ECOLOGY OF EPIFAUNAL CARIDEAN SHRIMPS IN THE HOPKINS RIVER ESTUARY, AND THE ROLE OF ESTUARIES IN THE LIFE HISTORY OF THE ATYID *PARATYA AUSTRALIENSIS* KEMP, 1917 IN SOUTH-EASTERN AUSTRALIA

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CANDIDATE'S CERTIFICATE

I certify that the thesis entitled "ECOLOGY OF EPIFAUNAL CARIDEAN SHRIMPS IN THE HOPKINS RIVER ESTUARY, AND THE ROLE OF ESTUARIES IN THE LIFE HISTORY OF THE ATYID *PARATYA AUSTRALIENSIS* KEMP, 1917 IN SOUTH-EASTERN AUSTRALIA" and submitted for the degree of DOCTOR OF PHILOSOPHY is the result of my own research, except where otherwise acknowledged, and that this thesis (or any part of the same) has not been submitted for a higher degree at any other institution.

Signed

Dated

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LIST OF ABBREVIATIONS

AHD	Above Australian Height Datum
ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
BP	Before Present
df	Degrees of freedom
FW	Fresh water
G	Value used in log-likelihood ratio test (Sokal and Rohlf, 1981)
HB	Hopkins Bridge
I_δ	Morisita's index of dispersion (Elliott, 1977)
JP	Jubilee Park
LG	Lake Gillear exit
MH	Pool below the confluence of Hopkins River and Mt Emu Ck
Mpi	Mannose-phosphate isomerase
MS	Mean square
msl	Mean summer level (water level in Hopkins estuary)
N	Number of individuals
n	Number of replicates
NS	Not significant
OCL	Orbit-carapace length
p	Precision
P	Probability
Pgi	Glucosephosphate isomerase
Pgm	Phosphoglocomutase
RF	Rowan's Flat
sd or s	Standard deviation
s^2	Variance
SE	Standard error
SS	Sums of Squares
SU	Sample unit
TS	Tooram Stones
UPGMA	Unweighted Pair Group Method of Analysis
x	Mean

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ABSTRACT

This study examined the factors affecting the distribution and abundance of epifaunal caridean shrimps in seagrass meadows of the Hopkins River estuary in south-western Victoria, Australia, and investigated the life history patterns of the freshwater *Paratya australiensis*, found for the first time in estuaries.

Adult and sub-adult shrimps were surveyed in seagrass meadows along the estuary over two years, and their planktonic larvae were surveyed in adjacent waters. Three species were collected.

The marine *Palaemon serenus* occurred only near the mouth, summer to autumn, in high salinities.

The marine/estuarine *Macrobrachium intermedium* occurred throughout the estuary. Adults were most abundant in late autumn, and least abundant in summer (unlike trends reported in marine meadows). Densities were higher and less variable in downstream meadows.

P. australiensis occurred in the upper estuary all year, most abundantly in spring, due to migration from the river after peak discharge. Ovigerous females dominated, while males, showing less migration into the estuary, dominated above estuarine influence. Adults disappeared from the estuary in summer as salinity rose.

Breeding period for *P. australiensis* was briefer in the estuary (September-December) than upstream (July-April). *M. intermedium* began breeding later in the upper estuary (November/December-March) than in the lower estuary (October-March), probably reflecting a physiological response to lower salinity, rather than an interaction with *P. australiensis*. No ovigerous *P. serenus* were found in the estuary.

Larvae of *P. australiensis* and *M. intermedium* occurred abundantly throughout the estuary, but *P. serenus* larvae did not. P. australiensis was an early coloniser to the plankton after peak discharge (November-December). Larvae concentrated in the deep saline layer at the head of the intruding salt wedge, thus probably maintaining longitudinal position. Diurnal vertical migrations were evident within the salt wedge, and in a deep pool above tidal influence.

M. intermedium larvae occurred October-May in the lower estuary and November-April in the upper estuary, peaking in abundance one to two months after *P. australiensis*. They were associated with low surface flows and surface salinities >10, over an anoxic deeper layer.

All three species exhibited extended development of euryhaline larvae in the laboratory. Tolerances and optimal salinities of larvae of the three species reflected their distributions. *M. intermedium* was the most euryhaline species. *P. australiensis* larvae were tolerant of higher salinities than juveniles of adults: capable of developing in salinity of at least 15.

Most *P. australiensis* juveniles recruited to the estuary November-December, after which numbers declined dramatically. After settlement, most recruits probably migrated upstream out of the estuary. Two cohorts of *M. intermedium* recruited to the estuary from larvae in summer (December and February), but some juveniles also migrated from adjacent coastal waters. Post-larval migration was at least as important a determinant of abundance as direct recruitment from estuarine, planktonic larvae in all three species.

Distributions among seagrass meadows along the estuary were determined primarily by physico-chemical patterns driven by hydrological changes. Seasonal variations in salinity and temperature were strongly associated with seasonal variations in shrimp abundance. Salinity tolerances of adults of the three species reflected their distribution patterns.

Biotic interactions were more important in determining distributions within meadows. *P. australiensis*, when abundant, were associated with seagrass biomass. *M. intermedium* were also, but when seagrass was sparsest and least extensive. The two species apparently partitioned the seagrass meadow according to depth in early summer. Laboratory experiments suggested *P. australiensis* was displaced from deeper water by *M. intermedium*. Preference for vegetative complexity and competition for position within meadows suggest the underlying importance of predation in regulating shrimp populations.

A survey of south-eastern Australian estuaries found *P. australiensis* larvae abundant in all stable, open, well-developed, salt-wedge estuaries where adults were abundant. Adults were most abundant in low salinities among submerged leafy macrophytes.

Reproductive traits of *P. australiensis* were compared in estuarine and fresh reaches of three rivers. Early in the breeding season, egg size was smaller, and (size-specific) egg number larger in estuaries than upstream. A trade-off between egg size and egg number resulted in no difference in total (size-specific) reproductive investment between locations. Reproductive investment tended to decrease at some locations over the breeding season, and this decrease was a result of decreased egg size in most cases. The decrease in reproductive investment probably reflected reduced food availability for the adult, while the reduced egg size was probably a response to improved conditions for larval development. In the Hopkins River, larger egg size at upstream sites was reflected in larger early stage larvae. Later stage larvae were larger in the estuary, suggesting more favourable conditions for larval development.

Allozyme electrophoresis showed the *P. australiensis* populations in each of the three rivers to be distinct. Allozyme frequencies were not different within the Hopkins River, but upstream and estuarine locations in the Curdies and Gellibrand were different. Although some variation in reproductive traits within catchments may have been due to genotypic differences, trade-offs between egg size and number, and decreases in egg size over summer were probably due to plastic responses to environmental cues.

It is proposed *P. australiensis* inhabits and reproduces in both estuarine and freshwater environments by plastic response to environmental conditions. Recruitment to estuaries is dependent on the presence of suitable adult, littoral habitat, and a stable salt wedge for larval retention. Estuaries are important recruitment sites for *P. australiensis*, potentially allowing an extra brood each year before riverine recruitment. Estuarine broods could constitute a large part of the total fecundity of *P. australiensis* females. Euryhaline larvae and estuarine recruitment of *P. australiensis* suggest marine transport of larvae between estuaries as a possible dispersal mechanism for *Paratya* species.

SUMMARY

Walsh, C.J. (1994). 'Ecology of epifaunal caridean shrimps in the Hopkins River estuary, and the role of estuaries in the life history of the atyid Paratya australiensis kemp, 1917 in south-eastern Australia.' Ph.D. Thesis. (School of Aquatic Sciences and Natural Resources Management, Deakin University.) 276 pp. (Supervised by Dr B. D. Mitchell, Deakin University and Dr M. J. Keough, University of Melbourne.)

This study examined factors affecting the distribution and abundance of shrimps inhabiting seagrass meadows in the Hopkins River estuary in south-western Victoria. Quantitative studies of distribution and population structure in seagrass meadows (adults and juveniles) and water column (larvae) were supplemented by laboratory experiments on physiological tolerances and interspecific competition.

The study also investigated the life history of the freshwater shrimp *Paratya australiensis*, which was found commonly in estuaries for the first time. Reproductive traits and genetic variation in this species were compared between estuarine and riverine populations in three rivers. Eggs were larger and broods smaller in riverine locations than in estuaries, and total reproductive effort tended to decrease for broods later in the breeding season. This variation was probably due to *P. australiensis* being able to adjust these traits in response to differing environmental cues. Such plasticity in reproduction may explain this species' widespread distribution.

Two other species were also collected in the Hopkins River estuary: the marine/estuarine *Macrobrachium intermedium* and the marine *Palaemon serenus*. Larvae of all three species were grown in the laboratory, and the development of *P. australiensis* was described for the first time. Only larvae of *P. australiensis* and *M. intermedium* were found in the estuary. *P. australiensis* larvae occurred in the deep saline layer of the estuary, soon after the annual flood, while *M. intermedium* larvae tended to occur later, when surface salinities had risen. Although many *P. australiensis* and *M. intermedium* recruited to seagrass meadows directly from planktonic larvae, migration after settlement—both between meadows, and into and out of the estuary—was an important determinant of distributions, particularly for *P. australiensis*.

The prime determinants of shrimp abundance and distribution along the estuary were physical factors as determined by hydrology. Distributions within meadows were more influenced by structure of vegetation and competition between species for deeper location, suggesting the underlying importance of predation as a population regulating mechanism. However, biotic factors appeared less important in determining larger-scale distributions within the estuary.

1. GENERAL INTRODUCTION

1.1. CARIDEAN SHRIMPS AND THE ECOLOGY OF SEAGRASS EPIFAUNA

Seagrass meadows are a predominant biotope in estuaries and coastal waters around the world (Kikuchi, 1980). Caridean shrimps are a common, often abundant element of the epifauna in these meadows, and are considered to play an important role in determining the structure and dynamics of seagrass communities (Kikuchi, 1974; Heck and Orth, 1980a; Bauer, 1985; Virnstein, 1987; Gray, 1991a). They are important predators on other seagrass macro- and meiofauna (Nelson, 1981; Howard, 1984), and are themselves prey for fish (Kikuchi, 1974; Adams, 1976; Howard, 1984) and wading birds (Howard, 1984; Howard and Lowe, 1984). The caridean families most commonly represented in studies of seagrass epifauna are the Palaemonidae, Hippolytidae, Processidae and Crangonidae. Only one study has been found which reported members of the Atyidae—a largely freshwater group—in seagrass meadows: a few juveniles of two freshwater species in a diverse caridean assemblage in the Caribbean (Bauer, 1985). The current study is the first to find an atyid species to be a significant element of a caridean assemblage in seagrass meadows.

Most studies of macrofauna in seagrass meadows have considered patterns in the composition and abundance of assemblages of macrofaunal species (e.g. Heck and Orth, 1980b; Bell and Westoby, 1986a, 1986b, 1986c; Holmquist et al., 1989). Comparatively few studies have reported patterns of distribution and abundance of individual species of caridean shrimps, and fewer have considered population dynamics (Table 1.1). As Gray (1991a) argued, such information is essential to assess the effects of caridean shrimps on other fauna in seagrass meadows. No studies of caridean shrimps in seagrass meadows have adequately quantified larval abundance and distribution in order to relate this to the recruitment of juveniles or the abundance of juveniles and adults in meadows. Indeed variation in recruitment from a planktonic larval phase has been proposed as the major determinant of abundance in marine and estuarine species (Sinclair, 1988). But the validity of this proposal is difficult to confirm for epifaunal caridean shrimps due to the lack of studies which integrate adult abundance in seagrass meadows with larval abundance in the plankton.

The study of epifaunal assemblages has proceeded largely from the observation that more species and individuals of animals are associated with seagrass than with adjacent bare substrata (Kikuchi, 1980). The importance of vegetative complexity in determining the abundance of motile epibenthic species and the composition of epifaunal assemblages in

Table 1.1. Studies of epifaunal caridean shrimp species in seagrass meadows and/or estuaries.

LH = studies which presented life-history data; RA, AA = studies of temporal and/or spatial variations in abundance (relative and absolute respectively).

C. = *Crangon*; *H.* = *Hippolyte*; *M.* = *Macrobrachium*; *Pn.* = *Palaemon*; *Ps.* = *Palaemonetes.*

Study	Caridean species	Habitat	Locality	Type of Study	
Höglund (1943)	*Leander (=Pn.) squilla*	*Zostera*?	W Sweden	LH	
Forster (1951)	*Leander (=Pn.) serratus*	not specified	S UK	LH	
Wood (1967)	*Ps. pugio*	*Zostera*?	S USA	LH	RA
Welsh (1975)	*Ps. pugio*	*Spartina*	NE USA	LH	AA
Thorp (1976)	*Ps. pugio, Ps. vulgaris*	*Spartina, Zostera*	E USA		RA
Walker (1979)	*M. intermedium, Pn.* n.sp.	*Heterozostera*	SE Australia	LH	RA
Berglund (1980)	*Pn. adspersus, Pn. squilla*	*Zostera* and others	W Sweden		RA
Siegfried (1980)	*C. franciscorum, Pn. macrodactylus*	nekton?, estuarine	W USA	LH	AA
Gore et al. (1981)	*Ps. intermedius, H. pleuracanthus*	*Syringodium, Halodule* and others	SE USA		AA
Howard (1981, 1984), Howard and Lowe (1984)	*M. intermedium*	*Heterozostera, Zostera*	SE Australia	LH	AA
Alon and Stancyk (1982)	*Ps. pugio*	unspecified, estuarine vegetation	E USA	LH	
Crivelli (1982)	*Pn. squilla, C. crangon*	*Ruppia*, FW weeds	SE France		RA
Pihl and Rosenberg (1982)	*C. crangon*	bare mud, *Ruppia*	W Sweden	LH	AA
Baden and Pihl (1984)	*Pn. adspersus*	*Zostera*	W Sweden	LH	AA
Berglund (1984)	*Pn. adspersus, Pn. squilla*	*Zostera*	W Sweden	LH	
Bauer (1985)	*Latreutes fucorum* and many others	*Thalassia, Syringodium*	Cent. America		AA
Howard (1985)	*H. pleuracanthus, Ps. intermedius*	*Halodule*	SE USA		AA
Emmerson (1986)	*Pn. pacificus*	*Zostera*	S Africa	LH	AA
Gray and Bell (1986)	*M. intermedium*	*Zostera*	E Australia		AA
Howard (1987)	*H. pleuracanthus, Ps. intermedius*	*Halodule, Syringodium*	SE USA		AA
Virnstein and Howard (1987b)	*H. pleuracanthus, Ps. intermedius*	*Halodule, Syringodium*	SE USA		AA
Holmquist et al. (1989)	*Thor floridanus* and others	unspecified seagrass	SE USA		AA

Table 1.1 (cont)

Study	Caridean species	Habitat	Locality	Type of Study	
Sogard (1989)	*H. pleuracanthus, Ps. vulgaris, C. septemspinosa*	*Zostera* and artificial seagrass	NE USA		AA
Gray (1985, 1991a, 1991b)	*M. intermedium*	*Zostera, Posidonia*	E Australia	LH	AA
Mellors and Marsh (1993)	3 families (to family only)	*Halodule* and others	NE Australia		AA

seagrass meadows has subsequently been the subject of many studies (e.g. Heck and Orth, 1980b; Orth et al., 1984; Bell and Westoby 1986a, 1986b, 1986c; Virnstein and Howard, 1987a). Such studies vary widely in approach and results: most concentrate on the diversity and abundance of whole macrofaunal assemblages while a few have presented data on individual species including caridean shrimps. Of studies which have investigated the abundance and diversity of epifaunal assemblages, many have shown positive correlations with seagrass biomass (e.g. Stoner, 1980; Gore et al., 1981; Homziak et al., 1982; Lewis and Stoner, 1983). However Bell and Westoby (1986b) found differing effects on species richness of epifaunal assemblages and individual species abundance of experimentally thinning and shortening seagrass leaves, depending on seagrass species. Furthermore, the trends observed in a single meadow were not repeated on a wider spatial scale (Bell and Westoby, 1986c; Bell et al., 1988). Thus although positive correlations between macrofaunal abundance and diversity, and seagrass abundance and structure have commonly been reported, there is by no means a universal relationship.

Several studies have reported the effect of vegetative complexity on the abundance of caridean shrimps. In some cases a positive correlation between seagrass standing crop and caridean abundance was found (Emmerson, 1986; Mellors and Marsh, 1993) or carideans were less abundant in experimentally thinned plots (Bell and Westoby; 1986a). However, Baden and Pihl (1984) found no relationship between the abundance of *Palaemon adspersus* and the standing crop of *Zostera*, but they did find increased abundance of shrimps when the macroalga *Fucus* was associated with the seagrass. Studies which have compared adjacent meadows of different seagrass species, which present varying levels of structural complexity, have found no effect of seagrass species on caridean abundance, when standardised to bottom surface area (Virnstein and Howard, 1987a; Gray, 1991a). Thus, although vegetative complexity has been correlated with caridean abundance in some cases and may play a part in determining distribution and abundance within a meadow or between adjacent meadows, other factors are likely to be involved.

More generally, correlations between habitat complexity and macrofaunal abundance have been reported often enough for the former to be considered an important determinant of the latter. Heck and Orth (1980b) argued that increased habitat complexity afforded by the greater density of vegetation or by seagrass species with more complex architecture provides refuge from predation and thus contributes to greater abundances of epifauna. Experimental studies have confirmed that predation on a variety of epifaunal taxa can be decreased with increased density of vegetation (e.g. Young and Young, 1978; Nelson, 1979; Crowder and Cooper, 1982; Stoner, 1982).

Several studies have considered predation on caridean shrimps. Coen et al. (1981) found predation intensity on *Palaemonetes vulgaris* and *Palaemon floridanus* was inversely related to the physical complexity of the experimental habitat, and Heck and Thoman (1981) found that although predation pressure on *Palaemonetes pugio* was not different on bare sand or in seagrass of low or intermediate density, it was decreased in seagrass of high density. Bell and Westoby (1986a) concluded that, for *Macrobrachium intermedium* and other non-caridean species, habitat preference rather than predation was the proximate cause of greater abundance in more complex habitat structure. This conclusion does not necessarily discount the importance of predation in shaping macrofaunal assemblages. Indeed they commented that habitat preferences may have been selected by predation pressure. Howard (1981) pointed to cryptic body pigmentation and diel patterns of activity as being suggestive of the major role of predation in the evolution of the caridean species he studied. Howard and Lowe (1984) showed that selective predation for large *M. intermedium* by wading birds skewed the sex ratio of an intertidal population, and decreased the survivorship of female cohorts.

Thus in many studies predation, or more often the implied protection from it afforded by the increased physical complexity of vegetation, has been considered the major determinant of epifaunal abundance and community structure in seagrass meadows. However the inconsistency of patterns observed within and between adjacent meadows (e.g. Bell and Westoby, 1986b) and the even greater inconsistencies on a wider spatial scale (Bell and Westoby, 1986c; Bell et al., 1988) point to other factors being important at least in some cases. This is particularly true of the epifaunal caridean shrimps, the abundance of which has not always shown a positive relationship with vegetative complexity.

Competitive interactions have been proposed in several studies of epibenthic caridean shrimps in seagrass meadows (Thorp, 1976; Walker, 1979; Coen et al., 1981), and niche differentiation has been described (Berglund, 1980, 1984). Siegfried (1980) suggested that the nektonic estuarine carideans *Crangon franciscorum* and *Palaemon macrodactylus* may compete for their common prey. However, the only experimentally proven cases of competitive interactions between epifaunal caridean shrimps have involved competition for refuge from predators in the increased habitat complexity of seagrass (Thorp, 1976; Coen et

al. 1981). Thus, in cases where interspecific competition has been proven, habitat complexity and predation have been found to be driving factors. In contrast Howard (1981), working on the distribution, behaviour and trophic relationships of a guild of epibenthic carideans, concluded that interspecific competition was unlikely to play a role in determining their abundances and distributions..

Wider scale comparisons between seagrass meadows within an estuary and between estuaries have revealed effects on caridean abundance, distribution and other demographic patterns (Wood, 1967; Siegfried, 1980; Alon and Stancyk, 1982; Emmerson, 1986; Bell et al., 1988; Sogard, 1989; Gray, 1991b). Few studies have reached firm conclusions to account for the observed spatial patterns, and the speculated causes have varied widely. Alon and Stancyk (1982) found considerable variation in the demography (abundance, reproduction, recruitment, growth and size structure) of *Palaemonetes pugio* in two neighbouring estuaries. While speculating that differences in growth may have been due to nutritional and physiological factors, differences in longevity due to predation, and differences in reproductive timing due to physiological stress or competition, they offered the study as no more than a data base for further work. Alon and Stancyk's study has been criticised by Gray (1991b) for its duration of only one year, because in Gray's study of *Macrobrachium intermedium*, levels of heterogeneity in those parameters between years at a single site were as large as heterogeneity between estuaries in a single year. Emmerson (1986) surmised differences in shrimp abundance between estuaries may have been due to differences in nutrient status and primary productivity. Wood (1967) attributed variation in demography along an estuary to responses of post-larval shrimp to physical conditions. Siegfried (1980) reached similar conclusions, attributing control of the upper distributional limit of *Crangon franciscorum* to low salinities, but relating the downstream distribution to prey availability. Bell et al. (1988) found the position of the seagrass meadow within an estuary lacking strong temperature and salinity gradients to have a significant effect on the abundances of many species of fish and decapods. They concluded variations in epifaunal abundance were due to variation in availability of competent larvae to settle in the meadows. Similarly Gray (1991b) hypothesised that the interaction of stochastic, abiotic factors with recruiting larvae was an important determinant of the distribution and abundance of *M. intermedium*. If epifaunal abundance within a meadow were determined by larval recruitment, then little post-larval migration between meadows should occur. However Sogard (1989) found high levels of migration into distant artificial seagrass beds by juveniles and adults of many epifaunal species including carideans. As she points out, the relative abundance of settling larvae versus post-larval migrants will determine which is the more important contributor to the population.

Despite the growing speculative importance placed on the larval phase in recent studies, the distribution of larvae in relation to the distribution of seagrass epifauna has received little attention. Recently a renewed interest in larval supply as a major influence on the structure and

dynamics of marine and estuarine populations has resulted in an emphasis on the need to integrate studies of the benthic and epibenthic phase with study of the dispersal phase (Sinclair, 1988; Underwood and Fairweather, 1989; Grosberg and Levitan, 1992). Consequently the current study is concerned with the distributions of both caridean shrimps in estuarine seagrass meadows and their planktonic larval stages.

The caridean species under investigation

This work reports on a study centred on the Hopkins River estuary in south-western Victoria, Australia (Fig. 1.1). The seagrass meadows of this estuary are inhabited by three epifaunal caridean shrimps— the freshwater atyid, *Paratya australiensis* Kemp, 1917, and two palaemonids; the marine/estuarine *Macrobrachium intermedium* Stimpson, 1860, and the marine *Palaemon serenus* Heller, 1865. *P. australiensis* is a common inhabitant of the fresh waters of south-eastern Australia and until this study had not been recorded in significant numbers from estuaries. A review of previous work on this species and other atyids is presented in section 1.3. While no studies in seagrass meadows have been conducted on either *P. australiensis* or *P. serenus*, several studies in southern Australia have focused on *M. intermedium*.

Walker (1979) investigated the overlapping distributions of *M. intermedium* and an undescribed species of *Palaemon* in near-shore and estuarine seagrass meadows of Tasmania. He reported *M. intermedium* occurring in coastal waters around almost all of Australia, while *Palaemon* n. sp. occurred in estuaries of Tasmania, Victoria and South Australia*. In meadows in which the two species co-occurred, there was some habitat partitioning that may have at least partly been an artefact of differentiation of distributions based on body size. Walker identified a number of factors which may have determined distribution including salinity and temperature, seagrass species, interspecific competition and fish predation, but his results were largely inconclusive. Howard (1981, 1984) studied the seasonal abundance patterns, population dynamics and trophic ecology of *M. intermedium* and three other caridean shrimps in seagrass meadows in Westernport, Victoria. *M. intermedium* was the dominant species in the caridean group. Although Howard (1981) identified predation by both fish and birds as a significant factor in modifying the population structure and productivity of the four species, he concluded that it did not control the abundance ranking of the species within the guild. He also discounted interspecific competition as a factor that might strongly influence the structure of the caridean assemblage. Gray (1985, 1991a, 1991b) studied the distribution, abundance and population dynamics of *M. intermedium* in predominantly marine seagrass

* While *Palaemon* n. sp. (Walker, 1979) was not collected in the Hopkins River estuary during the present study, the author has found it associated with *P. serenus* in estuarine seagrass meadows near the mouth of the Moyne River, 25 km west of the Hopkins River.

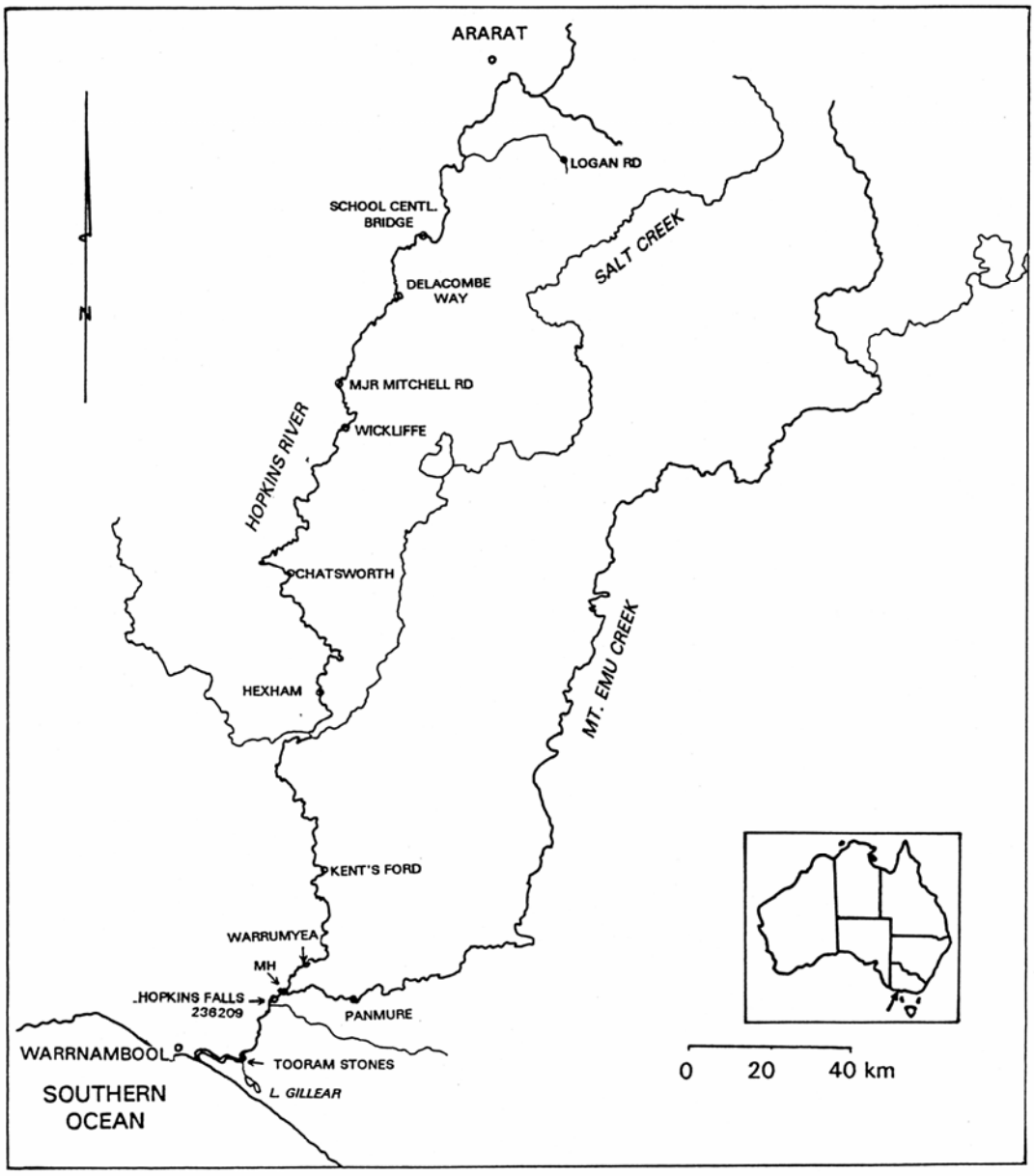


Fig. 1.1. The Hopkins River basin, indicating riverine sampling locations, and the Hopkins Falls gauging station.

meadows in three estuaries of the Sydney region. These more northern populations were reproductively active longer and produced more cohorts each year than the populations studied by Walker (1979) and Howard (1981). Gray (1985) found large variations in abundance and demographic patterns between adjacent meadows of different seagrass species, and equally large variations between meadows within and between estuaries and between years. He attributed these variations to 'stochastic factors extrinsic to the seagrasses themselves', suggesting abiotic influences on the larval phase as the most important factor (Gray, 1991b).

The Hopkins River estuary is the most freshwater-influenced environment in which a study of *M. intermedium* has been conducted, and also the most marine-influenced environment in which *P. australiensis* has been studied (see section 1.3). It provides an opportunity to compare life-history patterns with those observed in *M. intermedium* in more marine meadows (Walker, 1979; Howard, 1981; Gray, 1985) and with those observed in *P. australiensis* in rivers (Walker, 1972; Williams, 1977). The current study investigates the abundance of each caridean species in the seagrass meadows of the estuary in relation to: vegetative complexity; other caridean species; and physical factors such as depth, salinity and temperature within each meadow. Four small meadows spanning the length of the estuary were sampled to assess the effect of position within an estuary with a pronounced longitudinal variation in salinity patterns. Because the estuary is small and relatively enclosed, it is ideal for the study of larval distributions in an integrated way with juvenile and adult distributions in the fringing seagrass meadows.

1.2. RECRUITMENT AND CARIDEAN LARVAE IN ESTUARIES

Epifaunal Caridea generally possess complex life cycles; i.e. during a life cycle there is an abrupt change in the individual's morphology and ecology (Wilbur, 1984) resulting, in the case of carideans, in epifaunal juvenile and adult stages following a planktonic larval phase. Estuaries are an important habitat for many species which inhabit inland waters or the sea for part of their life cycle, and may be used as adult or larval habitat or both, resulting in a number of potential life cycle combinations. Within the Caridea almost all potential life cycles are represented in the Atyidae and the Palaemonidae (Table 1.2). Little research has been conducted on the larval ecology of the Caridea and in many cases the larval habitat has only been deduced speculatively from the evidence of juvenile recruitment patterns (e.g. Smith, 1987; Carpenter, 1983) or from salinities at which larvae grow optimally in the laboratory (e.g. Walker, 1979; Hunte, 1979a). Although atyids are usually exclusively freshwater as adults, the larvae of a number of atyid species inhabit estuaries and a few
species inhabit the sea as larvae. The Palaemonidae, while essentially a marine group, has

Table 1.2. The range of complex life cycles in the Palaemonidae and the Atyidae. Citations marked by an asterisk (*) are studies which used larval development in the laboratory or juvenile recruitment to infer larval habitat.

Aa. = *Atya*; *Au*. = *Australatya*; *As*. = *Atyopsis*; *C*. = *Caridina*; *M*. = *Macrobrachium*; *Ma*. = *Micratya*; *Pa*. = *Paratya*; *Pn*. = *Palaemon*; *Ps*. = *Palaemonetes.*

Dominant habitat of		Palaemonid and atyid examples	
Adult	Larva	Family	Species and study
Marine	Estuarine	Palaemonidae	*M*. sp. (Nguyen, 1976*)
Marine/ estuarine	Marine/ estuarine	Palaemonidae	*M. intermedium* (Walker, 1979; Howard, 1981; this study) *Ps. attrinubes* (Bray, 1976*)
Marine/ estuarine	Marine	Palaemonidae	*Pn. pacificus* (Emmerson, 1986) *Pn. serenus* (this study)
Marine/ estuarine	Estuarine	Palaemonidae	*Pn*. n. sp. (Walker, 1979*) *M. equidens* (Nguyen, 1976*)
Estuarine	Marine	Palaemonidae	*Pn. longirostris*, *Ps. varians* (Fincham and Furlong, 1984*)
Estuarine	Estuarine	Palaemonidae	*M. novaehollandiae* (Thorne et al., 1979) *Ps. pugio* (Wood, 1967, Sandifer, 1975) *Ps. vulgaris* (Sandifer, 1973*, 1975)
Estuarine/ freshwater	Estuarine	Palaemonidae	*Ps. australis* (Bray, 1976*)
Estuarine/ freshwater	Estuarine/ freshwater	Palaemonidae Atyidae	*M. nipponense* (Mashiko, 1990) *Pa. australiensis* (Walsh, 1993; this study)
Freshwater	Marine	Atyidae	*Au. striolata* (Smith, 1987*)
			Aa. innocous (Felgenhauer and Abele, 1983) *C. japonica* (Hayashi and Hamano, 1984*) *Ma. poeyi* (Hunte, 1979a*)
Freshwater	Estuarine	Palaemonidae	Many *Macrobrachium* spp. (Ibrahim, 1962; Raman, 1965; Choudhury, 1971*, Hughes and Richard, 1973; Moreira et al., 1980*; Holtschmit and Pfeiler, 1984; Moreira et al., 1986*).
		Atyidae	*Aa. africana*, *Aa. gabonensis*, *Aa. margaritacea* (Hobbs and Hart, 1982*)
			Aa. scabra (Abrunhosa and Moura, 1988*) *As. moluccensis* (Johnson, 1965; Chace, 1983) *Pa. curvirostris* (Ch'ng, 1973*; Carpenter, 1983*)
Freshwater	Estuarine/ freshwater	Atyidae	*Pa. compressa* (Yokoya, 1931; Shokita, 1979*)

both freshwater and marine species. Estuarine and marine larval stages are common in the Palaemonidae, and in many species either adults or larvae are euryhaline, occurring in either environment. Euryhalinity has been less commonly reported in the Atyidae. Only one palaemonid species was found which is suspected of having a solely estuarine larva while being marine as an adult (Nguyen, 1976). Table 1.2 shows that, in both caridean families of concern in this study, estuaries are often an important habitat for the larval stage. Yet little work has been conducted on the ecology of caridean larvae in estuaries, with most studies of decapod larvae concentrating on the Brachyura (e.g. Cronin and Forward, 1982; Sulkin, 1984; Dittel and Epifanio, 1990).

Because of the strong flushing nature of estuaries and rivers there has been an emphasis in studies of estuarine planktonic larvae on their retention in order to maintain populations (e.g. Strathmann, 1982). Strathmann recognised two modes of planktonic larval behaviour in estuarine invertebrates: behaviour which enhances retention of larvae in an estuary, and behaviour which enhances export of larvae. In the case of the latter, he considered the export of larvae to be migration to areas more suitable for larval development, ultimately followed by migration back to the parental habitat, rather than a mechanism of dispersal to colonise other areas or to maintain gene flow between estuaries. His emphasis was on retention and return to the adult habitat. In marine studies, particularly those with a biogeographical or evolutionary perspective, the emphasis has been more on planktonic larvae having the potential for dispersal (e.g. Jablonski and Lutz, 1983; Strathmann, 1985). McConaugha (1988) considered arguments for the selective advantage of larval retention (or return to the parental habitat after export) to be more persuasive than those for the selective advantage of larval export and dispersal. Sinclair (1988) reconciled these seemingly opposing arguments by considering them coupled components of a single phenomenon which may not be able to be considered separately—in a manner analogous to the coupled phenomena which frequently occur in physics, such as discontinuity/continuity. Sinclair interpreted retention as the more important phenomenon on a short time scale of interest to ecological studies. He argued the persistence of a population in a particular place is being selected for because of the geographical constraint of sexual reproduction. He suggested dispersal of larval stages out of an area, although considered an accidental artefact in some ecological considerations (Strathmann, 1982), may have considerable importance at an evolutionary level.

Distinct from the dualism of retention/dispersal is the occurrence of the two estuarine larval behaviours distinguished by Strathmann (1982), both of which have been found commonly in decapods: behaviour which promotes maintenance of position within an estuary, and behaviour which promotes export (with subsequent return as juveniles). In estuaries with two-layered circulation, the extent of larval retention or export for each species is related to: 1) larval duration; 2) the tolerances and requirements of the larvae; 3) the vertical distribution

and behaviour of larvae and; 4) nett seaward flow (Sastry, 1983a). Each of these aspects of larval biology has been studied in a variety of estuarine decapods, and is considered below.

Larval duration

Larval duration is a function of the number of ecdyses to metamorphosis and the length of intermoult periods. These factors have been found to be both intrinsically and extrinsically variable within species. The first three or four stages of caridean larval development tend to be isochronal (i.e. having a relatively constant intermoult period), and are therefore less variable. But subsequent instars are often irregular in number and duration (Gore, 1985). Species which exhibit abbreviated larval development, such as *Macrobrachium australiense*, tend to show a consistent, small number of instars, although the length of the intermoult period may vary under different environmental conditions (Lee and Fielder, 1981). Species with longer larval development often respond to sub-optimal conditions by increasing the intermoult period and undergoing more ecdyses, often with little morphological change—termed 'mark-time' moults by Gore (1985). In the Atyidae and Palaemonidae, several species such as *Atya innocous* (Hunte, 1979b) and *Palaemonetes vulgaris* (Broad, 1957) have long, intrinsically variable larval durations. As is reviewed below, several palaemonid species exhibit variable number and durations of instars in response to environmental variables such as temperature, salinity, and the nature and abundance of food, but such trends have been less commonly studied in the Atyidae. Geographical variation in larval duration and morphology within a species has been reported in both families. Such variation may be due to differing environmental conditions, but has often been found to be due to genetic differences—e.g. *Atyaephyra desmarestii* (Gurney, 1942; Salman, 1987b)

The duration of larval development for many caridean species, including many of the Atyidae and Palaemonidae, has been determined by rearing larvae in the laboratory. Of the species under investigation in this study, larval development of *Paratya australiensis* under moderately saline conditions (Walsh, 1993; Chapter five of this study) and the larval development of *Macrobrachium intermedium* under marine conditions (Williamson, 1972) have been described. The planktonic larval phases of both species are moderately long (28-45 days for 7-12 ecdyses in *P. australiensis* and 30-40 days for an estimated ten stages in *M. intermedium*). In both the Palaemonidae and the Atyidae, a range of development types is evident. Species which complete their development in freshwater tend to have abbreviated or direct development (i.e. the larval stage is bypassed), while species with marine larvae tend to exhibit extended larval development, and species with estuarine larvae have larval development of intermediate duration (Gore, 1985). The range of larval development observed among species of *Macrobrachium* was reviewed by Chong and Khoo (1987), as was the range observed within the atyid genus *Caridina* by Benzie (1982). A broader discussion of variation of larval development within the Atyidae is presented in Chapter 5 of this study.

Tolerances and requirements of larvae

Development of larvae to metamorphosis occurs within a well-defined range of physical factors such as salinity, temperature, dissolved gases, and photoperiod, characteristic to each species. Laboratory studies of development and survival rate of larvae for single and interacting environmental parameters have been conducted for a number of decapod species (see Sastry, 1983a). In the Caridea, temperature and salinity have most frequently been investigated. While both parameters have distinct ranges beyond which survival of larvae is reduced, temperature appears to be the more important factor in altering larval development patterns within the ranges of tolerance. In several palaemonid species, the temperature for maximal survival of larvae also allowed the fastest growth to metamorphosis. In *Macrobrachium australiense*, with abbreviated larval development, longer larval development at sub-optimal temperatures resulted from longer intermoult periods between the three fixed ecdyses (Lee and Fielder, 1981). In species with extended development such as *Palaemonetes vulgaris* and *Palaemon elegans*, longer development at sub-optimal temperatures was characterised by both increased intermoult periods and an increased number of ecdyses to metamorphosis (Sandifer, 1973; Rochanaburanon and Williamson, 1976). Salinity had no effect on the rate of development or the number of instars of larval *P. vulgaris*, *P. elegans* or *M. australiense*, (Sandifer, 1973; Rochanaburanon and Williamson, 1976; Lee and Fielder, 1981). Larval duration was affected by salinity in *Caridina japonica* and *Macrobrachium amazonicum* (Hayashi and Hamano, 1984; Moreira et al., 1986), but in neither case was the number of instars to metamorphosis investigated. Interestingly *C. japonica*, a freshwater shrimp whose larval ecology is not well studied, reached metamorphosis fastest in seawater, although survival was maximal at salinity of 17 (Hayashi and Hamano, 1984).

Changes in salinity tolerance during development have been reported for some freshwater carideans. Salinity tolerance of larvae decreased with age in *Macrobrachium americanum* (Holtschmit and Pfeiler, 1984), which undergoes larval development in estuaries. An increase in salinity tolerance in later larval stages and post-larvae of the exclusively freshwater *Palaemonetes kadiakensis* was interpreted as evidence of a recent marine ancestry (Hubschmann, 1975). Several workers have determined salinity tolerance of adult *Paratya australiensis* (Walker, 1972; Williams, 1984; Morris, 1991), although ontogenetic changes in physiological tolerances have not been studied in this or any atyid species.

Decapod larvae are planktotrophic, with most larvae requiring animal food (McConaugha, 1985). Little work has been done on the feeding ecology of estuarine or riverine decapod larvae, but many studies have investigated larval nutrition in a culturing context (see McConaugha, 1985). Most laboratory studies of decapod larvae have used *Artemia* nauplii as the primary food source due to the wide availability of *Artemia* cysts. The quality and quantity of food influences the frequency of ecdyses and the duration of larval development in

Palaemonetes—an algal diet was found to be equivalent to starvation (Broad, 1957) and reduced densities of *Artemia* nauplii increased the intermoult period and the number of instars to metamorphosis (Knowlton, 1974).

Vertical distribution and behaviour of larvae

The study of vertical distribution of planktonic larvae has primarily been approached by field studies in relation to water movement, while behaviour of larvae has primarily been studied by laboratory experiments designed to detect responses of larvae to specific environmental variables.

The use of tidal currents and two-layered circulation of estuaries for maintenance of position or migration has been widely reported for holoplankton (e.g. Wooldridge and Erasmus, 1980, and see Sinclair, 1988), fish larvae and eggs (see Norcross and Shaw, 1984), larvae of benthic invertebrates in general (see Sinclair, 1988), sergestid penaeid prawns (Xiao and Greenwood, 1992), and particularly for brachyuran decapod larvae (e.g. Cronin and Forward, 1982; Epifanio and Dittel, 1982; Sulkin and Van Heukelem, 1982; Epifanio et al., 1988; Johnson and Hester, 1989; Dittel and Epifanio, 1990). In most cases the observed retention or export has been achieved by vertical movement between layers of differing current, but lateral movement between areas of differing flow intensity has been observed in fish (Norcross and Shaw, 1984), mysids (Wooldridge and Erasmus, 1980; Hough and Naylor, 1992) and in post-larval penaeid prawns (Xiao et al., 1988). No decapod larvae have been found to maintain position in an estuary by lateral movement.

Vertical migrations by larvae of a number of decapod species, resulting in either retention in the estuary or export to coastal marine waters, have been demonstrated. Larvae of the xanthid crab *Rhithropanopeus harrisii* are maintained in the upstream portion of estuaries in eastern USA by rhythmic vertical migrations ranging above and below the depth of no nett flow (Cronin, 1982; Cronin and Forward, 1982). In contrast early stage larvae of the blue crab *Callinectes sapidus* utilise the outward flowing surface layer to permit export to coastal marine waters, with juveniles returning to the estuary after metamorphosis (Sandifer, 1975; Sulkin and Van Heukelem, 1982). Similar patterns have been found in other crab species (Epifanio and Dittel, 1982; Epifanio et al., 1988). Newton (1994) postulated that shrimp larvae in the Hopkins River estuary maintained position primarily by using the bottom boundary layer, migrating into the water column on slack tides. However, no caridean shrimp species has been proven to exhibit tidal migratory behaviour, although retention of estuarine *Palaemonetes* spp. by maintenance of position in the deep layer with nett upstream flow has been suggested (Sandifer, 1975).

The maintenance of a vertical position in a water column requires that the effects of negative buoyancy be overcome. No morphological or physiological mechanisms for regulating buoyancy are apparent in brachyuran larvae (Sulkin, 1984), nor presumably in caridean

larvae, so the effects of negative buoyancy must be modified by behavioural responses. There is a considerable body of experimental work on the behavioural basis of depth regulation in brachyuran larvae in relation to environmental factors such as gravity, light, hydrostatic pressure, salinity, temperature, food and pollutants (see review by Sulkin, 1984). The most comprehensively studied species is *Rhithropanopeus harrisii*: observed changes in vertical distribution have been related to tidal rhythms in phototaxis and locomotor activity (Cronin and Forward, 1982), and changes in phototaxis and geotaxis in relation to the degree of water stratification (Cronin, 1982; Latz and Forward, 1977), while the day-night cycle was found to have little effect on vertical migration (Cronin, 1982). The behavioural basis of larval depth regulation has received less attention in the Caridea. While not reducing their attention to specific taxes, Hughes and Richard (1973) found larvae of *Macrobrachium acanthurus* dropped to a lower position in the water column as salinity was reduced, and reverted to a higher position as salinity was increased. They interpreted these responses as a mechanism for the estuarine larvae to avoid downstream displacement, thus allowing subsequent migration upstream to the freshwater adult environment. No such results were detected for the estuarine larvae of *M. novaehollandiae* (Thorne et al., 1979). They found this species to be positively phototactic regardless of other factors, but they concluded downstream displacement was reduced by the semi-benthic nature of the larvae.

Nett seaward flow

In estuaries, changes in the nett seaward flow of the water body have two primary components: tidal and seasonal. Some estuarine decapod species show semi-lunar rhythms of larval release, related to tidal cycles. Christy and Stancyk (1982) found crab larvae of the genus *Uca* in an eastern USA estuary were maximally released on nocturnal ebb tides of the greatest magnitude, while Paula (1989) found a number of decapod species, including the carideans *Palaemon* spp. and *Crangon crangon*, were released on evening crepuscular high tides. Such synchronised release of larvae has been interpreted to be related to reducing predation risk by a swamping effect (Paula, 1989), while the timing of larval release to coincide with high tides results in export from the estuary (Christy and Stancyk, 1982) or at least prevention of upstream displacement (Paula, 1989).

Seasonal variation in nett seaward flow is primarily related to the hydrology of the inflowing streams. In many estuaries, including the Hopkins River estuary and others of south-west Victoria, floods cause annual scouring which removes all saline waters from the estuary (Sherwood and Backhouse, 1982; Sherwood, 1985). Persistence of planktonic larvae in estuaries at such times is unlikely and some freshwater carideans which have marine larval phases use spates to assist dispersal of larvae to the sea (e.g. Smith, 1987). The intrusion of a deeper saline layer as flow decreases and the establishment of two-layered circulation allows the retention of larvae within the estuary, but surprisingly little has been written of the

seasonal timing of larval production in relation to seasonal estuarine circulatory patterns. The timing of such events in a highly stratified salt-wedge estuary such as the Hopkins River estuary is vital to the distribution of larvae within the estuary. In larvae which require estuarine conditions for development, it is essential that the saline layer is stable and has sufficient dissolved oxygen for at least the duration of larval development.

* * *

The larval biology of estuarine carideans, as treated above, is linked to the study of caridean distributions in seagrass meadows by the processes of juvenile recruitment to seagrass meadows from the larval phase, and subsequent migrations between meadows. At a local scale, settling juveniles of fish and decapods have not been found to discriminate strongly among isolated seagrass habitats (Bell et al., 1988). But on a larger scale, the spatial distribution of late stage larvae within an estuary has immediate bearing on the distribution of settling juveniles. The importance of juvenile distributions in determining adult distributions of epifaunal species depends on the extent of post-larval migration. Post-larval migration between seagrass meadows within an estuarine system has been found to be significant in caridean shrimps (Sogard, 1989), and mass migrations have been reported or surmised for a number of freshwater caridean species. *Atya innocous* juveniles have been observed migrating from the marine larval habitat (Felgenhauer and Abele, 1983) and *Macrobrachium australiense* which spends its entire life cycle in the freshwater sections of rivers have been reported to undertake mass upstream migrations (Lee and Fielder, 1979).

Thus a study of carideans which aims to integrate larval and adult ecology needs to address each of these concerns: an understanding of the number and form of larval stages and their overall duration; a distributional survey to assess larval production and patterns of horizontal distribution in relation to seasonal variation in river discharge; a study of patterns of vertical distribution in relation to diurnal, tidal and seasonal changes in hydrology; an assessment of the effect of physical factors such as salinity and temperature on larval development; and a study of ontogenetic changes in tolerances and optimal conditions. Finally the patterns of settlement should be quantified and the extent of post-larval migration should be assessed. In the case of a freshwater species such as *P. australiensis* such work could help explain the observed distribution not only in the estuary in question but its absence from other estuaries and its larval production upstream.

1.3. ECOLOGY OF *PARATYA* AND THE ATYIDAE

Biogeography and taxonomy

Members of the Atyidae occur in all tropical regions of the world, almost exclusively in freshwater environments, and are also a common element of temperate freshwater faunas in many regions (Bishop, 1967). The wide distribution and differentiation of atyids in freshwater, and the lack of marine atyids have been used as evidence of a long history of freshwater evolution (Fryer, 1977): it is thought that the family arose as early as the Jurassic (Ortmann, 1894). Atyid species have colonised fresh waters of remote oceanic islands such as Hawaii and the Galapagos that lack true freshwater fish (Fryer, 1977). Such colonisation may have been possible through marine dispersal of larval phases. Some atyid species, such as those of the genus *Atya* and the *Atya*-like genera, while well adapted for life in freshwater lotic environments, have marine or estuarine larval phases (Hobbs and Hart, 1982; Chace, 1983; Felgenhauer and Abele, 1983). In contrast most *Caridina* species complete their larval development in freshwater environments (Benzie, 1982). Prior to the current study, little was known of the larval phase of any species of *Paratya*.

The genus *Paratya*, despite its name, is not *Atya*-like (sensu Chace, 1983). It shares the primitive characteristic of exopods on all pereiopods with what has been considered the most primitive extant genus of the family, *Xiphocaris* (Fryer, 1977). This latter species has recently been considered aberrant enough to warrant placement in a family of its own (Chace, 1992). Holthuis (1970) referred to "about a dozen species" of *Paratya*, but descriptions of only ten are available:

- an Australian species, *P. australiensis* Kemp, 1917; this, the most widely distributed *Paratya* species, is the most common riverine shrimp of south-eastern Australia, occurring in coastal streams from Adelaide to southern Queensland, with a wide distribution within the Murray-Darling Basin and from north-west to south-east Tasmania (Fig. 1.2). It also occurs less commonly as far north as north Queensland (Williams, 1977). Smith and Williams (1980) found *P. australiensis* to have very variable morphology, and Williams and Smith (1979) found variation in morphology between populations over its entire range to be no greater than within a single population. They thus reinstated a single species for Australian *Paratya*, which had previously been divided into a number of species by Riek (1953);
- a Japanese species (with two distinct sub-species), *P. compressa* de Haan, 1849, which is also recorded from Korea (Fig. 1.2) (Kemp, 1917, Roux, 1926);
- a New Zealand species, *P. curvirostris* Heller, 1862, which also occurs on Chatham Island (Fig. 1.2) (Kemp, 1917);
- *P. martensi* Roux, 1925 from Adonara Island near Flores, Indonesia (Fig. 1.2) (Roux, 1925);

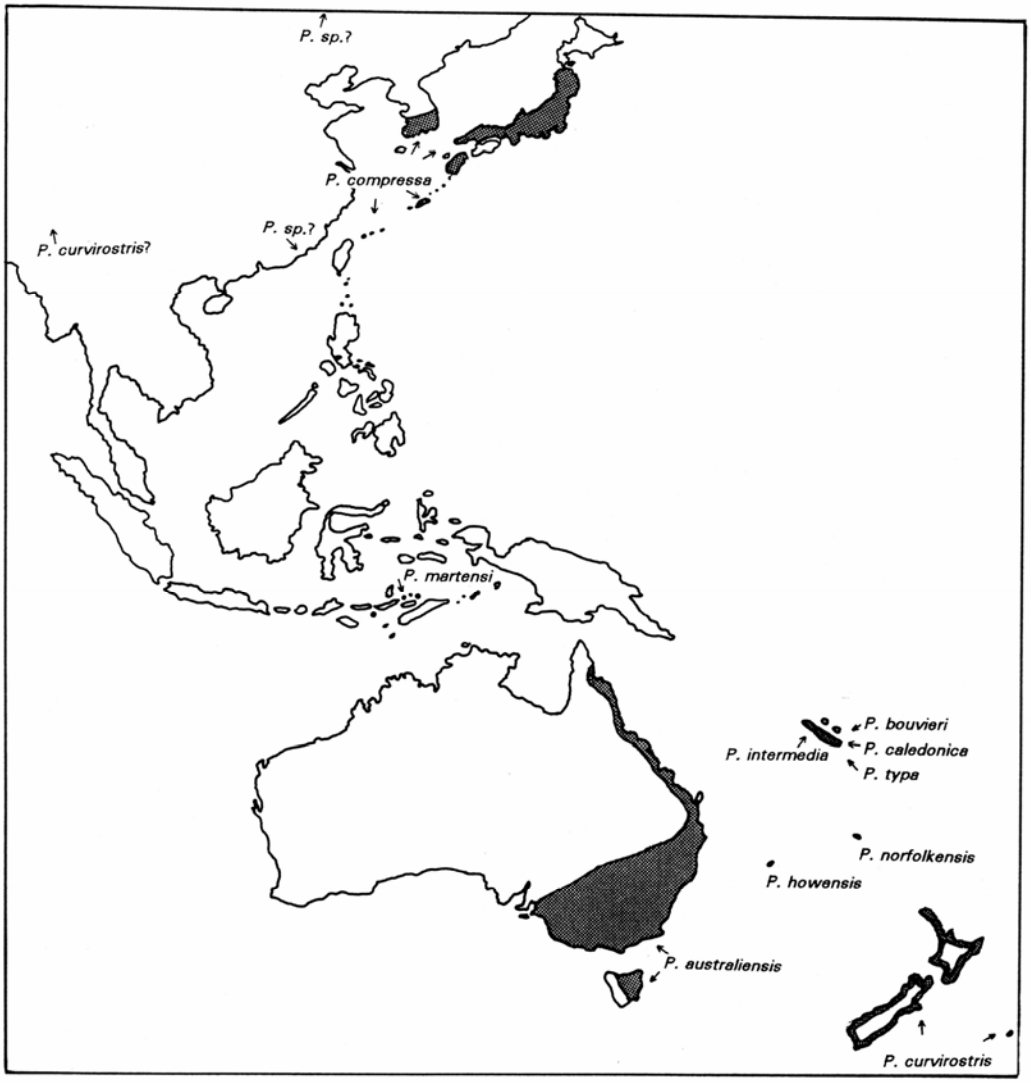


Fig. 1.2. Reported distributions of *Paratya* species.

- six species from oceanic islands of the south-west Pacific: *P. norfolkensis* Kemp, 1917 from Norfolk Island; *P. howensis* Roux, 1926 from Lord Howe Island; and *P. bouvieri* Roux, 1926, *P. caledonica* Roux, 1926, P. intermedia Roux, 1926 and *P. typa* Roux, 1926 from New Caledonia (Fig. 1.2) (Roux, 1926; Kamita, 1967; Holthuis, 1970).

- specimens assigned to *P. curvirostris* by Kemp (1917) have been collected from Assam, north-east India and other specimens have been collected from eastern Siberia and the Annam region of Vietnam (Fig. 1.2) (Holthuis, 1970).

The distributions of *Paratya* species in rivers and land-locked waters on widely separated land masses (Fig. 1.2) emphasise the need for further understanding of the ecology of the most likely dispersal phase of the genus: the larva. Bishop (1967) proposed that *P. australiensis*, the sole oriental element of the Australian freshwater decapod fauna, arrived in Australia by 'a series of "island-hopping" and "land-bridge-crossing" movements', but failed to speculate on the means of dispersal for these movements.

The ecology of *Paratya*

P. australiensis is found in freshwater lakes, reservoirs, farm dams, ditches, canals, streams and, most commonly, rivers (Williams, 1977). It has even been reported to be a facultative cave dweller (Dew, 1963; Williams, 1964). But Williams (1977) collected none from even moderately saline lakes, upland streams, highland lakes or temporary waters, and reported only very limited estuarine penetration. In Tasmania, although not found in highland streams, it is found in Lakes Sorell and Crescent on the edge of the central plateau (altitude 823 m) (Walker, 1972). M. Hancock (Griffith University, personal communication) has studied populations of *P. australiensis* occurring in the upland streams of south-east Queensland (altitude up to 800m). In southern Australia, however, there are no records of highland stream populations of *P. australiensis*. The status of *P. australiensis* as a primarily riverine shrimp is strengthened by the observation that in the Murray River, where it occurs sympatrically with *Caridina mccullochi*, *P. australiensis* occurred most commonly in the mainstream sections of the river while *C. mccullochi* occurred more commonly in the floodplains (Morris, 1991).

In all habitats, *P. australiensis* occurs more commonly in vegetation than elsewhere (Walker, 1972; Williams, 1977). Walker (1972) indicated a variety of macrophyte species in which it occurred most commonly. He found no *P. australiensis* in filamentous algae or in *Phragmites* stands, but did find small numbers under leaf litter and in rocky substrates. In contrast the rainforest streams of the Connondale ranges of south-east Queensland, which support populations of *P. australiensis*, have rocky substrates with no macrophytes other than filamentous algae (M. Hancock, Griffith University, personal communication).

Japanese and New Zealand *Paratya* appear to have similar habitat requirements to *P. australiensis*. In Honshu and the Ryukyu Islands, *P. compressa* occurs mainly among vegetation in a wide variety of habitats—swamps, ponds, canals, and streams—most commonly in the lower reaches of streams (Kamita, 1958a, 1958b; Shokita, 1979). *P. curvirostris* is associated with macrophyte beds or fringing vegetation in lowland streams, most commonly just above the level of tidal influence (Carpenter, 1982, 1983; Ch'ng, 1973). The only available ecological information on the four New Caledonian species are short distributional notes: *P. typa* and *P. intermedia* co-occur in streams at elevations of ≈100-300 m, while *P. bouvieri* occurs in streams from 8-260 m, and *P. caledonica* occurs only in lentic environments (Holthuis, 1970). No ecological study of other *Paratya* species has been found.

P. australiensis is both a browser and a filter feeder which subsists primarily on detritus and plant matter, with algae, diatoms, protozoans and small insects as minor dietary constituents (Gemmel, 1979a; 1979b). *P. australiensis* is undoubtedly an important prey item in lotic and lentic environments, but little work has been done on this aspect of its ecology. Sloane (1984) found *P. australiensis* to be the dominant dietary item of large eels (*Anguilla* spp.) in Tasmania.

Carpenter (1978) demonstrated *P. curvirostris* to be a protandrous hermaphrodite. Within the Atyidae, *Australatya striolata* has also been demonstrated to be protandrous (Smith and Williams, 1982) and three species of *Atyoida* and *Caridina richtersi* are suspected of partial or full protandry (Carpenter, 1978; Chace, 1983). Protandry, while not uncommon in the Atyidae or indeed the Caridea, shows no common systematic or ecological factors linked to its occurrence (Carpenter, 1978). There is no evidence of *P. australiensis* being protandrous.

Population studies in rivers of Tasmania (Walker, 1972) and southern Victoria (Williams, 1977) showed *P. australiensis* to live for two years, with most females breeding once or more in their second year. Females grew to a larger maximum size than males and the sex ratio did not diverge greatly from 1:1. Ovigerous females occurred from August or September until January in Victoria (and south-eastern Queensland—M. Hancock, Griffith University, personal communication) but did not occur until October in Tasmania. In Cardinia Creek, Victoria, larvae first appeared in November or December and juveniles occurred from December to April or May, coinciding with the period of low discharge when the creek dried to a series of pools with negligible surface flow (Williams, 1977). However, the first occurrence of small larvae in these pools, in December 1962, was four months after the first occurrence of ovigerous females. Because the period of embryonic development is probably of the order of one month (Walsh, 1993), some export of larvae from that section of the creek in the months prior to December 1962 is suggested. Williams (1977) also collected ovigerous females in rivers of south-eastern Queensland during high discharge periods. Thus although the occurrence of larvae and juveniles at the time of low discharge in Cardinia Creek may indicate a relationship between recruitment and stream discharge, the effect of discharge on breeding effort (as

indicated by the occurrence of ovigerous females) is unclear. M. Hancock (Griffith University, personal communication) has surprisingly found larvae in the highland streams of south-eastern Queensland to be abundant during peak flows. The fate of larvae produced from females ovigerous in periods of non-minimum discharge has not been satisfactorily addressed by any previous studies.

Estuaries have been sampled for *P. australiensis* with limited success. None were found in lower reaches of four south-eastern Queensland rivers under estuarine influence (Williams, 1977). At the upper limit of three Tasmanian estuaries, *P. australiensis* occurred only above estuarine influence while *Macrobrachium intermedium* occurred in the estuarine weedbeds with no overlap (Walker, 1972). Each of these surveys was conducted on a single occasion, so seasonal changes in distribution cannot be assessed. However, Walker (1972) reported collection of *P. australiensis* from two sites 'near or within areas of permanent or occasional tidal influence', one in brackish water. He implied these shrimps were likely to have been individuals washed downstream by floods rather than estuarine inhabitants. More recently *P. australiensis* has been collected from saline water in the Derwent River estuary, Tasmania, in December 1989 (P. Horwitz, Edith Cowan University, personal communication), and it was found to be the most numerous caridean in the upper Barwon River estuary, Victoria, throughout 1987 (Sherwood et al., 1988). In preliminary surveys I found large numbers of *P. australiensis* adults and juveniles in the seagrass meadows and larvae in the plankton of the Hopkins River estuary, particularly in the 3 months after the winter peak in discharge.

Little ecological study has been undertaken that has shown a degree of estuarine occurrence in other *Paratya* species. Shokita (1979) suggested larvae of *P. compressa* may develop in Japanese estuaries, despite the existence of landlocked population of this species. Similarly, Ch'ng (1973) and Carpenter (1983) postulated the development of larval *P. curvirostris* in estuaries in New Zealand.

The discovery of *P. australiensis* populations in estuaries opens up new avenues of study of this species. It provides the opportunity for the first study of population dynamics of *P. australiensis* in a non-riverine environment, and the potential to address the problem of the fate of larvae released upstream during non-minimum discharge. Given observations of the preference of *P. australiensis* for vegetation cover (Walker, 1972; Williams, 1977), its occurrence in seagrass meadows presents an opportunity to investigate the effect of vegetative complexity on the abundance of this species as considered in section 1.1.

The ecology of other atyids

Other than the studies on *P. australiensis* discussed above, the ecology of only two other Australian atyid species has been studied. Smith (1987) conducted a three-year study of the population biology of *Australatya striolata* in north Queensland. This species, which occurs in the same streams as *P. australiensis* in the southern part of its distribution, is mainly a

filter-feeder on particulate organic matter in low-order streams along the east coast of Australia. Smith (1987) concluded that abundance of *A. striolata* was not limited by food availability, predation or disease, but by rate of recruitment from its marine larval phase. However, he did not successfully study the ecology of the larvae. The work of Morris (1991) on habitat preference and physiological tolerance of *Caridina mccullochi* in the Murray River is the only study of this species other than a description of its abbreviated larval development (Benzie, 1982).

Ecological studies on atyids elsewhere are similarly sparse. The atyids of Sri Lanka are probably the best studied (Benzie and de Silva, 1988; de Silva, 1988a, 1988b, 1990; de Silva and de Silva, 1989). These studies of some of the ten *Caridina* species of Sri Lanka vary in intensity and duration, but provide at least a background to the variation in population dynamics of closely related tropical atyids. Breeding occurred all year round in all species studied and, although duration of larval development varied, abbreviated in-stream development was the norm. Dudgeon (1985) studied the population dynamics of the direct developing *Neocaridina serrata* in Hong Kong over fifteen months, and Hart (1981) conducted a fourteen month study of *C. nilotica* in a coastal South African freshwater lake with a relict estuarine fauna. The work of Shokita (1979, 1981) on Japanese freshwater shrimps contains useful distributional and life-history data for several atyid species and some demographic data for four species of *Caridina*. Mashiko et al. (1991) offered some fragmentary population data on the endemic atyid fauna of Lake Tanganyika, east Africa. The atyids of the West Indies and the Americas have received some attention but information on population dynamics has generally been anecdotal and secondary to functional morphology (Fryer, 1977; Felgenhauer and Abele, 1983) or large-scale distributional data (Hedgepeth, 1968; Hunte, 1978).

Although Hart (1981) studied *C. nilotica* in a relict estuarine lagoon, no study of atyid population ecology in a truly estuarine environment has been conducted. And although reports of juveniles of atyid species recruiting to estuaries are common (Felgenhauer and Abele, 1983; Hunte, 1978; Smith, 1987), recruitment rates to estuaries have never been quantified. The current study of *P. australiensis* in the seagrass meadows of an estuary in association with a study of larval distributions is the first such study for any atyid species.

Few previous studies of atyid shrimps have taken a quantitative approach to the determination of factors affecting distribution and abundance, or considered both larval and adult ecology. But most have presented useful life history data and, taken as a whole, they reveal that the Atyidae exhibit a diversity of approaches to the utilisation of the freshwater environment. *Caridina* and its closely related genera, while showing considerable interspecific variation, are characterised by relatively abbreviated in-stream larval development (see Benzie, 1982), while *Atya* and its closely related genera are characterised by extended marine or estuarine larval

development (see Hobbs and Hart, 1982; Chace, 1983). *Paratya* is of interest as it appears to span these two larval types, being able to develop in both estuarine and freshwater environments (Walsh, 1993).

1.4. VARIATION IN REPRODUCTIVE TRAITS BETWEEN FRESHWATER AND ESTUARINE ENVIRONMENTS

Egg size has been shown to be an accurate measure of energetic investment both within and between caridean shrimp species (Clarke, 1993a). The significance of larger eggs to fitness of offspring is less well studied, but large eggs in several invertebrate groups have been shown to produce larger, more competent larvae (see Clarke, 1993a). Mashiko (1985) showed larger *Palaemon paucidens* eggs hatched into larger larvae, which survived longer and developed further under starvation conditions than smaller larvae. Thus large eggs are likely to be more successful when food resources are limiting for larvae. But given a finite amount of energy available for reproduction, increased egg size must be at the expense of fecundity. The need to balance available resources between individual offspring, while maximising the total number of offspring is a central concern of life-history theory (Stearns, 1992). Life history models for marine invertebrates have sought to explain a perceived dichotomy in form between those species that produce large numbers of small eggs with planktotrophic development, and those that produce a small number of large eggs with direct or lecithotrophic development (Vance, 1973a; 1973b; Christiansen and Fenchel, 1979). However less extreme trade-offs between fecundity and egg size have often been reported: for instance between species with similar larval forms (eg Clarke, 1979; Mauchline, 1988), between populations of the same species (eg Mashiko, 1982; 1992; Clarke et al., 1991; Walsh, 1993), and within populations (eg Lawlor, 1976; Skadsheim, 1984; Willows, 1987; Clarke, 1993b)

The negative relationship between fecundity and egg size has most commonly been studied between closely related species. In many aquatic invertebrate groups, a tendency to larger broods and smaller eggs has been observed from higher to lower latitudes, and from shallower to deeper seas (eg Thorson, 1950; Clarke, 1979; 1992; Mauchline, 1988). Similar clinal trends with latitude have been observed within species, including in several carideans such as the freshwater *Palaemon paucidens* (Nishino, 1980), the Southern Ocean *Notocrangon antarcticus* (Clarke, 1979), the northern Atlantic *Eualus gaimardii* (Thorson, 1936) and the deep-sea *Pandalus borealis* (Clarke et al., 1991).

Of estuarine and freshwater carideans, altitudinal variation in egg size and fecundity within a single catchment has been reported in *Palaemon paucidens* (Mashiko, 1982), *Macrobrachium nipponense* (Mashiko, 1983a) and *Paratya australiensis* (Walsh, 1993). In addition, Thorson

(1950) noted anecdotally that *Palaemonetes varians* produced larger eggs in fresh than brackish water. *Palaemon paucidens*, which only occurs above estuarine influence, was found to possess larger eggs and smaller broods in running waters at lower elevations, and smaller eggs and larger broods in lentic habitats at higher elevations (Mashiko, 1982). *M. nipponense* and *P. australiensis* were both found to possess smaller eggs and larger broods in estuarine environments than upstream (Mashiko, 1983a; Walsh, 1993). In addition *M. nipponense* was found to have eggs and broods of intermediate size in brackish coastal lagoons (Mashiko, 1990).

Variation in egg size, fecundity and total reproductive output within populations over a breeding season has been reported in copepods (Hutchinson, 1951), cladocerans (Brambilla, 1982), amphipods (Skadsheim, 1984), and isopods (Willows, 1987). Brambilla (1982) proposed that variation in reproductive traits of *Daphnia pulex* was in response to changing predation regimes. But generally a decrease in egg size has been associated with increased food availability for larvae, while an increase in total reproductive output has been associated with increased food availability to the adult.

Early life history models for marine invertebrates (Vance, 1973a; 1973b; Christiansen and Fenchel, 1979) assumed constant reproductive effort, but recent more general models (e.g. Winkler and Wallin, 1987) have examined relationships between investment per offspring and total reproductive investment. Total reproductive effort, i.e. the proportion of the total energy assimilated by an organism devoted to gamete production, has rarely been measured adequately (Christiansen and Fenchel, 1979). Measurement of this proportion, the reproductive effort, requires measurement of not just the gonad production and total energy assimilated, but also the respiratory cost of gonad production, and the respiratory cost of behaviour associated with reproduction (Clarke, 1987). More commonly reproductive output, the weight-specific gonad production, has been determined, using measurements of egg size or mass, brood size and fecundity (which must include the frequency of brood production: Sastry, 1983b). For animals such as aquatic invertebrates, which do not nourish their young, these parameters can provide useful measures of the total reproductive investment and the investment per offspring.

Willows (1987) found variation in reproductive output of the rock slater *Ligia oceanica* to be expressed as variation in brood size with no effect on egg size. But the effect of reproductive output on brood size was small compared to the effect of the trade-off between brood size and egg size. Similar results were found in three polar caridean shrimps (Clarke, 1993b). Willows (1987) hypothesised that the observed patterns in reproductive traits were a result of individual slaters adjusting the use of resources on more or fewer offspring dependent on expected seasonal variation in the food resources available to those offspring.

The differences in reproductive traits between populations of *Macrobrachium nipponense* described above (Mashiko, 1990) were shown to be primarily due to genetic differentiation of

populations (Mashiko, 1983b; 1992). However, in addition to differences in fecundity and egg size, Mashiko (1990) also found variation in reproductive output of *Macrobrachium nipponense* (measured as a proportion of total egg weight to body weight) between locations. He postulated that these variations were in response to food availability to the adult, and found that differences in reproductive effort did not occur in controlled conditions (Mashiko, 1992). Egg size was found to be strictly genetically controlled in *M. nipponense*, but brood size, while having a genetic component, varied with environmental conditions. This finding is consistent with the relationship between reproductive output and the egg size/brood size trade-off found for *L. oceanica* (Willows, 1987).

In comparing reproductive traits between populations open to migration, it is important to assess the level of gene flow between populations so that observed patterns can be ascribed to either phenotypic plasticity or genetic differentiation of populations. *Paratya australiensis*, unlike *M. nipponense*, inhabits lotic habitats. It is therefore less likely to separate into reproductively isolated populations along a river system. Phenotypic plasticity may therefore be more important than genetic differences in explaining any egg size/brood size trade-off in this species. The final chapter of this work reports on variation in some reproductive traits in *P. australiensis* within and between catchments, and presents preliminary studies of the extent of gene flow within a catchment.

1.5. AIMS OF THE STUDY

In light of the preceding discussion, the aims of the present study are to:

1. identify and assess the importance of factors which determine the distribution and abundance of adult caridean shrimps in the seagrass meadows of the Hopkins River estuary, with attention to the factors that have been flagged as important in previous work: vegetative complexity and the protection it may afford from predation; physiological tolerances to salinity and temperature; patterns of recruitment from the planktonic larval phase and post-larval migration.
2. describe the life-history patterns which permit the freshwater shrimp *Paratya australiensis* to occur in a wide variety of habitats from lakes to running fresh waters to estuaries.

In addressing these aims, chapters 2-4 examine the patterns of distribution and abundance of adult and juvenile carideans in the seagrass meadows of the Hopkins River estuary, and chapters 5 and 6 examine patterns of distribution in the estuary, and the biology of planktonic caridean larvae, in particular *P. australiensis*. Chapter 7 takes a broader look at the occurrence of *P. australiensis* in south-eastern Australian estuaries, and compares life history patterns between estuarine, and upstream riverine and lacustrine environments, within and between three river systems. Chapter 7 also attempts to quantify the connectedness of *P.*

australiensis populations within a catchment, in order to assess the extent of reproductive isolation between estuaries and upstream.

The chapters have the following objectives:

Chapter 2
- to quantify the temporal and spatial variation in distribution and abundance of all epibenthic caridean shrimps in the seagrass meadows of the estuary
- to identify relationships between patterns of abundance of each caridean species and patterns of variation in vegetation structure and physico-chemical parameters.

Chapter 3
- from the relationships detected in chapter 2, to conduct laboratory experiments which test likely determinants of distribution
- to test hypotheses of competitive interactions between species
- to quantify tolerances to salinity over a range of temperature in juveniles and adults of each caridean species and relate tolerances to observed distributions.

Chapter 4
- to describe the population dynamics of *P. australiensis* and *M. intermedium* in the seagrass meadows of the Hopkins River estuary and compare the dynamics of the two species in locations where each species occurs alone and where they occur together to detect any patterns in population dynamics that may be the result of co-occurrence.

Chapter 5
- to describe the complete larval development of *P. australiensis*, and rear larvae of M. intermedium and P. serenus in order to permit differentiation of these two similar species. This will permit the identification of larval stages of each species collected from the wild
- to assess effects of salinity on the larval development of each species.

Chapter 6
- to describe the temporal and spatial trends in distribution and abundance of larvae in the Hopkins River estuary
- to relate the horizontal and vertical distributions of larvae to the seasonal hydrological patterns of the estuary, and the vertical distributions of larvae to diurnal and tidal cycles
- to correlate patterns of abundance of larvae with patterns of abundance of juveniles in weedbeds.

Chapter 7

- to identify the extent of estuarine occurrence of *P. australiensis* in southern mainland Australia and the characteristics of the rivers and estuaries which support large numbers of *P. australiensis* in their estuaries
- - to compare life-history patterns (timing and synchrony of breeding, larval size) and reproductive traits (egg size, brood size, reproductive output) of *P. australiensis* between lacustrine, riverine and estuarine environments
- - to assess genetic variation within and between the same lacustrine, riverine and estuarine populations of *P. australiensis*
- - to examine evidence of migration patterns in juvenile and adult *P. australiensis* within the Hopkins River.

2. TEMPORAL AND SPATIAL PATTERNS IN THE DISTRIBUTION OF ADULT AND JUVENILE CARIDEAN SHRIMPS IN THE SEAGRASS MEADOWS OF THE HOPKINS RIVER ESTUARY

2.1. INTRODUCTION

Distribution patterns of epifauna in seagrass meadows must be considered on at least two scales. Within an estuary such as the Hopkins, seagrass meadows are relatively discrete patches of habitat spread along the estuary, separated by stretches of no or little seagrass growth. Differences in epifaunal abundances have been widely reported at this scale of 'between-separate-meadows' (e.g. Alon and Stancyk, 1982; Bell and Westoby, 1986c; Bell et al., 1988; Gray, 1991b). Study of patterns of distribution *within* a meadow on a single occasion, and over time, may help elucidate factors which drive patterns on a larger scale. Several studies, particularly those concerned with the effect of seagrass structure and habitat complexity, have been conducted at this smaller, within-meadow scale, either within meadows (Bell and Westoby, 1986b) or between adjacent meadows (Gray, 1991a; Virnstein and Howard, 1987).

Bell and Westoby (1986b) used poisoning and nets over an area of 36 m^2 to detect gross changes in epifaunal abundance with differing seagrass structure, and Gray (1991a) used nets to collect from an area of 50 m^2. In both cases, information on small scale associations between epifauna and environmental factors, such as vegetation structure and physico-chemical data, would have been lost. Elliott (1977) recommends a small sample unit size to investigate patterns of distribution in organisms with aggregated distributions. In this chapter a pilot study is described which aimed to find the sampler size which maximised information on pattern of distribution within meadows, while providing accurate data on abundance in the meadow. The sampler chosen allows the simultaneous sampling of macrofauna and vegetation, and the measurement of physico-chemical data from small areas of seagrass meadow.

Using this sampler, a survey of the distribution and abundance of the caridean shrimps in four seagrass meadows, spanning the length of the Hopkins River estuary was conducted over a year. This quantitative survey was augmented by a year-long qualitative survey of caridean shrimps at two of the same meadows. The data collected in the quantitative survey allow analysis of associations between shrimp abundance and environmental factors. From this work a number of hypotheses are raised concerning determinants of shrimp distribution, which are investigated in subsequent chapters.

2.2. DESCRIPTION OF THE STUDY AREA: THE HOPKINS RIVER AND ITS ESTUARY

The catchment of the Hopkins River extends approximately 160 km from its northern boundary to the Southern Ocean, and approximately 60 km from east to west (Fig. 1.1). The catchment covers an area of 8 651 km^2 bounded to the north by the Great Dividing Range and by the Gariwerd (Grampians) Range to the north-west. The river flows south from these ranges through the western volcanic plain and the coastal plains, before draining into the Southern Ocean at Warrnambool. Major tributaries are the Mt. Emu Creek, draining the east of the basin, and Salt Creek and its tributary, Fiery Creek, which drain the centre of the basin.

Average annual discharge is 3.3×10^5 ML of which nearly half is contributed by the Mt. Emu Creek (Department of Water Resources Victoria, 1989b). The pattern of stream flow is strongly seasonal with 68% of mean annual flow from July to September with only 2% from January to March. The basin is almost entirely cleared for pasture and agriculture except for a small area in the north, and a few small remnants of forest near the coast (Department of Water Resources Victoria, 1989a).

Hopkins River estuary

The Hopkins River estuary is a drowned river valley (Gill, 1967) which extends for 9.5 km upstream of the mouth to Tooram Stones (Fig. 2.1a). The mouth of the estuary is shallow, being underlain by a rock bar (Gill, 1984). Upstream of the mouth, the estuary deepens into a single well-defined U-shaped channel averaging 2-3 m deep, with holes 8-12 m deep at Kinnear's Hut, Jubilee Park, and below Tooram Stones (Fig. 2.1b). The last two of these holes are 'plunge pools' downstream of shallow lava flows which formed waterfalls in periods of lower sea levels (Sherwood and Backhouse, 1982). Only one minor tributary, the Lake Gillear drain, enters the estuary.

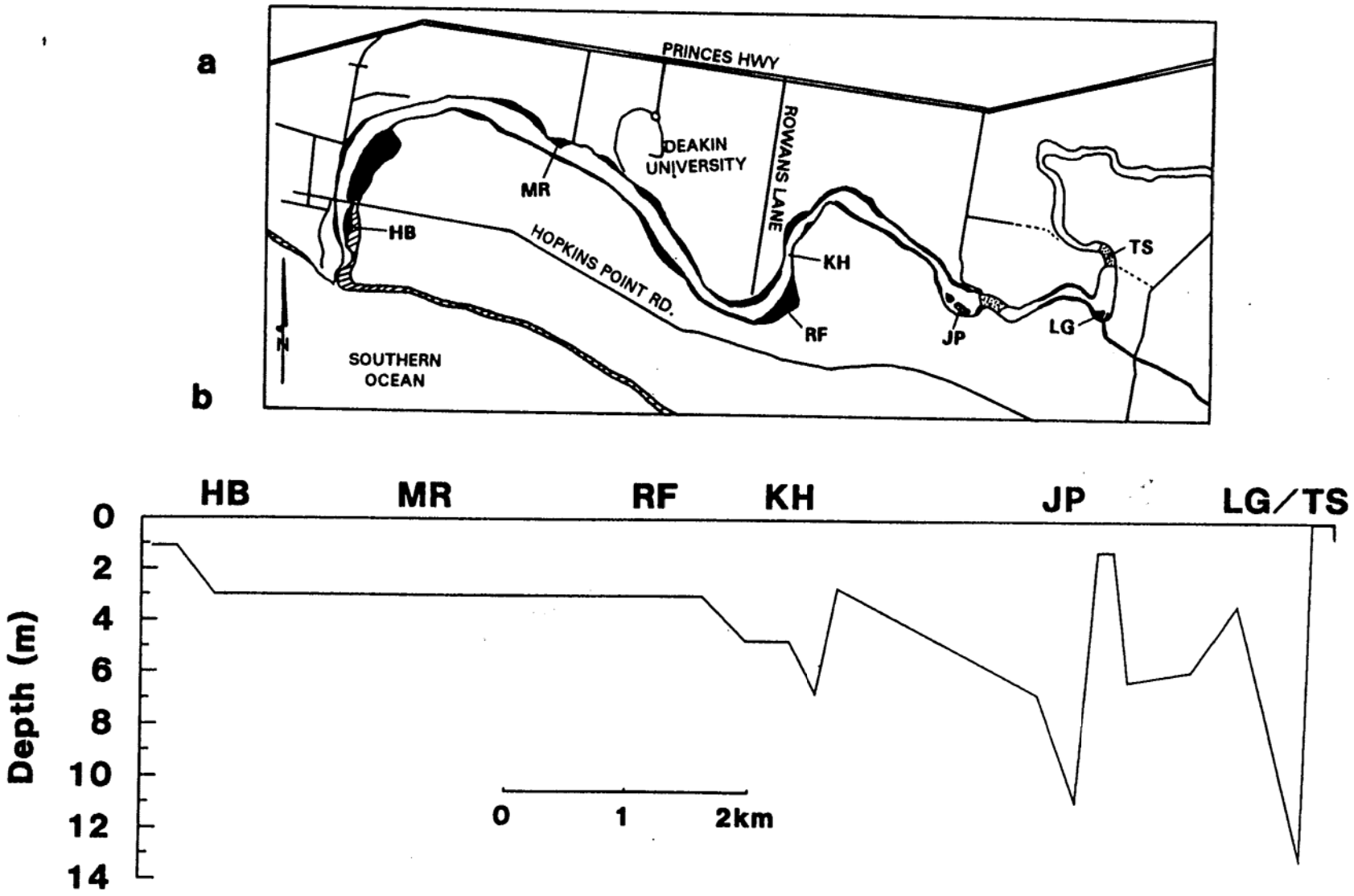
The estuary is a 'salt wedge' estuary, stratifying strongly with a surface fresh layer overlying more saline bottom water (Sherwood, 1985). When highly stratified, changes in salinity of 20 over vertical distances of less than 0.5 m are possible. But the sharpness of stratification and the extent of intrusion of the salt-wedge is influenced by the strongly seasonal stream flow input.

→

Fig. 2.1 The Hopkins River estuary (a) Locations of sampling sites: seagrass meadows and mudflats, black; lava flows, stippled; sand, hatched (See Fig. 1.1 for broader location.)

(b) Schematic representation of a longitudinal profile of the estuary indicating locations of deep holes, and sampling locations (After Sherwood and Backhouse, 1982)

HB, Hopkins Bridge; MR, Mahoney's Road; RF, Rowan's Flat; KH, Kinnear's Hut; JP, Jubilee Park; LG, Lake Gillear Exit; TS, Tooram Stones


a
b
PRINCES HWY
DEAKIN UNIVERSITY
ROWANS LANE
MR
HB
HOPKINS POINT RD.
KH
RF
JP
LG
TS
N
SOUTHERN OCEAN
HB
MR
RF
KH
JP
LG/TS
Depth (m)
0
2
4
6
8
10
12
14
0
1
2km

The following is a summary of the annual hydrodynamic cycle of the Hopkins River estuary, based on the description by Sherwood and Backhouse (1982). In most years, flooding in August and September flushes the salt wedge from the estuary, so the entire estuary fills with freshwater. In spring and early summer, the wedge advances upstream at speeds of up to 3 km per day. The advance of the wedge may be stalled by shallow barriers at Kinnears Hut and Jubilee Park, as observed in spring 1989 (Fig 2.2). In the early stages of advance, the wedge is characterised by small increases in salinity upstream with relatively high levels of dissolved oxygen. Over summer and autumn, with low stream flow, the wedge reaches its upstream limit at Tooram Stones and slowly stagnates. The mouth becomes smaller in cross-sectional area and may become totally blocked by a sand bar. Exchange of sea water at this time is slight, so the dissolved oxygen levels drop with the deep holes often becoming anoxic until flushed at the next flood.

Oceanic tides of this region are basically diel with a small semi-diel component. The daily tidal range in the estuary is typically between 0.1 and 0.6 m. When the mouth is blocked, the system becomes atidal and, on the rare occasions such as March 1989 when it is blocked for an extended period, the level of the estuary may rise by over a metre. The mean summer level (msl) of the estuary is 0.375 m above the Australian Height Datum (AHD), and the mean winter level is 0.475 m AHD (J. Sherwood, Deakin University, personal communication).

The estuary supports littoral stands of *Phragmites australis*, and subtidal stands of *Zostera muelleri* and *Ruppia maritima* (hereafter collectively referred to as seagrass meadows and individually as *Zostera* or *Ruppia* meadows) for most of its length. The extent of these meadows varied widely over the study period. In most sections of the river, seagrass grew in a band 1-2 m wide along the sides of the channel. In some sections, shallow mudflats supported more extensive seagrass meadows (see shaded areas in Fig. 2.1) five of which were used as sampling locations.

Four seagrass meadows and a site just upstream of the estuary were the focus of adult and juvenile shrimp collection in the estuary during the study, They, and a fifth seagrass meadow used in preliminary surveys, are described below.

Tooram Stones (TS) is a set of shallow rapids between basalt boulders approximately 150m long which forms a complex of channels and pools within tea tree scrub (*Leptospermum lanigerum*) at the upper limit of tidal influence in the Hopkins River (Fig. 2.1). Within the 'Stones' are a wide range of aquatic habitat types, from fringing grasses which become inundated during floods, to a diverse mosaic of submerged and emergent macrophytes in the channels and pools, dominated by *Triglochin procera*, *Potamogeton pectinatus*, and filamentous green algae.

Lake Gillear Exit (LG) (Figs. 2.1, 2.3): Three hundred and fifty metres south of Tooram Stones, a mudflat formed by the delta of the drain emanating from Lake Gillear (Fig. 1.1)

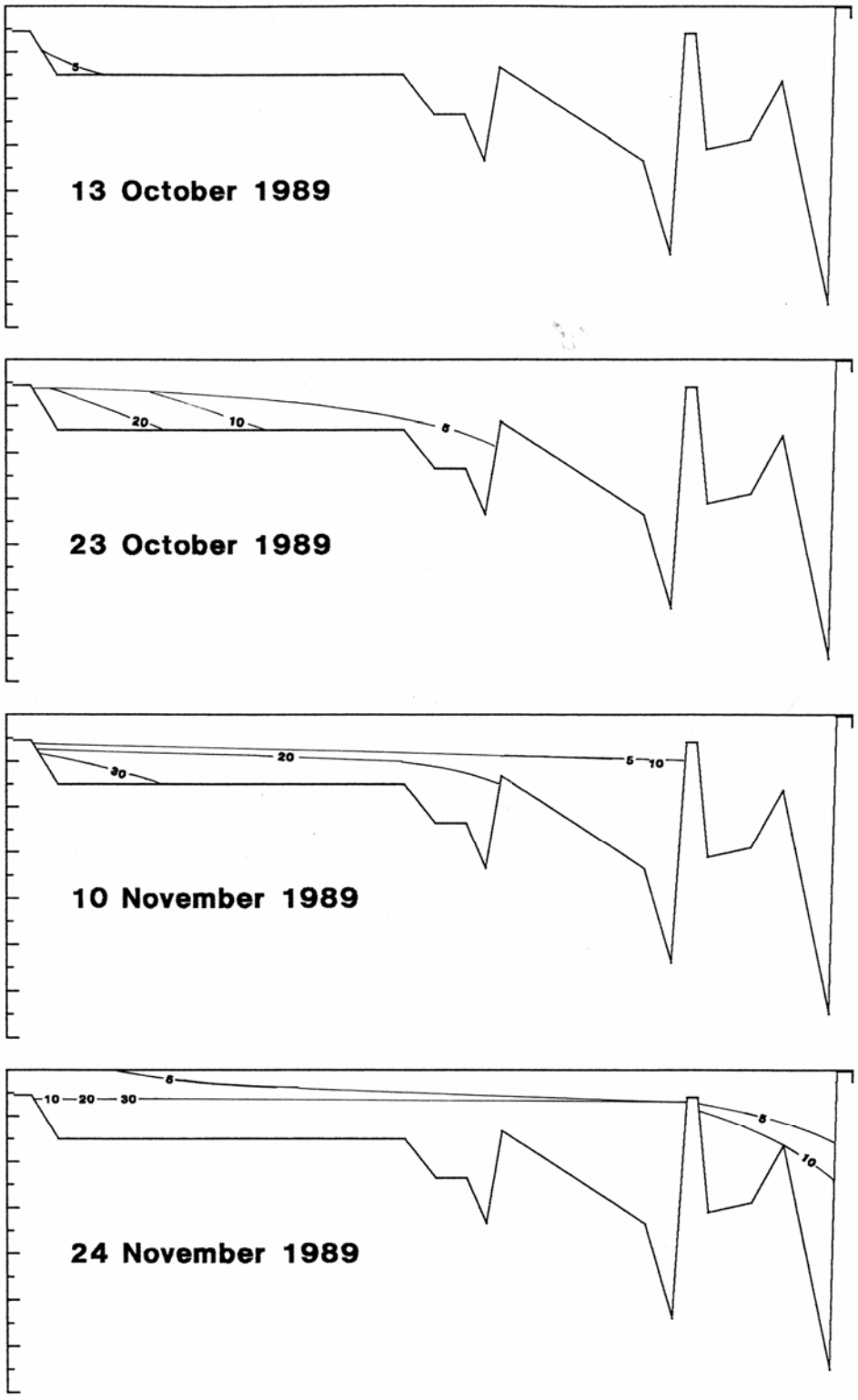


Fig. 2.2 Progressive intrusion of the 'salt-wedge' into the Hopkins River estuary after the flood of 1989 The long itudinal profile is as in Fig. 2.1, and salinity contours are extrapolated from salinity measurements at HB, RF, JP, and LG (see section 6.2).

supported a stand of *Ruppia* from November 1987 to April 1988 and from November 1988 to February 1989. During the low-flow period of late summer or early autumn, the plants developed a heavy epiphytic growth and died off. The meadow did not regenerate in the summer of 1990-1991. This meadow covered an area of approximately 1400 m^2, at a depth of 0.45-0.7 m below msl.

Jubilee Park (JP) (Figs. 2.1, 2.4): The *Zostera* meadows at this site, 8 km upstream of the mouth, mark the most upstream occurrence of this species in the estuary. Four separate meadows were sampled over the study period (Fig. 2.4a):

–Meadow 1 covered an area of ≈600 m^2 on 12 June 1988, but by 16 July 1988 the area covered by dense *Zostera* growth had receded to less than 200 m^2. The bottom of this meadow, which ranged from 0.35-0.95 m below msl, was littered with rocks which made sampling difficult. Meadow 1 was not sampled after 16 July 1988;

–Meadow 2 consisted of a strip of *Zostera* 1-2 m wide at 0.3-0.85 m below msl. It skirted the steep bank of the larger of the islands at Jubilee Park. This meadow covered an area of ≈150-240 m^2 over the study period.

–Meadow 3, around the smaller of the islands covered an area of ≈680 m^2 at its most extensive, but receded to an aggregation of patches totalling ≈360 m^2 during the period of peak discharge (Figs. 2.4a-d). *Zostera* in this meadow grew from 0.3 to 0.7 m below msl.

–Meadow 4 grew below the engineered wall on the north side of the estuary. This meadow, which covered an area of ≈200 m^2 from 0.25-0.6 m below msl, was sampled on 23 October 1988 when high water level prevented sampling at meadows 2 and 3.

Rowan's Flat (RF) (Figs. 2.1, 2.5): The broad sweep of the estuary opposite Rowan's Lane, 5.5 km upstream of the mouth, forms an expansive mudflat covering about 1 ha. The northern section of this mudflat did not support weed cover during the study period. A wedge-shaped meadow of *Zostera* in the southern third of the mudflat extended from 0.4 m to >1 m below the msl. This meadow expanded during the low-flow period, with dense *Zostera* growth at the deeper edge of the mudflat, and a sparser mixed stand of *Ruppia* and *Zostera* growing in the shallower regions adjacent to the main meadow.

Mahoney's Road (MH) (Fig. 2.1): Immediately west of Mahoney's Road, 2.5 km upstream of the mouth, a 0.65 ha mudflat supported an expansive stand of *Zostera* during 1988 and 1989. This meadow was used only for the preliminary sampling trials (section 2.3.1).

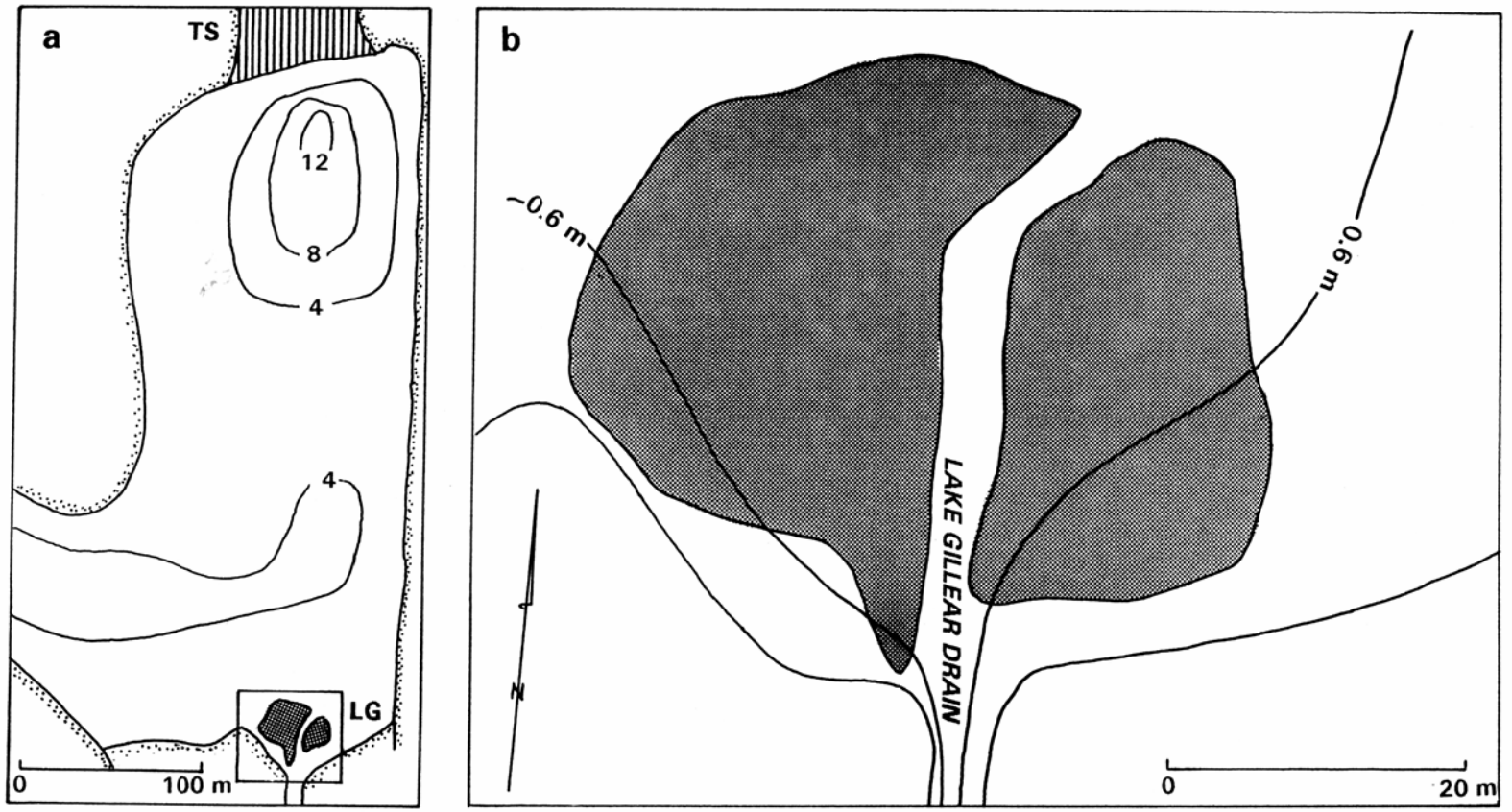


Fig. 2.3. (a) Upper limit of the Hopkins River estuary. (b) Detail of *Ruppia* meadow on the Lake Gillear drain delta; contours are depth below mean summer average level in metres; *Ruppia*, stippled area; rapids at TS, hatched (after unpublished data of J. Sherwood, Deakin University)

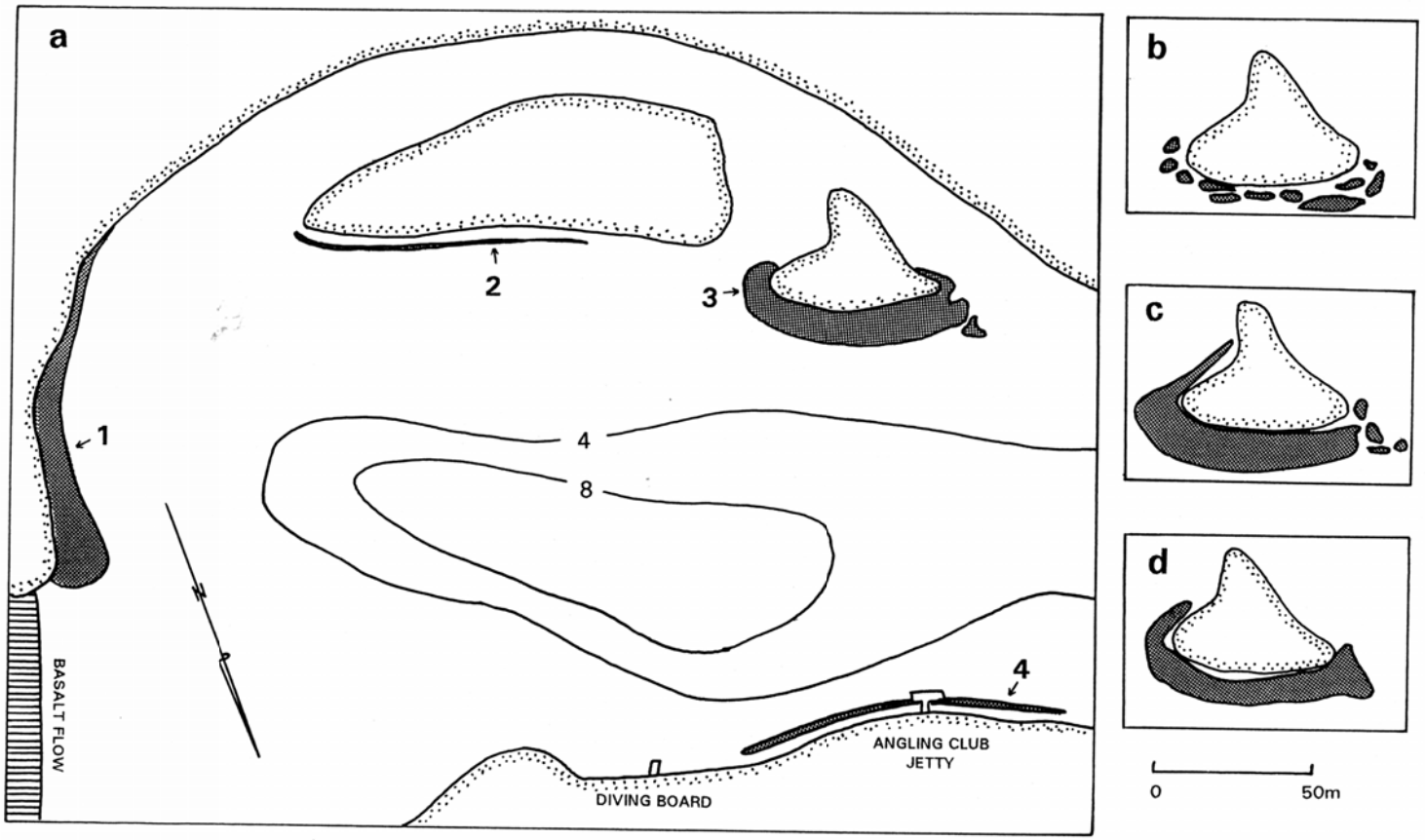


Fig 2.4. (a) Hopkins River estuary: Jubilee Park indicating location and extent of *Zostera* meadows (stippled), marked 1-4, on 12 June 1988; (b) extent of *Zostera* cover in the largest meadow—3—on 10 September 1988; (c) extent of *Zostera* cover in meadow 3 on 13 January 1989; (d) extent of *Zostera* cover in meadow 3 on 15 April 1989. Contours as in Fig. 2.3

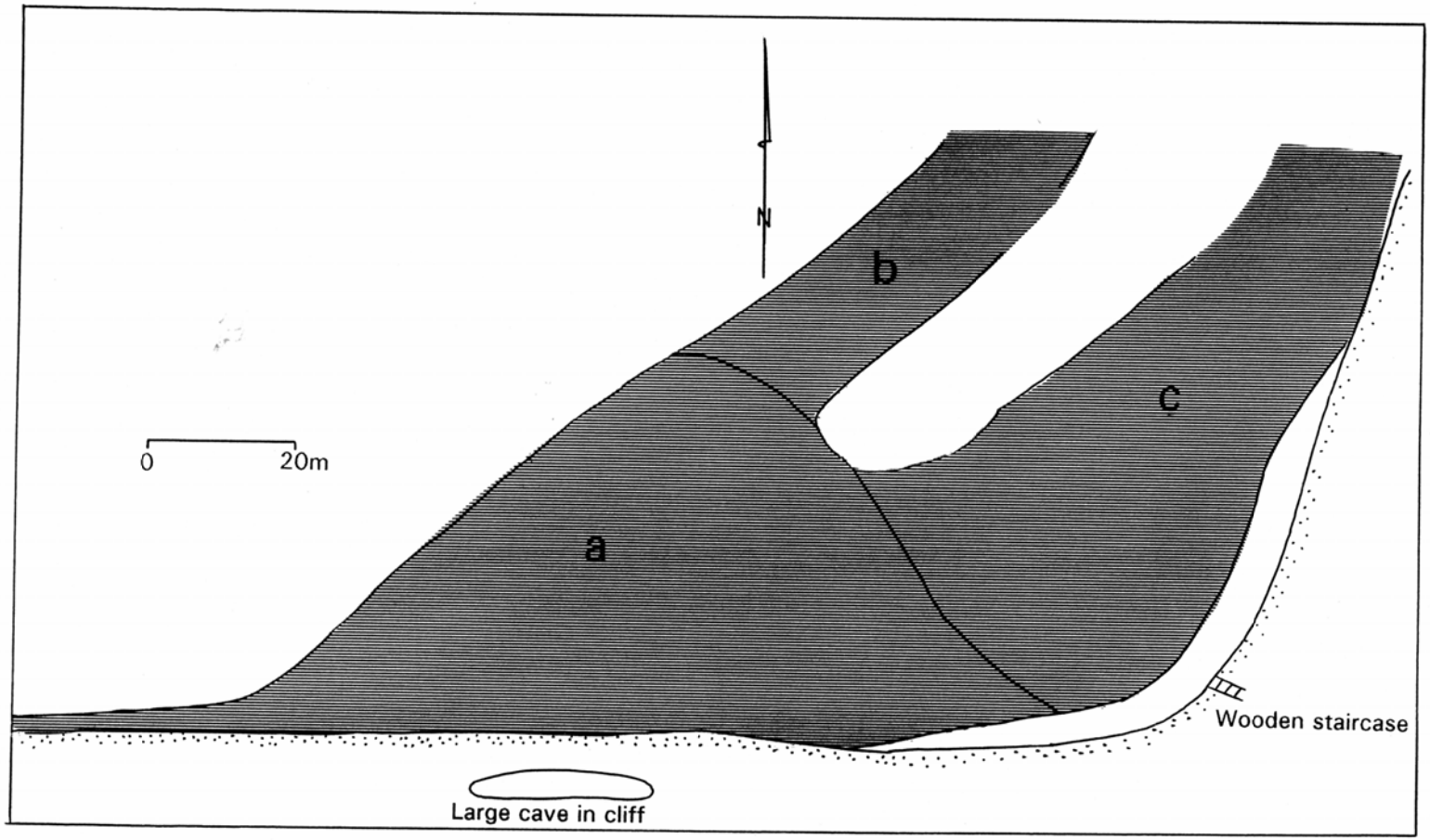


Fig. 2.5. Hopkins River estuary: the southern section of Rowan's Flat showing the extent of the *Zostera/Ruppia* meadow. (a) dense *Zostera* cover over entire sampling period; (b) *Zostera* cover from December 1988; (c) sparse cover of mixed *Zostera* and *Ruppia* from December 1988

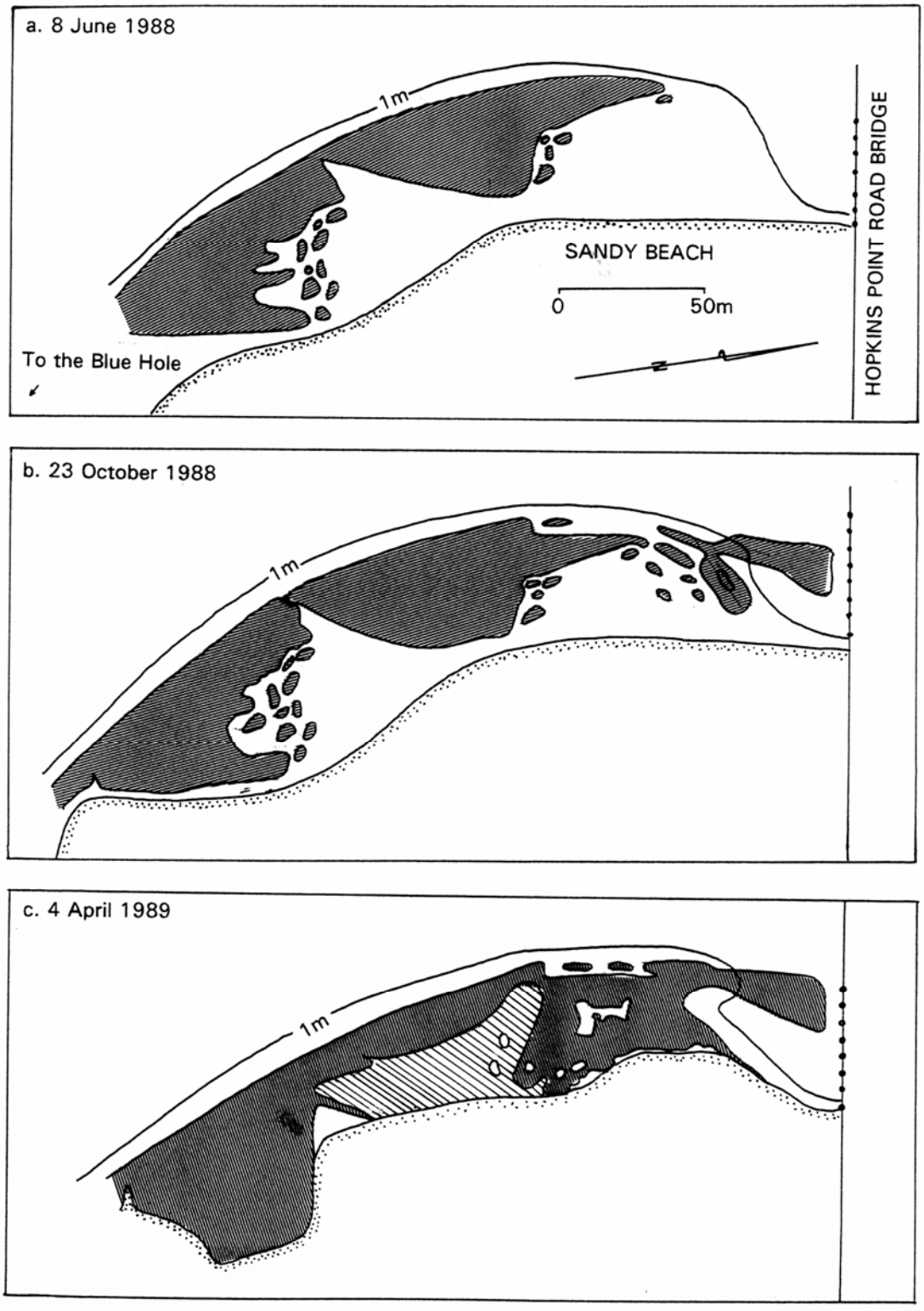


Fig 2.6. Hopkins River estuary: extent of the Hopkins Bridge *Zostera* meadow on three occasions. (a) 8 June 1988; (b) 23 October 1988; (c) 4 April 1989. Densely hatched, living *Zostera*; lightly hatched, senescent *Zostera*. Contour line shows approximate 1 m below msl.

Hopkins Bridge (HB) (Figs. 2.1, 2.6) Immediately south of the Hopkins Point Road bridge a meadow on the east bank stretched 250 m to the 'Blue Hole' within 400 m of the estuary mouth. The substrate of this meadow was firmer and more sandy than any of the meadows upstream, with *Zostera* (and rare patches of *Ruppia*) growing only 0.2-0.35 m below the msl over most of the flat. At the steep western boundary of the meadow formed by the drop off into the main channel, *Zostera* grew to a depth of ≈0.5 m below msl in a band 1-2 m wide. At the northern end of the meadow, a small extension of the *Zostera* cover grew to a depth of up to 1 m below msl on a mud substrate. The morphology of the beach and the flat itself varied over the study period, as did the extent of seagrass cover (Figs. 2.6a-c). It was common for the shallow main body of this meadow to be exposed at low tides— particularly in summer, when areas of senescent weed were common (Fig 2.6c). This meadow covered an area of 0.25-0.35 ha.

2.3. METHODS

2.3.1. QUANTITATIVE SAMPLING OF CARIDEAN SHRIMPS—PILOT STUDIES

Before a quantitative sampling program was undertaken, two pilot trials were conducted to determine an accurate and precise sampling technique for the estimation of caridean shrimp densities in the seagrass meadows of the Hopkins estuary.

2.3.1.1. REVIEW OF QUANTITATIVE METHODS IN PREVIOUS STUDIES

Methods used in previous studies to quantitatively sample caridean shrimps are summarised in Table 2.1. Studies that used nets to trawl for shrimps through seagrass meadows (Howard, 1981, 1984; Gray and Bell, 1986; Gray, 1991a, 1991b) reported densities of shrimp an order of magnitude less than studies that have used throw traps or core or grab samplers (Hart, 1981; Howard, 1981; Pihl and Rosenberg, 1982, Emmerson, 1986; Virnstein and Howard, 1987a; Holmquist et al, 1989). Intermediate densities of shrimps were reported by Gore et al. (1981) using large drop nets which were cleared by seining. Bauer (1985), using a pushnet, collected similar densities to Gore et al (1981), but such high densities may be explained by the tropical location of the study. These results suggest that the most efficient shrimp sampling techniques are throw traps, cores and grab samples, with trawl nets being least efficient.

Few studies have attempted to evaluate the accuracy or precision of the sampling techniques used (Table 2.1). Howard (1981) conducted two separate series of trials to assess the accuracy of his Riley push net samples. In three mark-recapture trials on *M. intermedium*, he found the push net recaptured 4.1%, 4.2% and 18.3% of marked shrimps expected to be in the path of the net in an enclosure. He also compared a collection using the Riley push net to an adjacent transect of twelve 0.1 m^2 core samples. The push net collected an average of 4.7% of the number of

Table 2.1. Studies which quantitatively sampled caridean shrimps in seagrass meadows (and a coastal FW lake: Hart, 1981). For seasonal studies, mean (and range) densities of dominant species are presented if they were reported or could be estimated from the published data. For studies that reported one set of samples, mean density is presented.

Study	Location	Sampling device & mesh size of collecting net	SU size (m^2)	Number of Replicates	Evaluation of precision and accuracy	Dominant species	Density reported (N m^{-2})
Hart (1981)	Lake Sibya, South Africa	Rectangular core; 0.3mm mesh	0.1	5 random	None	*Caridina nilotica*	(400-1400)
Howard (1981,1984)	Western Port, Victoria, Australia	Push net; 1.4 × 0.27 m; 1mm mesh Round core	235 0.1	1 12 along transect	Compared 2 methods and conducted a mark-recapture trial of push net.	1 *Macrobrachium intermedium* 2 *Pontophilus intermedius* 3 *Hippolyte caradina*	Net: sp. 1 (0.5-6); sp. 2 (0-1); sp. 3 (0-3) Core: 21, 83 and 3 times more efficient for species 1, 2, & 3 respectively
Gore et al. (1981)	Indian R., Florida, USA	Drop net; 2mm mesh	10	6	None	*Hippolyte pleuracanthus* *Palaemonetes intermedius*	50 (5-170) 10 (0-60)
Pihl and Rosenberg (1982)	W Sweden	Square core; 1mm mesh	0.5	30	Estimated accuracy and observed avoidance	*Crangon crangon*	(30-90)
Baden and Pihl (1984)	W Sweden	as for Pihl and Rosenberg (1982)				*Palaemon adspersus*	(2-50)
Bauer (1985)	N. Puerto Rico	Push net; 0.5 m wide 1 mm mesh	5	10	Compared night and day	*Latreutes fucorum* (and many others)	49 (5-250)-night 16 (1-80)-day
Emmerson (1986)	Eastern Cape South Africa	Square core sampler	0.5	1 in 4 strata	None	*Palaemon pacificus*	(28-211)
Gray and Bell (1986)	Pittwater NSW Australia	Beam trawl; 1 × 0.5 m 2 mm mesh and Poison	9	4 adjacent	Compared day/night trawls & poisoning	*Macrobrachium intermedium*	8 night, 6 day 0.2 poison
Virnstein and Howard (1987b)	Indian R. Florida, USA	Horizontal epifaunal grab	0.04	6 random in 3 grass spp.	None	*Hippolyte pleuracanthus*	114, 95, and 31
Holmquist et al. (1989)	Florida Bay, USA	Square throw trap	1	6 random, 3 transects	Precision and accuracy for fish (Kushlan,1981)	*Thor floridanus* and others	35-884
Gray (1991a)	Port Hacking NSW Australia	Beam trawl; 1 × 0.5 m 2 mm mesh	50	3 adjacent	None	*Macrobrachium intermedium*	(0-20)
Gray (1991b)	Sydney region NSW Australia	Beam trawl; 1 × 0.5 m 2 mm mesh	20	6 adjacent	cost/benefit analyisis for n (Young 1985)	*Macrobrachium intermedium*	(0-20)

M. intermedium collected by the core sampler per unit area. Given the push net collected at a 4-18% accuracy, the core sample was evidently much more accurate in assessing shrimp densities.

Pihl and Rosenberg (1982) observed avoidance reactions of mobile epifauna, finding that epifauna were not disturbed by the shade of an approaching 0.5 m^2 square core sampler. They did however detect avoidance reactions to a person moving at a distance of 0-1.5 m. They thus used two operators who held the sampler from either side using long poles to maintain a distance of 4 m during deployment. They also conducted an enclosure-recapture trial which showed this sampling method to have a very high accuracy.

Other studies have quantitatively attempted to compare the accuracy of alternative methods. Gray and Bell (1986) showed poisoning to be a less effective sampling method for caridean shrimps than trawling. These authors and Howard (1987) showed that larger numbers of carideans were captured at night than during the day.

In this work, the term 'sample units' (SUs) represents units of equal size that are collected from the sampling device. A group of these units randomly selected from a population of potential sample units, constitutes a 'sample' (Elliott, 1977). Sample unit size was much smaller in core samples than in any netting technique (Table 2.1). While the precision of a sample estimate is likely to increase with increasing size of sample units (Andrew and Mapstone, 1987), smaller sample units are likely to be more suitable to elucidate spatial patterns within an area (Elliott, 1977).

2.3.1.2. SAMPLE UNIT SIZE TRIAL

Because of the advantage of smaller sample units for studying spatial patterns, and because of the apparent greater accuracy of core samples than of netting techniques (Howard, 1981), it was decided to trial a core sampling technique for estimating abundance of caridean shrimps in this study.

A cylindrical, sheet metal core 1 m tall was used; a circular cross-section was used to minimise any edge effects. To collect a sample, the core was thrust vertically into the substrate, so that a water-tight seal was formed. The thrust was performed at full stretch with the core held aloft, thus ensuring that the operator was standing >2 m from the sampling location until the core was deployed. Water depth was recorded before emptying the core. All above-ground vegetation was removed from the core and a small square-mouthed, long-handled net was run through the remaining contents of the core, while a boat-based operator pumped the water from the core using a hand-operated bilge pump (Whale: Model Gusher Titan) through a large collecting net with 1 mm mesh. All material removed from the core was preserved in 5% formalin. On 30 January 1988, thirty random SUs were taken at Mahoney's Rd meadow. Ten SUs of each of three sizes were taken: 0.05 m^2 (S), 0.1 m^2 (M) and 0.2 m^2 (L).

Table 2.2. Statistics based on densities of adult *Macrobrachium intermedium* from a trial of three sample unit sizes, 30 January 1988 at Mahoney's Road meadow. See text for meanings of Precision, Morisita's Index and the ratio of adjacent indices.

Core Size (m^2) (q)	Density ($N.m^{-2}$) (x±sd)	n	Precision (p)	Morisita's Index I_δ	Ratio $\frac{I_{\delta\, q}}{I_{\delta\, 2q}}$
0.05(S)	79±9	7	0.095	1.34	-
0.10(M)	91±5	7	0.061	1.02	1.31
0.20(L)	60±19	9	0.206	1.20	0.85

A total of 269 *M. intermedium* were collected from the thirty sample units. However, seven units (3S, 3M, and 1L), which were taken in the shallowest regions of the meadow (depth <0.4 m), contained a total of only two individuals. These seven sample units were discarded from further calculations, as it was considered that this shallow part of the meadow represented a stratum of lower shrimp density than the deeper bulk of the meadow (depth 0.4-0.7m).

Shrimps were contagiously distributed, resulting in skewed distributions with heterogeneous variances. To correct for this, all shrimp numbers used in analyses were transformed by log (x+1). Reported means (and standard deviations) are the antilog(x)-1 of means (and standard deviations) calculated on the log (x+1)-transformed data. Significance was accepted at $P<0.05$ for all tests, unless otherwise stated.

An analysis of variance (ANOVA) comparing the mean densities from each of the three core sizes showed no significant differences ($P=0.625$). Thus no effect of core size on the accuracy of estimates of mean density was detected. Mean densities are presented in Table 2.2.

Precision (p) in Table 2.2 was calculated by the formula:

$$p = SE/x = (s/\sqrt{n})/x$$

(Andrew and Mapstone, 1987). The most precise estimate (smallest p) was the M core (0.1 m^2).

Morisita's Index of dispersion(I_δ) was calculated using untransformed data by the formula:

$$I_\delta = \frac{n.\Sigma[x(x-1)]}{\Sigma x(\Sigma x-1)}$$

Values of greater than 1 for this index indicate an aggregated distribution (Elliott, 1977). In this case, only data from the 'S' core departed significantly from a random distribution, using a χ^2 test as described by Elliott (1977), so the trend in Morisita's indices is indicative of an aggregated distribution of clumps smaller than 0.1 m^2. Elliott (1977) described a technique for analysis of pattern using this index for a series of sample unit sizes where each sample unit is twice the size of the previous sample unit. If the smallest sample unit is q m^2, the ratio

$$\frac{I_\delta \text{ for quadrat q}}{I_\delta \text{ for quadrat 2q}}$$

is assigned to unit size 2q. Maxima of this ratio occur when quadrat size and aggregation size of the population are approximately equal. Because this ratio was greater for the M core (Table 2.2), the population of *M. intermedium* at Mahoney's Road was grouped in aggregations of 0.1 m^2 or less. In light of the size and mobility of *M. intermedium,* it is likely that aggregations of 0.1 m^2 or less are the smallest for this species, although these small aggregations may group together to form larger aggregations (Elliott, 1977).

In summary, a sample unit size of 0.1 m^2 was chosen for this study for the following reasons:

- accuracy was not significantly different among the three sample units investigated.
- precision was greatest for the 0.1 m^2 unit. Edge effects are greater for smaller sampling units (Elliott, 1977), and this would appear a likely explanation for the lower precision of the smallest unit—particularly for such vagile organisms. Lower precision for the largest unit may have been a result of the unwieldiness of the core with which it was more difficult to achieve a seal with the substrate This unwieldiness may have resulted in less reliable capture of all enclosed shrimps.
- a 0.1 m^2 unit was at least as large as the smallest level of aggregation of the population in question, and should be most suitable for providing information on the pattern of distribution on this scale.

This pilot study has assessed the accuracy of core samples of differing sizes relative to each other, but has not quantitatively assessed the absolute accuracy of the technique. However, the studies of Howard (1981) and Pihl and Rosenberg (1982) suggest that such a technique is very accurate. The suitability of this technique for the assessment of the abundance of carideans other than *M. intermedium* has not been assessed, but it is assumed that the core would be equally suitable for *P. australiensis* and *P. serenus*, given their similar size ranges and habitat.

One possible error inherent in this technique, which is difficult to assess, is the result of changes in shrimp distribution while a set of sample units is being collected. Howard (1985) found a 20-50% turnover of carideans in three hours in an area of 0.56 m^2. As each sample unit in the current study took ten minutes to collect, a sample of twelve units took approximately two hours to complete. Samples were spread over meadows of total areas of >400 m^2 and as the sample was designed to estimate abundance of shrimp over this scale, it seems unlikely that a level of turnover on such a small scale as reported by Howard (1985) would have a large effect on estimates of abundance across a meadow.

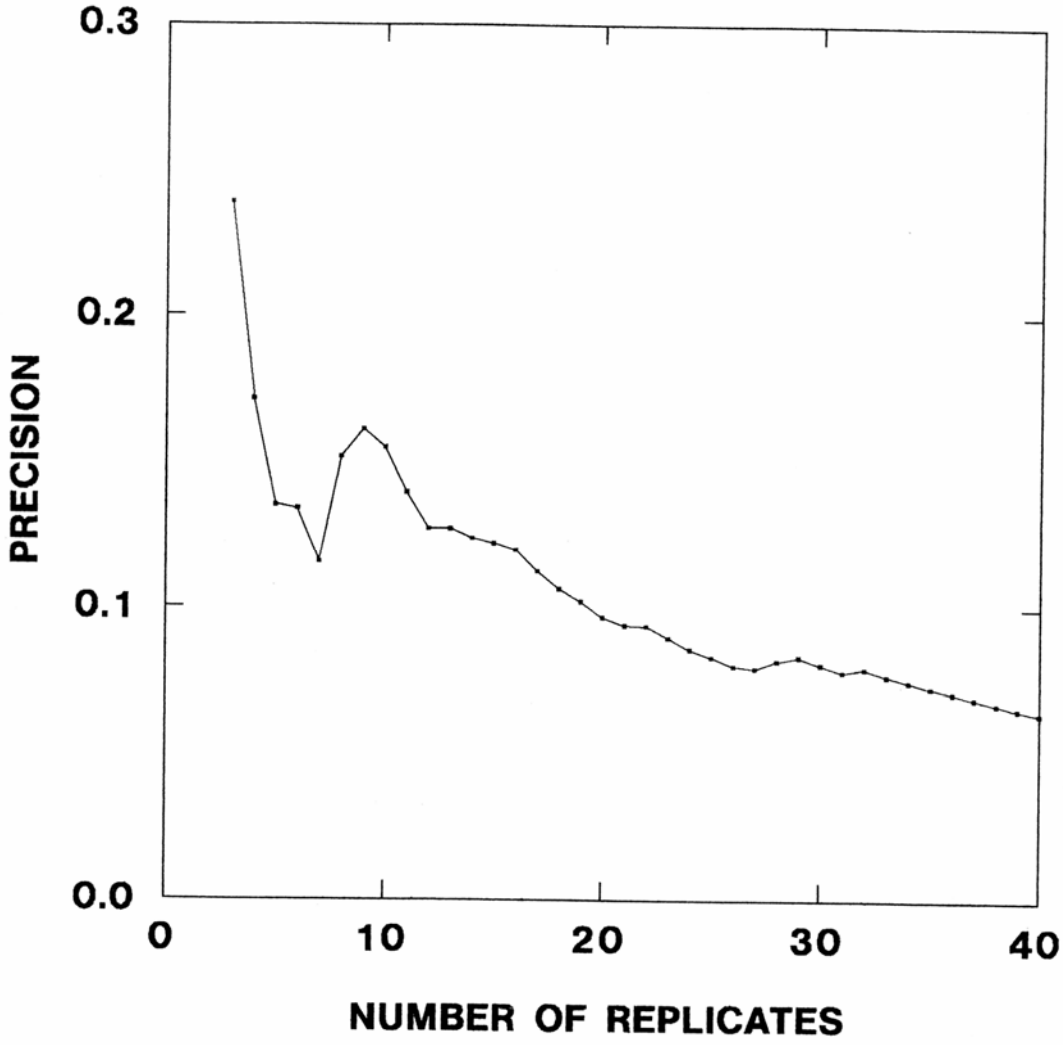


Fig. 2.7. Change in precision of the estimate of the mean of a sample of *Macrobrachium intermedium* from Mahoney's Rd on 10 April 1988 with increasing numbers of sample units

2.3.1.3. SAMPLE SIZE TRIAL

On 10 April 1988, forty random samples were taken at the Mahoney's Road meadow. Mean (±sd) density of *M. intermedium* was 199 ± 10 m^2. Precision of the estimate of the mean (see Section 2.3.1.2) was calculated for increasing numbers of sample units from three to forty (Fig. 2.7). A precision of 0.2 was deemed adequate, which was achieved after four replicates. However the level of precision was unstable below a sample size of twelve. Beyond a sample size of twelve, the increase in precision (decrease in p) was more gradual. Thus twelve was chosen as the minimum sample size required to achieve a reliable level of precision.

It is noteworthy that a higher level of precision was attained on 30 January 1988 in the sample unit size trial (Table 2.2), although this higher precision may have been an artefact of instability due to smaller sample size.

It is assumed that a sample size of twelve, appropriate for the estimation of abundance of *M. intermedium*, would also be an appropriate size for the other caridean shrimps of the Hopkins River.

2.3.2. SAMPLING PROGRAM

Caridean shrimps were collected from the Hopkins River estuary at approximately monthly intervals for two years. An initial qualitative collection was made by Dr. B. D. Mitchell (Deakin University, personal communication) from September 1983 to December 1984 at JP and HB. During the present study, quantitative samples were collected from June 1988 to May 1989 at LG (when *Ruppia* was present), JP, RF and HB. On occasions when water levels were too high for the quantitative collecting device (>1 m), qualitative samples were collected. Qualitative samples were also taken from July 1988 to May 1989 through the vegetation in the riffle at TS. Descriptions of all sample sites are given in section 2.3.1, and dates of all collections are presented in Appendix 1.

The 1983-84 qualitative samples were taken by sweeping a triangular-mouthed dipnet with a 1 mm mesh through the seagrass with a standard effort. Salinity and temperature on these sampling occasions were measured at a midstream site adjacent to the weedbeds using a Yellow Springs Instrument salinity and conductivity meter (model 33). The 1988-89 qualitative samples were taken with a square-mouthed dipnet (30 cm × 30 cm) with 1 mm mesh, using a standard effort of 2 minutes sweeping through vegetation.

For quantitative sampling, >20 sample unit sites was chosen randomly prior to each sampling occasion on a map of the maximum extent of each meadow. If the boundaries of the meadow had receded since first mapping, then units falling outside the meadow on bare mud were not used, and the new extent of the bed was noted. On several occasions, part or all of a meadow (particularly RF-see Appendix 1 for dates) was under a depth of water greater than 1 m. If more than 25% of the meadow could not be sampled due to high water, then a standard qualitative

sample only was taken through the vegetation at that site. The procedure for quantitative core sampling was described in Section 2.3.1.2.

Salinity and temperature at the surface and the bottom were measured at a minimum of three sample unit sites spanning the length of the meadow using a 'Yeo-Kal' salinometer (Model 602 Mk III).

In the laboratory, preserved samples were rinsed through a 350 μm mesh and all shrimps were removed and stored. Vegetation was sorted into species, and separated into: fresh leaves, senescent leaves and other detrital leaf fragments, drift marine algae, and two categories of epiphyte. Epiphytes were separated into the more common periphytic 'ooze' dominated by diatoms, and filamentous green algae, which tended to occur separately. The separated vegetation components were dried at 105°C for 48 h and weighed.

Shrimps were identified to species, and OCL measured using a dissecting microscope (×8-×40) with an ocular grid. Sex was determined, with ovigerous females being noted. Small individuals, for which sex could not be confidently assigned, were designated as juveniles.

Differences in density of adults and juveniles of *M. intermedium* and *P. australiensis* were compared among the four estuarine sites and among the eleven quantitative sampling occasions (see appendix 1) by two-way ANOVAs. In cases where differences between sites were obvious, sites with consistently low or zero densities were excluded from the analyses. ANOVAs on *M. intermedium* densities did not include LG. A one-way ANOVA for *P. australiensis* adult density was performed for JP only, and a two-way ANOVA on *P. australiensis* juveniles included all four levels of site, but only the three sampling occasions in which high densities were recorded (November to January).

Four outlier sample units with no or very few shrimps were excluded from these analyses because they contained no fresh seagrass leaves. The samples collected at HB on 19 November and 15 December 1988 were included as single adjusted means for each analysis because these samples were unusually stratified because of low water into shallow, warm sample units with very few shrimp, and deep, cool sample units with very high densities of shrimp, resulting in bi-modal distributions of shrimp densities.

Because only seven samples were collected from RF and three from LG, fully factorial design ANOVAs were not possible across all four sites. For *M. intermedium*, for example, ANOVAs were first conducted using just two levels of site (HB and JP), and then for HB, RF and JP with the seven levels of sampling occasions for which there were samples from all three sites. If no significant interactions between site and sampling occasion were detected, then a fractional factorial ANOVA was conducted using three levels of site (HB, RF and JP) with all eleven levels of sampling occasion, assuming no significant interaction between site and sampling occasion.

A two-way ANOVA was conducted on the biomass of fresh seagrass (*Zostera* and *Ruppia*) leaves in each sample unit (transformed by log (x+1) to correct for skewed distributions and heterogeneous variances) using two levels of site (HB and JP), and ten levels of sampling occasion (12 June 1988 excluded, because fresh leaves were not separated from dead leaves in these samples). Because of a significant interaction term in this analysis, an additional one-way ANOVA was conducted on seagrass material from the seven samples from RF.

Differences between means in all analyses were tested using Tukey's unplanned multiple comparison test. Because Tukey's test is sensitive to unequal sample sizes (Day and Quinn, 1989), when comparing means with differences in sample size >1, significance was only accepted at the $P < 0.01$ level.

2.4. RESULTS

2.4.1.1. PHYSICO-CHEMICAL PARAMETERS

Peak flow in the Hopkins River occurred from July to October with major floods in September 1983, 1984 and 1988 (Figs. 2.8a, 2.9a). Minimum discharge occurred during the January-March period in 1983 and 1988.

This flow regime is reflected in patterns of salinity over the seagrass meadows of the estuary (Figs. 2.8d, 2.9d). Salinity over LG, JP and RF was less than 5 from June to October 1988 and in May 1989 (Fig 2.8d), and surface salinities were less than 5 in September and October 1983 and in August, September and December 1984 (Fig. 2.9c). (The salinity ranges in Fig. 2.9c are so large because they indicate salinity to a depth of 1 m midstream rather than a true indication of salinity range over the meadow as in Fig. 2.8d.) As discharge declined in late 1988, salinities over the seagrass meadows increased. The more upstream sites remained less saline for longer, but by January 1989, all seagrass meadows in the estuary experienced salinities of greater than 20. As discharge increased after March 1989, salinities over the meadows decreased—more sharply at the upstream sites.

Temperature variation was typical of southern Australian waters (Figs. 2.8c, 2.9c) with warmest temperatures (20-25°C over the meadows) from November to February and coolest temperatures (10-12°C over the meadows) from June to September. Highest temperatures were reached at sites of low water level such as at HB, where a temperature of 29°C was recorded in shallow locations on 15 December 1988. A maximum-minimum thermometer placed in the seagrass meadow at JP recorded a range of 16.5-30.5°C during December 1988.

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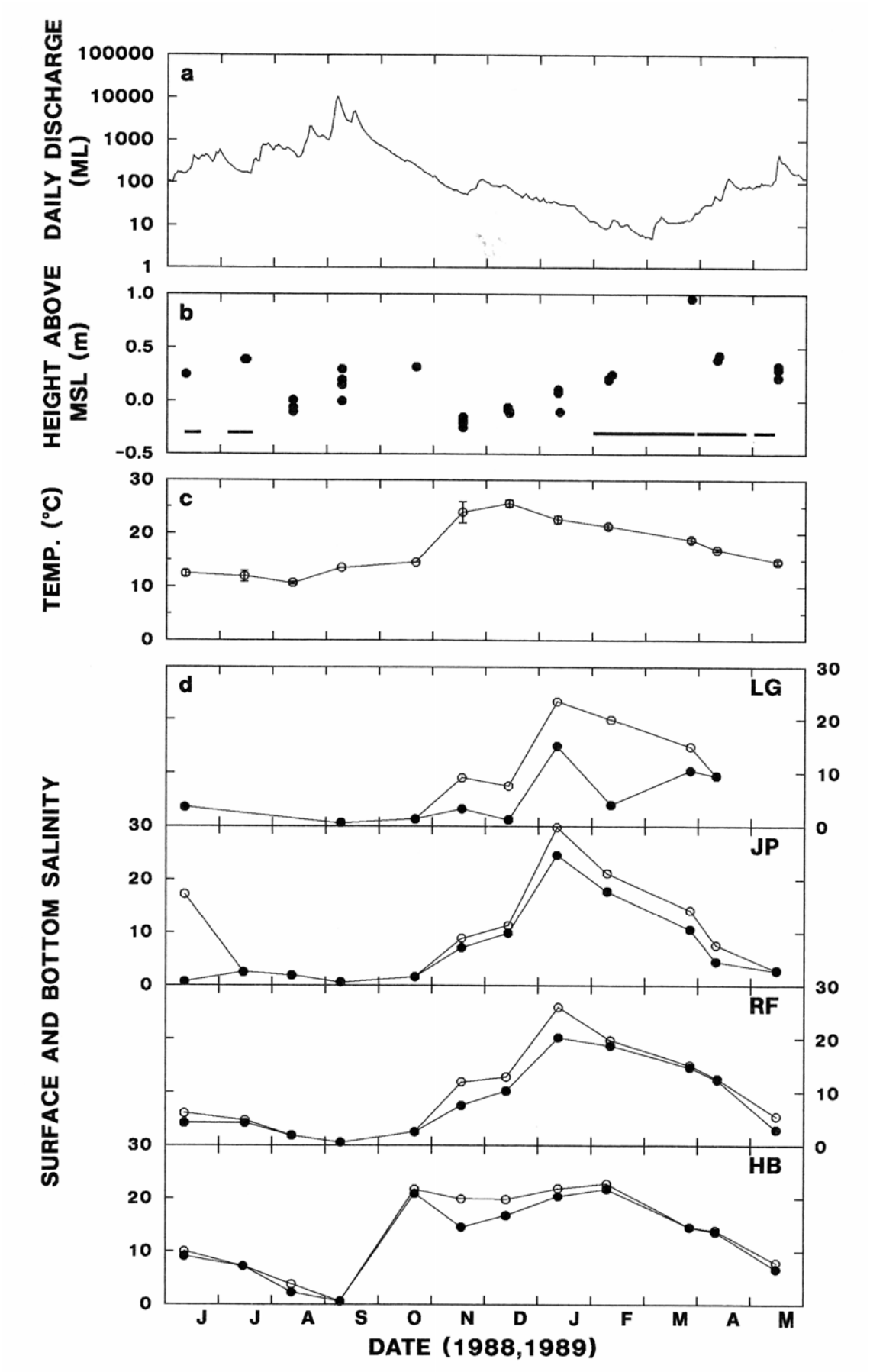
Fig. 2.8. Physico-chemical data for the Hopkins River estuary from June 1988 to May 1989. (a) Daily discharge in ML at Hopkins Falls gauging station (Fig. 1.1). Data supplied by the Rural Water Corporation Victoria. (b) Height of the estuary above msl at the time of each quantitative sample. Horizontal lines indicate periods during which the mouth of the river was closed by a sand bar. (c) Mean (and range throughout the seagrass meadow) temperature of water at JP recorded between 1300 and 1500 h on each sampling occasion. (d) Salinity at the surface (closed circles) and at the deepest part of the meadow (open circles) at the four meadows on each sampling occasion


DAILY DISCHARGE (ML)
100000
10000
1000
100
10
1
a
HEIGHT ABOVE MSL (m)
1.0
0.5
0.0
-0.5
b
TEMP. (°C)
30
20
10
0
c
SURFACE AND BOTTOM SALINITY
d
LG
JP
RF
HB
30
20
10
0
J J A S O N D J F M A M
DATE (1988,1989)

A sandbar at the mouth prevented outward flow for several periods ranging from one to eight weeks during the quantitative sampling period (Fig. 2.8b). During these times water level rose gradually, reaching the highest level in early March 1989. When the sandbar broke, the level of the estuary dropped rapidly— by as much as 0.5 m in a day. When the mouth was open, the estuary typically exhibited a tidal amplitude of 0.3-0.5 m. This is evident from the range of heights on each sampling occasion (Fig. 2.8b).

2.4.2. VEGETATION

The mean biomass of each vegetation type associated with quantitative shrimp samples is presented in Fig. 2.10. The dominant vegetation form in all meadows except LG was *Zostera*. *Ruppia* was the only seagrass present at LG and only from November 1988 to January 1989. Patches of *Ruppia* occurred at the other three sites at all times of the year except August to December 1988, but not commonly enough to treat this seagrass separately from *Zostera* in analyses of association with shrimp abundance.

Total seagrass biomass did not change significantly at HB over the sampling period. At JP, seagrass biomass was significantly lower in July 1988 than at any other time and peaked in February 1989, being significantly higher in that month than in the subsequent two samples. A similar trend was observed at RF with minimum fresh seagrass biomass being recorded June-August 1988 and maximum biomass being recorded in January 1989 (no February sample).

Heterogeneity of variances prevented a statistical analysis of the biomass of grass fragment and detritus, but some trends were evident. The mean biomass of grass fragments and detritus increased at all sites over the sampling period, although in the July-October 1988 samples variances were considerably larger than in later months—particularly at HB and RF (Fig. 2.10). At HB and RF, the density of detrital grass fragments declined in November, and a similar decline occurred at JP in December. Increases in grass fragments and detritus was associated with a greater degree of senescence in seagrass leaves. The most pronounced increase observed was at the ephemeral *Ruppia* meadow at LG, where there was a steady increase in total seagrass biomass from November to January, most of the increase in the last month being composed of a

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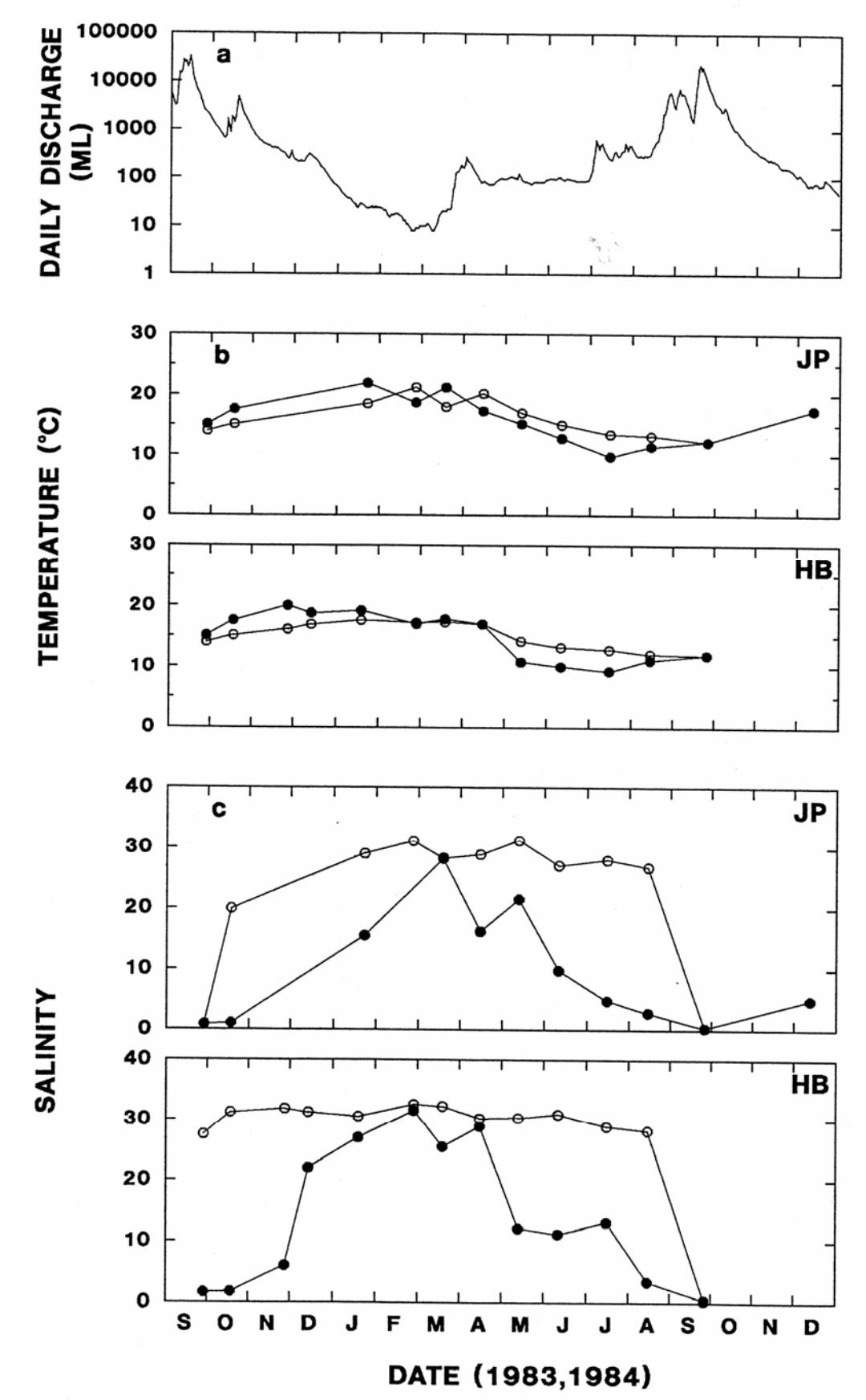
Fig. 2.9. Physico-chemical data for the Hopkins River estuary from September 1983 to December 1984. (a) Daily discharge in ML at Hopkins Falls gauging station (Fig. 1.1). Data supplied by the Rural Water Corporation Victoria. (b) Midstream temperature at the surface (closed circles) and at 1 m depth (open circles) at sites adjacent to the meadows at JP and HB. (c) Midstream salinity at the surface (closed circles) and at 1 m depth (open circles) sites adjacent to the meadows at JP and HB.


DAILY DISCHARGE (ML)
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10000
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100
10
1
a
TEMPERATURE (°C)
30
20
10
0
b
JP
HB
SALINITY
40
30
20
10
0
c
JP
HB
S O N D J F M A M J J A S O N D
DATE (1983,1984)

large amount of dead leaves. By February at LG there was only a very sparse distribution of fresh *Ruppia* plants over the generally bare mudflat. The gradual increase in senescence at other sites continued after the completion of sampling, and seagrass density and extent was greatly reduced in the following year (personal observation).

The decline of the *Ruppia* bed at LG in January 1989 was associated with an increase in epiphytic growth. Patterns of epiphytic growth in other parts of the estuary varied widely with site. Heterogeneous variances and numerous outlying values prevented statistical analysis of this variation. Epiphytic growth decreased from July to October 1988 at JP, with no measurable epiphytes from October to December. By January 1989 epiphytic growth was heavy at JP. Epiphytes were collected at JP in all subsequent samples. The meadow at RF supported some epiphytic growth on all sampling occasions with peaks in June and December 1988 and May 1989.

The meadow at HB supported the most diverse array of vegetation forms of all sites. Epiphytic filamentous green algae were as common as periphytic 'ooze'. Peaks in abundance of the former occurred in October 1988 and February 1989 and of the latter in October and December 1988 and April and May 1989. Drift marine algae occurred in small quantities in most months, particularly at the seaward end of the meadow, but no seasonal variation in its occurrence was discerned (Fig. 2.10).

Patterns of epiphytic abundance common to all sites are difficult to discern. A peak in periphytic 'ooze' occurred on 15-16 December 1988 at the two downstream sites, while a similar peak occurred on 13 January 1989 at the two upstream sites. An increase in epiphytic growth occurred at all three downstream sites in May 1989, coinciding with an increase in senescence.

In summary, variability in the density of seagrass was greatest at more upstream sites. Seagrass abundance peaked abruptly at LG in December, from a complete absence in October, and had disappeared completely by February. At JP and RF, seagrass was present in all months, but densities were lowest in winter and highest in summer. At HB, nearest the mouth, no significant seasonal differences in seagrass density were detected. At all sites, the extent of the meadows varied seasonally (eg Figs. 2.4, 2.6), with all meadows being most

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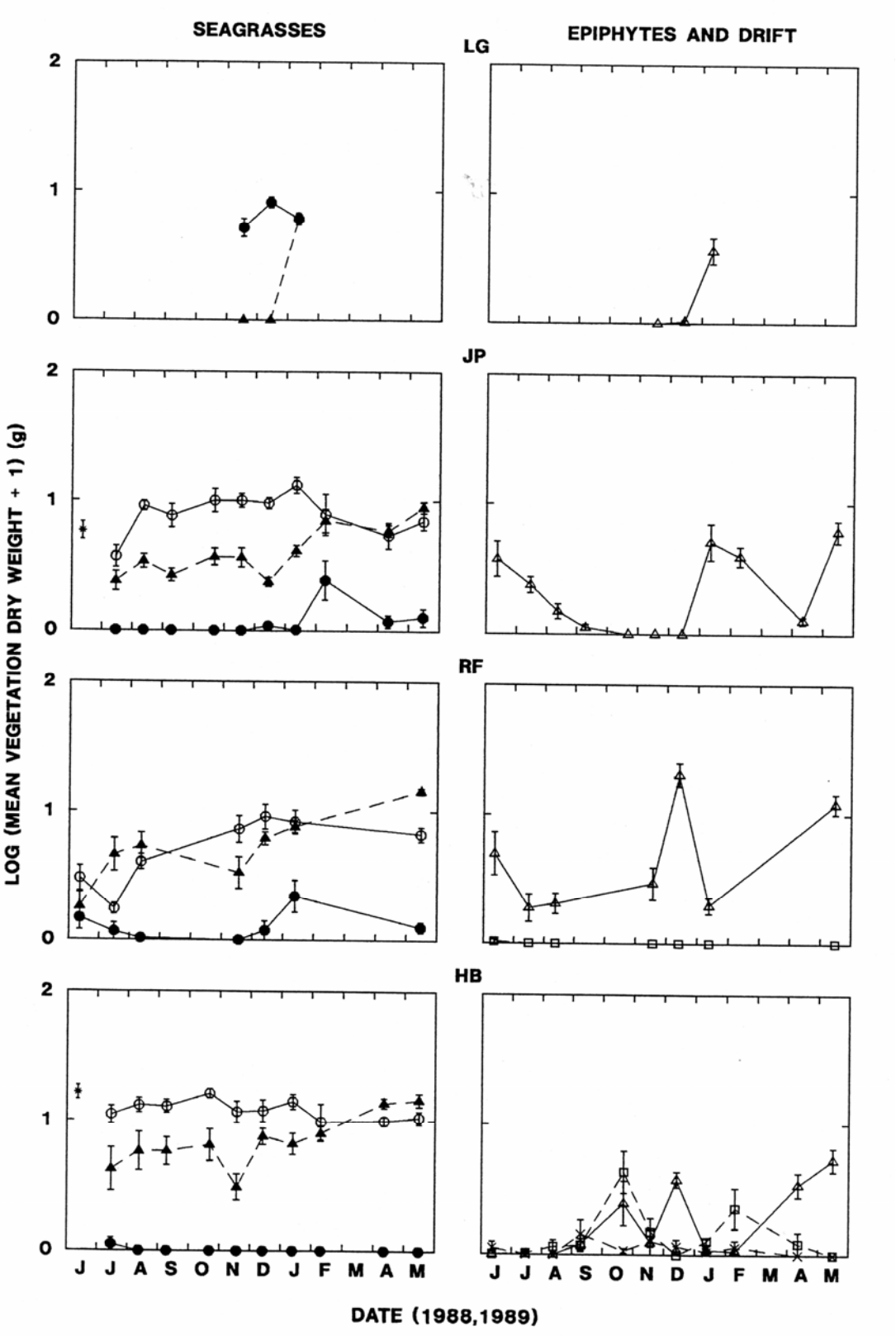
Fig. 2.10. Mean (± SE) biomass (g dry weight) of vegetation forms in the seagrass meadows of the Hopkins River estuary from 12 June 1988 to 20 May 1989. open circles, *Zostera muelleri* (fresh leaves); closed circles, *Ruppia maritima* (fresh leaves); closed triangles, grass fragments and detrital leaves; open triangles, periphytic 'ooze'; open squares, epiphytic filamentous green algae; crosses, drift marine algae; *, pooled value for grass fragments and fresh seagrass leaves for 12 June 1988 at JP and HB


SEAGRASSES
EPIPHYTES AND DRIFT
LG
JP
RF
HB
LOG (MEAN VEGETATION DRY WEIGHT + 1) (g)
0
1
2
J J A S O N D J F M A M
DATE (1988,1989)

extensive during summer, when seagrass density was highest. Thus habitat availability in terms of meadow area was highest throughout the estuary in summer and, in upstream sites, this increase in the extent of meadows was associated with increased habitat complexity in terms of seagrass densities. Epiphytic growth was highly variable within and between sites, but a summer increase in epiphytes was evident at all sites. Senescence increased over the sampling period at all sites.

2.4.3. PATTERNS OF ABUNDANCE

Fig 2.11 shows the density trends for adults and juveniles of each caridean species in the four seagrass meadows of the Hopkins River estuary over the quantitative sampling period. Temporal and spatial patterns for each species are considered separately below, concluding with an overview of patterns exhibited by all three species in Section 2.4.3.4.

2.4.3.1. MACROBRACHIUM INTERMEDIUM

M. intermedium was the most common shrimp in the three *Zostera* meadows of the estuary for most of the sampling period with a mean density (± sd) of 218±12 m^{-2} at HB, 148±13 m^{-2} at RF and 79±14 m^{-2} at JP.

No significant interaction between site and sampling occasion was detected for adult densities ($P=0.79$ for HB and JP with eleven sampling occasions, and $P=0.31$ for HB, JP and RF with seven sampling occasions). Significant differences were found in adult density between sites and between sampling occasions. Mean densities at HB and RF were both significantly higher than at JP. Lowest adult densities were recorded in November and December (Table 2.3). This decrease in densities was most pronounced at JP, while the decrease was least pronounced at HB (Fig 2.11). Peak densities were recorded in April and May (Table 2.3).

Mean adult densities (± sd) in each meadow ranged from minima on 13 January 1989 of 103±14 m^{-2} at HB, and on 15 December 1988, 47± 21 m^{-2} at RF and 18±12 m^{-2} at JP to maxima on 20 May 1989 of 584±4 m^{-2} for HB, 354±6 m^{-2} for RF and 188±4 m^{-2} for JP.

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Fig. 2.11. Mean (± SE) densities of adults and juveniles of the three caridean shrimp species in the Hopkins River estuary from 12 June 1988 to 20 May 1989. Closed circles, *Paratya australiensis*; open circles, *Macrobrachium intermedium*; triangles, *Palaemon serenus*. Asterisks indicate adjusted means to correct for stratification of shrimp distributions at HB.

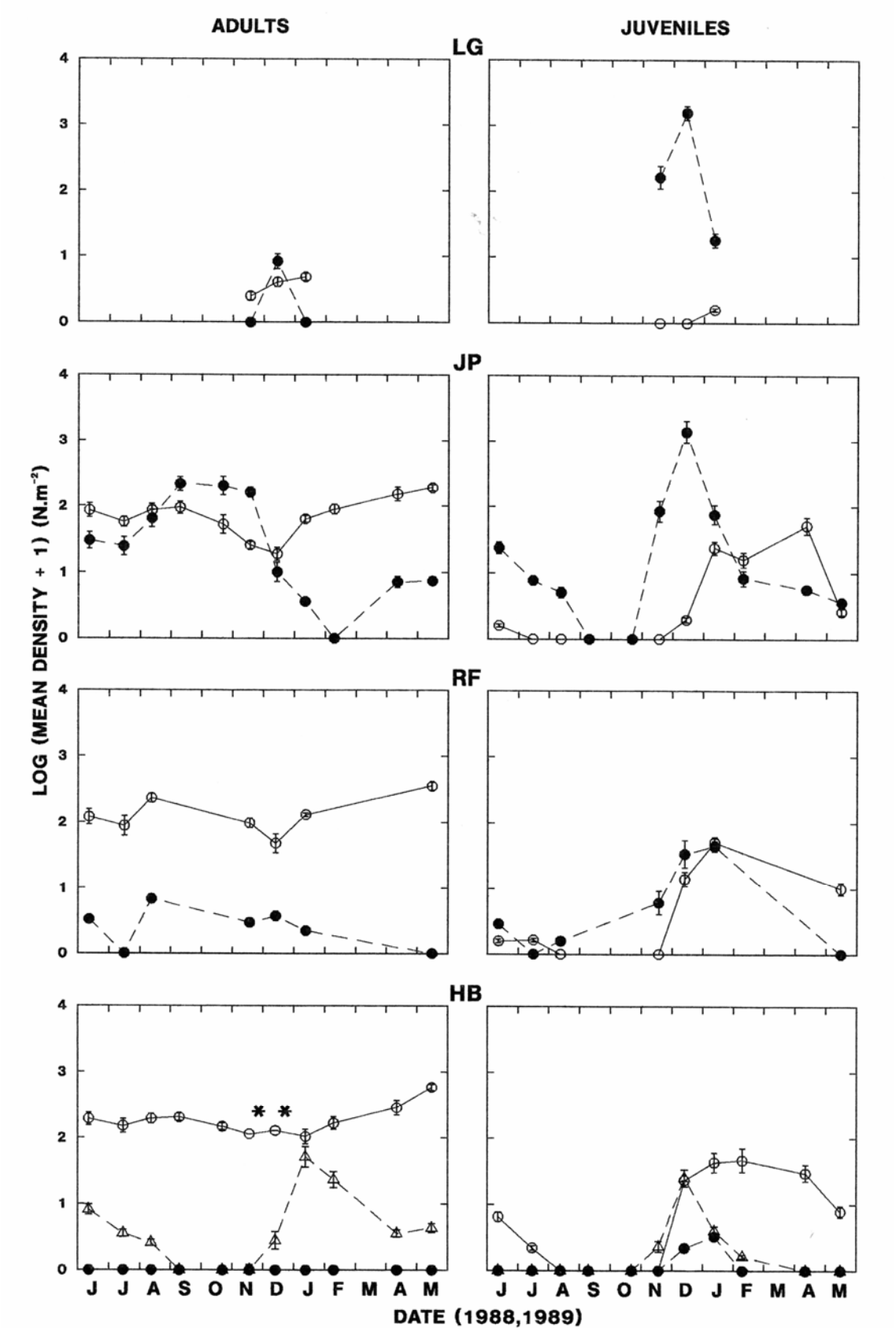
ADULTS
JUVENILES
LG
JP
RF
HB
LOG (MEAN DENSITY + 1) (N.m^{-2})
0
1
2
3
4
* *
J J A S O N D J F M A M
J J A S O N D J F M A M
DATE (1988,1989)

Table 2.3. Mean densities (m^{-2}) of adults and juveniles of the two dominant caridean species of the Hopkins River estuary on each sampling occasion from 12 June 1988 to 20 May 1989. Common lines join means which are not significantly different (based on ANOVAs and *a posteriori* Tukey's tests). Figures for *Macrobrachium intermedium* are overall means from the three *Zostera* meadows HB, RF and JP. *Paratya australiensis* adult means are from JP only. Statistical comparisons were made between mean densities of *P. australiensis* juveniles only in November, December and January. Sites are treated separately for *P. australiensis* juveniles due to a significant site-occasion interaction.

	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	APR	MAY
M. intermedium											
adults	136	91	157	140	91	51	32	95	121	208	335
juveniles	2	1	0	0	0	0	6	37	27	38	5
P. australiensis											
adults	34	23	64	213	200	160	9	3	0	6	6
juveniles											
all sites pooled	5	2	1	0	0	16	236	28	3	2	1
LG						162	1578	17			
JP	23	7	4	0	0	84	1383	85	7	5	3
RF	2	0	1			5	33	44			0
HB	0	0	0	0	0	0	1	2	0	0	0

The two-way ANOVAs conducted on juvenile *M. intermedium* produced non-significant interaction terms, although probability levels were quite low. (P=0.08 for HB and JP with eleven sampling occasions, and P=0.12 for HB, JP and RF with seven sampling occasions). These low probability levels may be due to the few juveniles collected at JP in December (1±4 m^{-2}) compared to HB (22 m^{-2}). After December, densities at the two sites were more similar (Fig 2.11). The fully factorial design ANOVA detected significant differences in densities between sites and between sampling occasions. Mean juvenile densities at both HB and RF were significantly higher than at JP. Juvenile densities from January to April were significantly greater than on other occasions (Table 2.3). At HB, mean juvenile densities ranged from 5±7 m^{-2} on 12 June 1988 to 46±29 m^{-2} on 11 February 1989. At JP, mean densities ranged from 1±4 m^{-2} on 15 December 1988 to 51±17 m^{-2} on 15 April 1989.

At LG small numbers of *M. intermedium* adults were collected in the three months that *Ruppia* was present, rising from a density of 1±4 m^{-2} on 19 November 1988 to 4±5 m^{-2} on 13 January 1989 (Fig. 2.11). Only one juvenile was collected at this site (on 13 January 1989).

Table 2.4. Mean (±sd) densities (m^{-2}) of shrimp in two strata sampled at HB on 15 December 1988, and corrected estimates of the mean densities for the entire meadow

	STRATA		Corrected
	Deep	Shallow	mean
Macrobrachium intermedium			
adults	429±15	6±9	127
juveniles	59±33	8±24	22
Paratya australiensis			
juveniles	4±6	0	1
Palaemon serenus			
total	70±19	9±9	26
Number of SUs	7	7	
Area of stratum (ha)	0.8	2	

The samples taken at HB on 19 November 1988 and 16 December 1988 were unusual because of low water level and on the latter day, high temperature. On 16 December 1988, 72% of the meadow was covered by a shallow layer (<0.2 m) of warm water, from which seven samples were collected. At the outer (western) edge and in the northern extreme of the meadow (Fig. 2.6a), *Zostera* grew in deeper, cooler water. Seven sample units were taken from the deeper portion of the meadow, ≤2 m from the outer edge (Fig. 2.12a). Fig. 2.12b shows that the deeper sample units generally contained greater numbers of *M. intermedium* (and *P. serenus*). Fig 2.12c shows that these deeper sites had a bottom water temperature ≤23.5°C, while the shallower sites varied from 23.6°C near the edge of the meadow to over 28°C 40 m into the meadow. By dividing the sample units into deep and shallow strata, two sets of statistics are attained for this sample (Table 2.4). Corrected estimates of mean densities for the entire meadow were calculated by weighting the means of each stratum by its area. On 19 November 1988, the shallow 72% of the meadow was either exposed or covered by ≤0.1 m of water. In this case in correcting the density estimate, it was assumed that the shallow portion contained no shrimps (none collected in two samples), and nine samples were taken from the deeper sections of the bed.

The correction for the 16 December 1988 sample increased the estimate of the mean for adult *M. intermedium* (from 75 to 127 m^{-2}) but decreased the estimate of the mean of juveniles (25 to 22 m^{-2}). This difference in the effect of correction is because of the different distributions of juveniles and adults in the meadow. Although *M. intermedium* adults tended to occur in greater numbers in the cooler sample units (Fig. 2.12b), juveniles were less common at the coolest sample units, and most common in sites at intermediate temperatures (23-24.2°C), which spanned both the deep and shallow strata.

Although it is tenuous to interpret variation in numbers collected in the qualitative samples as variation in abundance, patterns are evident in the 1983-1984 samples which can be compared to the quantitative survey of 1988, 1989. *M. intermedium* adults were present in most

qualitative samples at both JP and HB (Fig. 2.13). The two sampling occasions when no adults were collected were October 1983 at JP, which was the month in which the period of decline in adult density began at JP in 1988 (Fig. 2.11), and January 1984 at HB, which was the month of minimum adult density at HB in 1989 (and maximum *P. serenus* density in both years). In 1984, juveniles were present from January to May at JP and from February to June at HB (Fig. 2.13). In contrast, juveniles were present at all sites in December 1988, in smallest densities at JP. Juveniles persisted until June 1989 at JP and July 1989 at HB (Fig. 2.11). It is possible that juveniles may have been missed in periods of low density during the qualitative survey, such as in June and July 1984. However, it seems likely that the high densities of juveniles at HB in December 1988 and January 1989 represent a period of early recruitment that did not occur in December 1983 and January 1984.

In summary, both juvenile and adult *M. intermedium* were more common in the downstream part of the estuary. HB and RF supported greater numbers than JP, and very few were collected at the head of the estuary at LG. In 1988-1989, adults were most abundant in April and May, and least abundant in November and December. The summer decline in numbers was more pronounced at upstream sites. Juveniles were present in the estuary from December to July in 1988-1989, but did not occur until January or February in 1984. Juvenile densities were highest from January to April.

2.4.3.2. PARATYA AUSTRALIENSIS

P. australiensis adults occurred in highest densities at JP in 1988-1989 (Fig. 2.11). Densities at JP were highest from August to November, with a mean density over these four sampling occasions of 142 ± 16 m^{-2}. Densities dropped after December, with the lowest being recorded from December to May (Table 2.3). No adults were collected in the estuary in February. Small numbers of *P. australiensis* adults were collected at RF on most sampling occasions (Fig 2.11). None were collected at HB during the quantitative sampling period.

The interaction term was significant ($P<0.001$) in the two-way ANOVA conducted on *P. australiensis* juveniles from all four sites with three levels of sampling occasion (November, December, January). The interaction was primarily due to the sharp December peaks in

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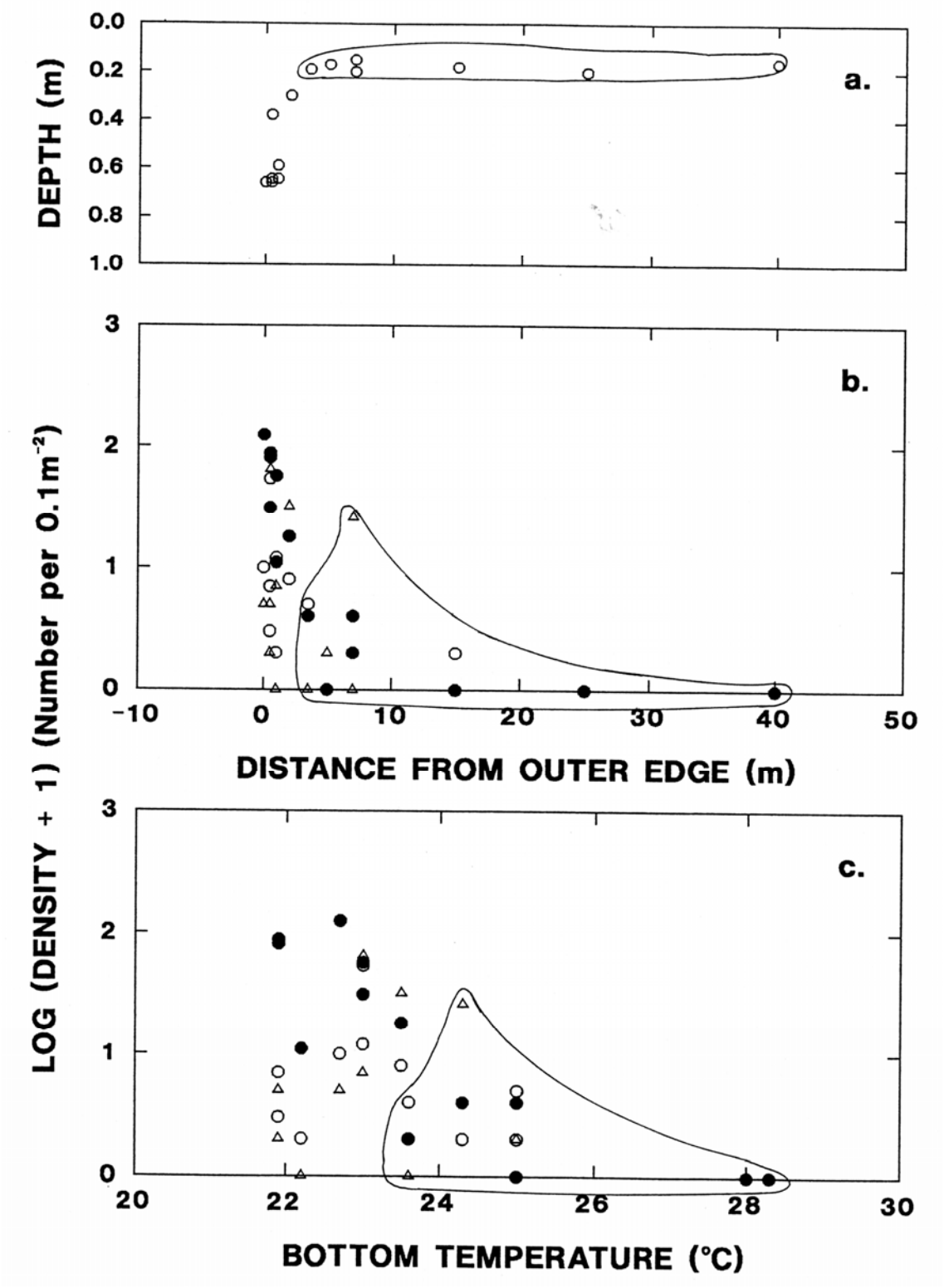
Fig. 2.12. Seagrass meadow at HB on 16 December 1988. (a) Depth of each sample unit plotted against distance from the outer (western) edge of the meadow; (b) Number of shrimps caught in each sample unit plotted against distance from outer edge; (c) Number of shrimps plotted against water temperature on the bottom at each sample unit. The data from the seven sample units from the shallow stratum are enclosed. Open circles, *Palaemon serenus*; closed circles, *Macrobrachium intermedium* adults; triangles, *M. intermedium* juveniles


DEPTH (m)
0.0
0.2
0.4
0.6
0.8
1.0
a.
LOG (DENSITY + 1) (Number per 0.1m^{-2})
3
2
1
0
b.
−10
0
10
20
30
40
50
DISTANCE FROM OUTER EDGE (m)
c.
20
22
24
26
28
30
BOTTOM TEMPERATURE (°C)

abundance recorded at the upstream sites, LG and JP, which were not apparent downstream: the small numbers of larvae collected at the downstream sites, RF and HB, were relatively consistent over the three months (Fig. 2.11, Table 2.3). The peak densities of *P. australiensis* juveniles coincided with the occurrence of the ephemeral *Ruppia* meadow at LG from November to January. Highest densities were recorded on 15-16 December 1988 at LG (1578 ± 13 m^{-2}) and JP (1383 ± 29 m^{-2}). Significantly lower densities were recorded downstream at RF and HB on the same occasion—at RF, 33 ± 42 m^{-2} and at HB, 1 m^{-2}. By 12-13 January 1989 densities had dropped to 17 ± 13 m^{-2} at LG and 75 ± 21 m^{-2} at JP, while densities at RF and HB were not significantly changed (Table 2.3). The more pronounced drop in numbers at LG than at JP is another component of the interaction term, and was associated with the decline of the meadow at LG (Fig. 2.10). No juveniles were collected at HB or RF after January 1989. *P. australiensis* juveniles were found most consistently at JP: from June to August 1988 and from November 1988 to May 1989.

While no *P. australiensis* adults were collected from HB during the 1988-1989 quantitative survey, small numbers were collected there in October, November and December 1983 (Fig. 2.13). No *P. australiensis* adults were collected at either JP or HB from January to May 1984, while only small numbers were collected at JP during these same months in 1989. Juvenile abundance peaked in December 1984 at JP, and to a small extent in December 1983 at HB (no sample was collected at JP in December 1983). This pattern corresponds to juvenile distribution patterns in 1988-1989. *P. australiensis* juveniles were present at JP in all 1983-1984 samples (Fig. 2.13), but were absent from the September and October 1988 samples (Fig. 2.11).

In summary, *P. australiensis* adults were most common at JP, the most upstream perennial seagrass bed of the estuary, less common at RF, and did not occur at HB at all in 1988-1989. They do, however, occur as far downstream as HB in some years. They were most abundant in the four months following peak discharge, from August to November, and were present in the estuary on most occasions for the rest of the year. They were present in very low densities (or absent) from January to May. Adults were present at LG in small numbers only in December, when this ephemeral meadow was at its maximum extent and density. Juvenile recruitment to the estuary was maximal in December: a very sharp peak compared to the extended period of recruitment in *M. intermedium* (Fig. 2.11). The period of *P. australiensis* recruitment

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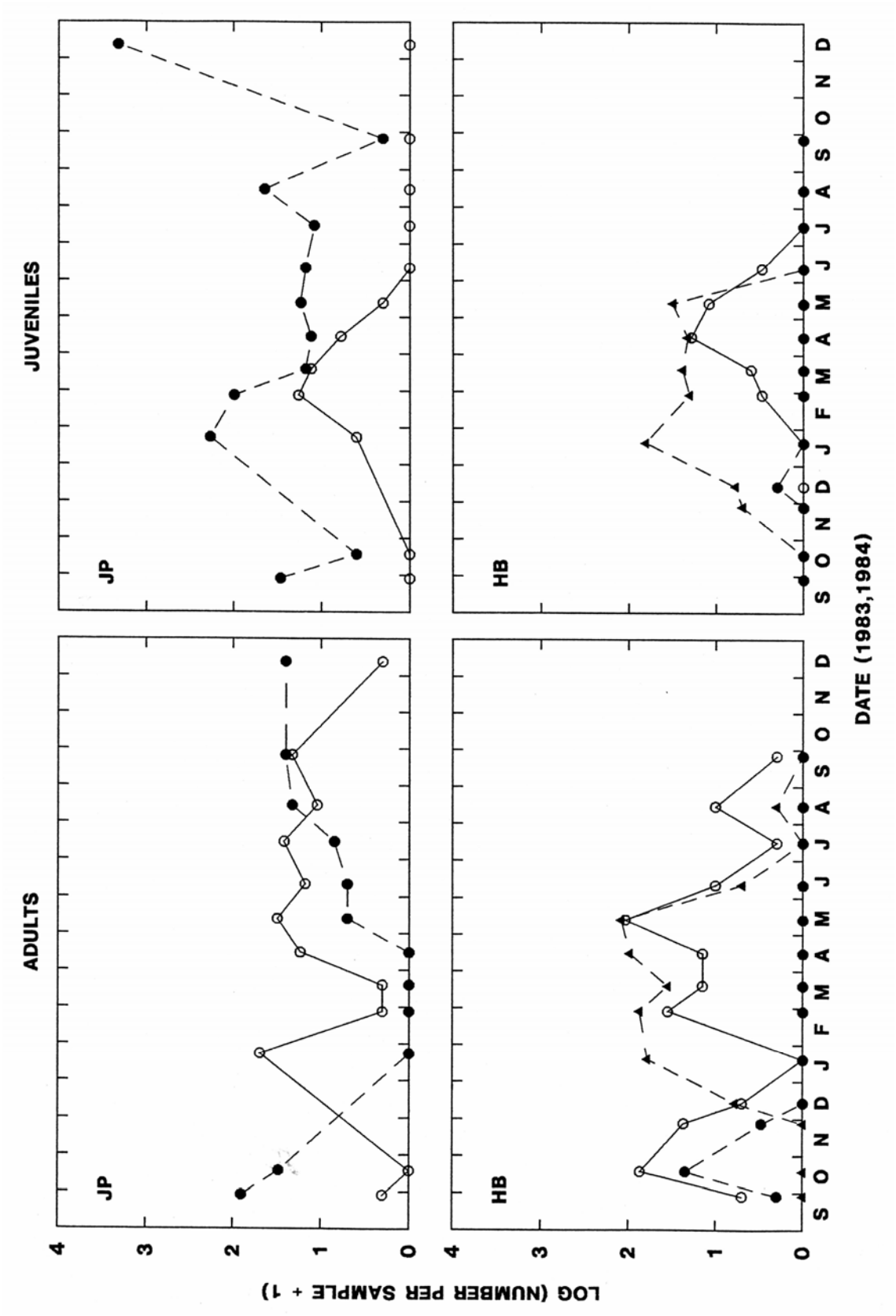
Fig. 2.13. Abundances of adult and juveniles of the three caridean shrimp species in the Hopkins River estuary sampled qualitatively from 29 September 1983 to 15 December 1984.. Closed circles, *Paratya australiensis*; open circles, *Macrobrachium intermedium*; triangles, *Palaemon serenus*


ADULTS
JUVENILES
JP
HB
LOG (NUMBER PER SAMPLE + 1)
DATE (1983,1984)
S O N D J F M A M J J A S O N D

coincided with the presence of the meadow at LG and, unlike adults, juveniles were most abundant in this meadow, and the *Zostera* meadow at JP. Juvenile densities were much lower at downstream sites, and did not exhibit a pronounced peak in December. Juveniles were most persistent at JP, occurring in all months sampled except September and October 1988.

2.4.3.3. PALAEMON SERENUS

P. serenus only occurred near the mouth of the estuary at HB, from December 1983 to August 1984, from November 1988 to May 1989, and from June to August 1988 (Figs. 2.11, 2.13). Highest densities were recorded from December to February, peaking at 62 ± 34 m^{-2} on 14 January 1989. Juveniles occurred in lower densities than adults and were present from November 1983 to March 1984 and from December 1988 to March 1989.

2.4.3.4. SEASONAL PATTERNS OF ABUNDANCE BETWEEN MEADOWS: AN OVERVIEW

The occurrence of *P. australiensis* adults in the Hopkins River estuary was closely associated with the peak river discharge. Densities were highest when salinity was low over the meadows, and the decline in *P. australiensis* adult density coincided with increases in salinity over the meadows (Figs. 2.8, 2.11). Nevertheless, *P. australiensis* adults occurred in greatest densities at JP, despite similar salinity conditions from September to October at RF. *P. australiensis* adults have been collected from all parts of the estuary, but there was a downstream decline in numbers from JP to RF to HB.

In contrast to *P. australiensis* , adults of *M. intermedium* were most common at downstream sites, but the differences between sites were not as marked as for *P. australiensis*. The period of maximum density for *P. australiensis* adults at JP coincided with a decline in density for *M. intermedium* adults (Fig. 2.11). However this decline was also observed at RF and HB in the absence of large numbers of *P. australiensis*, although the intensity of the decline decreased at downstream sites (the small decline at HB was not significant). This period of decline coincided with maximum seagrass densities —which, like the decline in *M. intermedium* adult densities, was least pronounced at HB (Fig. 2.10)—and meadow extent. At HB, the late summer, early autumn occurrence of *P. serenus* was associated with the minor (insignificant) decline in *M. intermedium* adults.

The brief, intense peaks in *P. australiensis* juvenile recruitment occurred at JP one month before *M. intermedium* recruitment reached maximum levels. Densities of *M. intermedium* juveniles were comparable throughout the lower three sites (JP, RF, HB), whereas, *P. australiensis* occurred in very high densities at LG and JP, but only in small numbers at RF and HB. In contrast to the intense peaks of *P. australiensis* recruitment, *M. intermedium* juveniles maintained relatively constant, moderate densities from December to April.

In summary, hydrological conditions appear to be strongly associated with *P. australiensis*, which was highly variable in its occurrence between sites and between occasions. *M. intermedium* showed much less variation with hydrological cycles, although juveniles of this species occurred primarily during periods of highest salinity. *M. intermedium* densities, while greater nearest the mouth, varied little amongst *Zostera* meadows of the estuary, compared to *P. australiensis*.

2.4.4. PATTERNS OF CARIDEAN ABUNDANCE WITHIN MEADOWS: ASSOCIATIONS

2.4.4.1. RELATIONSHIPS BETWEEN THE DISTRIBUTIONS OF *M. INTERMEDIUM* AND *P. AUSTRALIENSIS*

For each quantitative sample taken at JP, a regression was calculated for the number of *P. australiensis* adults as a function of the number of *M. intermedium* adults and (Appendix 2a), and for the number of adults of each species as a function of the biomass of fresh seagrass leaves (Appendix 2b), and for the number of adults of each species as a function of water depth (Appendix 2c).

The trend in slopes of relationships between *M. intermedium* and *P. australiensis* over the study period is presented in Fig. 2.14a. From January to May 1989, the slope was close to zero due to the small numbers of *P. australiensis* at JP over those periods. Differences between regression lines were tested for the seven samples up to 15 December 1988 (after which very few or no adult *P. australiensis* were present). Homogeneity of slopes was tested by analysis of covariance (ANCOVA) on log (x+1)-transformed number of *P. australiensis* adults over seven sampling occasions with transformed number of *M. intermedium* adults as the covariate. The interaction term between the covariate and sampling occasion was significant indicating heterogeneous slopes (Sokal and Rohlf, 1981). Pairwise unplanned multiple comparisons of the slopes were made using the Games and Howell method (Day and Quinn, 1989) which is suitable for comparisons where variances are unequal.

The negative relationships of November and December 1988 were significantly different from all preceding samples, which showed positive or near zero relationship between the species. The relationships for 16 July 1988 and 10 September 1988 were most clearly positive, being significantly different from 12 June 1988 and 13 August 1988. By January, when the number of *P. australiensis* had declined, making the slope of the regression close to zero, *M. intermedium* numbers had increased (Fig. 2.11). The negative relationship between species in November and December, followed by the decline of one species and the rise of the other is suggestive of competitive interaction. At other sites in November and December, numbers of one species were insufficient to perform a similar analysis: numbers of *P. australiensis* were very low at RF, and zero at HB, while numbers of *M. intermedium* were very low at LG. Sample sizes were too

small to conduct contingency table analysis with acceptable power to test for an interaction between species.

The switch in relationship between the abundance of the two species is reflected in the regressions against water depth (Fig. 2.14b). On 19 November 1988 and 15 December 1988, when regressions between the species were negative, *M. intermedium* was more common in deeper SUs and *P. australiensis* was more common in shallower SUs.

Although numbers of adult *M. intermedium* were low at LG and numbers of adult *P. australiensis* were low at RF on 15 December 1988, similar trends to those observed at JP on this occasion were evident using analyses of covariance. ANCOVAs were conducted on the log (x+1)-transformed abundance of adults of each species for three levels of site (LG, JP and RF) with depth as the covariate. Because of the low numbers at LG and RF, the nine SUs in which no adults of either species were collected were excluded from the analyses. To ensure equality of covariate range, SUs from outlying depths (one shallow from JP and one deep from RF) were also excluded.

The slopes of *M. intermedium* against depth were not significantly different between the three sites ($P = 0.264$ for the site×depth interaction term). The effect of depth was significant ($P=0.023$, after removal of the interaction term). For *P. australiensis*, the slopes were significantly different between sites ($P=0.014$). However, only the two shallowest SUs at RF contained *P. australiensis* adults, and the large number of zero values brought the slope of the relationship closer to zero than at the other two sites. If the ANCOVA on *P. australiensis* was performed for LG and JP only, the site×depth interaction was not significant ($P=0.788$). (The site terms in these analyses are not interpretable, because abundances of shrimps will have been biased by the exclusion of SUs without shrimp.) Thus the positive regression of *M. intermedium* on depth and the negative regression for *P. australiensis* on depth was evident at all three sites at which *P. australiensis* occurred on 15 December 1988.

The switch in relationship from October to November at JP was not apparent when considering regressions of adult abundance against biomass of the various components of vegetation. Neither species was significantly related to biomass of epiphytic growth or to grass fragments and detritus. Some interesting patterns were discernible however, in regressions of adults as a function of biomass of fresh seagrass leaves (Fig. 2.15). At JP, *M. intermedium* was positively related with seagrass biomass in April and May 1989, and from June to September 1988, when seagrass density was low, but showed no relationship from October 1988 to February 1989, when seagrass density was high (Figs. 2.10, 2.15c). *P. australiensis* at JP, on the other hand, was positively related to seagrass biomass in July and from September to December 1988, showing no relationship at other times of the year.

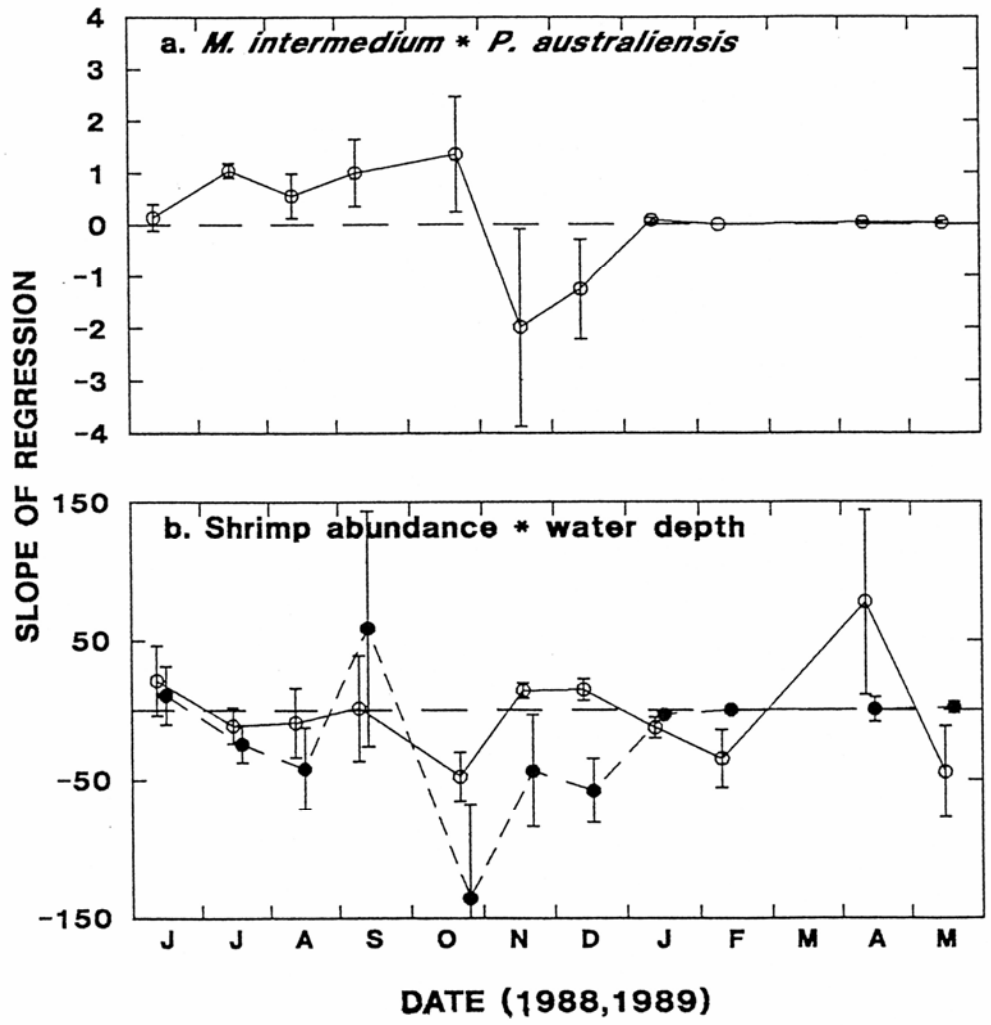


Fig. 2.14. (a) Slopes of regressions (± SE) for the number of *Paratya australiensis* as a function of the number of *Macrobrachium intermedium* in each sample taken at JP, June 1988 to May 1989.
(b) Slopes of regressions (± SE) for the number of each shrimp species as a function of water depth in each sample taken at JP 1988-1989. Closed circles, *P. australiensis*, open circles, *M. intermedium*.

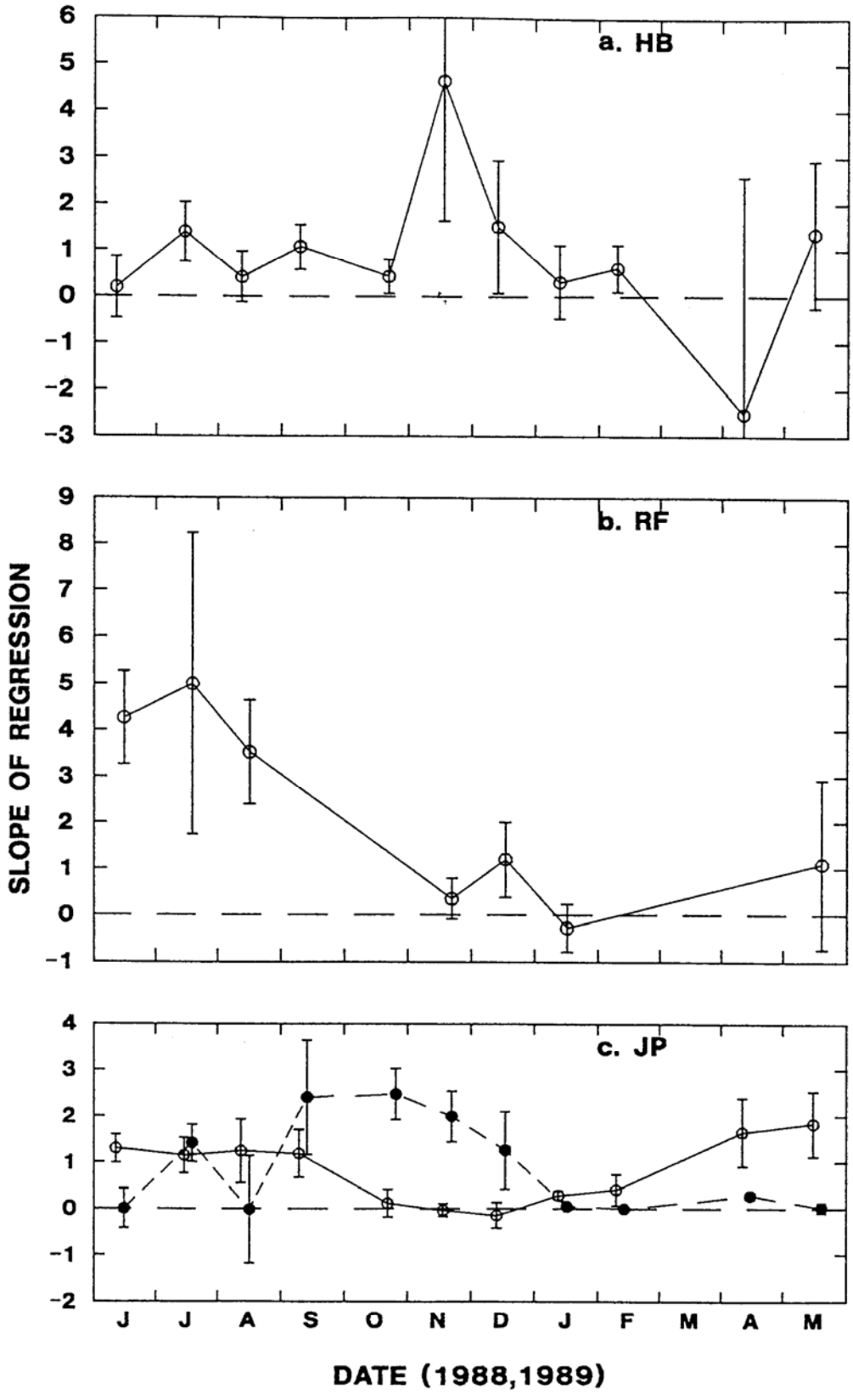


Fig. 2.15. Slopes of regressions (± SE) of the number of shrimps against the biomass of fresh seagrass leaves at (a) HB (b) RF (c) JP.

Closed circles, *Paratya australiensis*: open circles, *Macrobrachium intermedium*

At RF, *M. intermedium* showed a positive relationship to seagrass biomass in June, July and August 1988, but was not strongly related in subsequent samples (Fig. 2.15b). At HB, *M. intermedium* was not strongly related to seagrass biomass on any occasion, although a sharp increase in slope was recorded on 19 November 1988, when its distribution was restricted to the outer deep edge of the meadow (Fig. 2.15a). However the regression was not significant (P=0.161).

Potential for association between juveniles of the two species was limited to December at JP and RF, and January at JP, due to the differing periods of recruitment (Fig. 2.11). No clear trends in relationship with depth or seagrass biomass were apparent for juveniles of either species across sites. *P. australiensis* tended to be negatively related with depth at JP (significantly in January and February), but was positively related or showed no association with depth at LG or RF. *M. intermedium* was positively related with depth at RF in May, but the only other significant regression between *M. intermedium* juveniles and depth was negative, at JP in February. Thus *P. australiensis* and *M. intermedium* juveniles both tended to occur in shallow sites at JP in January, but showed no consistent association at other sites or on other occasions. *P. australiensis* was positively related with seagrass biomass at JP in December and January, as was *M. intermedium* in February, but no other significant regressions were recorded..

2.4.4.2. FACTORS AFFECTING SHRIMP ABUNDANCE IDENTIFIED BY CANONICAL CORRELATION ANALYSIS

Canonical correlations were performed between sets of shrimp abundances and sets of environmental variables for quantitative samples collected at JP, RF and HB.

At JP and RF, the shrimp set was composed of *M. intermedium* adults, *P. australiensis* adults, *M. intermedium* juveniles, and *P. australiensis* juveniles. The environment set was composed of:

- depth of SU;
- bottom salinity, which was highly correlated to both surface salinity and temperature. Thus surface salinity and temperature were not included to avoid the problems of collinearity (Gittins, 1985);
- biomass of fresh seagrass leaves (*Ruppia* was lumped with *Zostera* because of its rare, irregular occurrence, and subsequent non-normal distribution at these sites);
- biomass of grass fragments and detritus;
- biomass of epiphytes.

At HB, the shrimp set was composed of *M. intermedium* adults and juveniles and *P. serenus* (all individuals of this species were lumped to minimise skewness of distribution) and the environment set was composed of the same variables as above, with the inclusion of a measurement of distance from the mouth (included because the proximity of this meadow to

Table 2.5. Canonical correlation analyses of shrimp abundance (*Macrobrachium intermedium* adults and juveniles separated, and all *Palaemon serenus* together), and a set of environmental data for the Hopkins Bridge meadow (HB)

	First canonical variate		Second canonical variate	
	Correlation	Coefficient	Correlation	Coefficient
Shrimp set				
M. intermedium-adults	-0.56	-0.63	0.73	0.58
-juveniles	0.56	0.51	0.80	0.726
P. serenus	0.72	0.51	0.09	-0.11
Proportion of variance	0.38		0.40	Total = 0.78
Redundancy	0.25		0.10	Total = 0.35
Environment set				
Seagrass	0.12	0.31	0.21	0.23
Grass fragments	0.12	0.13	0.31	0.40
Epiphytes	0.15	0.51	-0.06	-0.37
Depth	0.38	0.25	0.62	0.76
Distance	0.31	0.15	0.25	0.61
Bottom salinity	-0.79	-0.93	0.28	0.63
Proportion of variance	0.15		0.11	Total = 0.26
Redundancy	0.10		0.03	Total = 0.13
Canonical correlation	0.81		0.49	

the mouth resulted in a longitudinal variation in marine influence, which may not have been detected by salinity readings taken during a single sample).

To improve linearity of relationship between variables and normality of their distributions, log (x+1) transformations were applied to shrimp abundances and vegetation biomass measurements, except for seagrass biomass at HB, where the untransformed distribution was more normal. Several multivariate outliers were identified from the stratified samples of 19 November 1988 and 15 December 1988 at HB. Because of the unusual nature of these two samples, with habitat availability restricted due to low water, no data from them were included in the analysis. At RF, two SUs with large numbers of *P. australiensis* juveniles were univariate outliers and one was an outlier for adults. At JP, one SU had a high, outlying abundance of *M. intermedium* juveniles. The exclusion of these outlier SUs did not alter the results of the analyses, so they were included. Samples from HB and JP on 12 June 1988 were not included due to inadequate vegetation data. Thus for HB, N = 94, for RF, N = 81, and for JP, N = 116. Assumptions regarding within-set multicollinearity were met.

HOPKINS BRIDGE MEADOW (HB)

The first canonical correlation was 0.81 (65% of variance); the second was 0.49 (24% of variance); the third was 0.22 (5% of variance). With all three canonical correlations included, χ^2 (18 df) = 122.4, $P < 0.001$, and with the first canonical correlation removed, χ^2 (10 df) = 29.1,

$P < 0.001$. The χ^2 test for the third canonical correlation was not significant. Thus the first two pairs of canonical variates accounted for the significant relationships between the two sets of variables.

Data on the first two pairs of canonical variates are shown in Table 2.5. Proportions of variance and redundancies indicate that both pairs of canonical variates were moderately related and, while having good explanatory power in the species set (0.78 of total variance), the explanatory power in the environment set is only moderate (0.26 of total variance).

The first canonical variate was most strongly correlated to *P. serenus* (0.72), and was also correlated negatively to adult *M. intermedium* (-0.56) and positively to juvenile *M. intermedium* (0.56). Among the environmental variables, the first canonical variate was correlated with bottom salinity (-0.79) and, to a lesser extent, water depth (0.38) and the distance along the meadow (0.31). Thus the first pair of canonical variates point to the tendency of *P. serenus* to occur most commonly at the seaward end of the meadow, and in deeper sites with higher bottom salinity. While juveniles of *M. intermedium* tended to show the same trends, most strongly in relation to bottom salinity, adults showed the opposite tendencies.

The second canonical variate in the shrimp set was composed of both juvenile and adult *M. intermedium* (0.80 and 0.73 respectively), while the corresponding canonical variable of the environment set most strongly correlated with depth (0.62) and weakly correlated with grass fragments (0.31). This pair of variates thus indicate the tendency of *M. intermedium* to occur most commonly in deeper sites with higher levels of grass fragments and detritus.

ROWAN'S FLAT MEADOW (RF)

The first canonical correlation was 0.79 (62% of variance); the second was 0.53 (28% of variance); the third was 0.31 (10% of variance); the fourth was 0.12 (1% of variance). With all 4 canonical correlations included, χ^2 (20 df) = 106.0, $P < 0.001$, and with the first canonical correlation removed, χ^2 (12 df) = 32.9, $P < 0.001$. Subsequent χ^2 tests were not significant. Thus the first two pairs of canonical variates accounted for the significant relationships between the two sets of variables.

Data on the first two pairs of canonical variates are shown in Table 2.6. Proportions of variance and redundancies indicate that both pairs of canonical variates were moderately related.

The first canonical variate in the shrimp set was correlated with juveniles of both *M. intermedium* (0.91) and *P. australiensis* (0.77), while the corresponding variate in the environment set was correlated to bottom salinity (0.95) and, less strongly, to seagrass biomass (0.59). This pair of variates thus reflects the tendency of juveniles of both species to be associated with deeper sites with more fresh seagrass.

Table 2.6. Canonical correlation analyses of shrimp abundance (*Paratya australiensis* and *Macrobrachium intermedium* separated into juveniles and adults) and a set of environmental data for Rowan's Flat meadow (RF)

	First canonical variate		Second canonical variate		
	Correlation	Coefficient	Correlation	Coefficient	
Shrimp set					
M. intermedium-adults	-0.23	-0.12	0.85	0.85	
-juveniles	0.91	0.70	0.24	0.50	
P. australiensis-adults	-0.14	0.00	0.33	0.34	
-juveniles	0.77	0.43	-0.16	-0.27	
Proportion of variance	0.38		0.23		Total = 0.61
Redundancy	0.23		0.06		Total = 0.29
Environment set					
Seagrass	0.59	-0.05	0.64	1.15	
Grass fragments	0.28	0.14	0.57	0.52	
Epiphytes	0.14	0.20	0.11	-0.26	
Depth	-0.24	0.18	-0.27	0.09	
Bottom salinity	0.95	1.05	-0.02	-0.80	
Proportion of variance	0.28		0.17		Total = 0.45
Redundancy	0.18		0.05		Total = 0.23
Canonical correlation	0.79		0.53		

The second canonical variate was correlated with adult *M. intermedium* (0.85) and weakly with adult *P. australiensis* (0.33), while the corresponding variate in the environmental set was composed of biomass of seagrass (0.64) and grass fragments and detritus (0.57). Thus this pair of variates shows an association of adults of both species with more densely vegetated areas.

JUBILEE PARK MEADOW (JP)

The first canonical correlation was 0.75 (56% of variance); the second was 0.71 (50% of variance); the third was 0.52 (27% of variance); the fourth was 0.364 (13% of variance). With all four canonical correlations included, χ^2 (20 df) = 216.3, $P < 0.001$; with the first canonical correlation removed, χ^2 (12 df) = 126.1, $P < 0.001$; with the first two canonical correlations removed, χ^2 (6 df) = 49.9, $P < 0.001$; with just the last canonical correlation χ^2 (2 df) = 15.6, $P < 0.001$. Thus all four pairs of canonical variates could account for the significant relationships between the two sets of variables. However, because redundancies for the fourth pair of variates were < 0.03, only the first three pairs of variates were considered.

Table 2.7. Canonical correlation analyses of shrimp abundance (*Paratya australiensis* and *Macrobrachium intermedium* separated into juveniles and adults) and a set of environmental data for the Jubilee Park meadow (JP)

	First canonical variate		Second canonical variate		Third canonical variate	
	Corr.	Coeff.	Corr.	Coeff.	Corr.	Coeff.
Shrimp set						
M. intermedium-adults	-0.15	0.19	-0.66	-0.52	0.65	0.57
-juveniles	-0.64	-0.44	0.22	0.39	0.71	0.69
P. australiensis-adults	0.89	0.78	-0.10	0.07	0.22	0.53
-juveniles	0.17	0.34	0.88	0.66	0.06	0.32
Proportion of variance	0.31		0.32		0.24	Total = 0.87
Redundancy	0.17		0.16		0.07	Total = 0.40
Environment set						
Seagrass	-0.18	-0.42	-0.21	0.20	0.86	0.92
Grass fragments	0.44	0.42	0.31	0.18	0.51	0.42
Epiphytes	0.56	-0.03	0.37	0.48	-0.05	-0.42
Depth	0.49	0.47	0.66	0.44	-0.10	0.38
Bottom salinity	0.64	0.83	-0.62	-0.84	0.23	-0.04
Proportion of variance	0.24		0.22		0.21	Total = 0.67
Redundancy	0.13		0.11		0.06	Total = 0.30
Canonical correlation	0.75		0.71		0.52	

Data on the first three pairs of canonical variates are shown in Table 2.7. Proportions of variance and redundancies indicate that all three pairs of canonical variates were moderately related.

The first canonical variate was positively correlated to *P. australiensis* adults (0.89) and negatively correlated to *M. intermedium* juveniles (-0.64). Among the environmental variables, the first canonical variate was positively correlated to bottom salinity (0.64), epiphytes (0.56), depth (0.49) and grass fragments and detritus (0.44). This indicates the tendency of *P. australiensis* adults to occur at periods of low salinity, when epiphyte growth and leaf senescence are low, in shallower sites, while *M. intermedium* juveniles tend to occur in deeper sites when salinity is high and epiphyte growth and leaf senescence is high.

The second canonical variate was composed of *P. australiensis* juveniles (0.88) and the negative of *M. intermedium* adults (-0.66). The corresponding variate for the environment set was positively correlated to depth (0.66) and negatively correlated to bottom salinity (-0.62), with weak correlations to epiphytes (0.37) and grass fragments (0.31). Thus vegetation form is less important to this pair of variates, which reflect the tendency of *P. australiensis* juveniles to occur at times of high salinity in shallower sites, while *M. intermedium* adults occur most abundantly in deeper sites at times of low salinity.

The third canonical variate was composed of adults and juveniles of *M. intermedium* (0.65 and 0.71 respectively). The corresponding variate in the environment set was composed of biomass of seagrass (0.86) and grass fragments and detritus (0.51). Thus this pair of variates suggest the tendency of *M. intermedium* to be associated with more heavily vegetated SUs.

Trends across sites

Bottom salinity was the most influential environmental variable on the abundance of shrimps at all three sites, being the consistently dominant environmental variable of the first canonical variate. Changes in salinity in this data set are almost entirely the result of temporal hydrological changes in the estuary, rather than within sample variation. Juveniles of all species were abundant at times of high bottom salinity (and correspondingly high surface salinity and high temperature). *P. serenus* was most common at HB at high salinity, while adults of *M. intermedium* at this site were more associated with low salinity. The influence of salinity on *M. intermedium* adults was not strong at RF, but at JP, they were most commonly associated with low salinity. *P. australiensis* adults were strongly associated with low salinity at JP.

Depth was an important variable associated with the abundance of *M. intermedium* at both HB and JP, where both adults and juveniles were most common in deeper water. At JP, *P. australiensis* was associated with shallow water.

Vegetation biomass was not highly correlated with shrimp abundance at HB, but *M. intermedium* adults were associated with greater seagrass biomass (both fresh and senescent fragments) at RF and JP, where a similar association for juveniles was also identified. *P. australiensis* was not strongly correlated with seagrass biomass, but was weakly negatively correlated to grass fragments and epiphytic growth at JP, which may reflect the tendency of this species to occur at periods of low salinity when epiphyte growth and senescence are at a minimum.

2.5. DISCUSSION

Mean densities of caridean shrimps collected in the Hopkins River estuary are as high as recorded in any other study of carideans in seagrass meadows. Mean densities of adult *M. intermedium* ranged from 18 m^{-2} at JP on 15 December 1989 to 584 m^{-2} at HB on 20 May 1989 (Fig. 2.11). In comparison, other studies using comparably accurate methods to sample caridean shrimps in seagrass meadows have generally recorded lower densities, although mean densities of *Thor floridanus* in marine meadows in Florida ranged from 35 to 884 m^{-2} (Holmquist et al., 1989). Mean densities of *Palaemon pacificus* in South African estuarine meadows were 28-211 m^{-2} (Emmerson, 1986). Pihl and Rosenberg (1982) and Baden and Pihl (1984) did not record densities greater than 100 m^{-2} for carideans in Swedish seagrass meadows. Howard (1981) recorded peak densities of *M. intermedium* in a Victorian marine meadow of 100-120 m^{-2}, but these high densities were influenced by the recruitment of large numbers of juveniles in summer months. More usual densities in that study were 10-60 m^{-2}. The mean density of adult *P. australiensis* at JP from September to November of 179 m^{-2} with peaks of 1590 m^{-2} juveniles at LG is comparable to the densities of 400-1400 m^{-2} recorded for *Caridina nilotica* in a coastal lake by Hart (1981). No other studies have recorded such high caridean densities. Thus, compared to carideans of other seagrass communities, those of the meadows of the Hopkins River estuary, are highly abundant and productive.

Gray (1991b) criticised the study of Alon and Stancyk (1982) for concluding between-site heterogeneity on the basis of a single year's data. The quantitative sampling of this study over a single year is open to the same criticism, but this data is backed up by qualitative data which at least confirms the consistency of major annual trends over a longer time scale. The core-sampling technique was labour-intensive, and to continue sampling beyond a year would have been at the expense of other aspects of this study. The advantage of the technique is its ability to elucidate patterns of distribution, not only between meadows in an estuary, but within each meadow.

The three methods of data analysis employed in this chapter have been directed at different spatial and temporal scales. The ANOVAs of mean densities in each sample detected differences *between* meadows and seasonal differences between and within sites. The analysis of correlations of shrimp abundance against depth and seagrass biomass, and between species detected associations *within* each meadow on each sampling occasion, and described changes in these patterns over the year. Canonical correlation analyses also investigated patterns *within* each meadow, but used the entire year's data as a block. This last technique takes a broad perspective on within-meadow distributions to identify factors of overriding importance.

Three factors showed associations with adult shrimp abundance and distribution: physico-chemical conditions driven by hydrological patterns, vegetative structure, and depth. The

effects of each factor are discussed below, after which the factors affecting juvenile distribution and abundance are discussed.

HYDROLOGICAL PATTERNS

The canonical correlation analyses point to the overriding influence of physical factors in shaping abundances of caridean shrimps in the Hopkins River estuary, with the exception of *M. intermedium* adults. The most influential environmental variable at all sites, bottom salinity, was highly correlated to temperature and surface salinity, so variations in all three factors were associated with patterns in shrimp abundance within meadows. Almost all the within site variation in these variables was temporal, due to changes in hydrological conditions. The occurrence of *P. serenus* at HB was associated with raised salinities. It was absent from September to November, the three months after maximum discharge, in both 1983 and 1988. It peaked in abundance in January 1989, and maintained high numbers from January to May 1984, when salinity and temperature were maximal. *P. australiensis* adults were associated with low salinity at JP because they occurred most commonly in the three months after maximum discharge. The disappearance of *P. australiensis* adults from JP after December coincided with an increase in both temperature and salinity over the meadow.

Salinity and temperature may directly determine distributions if fluctuations in these parameters approach the limits of physiological tolerance, thus causing mortality or migration away from a location. To assess the importance of tolerances to these parameters on the observed distributions of the Hopkins River caridean shrimps, a series of tolerance experiments was conducted and their results are presented in Chapter 3.

Despite the importance of seasonal hydrological patterns to the abundance of *P. australiensis* at JP and RF, the differences in density of *P. australiensis* adults along the estuary on each occasion were not as clearly associated with physical conditions. In the months after peak discharge, when *P. australiensis* was abundant at JP, densities downstream were significantly lower despite similar salinity and temperature conditions throughout the estuary. The differences are likely to be due to the availability of *P. australiensis* stock, and their ability to migrate from upstream of the estuary. Migration is considered in Chapter 7.

The density of *M. intermedium* adults showed less variation with hydrological conditions than *P. australiensis* density, a trend borne out by the canonical correlation analyses. *M. intermedium* adult density was not strongly associated with physical conditions at RF, but was moderately associated with low salinity at JP, and HB. This was probably due to the decline of *M. intermedium* adult densities in summer.

Previous studies on the distribution and abundance of *M. intermedium* have reported seasonal trends that differ from those observed in the Hopkins River estuary. Gray (1991a), Howard (1981) and Walker (1979) all reported peak abundance of *M. intermedium* in the warmest

months of the year, and yet in the Hopkins River, peak abundances were generally found around late Autumn. This was the case for all sites for the quantitative sampling period (Fig. 2.11), and although abundance values are less reliable for the qualitative dipnet samples, a similar peak in abundance in April-May 1984 is evident at HB, but not at JP, where total *M. intermedium* numbers were reasonably constant through out the year (Fig. 2.13). Howard (1981) linked summer increases in total abundance of *M. intermedium* to the recruitment of large numbers of juveniles to the seagrass meadows. Recruitment of *M. intermedium* juveniles in the Hopkins River estuary was not strong, and while peaking in January and February at HB, relatively large numbers of juveniles were found at HB and JP in April. It appears that the April-May increase in *M. intermedium* numbers may be due to the cumulative effect of an extended period of recruitment. This will be discussed in Chapter 4.

In studies of *M. intermedium* in marine environments with little fluctuation in salinity, Gray (1985) found minimum abundances in winter, and Walker (1979) and Howard (1981) in late winter to spring. In the current study, minimum abundances occurred in late spring to early summer, although the minimum was not pronounced downstream at HB (Fig. 2.11). Walker (1979) reported an estuarine population declining sharply in mid-winter, which he attributed to migration out of the estuary due to the winter flood lowering salinity and temperature severely. This was certainly not the case in the Hopkins River estuary where normal densities of *M. intermedium* were maintained through the flood at all sites. The summer decline in *M. intermedium* densities in the Hopkins River coincided with the period of maximum seagrass density and extent. It was during this time that *M. intermedium* adult densities showed no relationship with seagrass biomass. One interpretation of these trends is that *M. intermedium* densities decreased at this time due to increased habitat availability afforded by more extensive meadows.

VEGETATIVE STRUCTURE

Recent studies of epifaunal abundance in relation to habitat complexity in seagrass meadows, have increasingly emphasised plant morphology and total surface area as measures of complexity (e.g. Orth et al., 1984; Bell and Westoby, 1986b; Virnstein and Howard, 1987a). In the present study, the meadows were composed almost entirely of *Zostera* (except LG, which was entirely *Ruppia*). On each occasion, leaf height and width were relatively uniform across each meadow, although *Zostera* at HB tended to have wider leaves than *Zostera* upstream (personal observation). It was thus assumed that, within each sample, fresh *Zostera* leaf morphology was constant, and that fresh seagrass biomass provided a good estimate of fresh leaf density in each sample unit. A more comprehensive measure of habitat structure was afforded in this study by the measurement of epiphytic growth and senescence of seagrass (mass of detrital grass fragments).

The canonical correlation analysis found no strong association with any component of vegetation at HB, but did find a moderate association with seagrass biomass for *M. intermedium* adults at RF and JP. A clearer picture of variation in association with seagrass biomass within sites was afforded by inspection of regressions in each sample (Fig. 2.15). Within each seagrass meadow, *M. intermedium* adult densities were never negatively related to seagrass biomass. At RF, and particularly at JP, they were positively related in months when seagrass biomass was lowest and meadows were least extensive. At HB, where seagrass biomass per m^2 was constant throughout the year, they were not significantly related on any occasion. However, a sharp increase in slope of the relationship was observed on 19 November 1988. This sample, in which shrimps were restricted to the outer band of the meadow due to low water, was not included in the canonical correlation analysis. These results suggest that *M. intermedium* adult densities only showed association with seagrass density when the amount of seagrass was limiting, either through decreased density of seagrass or through increased densities of *M. intermedium*. If this were the case, then seagrass density was limiting for *M. intermedium* adults in the upper part of the estuary from June to September 1988, and in April and May 1989 (Fig. 2.15).

Zostera biomass was not identified by the canonical correlation analyses as an important component associated with *P. australiensis* adults. However, in individual samples at JP, *P. australiensis* showed a trend similar to *M. intermedium* in that its density was either positively or not significantly related to seagrass biomass. *P. australiensis* density was significantly related to seagrass biomass in October and November 1988 at JP, when *P. australiensis* densities were highest (Fig. 2.11). and when *M. intermedium* densities showed no relationship with seagrass biomass (Fig. 2.15). The canonical correlation analyses did identify that *P. australiensis* was negatively correlated to detrital fragments and epiphytic growth. *P. australiensis* is a browser (Gemmel, 1979a, 1979b) that feeds on epiphytic growth on *Zostera* in laboratory aquaria, effectively cleaning seagrass leaves bare. It is possible that *P. australiensis* was negatively correlated to the amount of epiphytic growth because it cleans off the growth from seagrass leaves. This proposition may warrant further investigation.

Thus both *M. intermedium* and *P. australiensis* adults showed at least some tendency to be associated with seagrass biomass within meadows. For *M. intermedium,* associations with seagrass biomass occurred most frequently when available seagrass cover was lowest. Both seasonal fluctuations in seagrass abundance and tidal variations in seagrass availability appeared important: the latter only at HB, which was the meadow most prone to exposure at low tide.

Despite a prevailing interest in the importance of habitat complexity to the abundance of epifauna, positive correlations between seagrass biomass or structure and caridean abundance have rarely been demonstrated. Emmerson (1986) and Mellors and Marsh (1993) both found an overall positive correlation of abundance of *Palaemon pacificus* with *Zostera* biomass, and Bell and Westoby (1986a) found carideans in lower densities in experimentally thinned plots. In the

current study, although positive relationships have been recorded between *M. intermedium* adult abundance and seagrass biomass, vegetative complexity appears only to be important at times when seagrass is limited due to seasonal or tidal fluctuations. *P. australiensis* adult densities were positively related to seagrass biomass in months in which they were highest.

DEPTH

Canonical correlation analyses found *M. intermedium* juveniles and adults to be more associated with deep water at both JP and HB, and *P. australiensis* adults at JP to be associated with shallow water. In regressions for each sample, *P. australiensis* showed either a negative or no significant relationship with depth. The most negative slopes were from October to December. The association of *M. intermedium* adults with deeper water was not strongly evident on any occasion at JP, and they were negatively related in October, but a weakly positive relationship with depth was significant in November and December (Fig. 2.14).

Relationship to water depth within a single meadow may be affected by the height of the estuary at the time of sampling, which will change the range of depths available to the shrimp. A tendency for *M. intermedium* adults to occur in deeper water was most pronounced at HB on 16 December 1988 due to extremely shallow water over most of the meadow, and restriction of available habitat to the deeper portions of the bed. However, no consistent effect on distributions was observed when levels were less extreme: for instance: strong negative associations with depth were recorded for both species in October 1988 when the river was high, but this trend was not apparent in July 1988 or April 1989 when the estuary was just as high.

Gray (1985) found *M. intermedium* tended to occur in shallower water, but his study was performed at sites with much greater variation in depth than the Hopkins River estuary seagrass meadows—he found less *M. intermedium* in depths 2.5-4 m. An opposite trend was observed by Baden and Pihl (1984) who found no differences in abundances of *Palaemon adspersus* and *P. elegans* between 0.7 and 1.5 m, but caught greater numbers of *P. adspersus* in 1.5-3.0 m. In contrast to the wide ranges of depth in these studies, the deepest seagrass growth in the Hopkins River estuary is not much greater than 1 m below msl at RF, so there is limited scope for an effect of depth on shrimp abundance. Even so, depth appeared an important determinant of distribution in *P. australiensis* and *M. intermedium* adults in November and December 1988.

The negative relationship between abundances of *M. intermedium* and *P. australiensis* at JP in November and December 1988 (Fig. 2.14b) is of interest as it suggests habitat partitioning. The consistency of relationship of each species to depth (positive for *M. intermedium* and negative for *P. australiensis*) in all sites where they co-occurred in December 1988, points to depth being an important factor in this partitioning. On that occasion, all the variation in salinity over the meadow at JP (range 1.4) was between sample units, with no vertical stratification. However stratification was observed at RF and LG. Thus, although salinity gradients may play a part in

determining distributions, the apparent habitat partitioning at JP occurred in the absence of a vertical salinity gradient.

Other than the opposite relationships of *M. intermedium* and *P. australiensis* observed in November and December 1988, no consistent association between depth and the abundance of any species was apparent. Notably, November and December were the months in which no association was evident between *M. intermedium* and seagrass biomass at JP. Perhaps during this period, when seagrass was abundant and *M. intermedium* density was low, depth became the more critical aspect of habitat. The importance of vegetative complexity and depth to the distributions of *P. australiensis* and *M. intermedium*, and the potential for habitat partitioning are investigated further in Chapter 3.

JUVENILE DISTRIBUTIONS

Juveniles of both species were associated strongly with periods of high salinity by the canonical correlation analyses, but the brief, intense period of juvenile recruitment in *P. australiensis* was prior to the more extended, less intense period of recruitment in *M. intermedium*, with little overlap (Fig 2.11). Indeed in December at JP, when *P. australiensis* juveniles were very abundant, *M. intermedium* juvenile numbers were low, although at HB, *M. intermedium* juveniles were much more abundant, while very few *P. australiensis* juveniles occurred. Thus the distinctiveness of estuarine recruitment patterns of the two species has spatial and temporal components. In the following month, when *P. australiensis* juvenile densities declined at JP, *M. intermedium* juvenile densities rose to levels comparable to the rest of the estuary. Where there was overlap in occurrence of moderate numbers of juveniles of the two species, they showed no clear associations to each other, or to depth or vegetation structure.

The increasing abundance of *P. australiensis* juveniles upstream followed a salinity gradient, and may be associated with physiological tolerance, but it may also have been due to the distribution of settling larvae in the estuary. Physiological tolerance of *P. australiensis* juveniles is investigated in Chapter 3, and larval distributions in relation to juvenile recruitment in the Hopkins River estuary are investigated in Chapter 6. *M. intermedium* juveniles, on the other hand, occurred in comparable densities in *Zostera* meadows throughout the estuary, despite longitudinal variation in salinity.

The occurrence of *M. intermedium* juveniles was followed at all sites in April and May by an increase in adult density. This was not the case for *P. australiensis*: adults were absent from the estuary, or present in very low densities, in the months after peaks in juvenile densities. Migration or mortality must account for the losses of *P. australiensis* from the estuary in summer. The fate of juveniles of both species is investigated in Chapters 4 and 7.

The canonical correlation analyses identified *M. intermedium* juveniles as being moderately associated with seagrass biomass at JP and RF, and juveniles of *M. intermedium* and *P.*

australiensis were significantly related to seagrass biomass on one and two occasions respectively. Juveniles of neither species showed consistent association with depth, but juvenile *M. intermedium* showed a less pronounced tendency to occur in the deeper SUs in the 16 December 1988 HB sample (Fig. 2.12). Emmerson (1986) found a positive correlation between shrimp size and depth in *Palaemon pacificus*, and thus inferred that smaller shrimp tended to be found at shallower depths. He attributed this to habitat preference, and the effect of matted *Zostera* leaves in shallow water effectively excluding large shrimp (and presumably predators). Kneib (1987) found juveniles of *Palaemonetes pugio* occurring predominantly in intertidal pools of a salt marsh, not migrating out at low tide as adults do. *M. intermedium* juveniles did not occur in shallow water to this extent, but it would appear from the 16 December 1988 HB sample that migration of juveniles out of shallow water at low tide is not as great as for adults.

CONCLUSIONS

The quantitative survey has shown *P. australiensis* to be an abundant element of the seagrass community of the Hopkins River estuary, particularly in the upper section of the estuary from spring to early summer. *M. intermedium* is the dominant caridean of the seagrass community, occurring in densities greater than reported elsewhere. It was most common in the lower section of the estuary. *P. serenus*, present only during periods of high salinity, and only at the site nearest the estuary mouth, was abundant at times, but was a less important member of the seagrass community on the scale of the whole estuary.

Hydrological patterns have been identified as the major determinant of adult shrimp distributions between meadows within the estuary, given the availability of recruiting stock. Patterns of salinity and temperature variation were associated with varying abundances within each meadow over the year, but had little effect on distributions within meadows on each occasion. Habitat structure, as estimated by fresh seagrass biomass, was associated with shrimp abundance, in particular *M. intermedium* in winter months when seagrass was least abundant. Within meadows, *P. australiensis* and *M. intermedium* both varied in their association with depth, although *P. australiensis* was more commonly associated with shallow water, and *M. intermedium* was more common in deeper water. Depth relationships within meadows were important in November and December when *M. intermedium* and *P. australiensis* appeared to be partitioning the meadow habitat.

Results of laboratory experiments designed to assess the importance of vegetation structure and water depth in determining distributions of these two species are presented in Chapter 3. The results of physiological tolerance experiments are also presented. These will elucidate the extent to which distribution patterns, associated with hydrological patterns, are driven by tolerance to physical and chemical conditions. Between-site differences may have been due to variation in the availability of immigrants. Patterns of migration may be elucidated by investigation of population structure (Chapter 4) and are discussed further in Chapter 7.

Juveniles of *P. australiensis* and *M. intermedium* showed distinct periods of recruitment with little overlap. *P. australiensis* juveniles were most abundant in the upper parts of the estuary, while *M. intermedium* was abundant in all parts of the estuary where *Zostera* grew. Juveniles of both species were associated less strongly with depth than adults, but did show moderate association with seagrass biomass. Juvenile distribution patterns between meadows are most likely to be determined by larval distributions, which are investigated in Chapter 6.

3. PHYSIOLOGICAL TOLERANCES AND COMPETITIVE INTERACTIONS IN CARIDEAN SHRIMPS OF THE HOPKINS RIVER ESTUARY

3.1. INTRODUCTION

The Hopkins River exhibits a strongly seasonal pattern of flow, which results in wide annual variation in salinity over the seagrass meadows of its estuary. In Chapter 2, it was demonstrated that the distribution and abundance of the epifaunal caridean shrimps in the estuarine seagrass meadows were strongly associated with these wide annual fluctuations in salinity (and associated fluctuations in temperature). Such trends suggest physiological tolerances to salinity and temperature may be one of the factors ultimately determining shrimp distributions in the Hopkins River estuary. Thus studies of tolerances to salinity were undertaken for the three caridean species.

Acute toxicity tests have been widely used on Australian aquatic fauna to gauge tolerance to salinity (e.g. Williams, 1984). Measures derived from such tests are useful for determining the immediate effects of short term exposure, and for comparing the acute sensitivities of different species (American Society for Testing and Materials, 1988). The most commonly used acute toxicity measure for aquatic invertebrates is the 96 h LC_{50} (the median lethal concentration), and several workers have determined this (or 48 h LC_{50}) measurement for salinity in *P. australiensis* (Walker, 1972; Williams, 1984; Morris, 1991). The lower lethal salinity for *M. intermedium* was estimated in an unreplicated series of tests by Walker (1979).

The salinity tolerances of these species and *P. serenus* were determined in the present study to compare acute sensitivities of the three species, and to compare salinity tolerances of the Hopkins River populations of *P. australiensis* and *M. intermedium* with tolerances derived for other populations. The Hopkins River estuary is the most marine influenced environment in which *P. australiensis* has been studied, and the most riverine environment in which *M. intermedium* has been studied. A comparison of species differences in salinity tolerance to distributional differences in relation to salinity patterns in the Hopkins river estuary may elucidate the importance of physiological tolerances in driving distributional patterns.

The overriding importance of physical conditions to seasonal and large scale spatial patterns of caridean distribution and abundance in the Hopkins River estuary was identified in Chapter 2. However at a critical time of increased salinity over the meadows of the upper estuary, when *P. australiensis* densities were declining, study of distributions *within* meadows pointed to possible habitat partitioning based on depth, with *P. australiensis* tending to occur in shallow water and

M. intermedium in deep water. This partitioning was observed at all locations where the two species occurred together in December. The observed differences in within-meadow distribution may have been due to habitat preference. Each species may prefer a position in the meadow in response to salinity variation, irrespective of the other species. But the differences may also have been the result of competitive displacement of *M. intermedium* from shallower water by *P. australiensis*, or competitive displacement of *P. australiensis* from deeper water by *M. intermedium*.

The relative importance of interspecific competition as a determinant of the structure of natural communities has been the subject of much debate. Many of the patterns observed in natural communities that could be explained by contemporary competitive interactions, might in fact be explained by historical competition, which may have resulted in the evolution of narrower niches and habitat partitioning, which serve to reduce the intensity of contemporary competition (Schoener, 1986). The importance of field experimentation to detect competitive interactions has been emphasised frequently (Connell, 1983; Schoener, 1983; Underwood, 1986). The reviews of Connell (1983) and Schoener (1983) may exaggerate the frequency of competition, because papers demonstrating an interaction are more likely to be accepted for publication. Furthermore, Underwood (1986) questioned the validity of many of the experiments reviewed by Connell (1983) and Schoener (1983), rueing the paucity of well-designed experiments testing for competition.

In seagrass communities, competition for enemy (predator)-free space has been suggested as an important determinant of community structure (Heck and Orth, 1980b). Competition for habitat complexity, which provides increased protection from predators, has been demonstrated between caridean species (Thorp, 1976; Coen et al., 1981). Logistical problems prevented field experiments on the carideans of the Hopkins River estuary, but two series of laboratory experiments were undertaken to test for competitive interactions between *M. intermedium* and *P. australiensis*: one experiment to test for competition for differing depths, and one to test for competition for more complex habitat in the form of vegetative cover. Such experiments may elucidate the importance and nature of competitive interactions, at least as a determinant of the observed small-scale partitioning of habitat in the Hopkins River carideans.

3.2. METHODS

3.2.1. SALINITY AND TEMPERATURE TOLERANCE EXPERIMENTS

3.2.1.1. TOLERANCE IN ADULT AND JUVENILE *P. AUSTRALIENSIS*

P. australiensis adults were collected from the Hopkins River at Warrumyea Bridge on 15-16 August 1991 in water of salinity of 0.8 at of 9.6°C. In the laboratory, they were placed in three large (2-3 m^3) tanks in 30 cm of tap water that had been aerated for at least 24 h, and had $CaCO_3$ added to achieve a calcium concentration of 50 $mg.L^{-1}$ (a typical level for Hopkins River water). Shrimps were stocked at a density of ≈400 m^{-2} at (mean±range) 10±0.2°C, in a light regime of 16:8 light:dark. One tank was maintained at 10°C for 1 week, and the temperature of the remaining two was raised by 0.5-1C° each day until the experimental temperatures of 21.5° C in one and 28.5°C in the other were reached. Once the experimental temperatures were attained, acclimation at these temperatures was continued for at least three days.

Five blocks of five salinity treatments (at salinity intervals of ≈2), and one control (acclimation water) were used. Experimental salinities were adjusted by mixing tap water, treated as above, with sea water collected from Lady Bay, Warrnambool. Salinities were determined by using a calibrated 'Yeo-Kal' salinometer (Model 602 Mk III), and were measured in each experimental aquarium at each observation. If salinity had increased due to evaporation, treated tap water was added to return salinity to its original level. Increases in salinity between observations were never more than 0.5 at the two lowest temperature treatments, and never more than 1 in the 28.5 °C treatment. The salinity value used for each aquarium in the calculation of results was the mean level during the experimental period. Salinity treatments were determined by pilot experiments at each temperature, and mean salinities of all aquaria in each treatment for each temperature are presented in Table 3.1.

Ten adults (3.8-9.0 mm OCL) were placed in each experimental covered glass aquarium measuring 22×12.5 cm in 15 cm of water. Treatments were randomised. Dead shrimps were removed, and the number of survivors in each tank counted at least daily up to 96 h, although the 28.5°C treatment was not continued past 48 h due to a failure in temperature regulation. Treatment tanks at 10°C and 21.5°C were not aerated, and the dissolved oxygen did not drop below 77% saturation during the experiment. Tanks at 28.5°C were aerated as decreases in oxygen concentration were considered a possible complicating factor.

Juvenile *P. australiensis* were collected from the *Ruppia* meadow at LG on 10 December 1991 from water of salinity 1.5, and temperature 20°C. In the laboratory, they were placed in tap water treated as described above at a density of ≈1000 m^{-3} amongst vegetation in large

Table 3.1. Mean (±sd) experimental salinities in each treatment in salinity tolerance experiments on the caridean shrimps of the Hopkins River estuary. Each mean is calculated from five salinity values which were themselves mean values of salinity in each aquarium over the experimental period.

Temperature	Salinity treatments					
	Control	1	2	3	4	5
Paratya australiensis						
Adults						
10	0.2	21.1±0.3	22.7±0.1	24.8±0.1	26.7±0.1	28.6±0.1
21.5	0.2	21.0±0.2	23.0±0.3	25.0±0.2	26.6±0.4	29.5±0.4
28.5	0.4±0.2	14.3±0.2	16.4±0.2	18.3±0.1	20.5±0.2	22.3±0.2
Juveniles						
20	0.2	20.2±0.1	22.2±0.1	24.2±0.1	26.2±0.1	28.3±0.1
Macrobrachium intermedium						
20	11.5	0	1.0±0.1	2.0±0.1	4.0±0.1	6±0.1
Palaemon serenus						
9	35.5±0.5	1.5±0.3	3.3±0.2	6.3±0.1	10.1±0.3	14.8±0.3
20	35.1±0.5	2.1±0.1	4.9±0.5	8.8±0.4	13.0±0.4	16.7±0.1
20	11.6±0.1	1.0±0.1	2.2±0.1	4.3±0.0	6.1±0.1	8.9±0.1

(0.15 m^2) aquaria at 20±0.5°C. A salinity tolerance experiment was conducted at 20±0.5°C as described above for adults. Salinity treatments used are shown in Table 3.1.

Fifty percent lethal salinities (LC_{50}) were calculated by logistic regressions (Steinberg and Colla, 1991) on the number of survivors and deaths in each aquarium against the log of mean salinity. Salinity for 50% survivorship was estimated from the regression and 95% fiducial limits were calculated by Fieller's theorem (Finney, 1978).

3.2.1.2. TOLERANCE IN ADULT *M. INTERMEDIUM* AND *P. SERENUS*

As both *M. intermedium* and *P. serenus* are known to inhabit the marine environment, and this study is concerned with their occurrence in the estuarine environment, it was of most interest to investigate the tolerances of these species to low salinities.

M. intermedium adults were collected in October 1988 in a *Zostera* meadow just south of HB in water of salinity of 11.5 at 14°C, and were placed in large (0.15-0.4 m^2) aquaria in the laboratory in water of the same salinity made from a mixture of tap water that had been aerated for several days and seawater from Lady Bay. Shrimps were acclimated for four days at 20±2° C.

P. serenus adults were collected from a *Zostera* meadow north of Griffith Island at the mouth of the Moyne River, 25 km west of the Hopkins River mouth in September and October 1988, in water of salinity of 34.8 at 16°C. In the laboratory, all shrimps were placed in large (0.15-0.4 m^2) aquaria in seawater, at a density of ≈200 m^{-2} at 20±1.5°C. Salinity in one aquarium was

reduced over 8 h to 11.5 by the addition of Hopkins River water, and shrimps were maintained at that salinity for four days, Temperature in another aquarium was gradually reduced to 9±1.5° C, and shrimps were maintained at that temperature for four days. A third group of *P. serenus* was maintained at 20±1.5°C in seawater.

For each trial, three blocks of five salinity treatments and one control (acclimation salinity) were used as in Table 3.1. A single trial was conducted at 20°C for *M. intermedium* acclimated at salinity 11.5. Two trials were conducted at 20°C for *P. serenus*: one with shrimps acclimated at salinity 11.5 and one with shrimps acclimated in seawater. One experiment was conducted at 9° C for *P. serenus* acclimated in seawater. Experimental procedures were as described for *P. australiensis*.

3.2.2. LABORATORY EXPERIMENTS ON COMPETITIVE INTERACTIONS BETWEEN ADULT *M. INTERMEDIUM* AND *P. AUSTRALIENSIS*

3.2.2.1. COMPETITION FOR DEPTH

Experiments were designed to simultaneously test the effect of both inter- and intraspecific associations. Underwood (1986) recommends such simultaneous experiments because of the interdependence of the two types of competition. Interactions can be masked if both types of interaction are not taken into account. Three experimental treatments were conducted:
1. each species alone at 15 per tank (1N). (a) *P. australiensis* and (b) *M. intermedium*;
2. each species alone at 30 per tank (2N). (a) *P. australiensis* and (b) *M. intermedium*;
3. both species at 15 each per tank (1N) (see Fig. 3.1).

Treatments 1 and 2 tested for the effect of intraspecific interactions on the distribution within the tank, while treatment 3 tested for interspecific effects. These densities (1N) correspond to 93 m^{-2}, which approximated natural adult densities recorded at JP in November 1988 (160 m^{-2} *P. australiensis*, 25 m^{-2} *M. intermedium*) but was greater than those recorded in December 1988 (9 m^{-2} *P. australiensis*, 18 m^{-2} *M. intermedium*) (see Section 2.4.3).

Trials were conducted at a salinity of 2 on 13 January 1990, 20 January 1990 and 21 January 1991 and at a salinity of 10 on 3 January 1990, 4 January 1990 and 15 January 1991. Only five tanks were used, so there was no replication of treatments at each trial.

P. australiensis were collected from TS and from the Fitzroy River estuary (see Section 7.2). *M. intermedium* were collected from HB. Shrimps were held in large single-species tanks at 19-21°C at the experimental salinity (1.8-2.2 or 10-10.5) at densities of 200-300 m^{-2} for at least one week prior to experimentation. Acclimation and experimental water in this and subsequent laboratory experiments was a mixture of tap water, which had been aerated for at least 24 h, with $CaCO_3$ added to achieve a Calcium concentration of 50 $mg.L^{-1}$ (a typical level for Hopkins

River water), and sea water collected from Lady Bay, Warrnambool. The mixture was adjusted to the required salinity using a 'Yeo-Kal' salinometer (Model 602 Mk III).

P. australiensis were fed epiphyte-covered *Zostera*, and *M. intermedium* were fed chopped frozen bivalve mollusc (*Plebidonax deltoides*).

Experimental tanks were 50×30×30 cm, fitted with a diagonal base that was covered by beach sand over 1 cm of gravel so that there was a water depth gradient along the long axis of the aquarium from approximately 4 cm to 23.5 cm (Fig. 3.1).

All tanks were blackened on two ends and placed in a black enclosure lighted from above by 'Biolux' fluorescent lights that were damped by two layers of 70% shade cloth. A 14:10 light: dark cycle was maintained during the experimental period, which approximated the natural diurnal cycle. Observations at night were carried out using a red darkroom lamp (Philips B22 PF712B) aimed from above directly onto the diagonal plane of the experimental substrate. All aeration equipment was removed prior to the initiation of the experiment to keep the substrate as simple as possible. Dissolved oxygen throughout each aquarium was measured with a Yellow Springs Instruments dissolved oxygen meter (Model 57), after the last observation to ensure that dissolved oxygen had not declined below 75% saturation.

During experimental observations, each tank was divided into four equal sections of 12.5 cm width. Four depth ranges were thus delineated; section one, 3.5-9 cm; section two, 9-14 cm; section three, 14-19 cm; section four, 19-23.5 cm (Fig. 3.1). Shrimps were introduced near the centre of the experimental tanks without food at least two hours before observations began at 1700 h. Observations were made at hourly intervals for six hours: three observations under light and three observations in the dark. The number of individuals of each species in each section was noted at each observation.

In analysing the effect of treatment, mean longitudinal position was used. To calculate this value, each section of the tank was given a value corresponding to its distance from the centre. Thus section 1=-2, section 2=-1, section 3=1 and section 4=2. The mean position of each species was then calculated for each observation by the formula:

$$\text{Mean position} = -2a - b + c + 2d$$

where a, b, c and d are the proportion of each species in sections 1,2,3, and 4 respectively.

In summary, six trials were conducted, three at each salinity. Because single trials of each treatment were conducted over six days, 'trial' was treated as a separate effect with no replication (Sokal and Rohlf, 1981). Therefore each salinity, the analysis of mean position for each species had three levels of treatment (Fig. 3.1), three levels of trial, and six levels of observation, which was treated as a repeated time effect. The effect of treatment on the position of each species in the experimental aquaria was thus tested by repeated-measures ANOVAs. Greenhouse-Geiser adjustment of P-values was used to test the repeated time effect

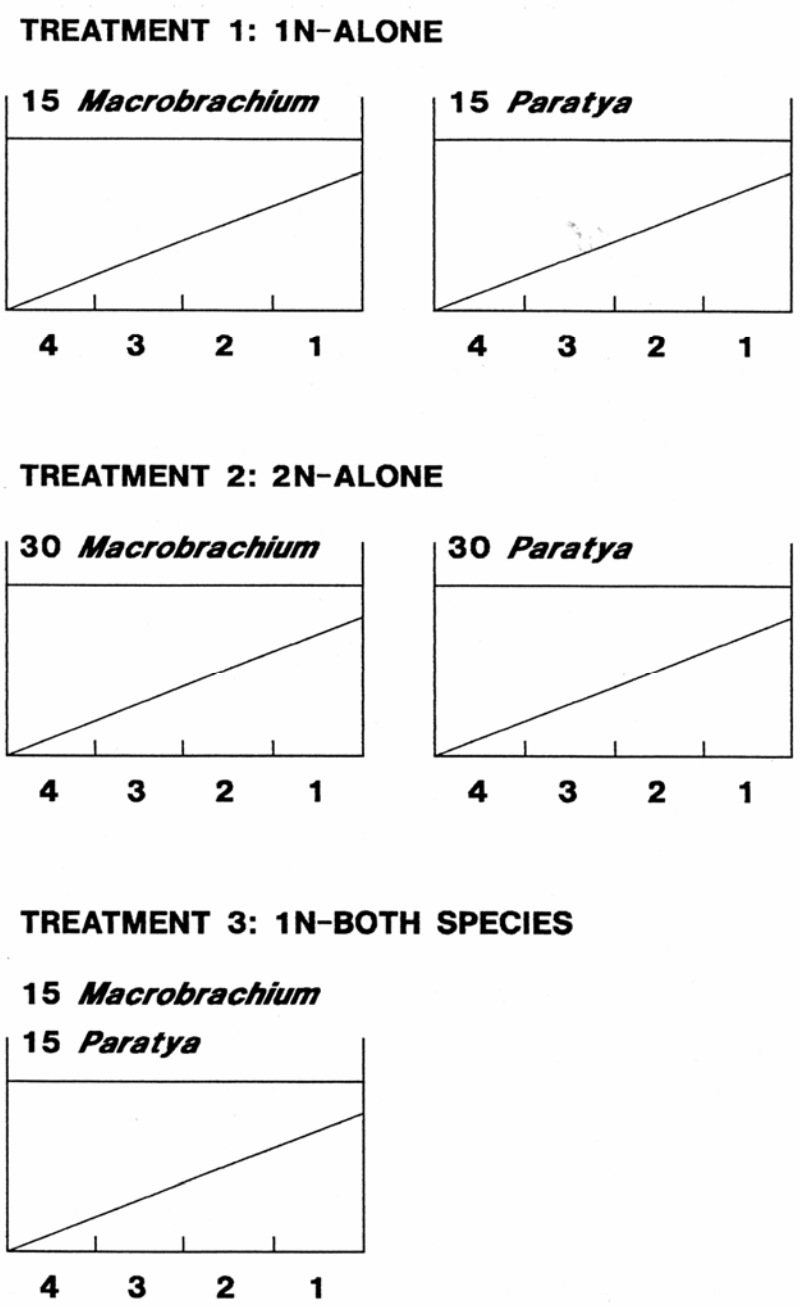


Fig. 3.1. Design of laboratory experiment to test for inter-and intraspecific interactions between *Paratya australiensis* and *Macrobrachium intermedium* in relation to depth. The four sections of each aquarium from shallow (1) to deep (4) are indicated.

(Wilkinson, 1990). If the treatment effect was significant, planned comparisons for intraspecific interaction (2N alone vs 1N alone) and for interspecific interaction (1N both species vs 1N alone) were conducted. If the time effect was significant, a planned comparison of the three lit trials vs the three dark trials was conducted. Separate analyses were performed for each species at each salinity with three levels of trial.

3.2.2.2. COMPETITION FOR VEGETATIVE COVER

The design of this experiment was the same as the previous experiment with three treatments designed to detect the effect of both interspecific and intraspecific associations. Experimental animals were collected and acclimated as described in the previous section.

A trial was conducted on 2 February 1991 with three replicates of each treatment, and a similar trial was conducted on 31 December 1991, but without the 2N treatments. Both trials were conducted at a salinity of 10.5.

Experimental tanks were 50×30×30 cm, with a substrate of beach sand over gravel, filled to a depth of 26-28 cm. *Zostera* was collected from 0.075 m^2 quadrats at HB (50-70 turions per quadrat) and transplanted into one randomly chosen half of each aquarium. The leaves were trimmed so that one half of the aquarium had a natural covering of vegetation and the other half was exposed sand. Aquaria were left to settle overnight with aeration.

Shrimps were added to the bare half of the aquaria, after the removal of the aeration, at least three hours before observations began. Treatments were allotted to tanks randomly. Observations were made at the same times, and lighting conditions were as in the previous experiment. At each observation, the number of each species in the bare half of the aquarium was counted. Dissolved oxygen was measured after the last observation as for the depth experiment.

The effects of treatments on the proportions of each species in the unvegetated half of the aquaria were analysed by repeated-measures ANOVAs. 'Trial' was considered an unreplicated effect with two levels. In the first trial, there were three replicates of each of the three treatments. In the second trial, there were three replicates of two treatments (no '2N' treatment). An initial ANOVA was conducted for each species with two levels of trial and two levels of treatment. If neither the trial effect nor the trial×treatment effect was significant, the trials were pooled, and a second ANOVA was conducted with three levels of treatment, and six levels of the repeated time effect. If either effect was significant in the initial ANOVA, then separate analyses were conducted for each trial.

3.3. RESULTS

3.3.1. SALINITY AND TEMPERATURE TOLERANCE EXPERIMENTS

P. AUSTRALIENSIS

Table 3.2 shows the 48 h LC_{50} values for adult *P. australiensis* at 10, 21.5 and 28.5°C and for juveniles at 20°C, and 96 h LC_{50} values for adults at 10 and 21.5°C and for juveniles at 20°C. Tolerance of high salinities decreased in adults with increase in temperature. A second logistic regression was conducted with age as an effect as well as salinity, to test for a difference in the response curve in adults and in juveniles. The interaction of salinity and age was not significant (P=0.233), and with the interaction term removed, the age effect was significantly different (P<0.001). Thus the LC_{50} for juveniles was significantly lower than for adults in *P. australiensis*.

M. INTERMEDIUM

Survivorship of *M. intermedium* adults over 96 h was greater than 95% in salinities of 1.0 and greater, but only 10% of *M. intermedium* survived 48 h, and 5% survived 96 h in freshwater (tap water that had been aerated for several days). The LC_{50} at 20°C for *M. intermedium* acclimated at salinity 11.5 therefore lies between 0 and 1. More accurate investigations were not pursued as this value falls below the minimum salinity of Hopkins River water.

P. SERENUS

Table 3.2 shows the 48 h and 96 h LC_{50} values at 9°C and 20°C for adult *P. serenus* acclimated in seawater, and at 20°C acclimated at salinity 11.5. Although tolerant of low salinities, *P. serenus* is less tolerant than *M. intermedium* under the same conditions. Tolerance of low salinity was increased by acclimation at a lower salinity, and *P. serenus* was less tolerant of low salinity at 9°C than at 20°C.

3.3.2. COMPETITIVE INTERACTIONS BETWEEN ADULT *P. AUSTRALIENSIS* AND *M. INTERMEDIUM*

INTERACTIONS IN RELATION TO DEPTH

The distribution of *P. australiensis* in the aquaria for each of the three treatments, at salinities of 2 and 10 are presented in Fig. 3.2. Each bar in the histograms represents the mean (±SE) proportion of individuals in each of the four segments of the aquaria, for the three trials at salinity 10 and the three trials at salinity 2. A similar depiction of distributions of *M. intermedium* is presented in Fig. 3.3.

When they were the sole species present, both *P. australiensis* and *M. intermedium* showed a consistent preference for the deeper portions of the aquaria (the greatest proportion being in section 4 in almost all cases). With both species present, *M. intermedium* still showed a preference for the deeper section of the tank, but *P. australiensis* was found more commonly at the shallower end, usually motionless on the incline, facing down the slope. *M. intermedium* was the more active species, moving around the aquarium with antennae sweeping at most times, but more actively after dark. *P. australiensis*, on the other hand, tended to remain motionless most of the time, most commonly moving with an escape response (rapid flex of the abdomen) if approached by an individual of the other species. Escape responses in *P. australiensis* were less common to individuals of the same species. More commonly if approached by another *P. australiensis*, there was either no response or a mutual antennal sweep, until one individual moved on.

In none of the analyses of mean position for each species at each salinity was effect significant for *M. intermedium*, however the treatment effect was significant for *P. australiensis* at salinity 10 (Table 3.3). In testing for interspecific and intraspecific interactions, use of multivariate statistics were not possible due to lack of trials in comparison to repeated measures. Thus a series of univariate tests was made for each time, necessitating the adjustment of the level of P at which significance is accepted. For six comparisons, the Dunn-Sidák method (Sokal and Rohlf, 1981) reduces α to 0.009. No test for intraspecific interaction was significant. One test for interspecific interaction was significant, and for five of the six other tests, probabilities were low (Table 3.3).

At a salinity of 10, the effect of repeated observations (time) was significant for *P. australiensis*, with mean position being significantly (P=0.025) more towards the shallow end in the dark than in the light (Table 3.3, Fig. 3.2).

These analyses suggested a weak interspecific interaction at salinity 10. Figs. 3.2 and 3.3 show both species preferring the deeper section of the tank when they are the only species present, but *P. australiensis* being more common in the shallower end of the tank in the presence of *M. intermedium*. This trend is also apparent, albeit more weakly, at salinity 2.

→

Fig. 3.2. Laboratory experiment to test for interspecific and intraspecific interactions between *Paratya australiensis* and *Macrobrachium intermedium* in relation to depth. Mean (±SE) proportions of *P. australiensis* in four sections along a depth gradient of experimental aquaria (segment 1, 3.5-9 cm; 2, 9-14 cm; 3, 14-19 cm; 4, 19-23.5 cm) in three treatments: both species at 1N (15 adults of each species in each aquarium); *Paratya* only at 1N (15 adult *P. australiensis* only in each aquarium); *Paratya* only at 2N (30 adult *P. australiensis* only in each aquarium). Abundances were observed hourly on six occasions: three observations in the light (1700 - 1900 h) and three observations in the dark (2000 - 2200 h), and at two salinities (10 and 2)

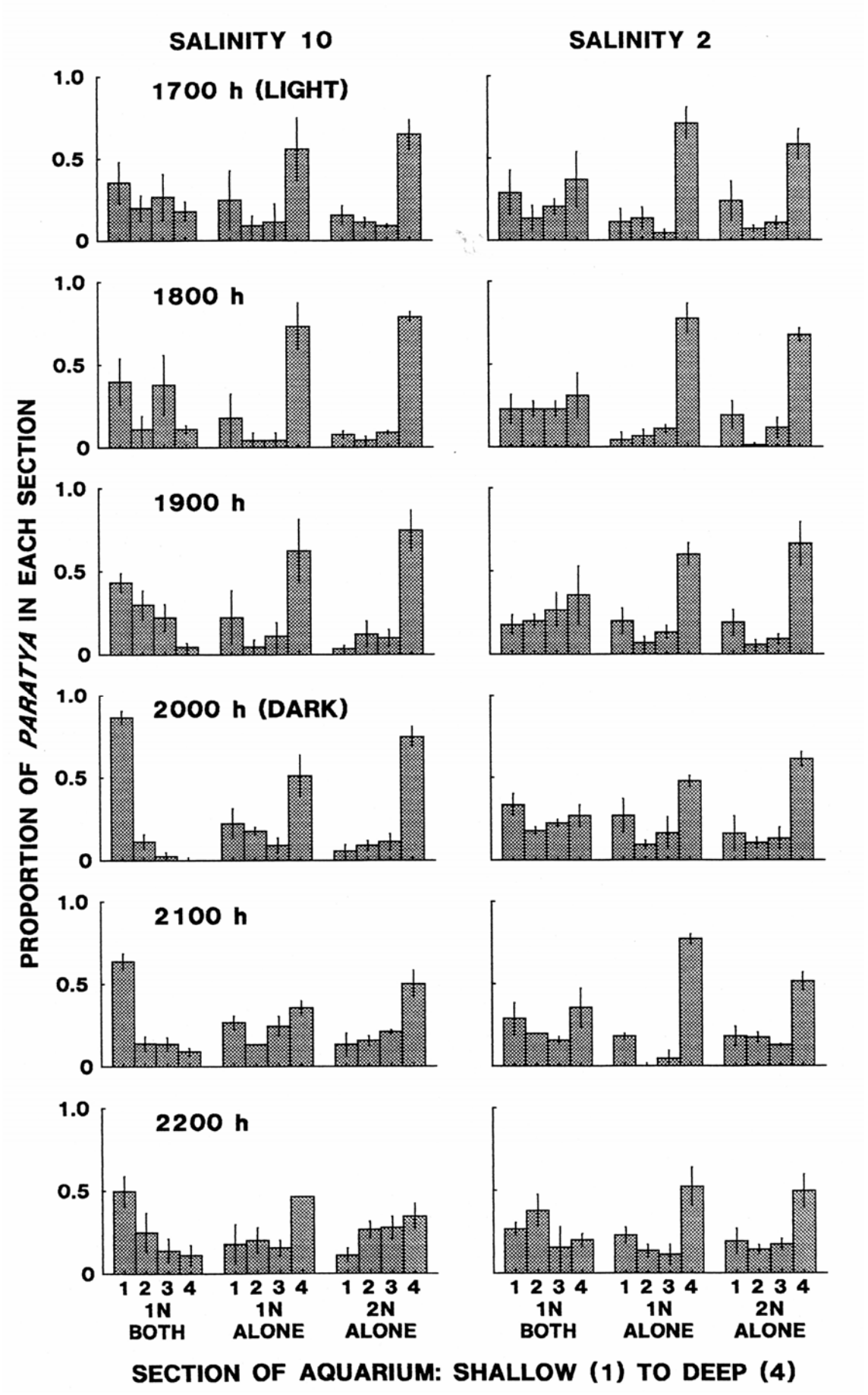

SALINITY 10
SALINITY 2
1700 h (LIGHT)
1800 h
1900 h
2000 h (DARK)
2100 h
2200 h
1.0
0.5
0
PROPORTION OF PARATYA IN EACH SECTION
1 2 3 4
1N BOTH
1N ALONE
2N ALONE
SECTION OF AQUARIUM: SHALLOW (1) TO DEEP (4)

Table 3.3. Results (P values) of repeated-measures ANOVAs for the mean position of each species in experimental aquaria designed to test for interspecific and intraspecific interactions in relation to depth. Results are for three trials at salinity 10, three at salinity 2, and all six trials together.

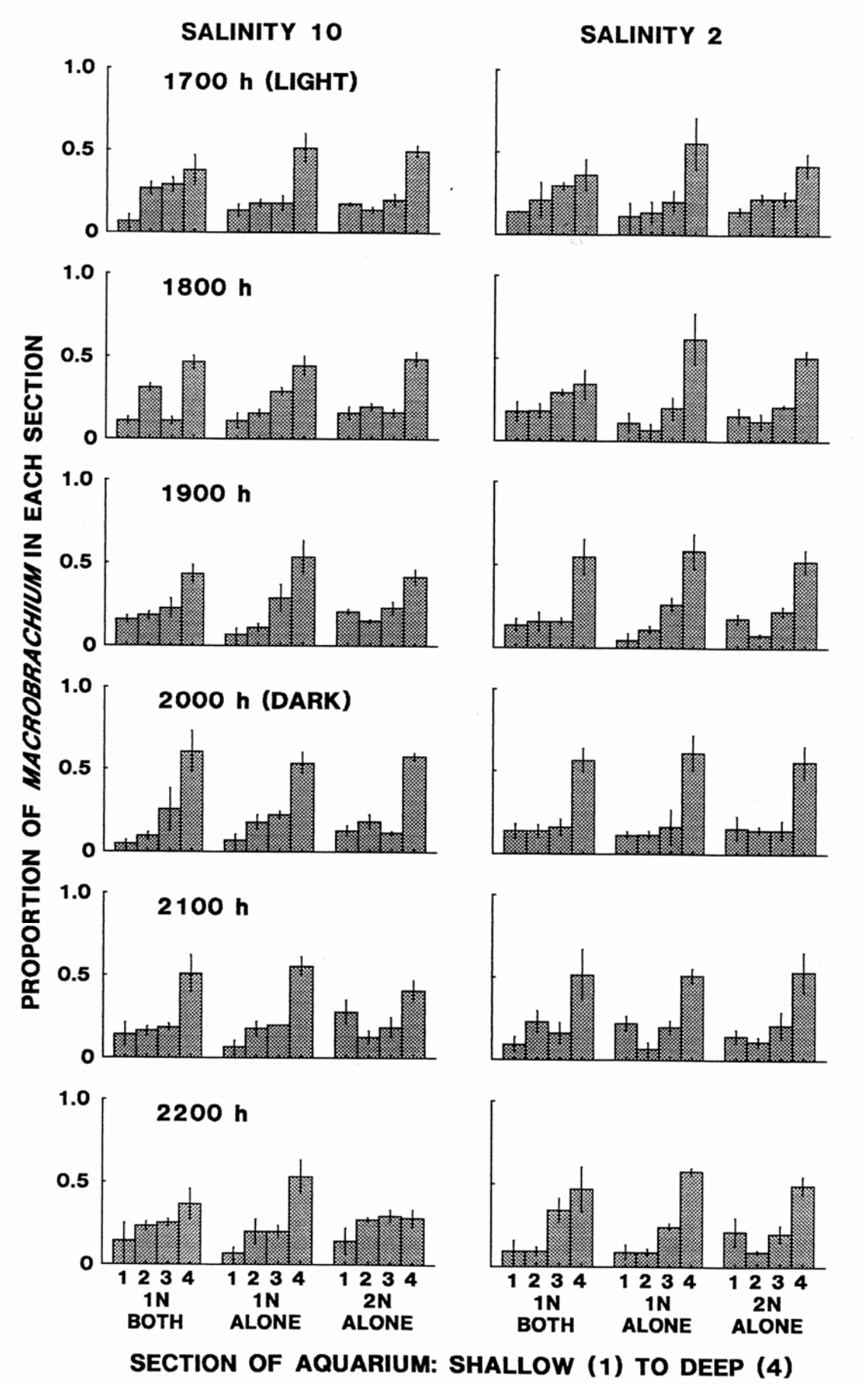
Effect	*Paratya australiensis*					*Macrobrachium intermedium*		
	df (10,2)	salinity 10	salinity 2	df	Pooled	salinity 10	salinity 2	Lumped
WITHIN REPLICATES								
time	5	*0.027	0.102	5	*0.001	0.352	0.617	0.340
treatment×time	10	0.121	0.401	10	0.151	0.680	0.772	0.690
trial×time	10	0.177	0.376	25	0.254	0.787	0.275	0.485
BETWEEN REPLICATES								
treatment	2	*0.010	0.228	5	*0.003	0.192	0.345	*0.047
trial	2	0.358	0.737	2	0.587	0.666	0.307	0.321
-test for light vs dark		*0.025	-		*0.006	-	-	-
-test for intraspecific interaction								
Light 1700 h		0.695	-		0.942	-	-	0.314
Light 1800 h		0.410	-		0.909	-	-	0.268
Light 1900 h		0.367	-		0.464	-	-	*0.002
Dark 2000 h		0.058	-		0.160	-	-	0.345
Dark 2100 h		0.183	-		0.873	-	-	0.459
Dark 2200 h		0.882	-		0.980	-	-	0.111
Multivariate test; Wilk's λ		-	-		0.813	-	-	0.114
-test for interspecific interaction								
Light 1700 h		0.274	-		0.119	-	-	0.247
Light 1800 h		0.021	-		*0.003	-	-	0.054
Light 1900 h		0.031	-		0.029	-	-	*0.004
Dark 2000 h		*0.003	-		*0.009	-	-	0.740
Dark 2100 h		0.011	-		*0.003	-	-	0.798
Dark 2200 h		0.016	-		*0.001	-	-	0.370
Multivariate test; Wilk's λ		-	-		*0.004	-	-	0.190

The separate analyses for the different salinities suffer from low power, so to increase power all six trials were analysed together (Table 3.3). This analysis assumes no significant (statistical) interaction between trial and treatment, so the results should be viewed with caution.

With all 6 trials pooled, time and treatment effects were both highly significant for *P. australiensis* (Table 3.3). Mean position in light was more shallow than in dark. The multivariate test for interspecific interaction was significant, with four of the six univariate

→

Fig. 3.3. Laboratory experiment to test for interspecific and intraspecific interactions between *Paratya australiensis* and *Macrobrachium intermedium* in relation to depth. Mean (±SE) proportions of *M. intermedium* in four sections along a depth gradient of experimental aquaria in three experimental treatments over six observations at two salinities (Details as in Fig. 3.2)


SALINITY 10
SALINITY 2
1700 h (LIGHT)
1800 h
1900 h
2000 h (DARK)
2100 h
2200 h
1.0
0.5
0
PROPORTION OF MACROBRACHIUM IN EACH SECTION
1 2 3 4
1N BOTH
1N ALONE
2N ALONE
SECTION OF AQUARIUM: SHALLOW (1) TO DEEP (4)

tests being significant. Treatment effect was also significant for *M. intermedium*, but the multivariate tests for interspecific and intraspecific interaction were not. The 1900 h observations showed significant differences for both tests (Table 3.3), with more individuals of *M. intermedium* being found towards the shallow end in the '2N' and '1N-both species' treatments than in the '1N-alone' treatment. However these differences were not large (Fig. 3.3).

In summary, this experiment has shown an interspecific interaction between *P. australiensis* and *M. intermedium*, in which *P. australiensis* was more common in less preferred shallow water in the presence of *M. intermedium*. This trend was more pronounced in the dark, when *M. intermedium* was most active. *M. intermedium* did not show any consistently significant change in distribution in the presence of *P. australiensis*, but at one time (1900 h), was more likely to occur in deeper water at low density, than either at high density or in the presence of *P. australiensis*. It is possible that the intensity of the interspecific interaction may be greater at salinity 10 than at 2, but this experiment was not explicitly designed to test this hypothesis.

INTERACTIONS IN RELATION TO VEGETATION STRUCTURE

The overall mean (±SE) proportion of each species in the unvegetated half of the experimental aquaria for the three treatments over the six observations is shown in Fig. 3.4. At a density of 15 per aquarium, *M. intermedium* tended to occur on the bare sand in greater numbers than *P. australiensis*, usually actively moving around the aquarium. At a density of 30 per aquarium *M. intermedium* was less common proportionately on the bare sand, although the absolute numbers were similar to the 1N treatments.

For *P. australiensis*, neither trial effect nor the trial×treatment effect was significant (Table 3.4), so a second ANOVA was conducted for three levels of treatment with trials pooled. No effect for treatment was found for *P. australiensis*, but a significant effect of time (the repeated effect) was detected. The proportion of individuals in the unvegetated half were greater in dark observations than light observations. The significant treatment×time term indicates that the trend to more individuals in the unvegetated half was stronger in the absence of *M. intermedium* (Fig 3.4).

The treatment×trial effect was significant in the initial ANOVA for *M. intermedium*, and therefore separate analyses were conducted for each trial (Table 3.4). No significant

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Fig. 3.4. Laboratory experiment to test for interspecific and intraspecific interactions between *Paratya australiensis* and *Macrobrachium intermedium* in relation to vegetation structure. Mean (±SE) proportions of *M. intermedium* and *P. australiensis* in the unvegetated half of experimental aquaria in three experimental treatments over six observations as in Fig. 3.2.

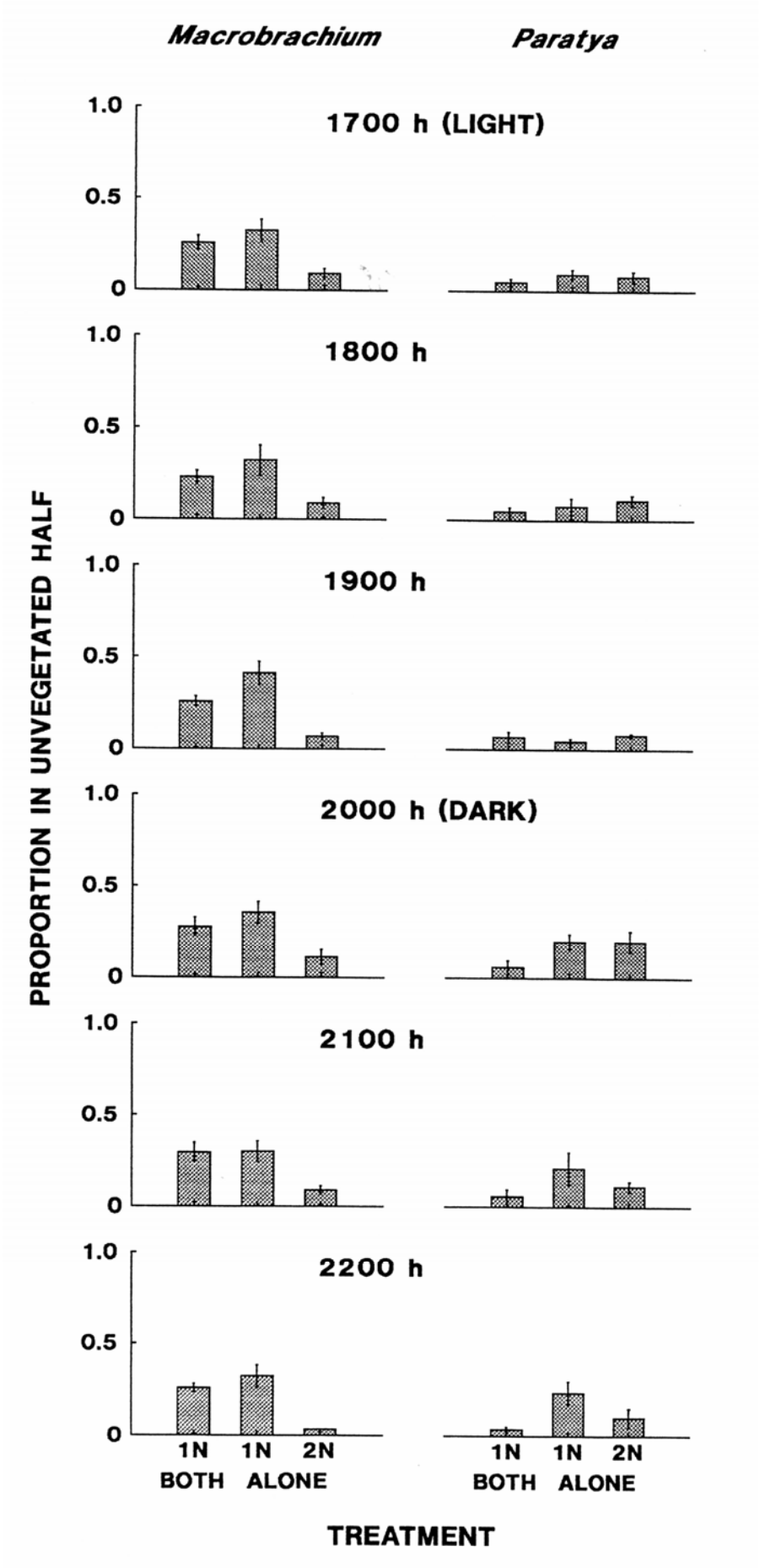

Macrobrachium
Paratya
1700 h (LIGHT)
1800 h
1900 h
2000 h (DARK)
2100 h
2200 h
1.0
0.5
0
PROPORTION IN UNVEGETATED HALF
1N BOTH
1N ALONE
2N
TREATMENT

Table 3.4. Results (P values) of repeated-measures ANOVAs performed on proportional abundances of each species in the unvegetated half of aquaria in an experiment designed to test for interspecific and intraspecific interactions in relation to vegetation structure

		Paratya australiensis				*Macrobrachium intermedium*					
Effect		Trial as an effect		Trials lumped		Trial as an effect		Trial 1		Trial 2	
		df	P	df	P	df	P	df	P	df	P
WITHIN REPLICATES											
time		5	*0.035	5	*0.027	5	0.544	5	0.358	5	0.473
treatment×time		5	*0.024	10	*0.039	5	0.546	10	0.566	5	0.541
trial×time		5	0.167			5	0.248				
treatment×time×trial		5	0.641			5	0.704				
BETWEEN REPLICATES											
treatment effect		1	0.065	2	0.101	1	*0.015	2	*0.001	1	0.899
trial effect		1	0.964			1	0.921				
treatment×trial		1	0.118			1	*0.020				
-test for light vs dark			-		*0.003		-		-		-
-test for intraspecific interaction											
Light	1700 h		-		-		-		0.011		-
	1800 h		-		-		-		0.108		-
	1900 h		-		-		-		*0.001		-
Dark	2000 h		-		-		-		*0.007		-
	2100 h		-		-		-		0.083		-
	2200 h		-		-		-		*0.003		-
-test for interspecific interaction											
Light	1700 h		-		-		-		0.060		-
	1800 h		-		-		-		0.462		-
	1900 h		-		-		-		0.027		-
Dark	2000 h		-		-		-		0.027		-
	2100 h		-		-		-		0.574		-
	2200 h		-		-		-		0.097		-

interspecific interaction was detected in either trial (the second trial *only* tested for interspecific interaction). *M. intermedium* showed a significant intraspecific interaction. A significantly smaller proportion was found in the unvegetated half under high density at three times, and probabilities were low at the other three times (Table 3.4). This suggests that *M. intermedium* showed intraspecific displacement, not from the vegetated side, but from the unvegetated side.

In summary, no interspecific interaction was detected in relation to vegetation structure. *M. intermedium* was found in similar absolute numbers in the unvegetated part of the aquaria, independent of total density. This trend was detected as an intraspecific interaction when analysing proportional abundances. *P. australiensis* occurred in greater numbers in the

unvegetated half after dark than in the light, but showed no significant effect of interspecific or intraspecific interactions.

3.4. DISCUSSION

Trends in acute sensitivities to salinity in the three caridean species of the Hopkins River estuary are reflected in their distributions. *P. australiensis*, which is absent or present in very low numbers during periods of high salinity, was unable to tolerate marine conditions in the laboratory. *M. intermedium*, the dominant caridean of the estuary, was the most euryhaline of the three species. *P. serenus*, which was only present during periods of high salinity, and only at HB near the estuary mouth was unable to tolerate salinity as low as Hopkins River water (above estuarine influence).

The disappearance of *P. australiensis* from the estuary after January 1989 was possibly due to physiological stress, as temperature over the bed at this time ranged between 20 and 30°C, and salinities over the meadows at JP reached levels around the LC_{50} for adults at 21.5°C and well above the LC_{50} for 28.5°C (Fig. 2.8, Table 3.2). Physiological stress may also be responsible for the dramatic decline in the number of *P. australiensis* juveniles in the estuary from December to January. An anomaly in these LC_{50} results is the lower value for *P. australiensis* juveniles than adults, and yet small numbers of juveniles persisted over the entire year (Fig. 2.11), including moderate densities of juveniles at JP in January when salinity over the meadow exceeded 25.

The LC_{50} values for *P. australiensis* at 20°C derived in this study fall between the high value derived by Williams (1984), and the low value derived by Morris (1991). At 10°C, the 48 h LC_{50} derived by Walker (1972) was much lower than the equivalent statistic of this study (Table 3.2). It is tenuous to draw conclusions from this disparate collection of data. Although the data show differences, in all cases LC_{50} values were greater than 20, except in high temperature conditions. Thus across its southern range (where all these studies were based), the freshwater *P. australiensis* shows considerable tolerance to salinity, and thus the potential to inhabit the estuarine environment. The occurrence of *P. australiensis* in other estuaries is considered in Chapter 7.

There is no evidence that stress caused by low levels of salinity affect the distribution of *M. intermedium*, as its abundance did not decrease with decreases in salinity during floods. Canonical correlation analyses (section 2.4.4.2) indicated little association of *M. intermedium* adults with salinity at RF, while they were more strongly associated with low salinity at JP and HB. This was probably due to lower abundances in summer, rather than a preference for low salinity. Although *M. intermedium* was found to be tolerant of very low salinity, it is less tolerant than *P. australiensis* which can survive in aerated tap water indefinitely, while *M. intermedium* can not. So although both species are capable of survival in Hopkins River water (salinity 0.8-2), it is likely that *M. intermedium* may experience sub-lethal stress at such low

salinities, which may explain its low abundance in the upper portion of the estuary, and its absence from further upstream. The LC_{50} for *M. intermedium* from the Hopkins River estuary was less than that reported by Walker (1979) for specimens from a marine environment in Tasmania (Table 3.2). It is unclear if the greater tolerance of low salinities by Hopkins River specimens was entirely due to a lower acclimation salinity or if there is some geographical variation in tolerance between populations. Canonical correlations also indicated an association between high salinity and the abundance of *M. intermedium* juveniles, but this association is more likely to be a result of recruitment during periods of high salinity rather than a direct influence of salinity tolerance on the distribution of juveniles.

Conditions typical throughout the estuary in late winter and early spring with surface temperatures at 10-14°C and surface salinities <5 (Figs. 2.8, 2.9), would be beyond the tolerance of *P. serenus*, which could explain its absence from the estuary from September to November 1988 (Fig. 2.10) and July to October 1984 (Fig. 2.12). Such a conclusion is consistent with the identification of salinity as an important factor associated with the abundance of *P. serenus* at HB identified by the canonical correlation analysis (Table 2.5). Although salinity tolerance can explain the absence of *P. serenus* from HB during periods of high flow, further explanation is necessary to explain its absence from further upstream where, although salinity remained low for a longer period than at HB, surface salinities were >10 for five consecutive months in 1988/1989. HB was unique among the meadows studied in that, on several occasions, there was a longitudinal variation in salinity due to proximity to the mouth of the estuary. Such variation and the more dynamic nature of salinity conditions at this site would allow *P. serenus* to move within the meadow to areas of higher salinity, which would not be possible in meadows further upstream. The correlation of *P. serenus* abundance with both high salinity and distance along the meadow (Section 2.4.6) supports this contention. The nature of recruitment of *P. serenus* to the estuary is probably also important in determining distribution, and this aspect is investigated in subsequent chapters.

The laboratory experiment that showed competitive displacement of *P. australiensis* from the preferred deeper water is consistent with the opposing correlations of the two species in relation to depth at all sites in November and December 1988. The bare sand in the experimental aquaria without vegetation is a situation quite different from the seagrass meadow of Jubilee Park, and this should be taken into account when assessing the validity of the experiment. It did, however, serve to show different behavioural responses of the two species and to show *P. australiensis* as vulnerable to displacement by *M. intermedium*, consistent with the observed distributional patterns. A field experiment using enclosures in a sloped section of seagrass meadow would better test the hypothesis of competitive displacement. Such an experiment was planned for December 1991 on the narrow strip of *Zostera* in meadow 2 at JP (Fig. 2.4), but a lack of seagrass throughout the upper part of the estuary in that year prevented its completion.

Underwood (1986) stressed the importance of intraspecific competition and suggested that demonstration of an intraspecific interaction was a prerequisite for the demonstration of interspecific competition. No intraspecific effect was detected for *P. australiensis*. At one time (1900 h), *M. intermedium* showed a decreased preference for deep water at high densities, regardless of the species composition. Thus *M. intermedium* showed intra- and interspecific interactions of similar (low) intensity. By far the strongest effect was that of the presence of *M. intermedium* on *P. australiensis*.

It is of interest that *P. australiensis* adults virtually disappear from the estuary after December and that habitat partitioning seems to only occur in November and December. It is uncertain whether this behavioural interaction causes the displacement of *P. australiensis* from the estuary or migration occurs due to physiological stress. Differences in physiological tolerances may be a component of competitive advantage, and *P. australiensis* may become more susceptible to competitive exclusion if stressed.

To have proven that competitive displacement occurs in relation to depth does not demonstrate clearly the resource for which the two species are competing. A possible answer is competition for refuge from predators in the form of wading birds. Howard and Lowe (1984) found that predation of large shrimps in shallow water by royal spoonbills (*Platalea regia*), white-faced heron (*Ardea novaehollandiae*) and sacred ibis (*Threskiornis aethiopicus*), increased the mortality of large females. All three species of bird are common in the Hopkins River estuary and large females dominated the adult portion of the *P. australiensis* population at JP in these months (see Chapter 4). So the decline in *P. australiensis* numbers after December may be due to increased predation in shallow waters, but it may also be a result of emigration from the estuary to upstream sites. The possibility of migration is explored in Chapter 7.

Although previous studies identifying habitat partitioning of caridean species have found habitat structural complexity to be an important resource for competition (Thorp, 1976; Coen at al., 1981), distributional patterns of *M. intermedium* and *P. australiensis* in the Hopkins River estuary have revealed vegetative structure to be less associated with relative abundances of the two species than depth (Figs. 2.14, 2.15).

The laboratory experiment on competition for vegetation cover did not show vegetated areas to be a limiting resource in densities about those found in the field. A similar experiment by Coen et al. (1981) showed *Palaemonetes vulgaris* excluded by *Palaemon floridanus* from vegetated habitats. It would appear that, in the current study, the displacement that occurs is for position within a meadow (depth) rather than for habitat space.

An intraspecific effect was detected for *M. intermedium*, which showed that, rather than increased density decreasing the proportion of *M. intermedium* in the seagrass, it decreased the proportion in the unvegetated side. The absolute density of *M. intermedium* adults on the bare substrate remained constant despite the increased stocking density This suggests that in making

forays into the bare sand substrate, *M. intermedium* individuals are more sensitive to increased density than they are in the cover of the seagrass. It also shows higher *M. intermedium* densities can be supported in the more complex habitat of vegetation than on bare substrate. The observation in Chapter 2 of *M. intermedium* densities only being correlated to seagrass abundance when *M. intermedium* densities were high and/or seagrass densities and meadow extent were low is consistent with *M. intermedium* only maintaining a low density in unvegetated areas.

In summary, acute toxicity tests to high and low levels of salinity supported the proposition of the overriding importance of physical factors in determining the distribution and abundance of the three caridean shrimps in the Hopkins River estuary. Laboratory experiments showed competitive interactions for position (depth) in aquaria, consistent with patterns observed in the estuary. If the partitioning of habitat observed in the Hopkins River estuary was the result of competitive displacement, competition would be of only limited importance in determining the overall distributions of carideans within the estuary. It would remain the proximate mechanism in separating species on a local scale, in response to the ultimate determinant of distributions on a broader scale: limits to physiological tolerance of *P. australiensis* to rising salinities.

Despite the importance of physical factors to the distribution of the caridean shrimps in the estuary, some spatial trends (e.g. the lack of *P. australiensis* adults downstream of JP in the months following maximum discharge) cannot be explained by response to physiological tolerance alone. Availability of juvenile recruits or adult immigrants is probably an important factor in such cases. An initial understanding of recruitment patterns can be gained from investigation of population dynamics of each species. This area is pursued in Chapter 4.

4. DEMOGRAPHIC PATTERNS OF CARIDEAN SHRIMPS IN THE SEAGRASS MEADOWS OF THE HOPKINS RIVER ESTUARY

4.1. INTRODUCTION

The population ecology of *M. intermedium* has been investigated in marine seagrass meadows of Western Port, Victoria (Howard, 1981; 1984; Howard and Lowe, 1984), in essentially marine estuaries on the central New South Wales coast (Gray, 1985; 1991a; 1991b), and in a strongly marine-influenced estuary in south-eastern Tasmania (Walker, 1979). Variation in demographic patterns was evident between the populations of these three latitudinally distinct studies. The Hopkins River estuary is at about the same latitude as Western Port (see Fig. 7.4), but the meadows in which *M. intermedium* was sampled in this study were more freshwater-influenced than the meadows of any earlier study. Demographic patterns observed in this study may help separate variation between populations due to latitudinal differences from variation due to differences in marine influence between study locations.

P. australiensis has been studied in several central-eastern Victorian coastal streams (Williams, 1977), in coastal streams of Tasmania (Walker, 1972), and in upland streams of south-eastern Queensland (M. Hancock, Griffith University, personal communication). In all cases, reproductive activity peaked in spring and summer, with juveniles recruiting to the rivers from November to January. Recruitment mechanisms were not clearly explained by any study. Recruitment occurred in periods prior to minimum discharge, and in the case of south-eastern Queensland, *during* peak discharge. Williams (1977) pointed to the enigma of such recruitment patterns in light of the planktonic larval stage of this species, stating "...[riverine] occupation seems scarcely possible". *P. australiensis* has never been recorded in significant numbers in estuarine seagrass meadows, and thus an investigation of the population ecology of *P. australiensis* in the Hopkins River estuary may shed light on not only recruitment processes, but also the importance of recruitment and immigration to adult distribution and abundance.

In light of interactions detected between adults of *M. intermedium* and *P. australiensis* in Chapters 2 and 3, study of the population dynamics of the two species in locations where they occur separately and where they occur sympatrically may detect other interspecific effects, such as changes to population structure, reproductive patterns or growth rates. The preceding chapters identified the overriding importance of hydrologically driven changes in physico-chemical conditions in determining distributions of all three species of caridean shrimp in the Hopkins River estuary, but physico-chemical conditions alone were inadequate to explain some spatial patterns, for which the availability of immigrants and recruits was suggested as a likely

determinant. Study of population structure in these populations may help clarify the importance of recruitment and migration.

While the population ecology of *P. serenus* has not been investigated prior to this study, previous studies of both *M. intermedium* and *P. australiensis* have used a variety of morphometric measurements in the analysis of population structure. Howard (1981) derived relationships between orbit-carapace length (OCL) and total length and dry weight in *M. intermedium*, to calculate standing crop, and his equations can be used for comparisons with other studies. No such relationships are available for *P. australiensis*, and therefore this chapter reports the same relationships for this species.

This chapter investigates the population dynamics of the three epibenthic caridean species of the Hopkins River estuary seagrass meadows. Data collected over two years from two meadows, JP and HB, and over one year from RF and from the freshwater habitat of TS are analysed. Reproductive and recruitment patterns, sex ratios and growth rates are investigated.

4.2. METHODS

Regressions between morphometric measurements and dry weight were calculated for *P. australiensis* to permit comparison of sizes reported in the present study with other studies that used different measurements. The following measurements were taken on thirty-three male *P. australiensis* and sixty-four juveniles and females:

- -Orbit-carapace length (OCL), measured from the antero-dorsal margin of the carapace behind the eye to the latero-posterior edge of the carapace;
- -Rostrum length, measured from the anterior tip of the rostrum to that point on the mid-line of the carapace in line with the antero-dorsal margin of the carapace behind the eye;
- -Total length, measured from the antero-dorsal margin of the carapace behind the eye to the midline of the posterior edge of the telson, excluding setae;
- -Dry weight, individuals were dried at 85-90°C until constant weight was achieved after 96 hours. (Ovigerous females were not used.)

The size range of *P. australiensis* used for the calculation of regressions was 1.6-8.5 mm OCL, which almost spanned the size range of shrimps collected from the Hopkins River. A few large females >8.5 mm OCL were collected, but as they were damaged, they were not used in these analyses. All measurements were made using a dissecting microscope (×8-×40) with an ocular grid, except for total lengths greater than 10 mm, which were made using vernier calipers. Relationships between the three morphometric measurements and the cube-root of dry weight were derived by linear regression for each sex.

Other sampling and laboratory methods for the data in this chapter are outlined in section 2.3.2. Some quantitative sample units and qualitative samples contained large numbers of juveniles. In these cases, after counting the total number of juveniles, OCL was measured for sub-samples of juveniles taken using a Folsom splitter, ensuring homogeneous size distributions were achieved (Griffiths et al., 1984). Total size frequency distributions were then calculated by incorporating the estimate of juvenile size frequencies into the total sample.

Patterns in sex ratios were investigated in *M. intermedium* and *P. australiensis*. Log-likelihood ratio tests (the G-test of Sokal and Rohlf, 1981) were conducted for each sample in which the number of post-juveniles was >10 on the null hypothesis that sex ratio=1:1, and the pooled, total and heterogeneity G values between sampling occasions were calculated. Three-way tables of sex, site and sampling occasion were analysed using log-linear models to test for a three-factor interaction (Sokal and Rohlf, 1981).

Growth in *M. intermedium* and *P. australiensis* was estimated from the monthly size-frequency data. Individual cohorts of different mean size were extracted for each sample using probability plots (Cassie, 1954).

4.3. RESULTS

4.3.1. MORPHOMETRIC RELATIONSHIPS

An ANCOVA performed on the cube-root of dry weight of *P. australiensis* between the sexes over the range of common size, with OCL as the covariate, detected a significant difference between the sexes (P=0.011), after heterogeneity of slope was not detected (P=0.768). The results of regressions for each sex of *P. australiensis* are:

males: $\sqrt[3]{\text{Dry weight (g)}} = -0.022 + 0.052$ OCL (mm) (N=33, R^2=0.977)

juveniles and females: $\sqrt[3]{\text{Dry weight}} = -0.008 + 0.048$ OCL (N=64, R^2=0.978)

However it is likely that the difference between the sexes is a result of the high sensitivity of the test rather than a meaningful biological difference. Thus it is probably more useful to calculate the regression equation for all individuals together:

$\sqrt[3]{\text{Dry weight}} = -0.009 + 0.049$ OCL (N=97, R^2=0.975)

Differences between the sexes for relationships between total length and OCL and between rostrum length and OCL were more pronounced, so regressions were only calculated separately for each sex:

males: Total Length = -0.122 + 3.705 OCL (N=33, R^2=0.962)

juveniles and females: Total Length = -0.012 + 3.464 OCL (N=68, R^2=0.993)

males:	Rostrum Length = -0.447 + 0.974 OCL	(N=33, R^2=0.926)
juveniles and females:	Rostrum Length = -0.251 + 0.856 OCL	(N=66, R^2=0.973)

The following equations for *M. intermedium* are derived from Howard (1981):

males:	Total Length = 3.161 + 3.937 OCL	(N=25, R^2=0.937)
juveniles and females:	Total Length = 2.197 + 3.861 OCL	(N=44, R^2=0.968)

4.3.2. SIZE STRUCTURE OF POPULATIONS

M. intermedium

Female *M. intermedium* grew to a larger size than males. The largest female collected in the Hopkins River estuary was 11.1 mm OCL, and the largest male was 7.3 mm OCL. The sex of sub-adults was generally identifiable in individuals greater than 3.2 mm OCL.

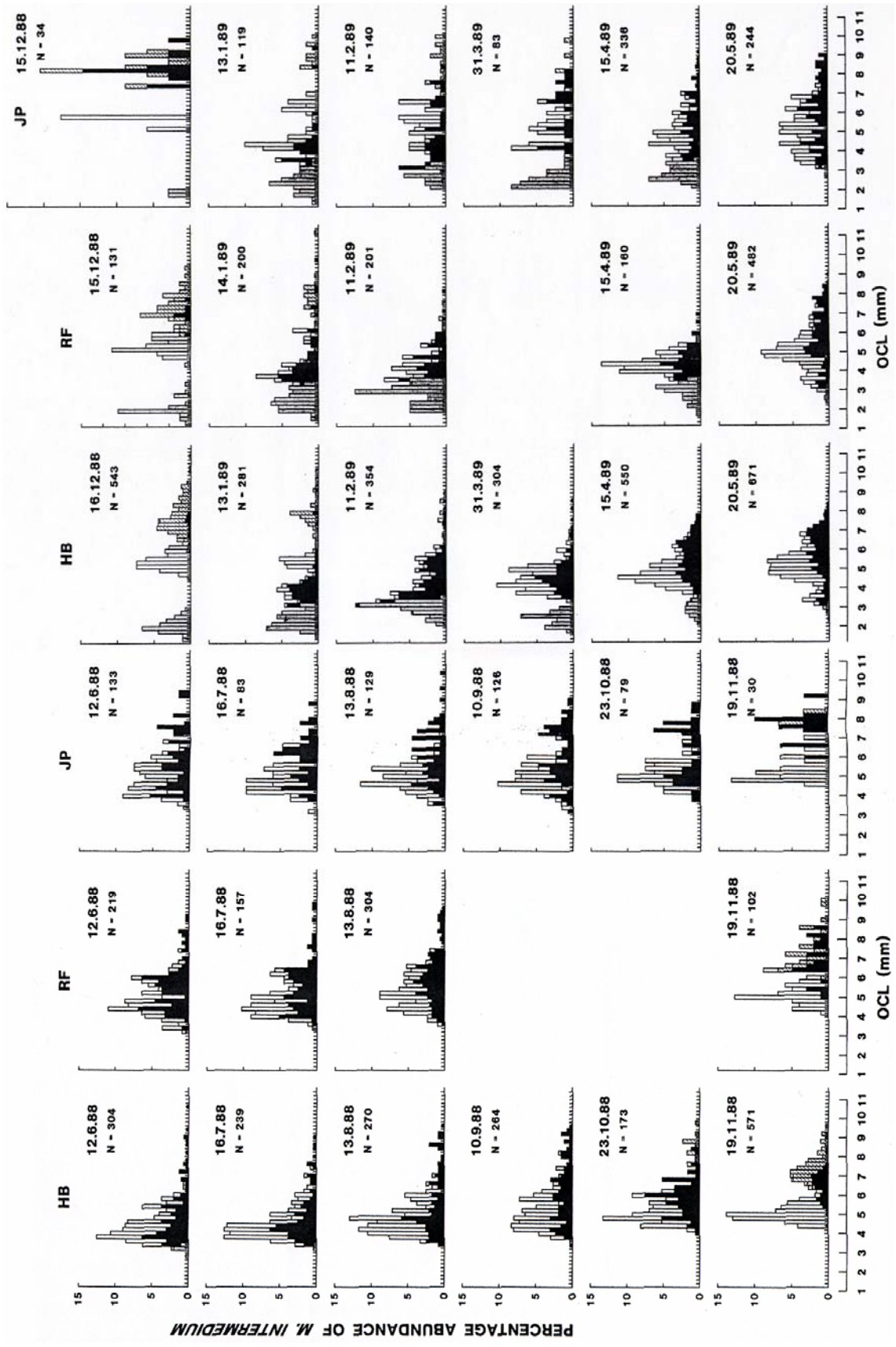
The population structure of *M. intermedium* was similar over the quantitative sampling period at HB, RF and JP (Fig. 4.1). The first juvenile recruits were collected on 15 December 1988. A second, older cohort, composed of sub-adults, was collected at each site on 13-14 January 1989, possibly having migrated from adjacent coastal waters. A third cohort was identifiable (most clearly at HB) on 31 March 1989.

On 12 June 1988, the difference in size between the sexes was not apparent in the dominant cohort, which probably was composed of the late recruits of that year. Some larger females (>6 mm OCL) —probably earlier recruits of 1988—also occurred on this occasion, and persisted at least until 23 October 1988. The late 1988 recruits differentiated into a clear bimodal size distribution of smaller males and larger females by 23 October 1988. This bimodality continued until 11 February 1989, after which very few of the 1988 recruits remained. The early 1989 recruits had begun to differentiate into a sex-based bimodal distribution by 20 May 1989. (This early cohort appeared to be dominant in 1989, but the later cohort appeared dominant in 1988.)

The qualitative samples of *M. intermedium* at HB in 1983 and 1984 were generally too small for a clear separation of cohorts from the size-frequency distributions (Fig. 4.2). However, the distributions exhibit trends that are consistent with those observed in Fig. 4.1.

→

Fig. 4.1. *Macrobrachium intermedium*. Seasonal changes in size frequency distributions in populations at HB, RF and JP over the quantitative sampling period, 1988-1989. Stippled bars, juveniles; open bars, males; black bars, non-ovigerous females; hatched bars, ovigerous females


HB
RF
JP
HB
RF
JP
12.6.88 N - 304
12.6.88 N - 219
12.6.88 N - 133
16.12.88 N - 543
15.12.88 N - 131
15.12.88 N - 34
16.7.88 N - 239
16.7.88 N - 157
16.7.88 N - 83
13.1.89 N - 281
14.1.89 N - 200
13.1.89 N - 119
13.8.88 N - 270
13.8.88 N - 304
13.8.88 N - 129
11.2.89 N - 354
11.2.89 N - 201
11.2.89 N - 140
10.9.88 N - 264
10.9.88 N - 126
31.3.89 N - 304
31.3.89 N - 83
23.10.88 N - 173
23.10.88 N - 79
15.4.89 N - 550
15.4.89 N - 160
15.4.89 N - 336
19.11.88 N - 571
19.11.88 N - 102
19.11.88 N - 30
20.5.89 N - 671
20.5.89 N - 482
20.5.89 N - 244
PERCENTAGE ABUNDANCE OF M. INTERMEDIUM
OCL (mm)
OCL (mm)

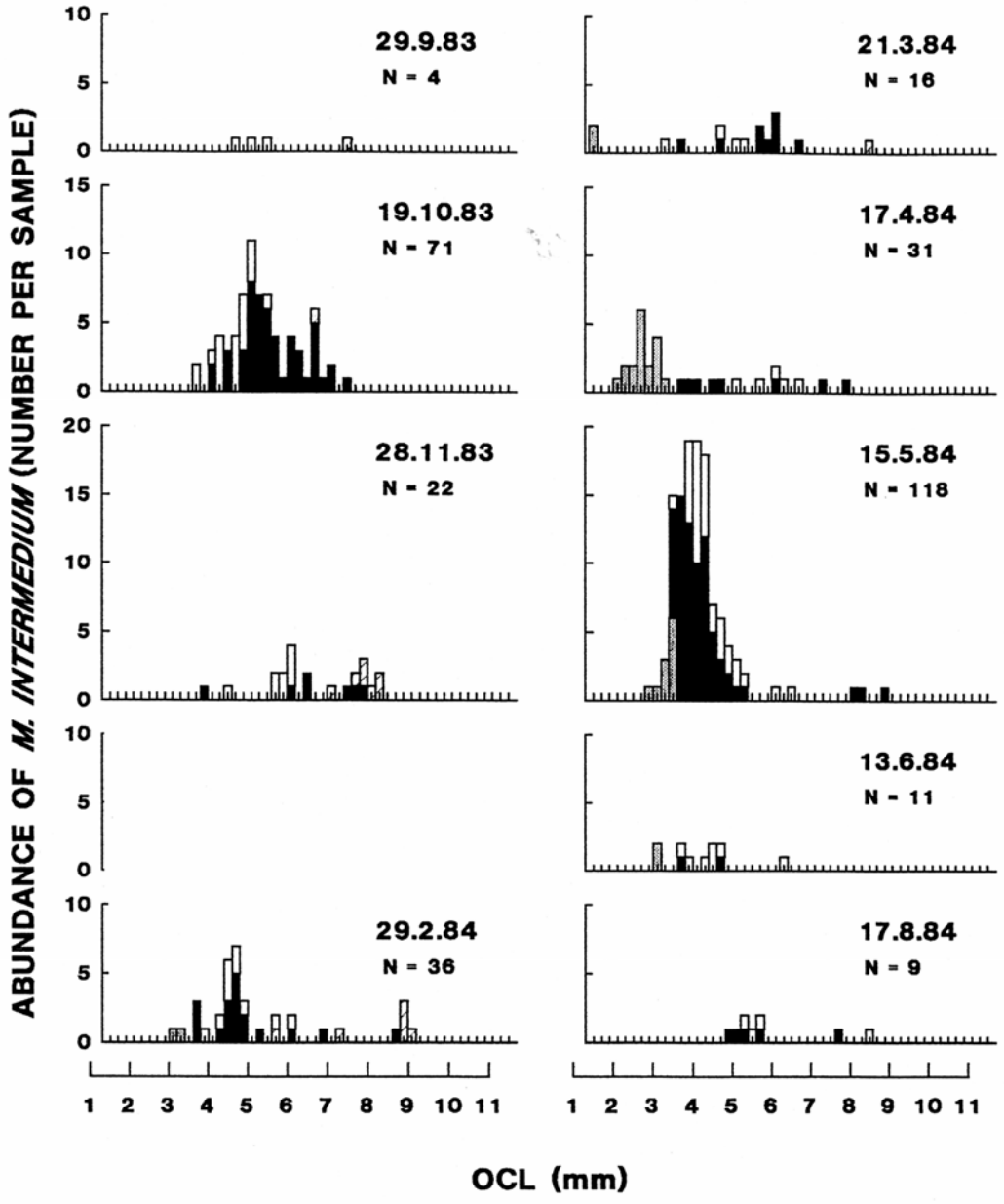


Fig. 4.2. *Macrobrachium intermedium*. Seasonal changes in size frequency distributions in populations at HB over the qualitative sampling period, 1983-1984. Shading scheme as in Fig. 4.1

P. australiensis

The largest female *P. australiensis* collected in the Hopkins estuary was 9.8 mm OCL The largest male collected in the Hopkins estuary was 7.2 mm OCL. The sex of sub-adults was identifiable in individuals greater than 3.4 mm OCL, although some males had begun to develop a sternal process while as small as 3.2 mm OCL.

The trends in population structure of *P. australiensis* over the 1988-1989 sampling period were similar at JP and at TS (Fig. 4.3). Although bimodal, the distribution at TS on 15 April 1989 exhibited indistinct cohorts, suggesting an extended period of recruitment from November to April. The recruitment at JP was concentrated much more markedly around November and December (Figs. 2.11, 4.3), although a less numerous second cohort of recruits was apparent in April and May (see section 4.3.5).

Females grew larger than males with small numbers of large females (>6.5 mm OCL) being collected at TS on all occasions. Many large females were collected at JP on 10 September 1988. This cohort had not been present at this site before September, but was present in large numbers at both JP and TS on 23 October 1988 and 19 November 1988. In 1983, large ovigerous females were collected from as far downstream as HB. Evidently these large females migrated from upstream reaches into the estuary. In both sampling periods, the cohort of females, common in October and November, became less common on following sampling occasions, even allowing for the dominance of the new recruit cohort.

At TS, a dominant mode of male size between 4.6 and 5.4 mm OCL persisted throughout the year, although a cohort can be followed from just post-juvenile size (≈4 mm OCL) on 16 July 1988 to a mode of ≈5 mm OCL on 23 October 1988. At JP, there was not a persistently dominant male size-class, with a larger modal size class of 5.2-5.8 mm OCL present on 10 September and 23 October 1988.

Fig. 4.4 shows size frequency histograms of *P. australiensis* from qualitative samples taken at JP during 1983 and 1984. Seasonal trends in this sampling period were similar to those in 1988 and 1989. Particularly noteworthy is the appearance of the large size classes of males and females in September of 1983, 1984 and 1988. Some differences, however are apparent:

- In 1989, a few large males and females persisted at JP until 13 January 1989. Despite a larger sample size, none were collected on 24 January 1984.
- A cohort of females (4.5-6.5 mm OCL) and males (4.0-5.5 mm OCL) occurred from 12 June to 13 August 1988 and 15 April to 20 May 1989, which was absent during the same months in 1984. This cohort may have corresponded to early recruits of the previous season. In 1984, the size frequency distributions were dominated by late recruits.

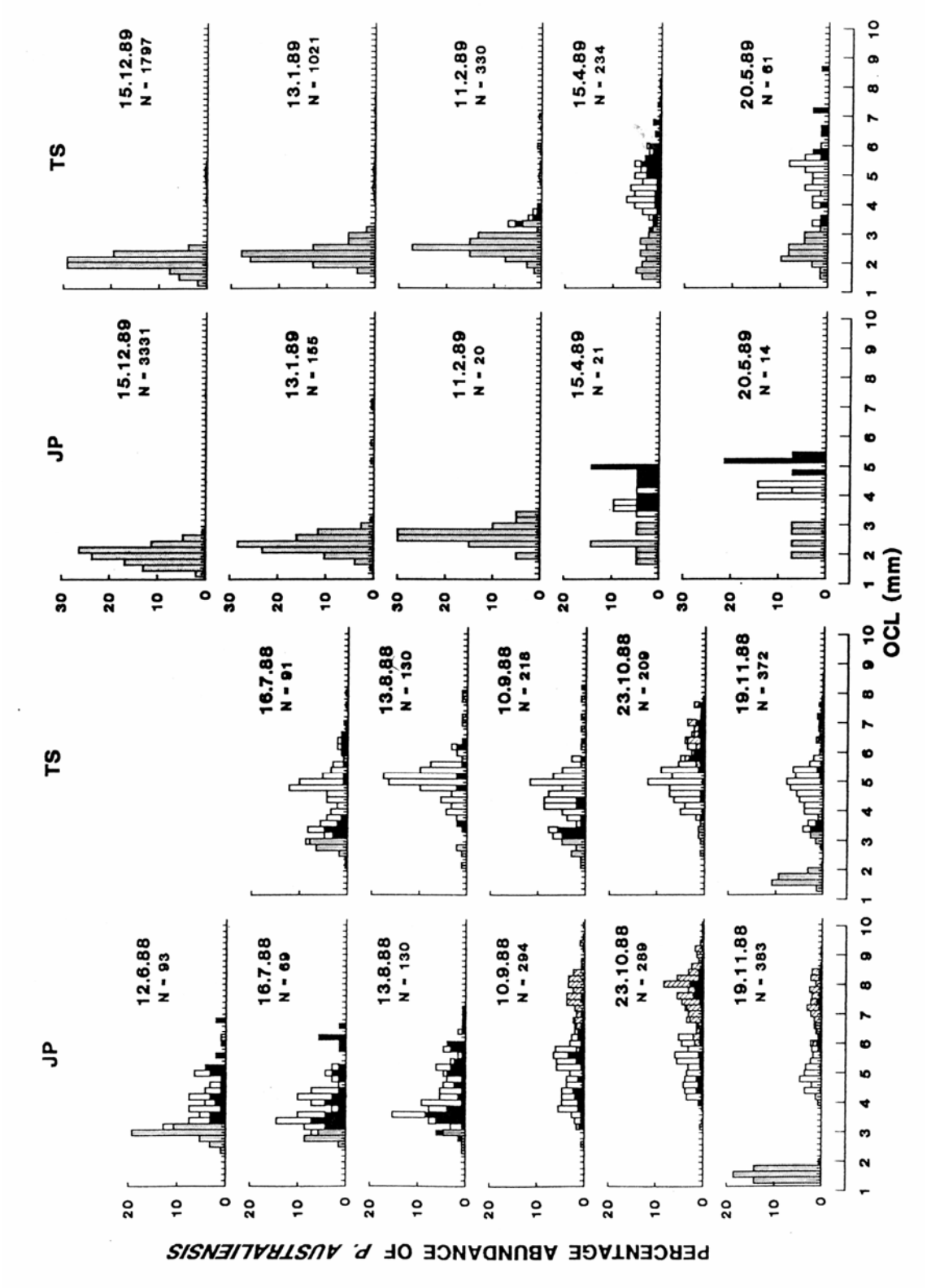


Fig. 4.3. *Paratya australiensis*. Seasonal changes in size frequency distributions in populations at JP and TS over the quantitative sampling period, 1988-1989. Stippled bars, juveniles; black bars, non-ovigerous females; hatched bars, ovigerous females; open bars, males

- In 1984, a cohort of large juveniles and small sub-adults (2.0-3.4 mm OCL) persisted until 19 October 1983, and 28 September 1984, but was not well represented at JP in September and October 1988.

P. serenus

The largest *P. serenus* collected was a female of 8.8 mm OCL. It is not clear from the Hopkins River samples if females grew to a larger size than males because very few males were collected in 1988 and 1989 (Fig. 4.5), and trends were not consistent in 1983-1984—mean male size was greater than female size on 17 April 1984, but was smaller in the following sample (Fig. 4.6). No ovigerous females were collected in the estuary.

Juveniles first occurred in November in both years, and large numbers of juveniles were collected on 16 December 1988, and 20 January 1984 (Figs. 4.5, 4.6). In both years, the smallest juvenile collected in November was larger than the smallest juveniles collected in subsequent months, which suggests that these juveniles did not recruit to the estuary directly from a larval planktonic phase. It seems likely that juveniles migrated into the lower part of the estuary from adjacent coastal waters from November to January. Older cohorts, mostly females, also migrated into the estuary in February and subsequent months in 1984 (Fig. 4.5), and a similar cohort of predominantly female adults migrated into the estuary just before the closing of the mouth at the end of 1988 (Fig. 4.6). In no case was *P. serenus* found to migrate further upstream than HB. Because the estuary was closed in January and February 1989 (Fig. 2.8), it is likely that the decline in numbers of *P. serenus* between January and February 1989 was due entirely to mortality. Because no ovigerous females were present in the estuary, and because *P. serenus* was only found at one site during the study, other aspects of the population dynamics of this species are not pursued.

* * *

The size distributions of all three species point to post-larval migration being an important factor determining their distributions within the estuary. Both adult and juvenile *P. serenus* migrated into the lower part of the estuary, but not further upstream, in summer and autumn. Adult *P. australiensis* migrated into the estuary (as far downstream as RF in 1988, and as far as HB in 1984) in September or October. A cohort of juvenile *M. intermedium* also apparently migrated into the estuary from adjacent coastal waters in summer (see Section 4.3.5). While *P. serenus* appeared not to recruit directly from planktonic larval stages to the estuarine seagrass meadows, both *P. australiensis* and *M. intermedium* did—in large numbers (see Chapter 6). A single, numerous cohort of *P. australiensis* recruited to JP in November and December, with a lower level of recruitment continuing in subsequent months.

M. intermedium showed three distinct, numerous cohorts that persisted at each site throughout the year, two of which were apparently composed of recruits direct from larvae in the estuary.

4.3.3. REPRODUCTIVE PATTERNS

M. intermedium

The smallest ovigerous *M. intermedium* collected was 5.8 mm OCL, which was used as the minimum size for mature females. At HB, females began to carry eggs in October 1988 (and September 1983), reaching a peak of reproductive activity with 92% of mature females carrying eggs on 15 December 1988 (Fig 4.7). The last ovigerous female collected in the quantitative sampling period was at HB on 11 February 1989 (and 21 March 1984). Fig. 4.8 shows that most smaller mature females (<7 mm OCL) did not become ovigerous until December, while the majority of ovigerous females in October and November at HB were larger (>7 mm OCL).

Ovigerous females were first collected at JP on 19 November 1988, a month later than at HB. Very few *M. intermedium* were collected at JP in 1983-1984, and therefore reproductive trends are not clear for this period. Most females at JP did not become ovigerous until 13 January 1989, when 83% of mature females were ovigerous. Ovigerous females were collected as late as 31 March 1989 at JP (Figs. 4.7 and 4.8).

The pattern of reproductive activity at RF more closely resembled that at HB, although abundances and proportions of females that were ovigerous were consistently lower (Fig. 4.7).

P. australiensis

The smallest ovigerous female collected was 5.3 mm OCL, but as ovigerous females as small as 5.0 mm OCL were collected at upstream locations (see Chapter 7), the latter was used as minimum size for mature females. Ovigerous females were present at TS from July 1988 until February 1989 (Fig. 4.7), despite low numbers of mature females collected at this site on most occasions (Fig 4.8: no sample taken in March 1989).

At JP, ovigerous females were not collected until 10 September 1988. Mature females were collected at this site in the preceding months, but the September sample marked the arrival of a cohort of larger females (>7 mm OCL), most of which were ovigerous (Fig. 4.8). Large numbers of ovigerous females were collected at JP from September to November 1988, with

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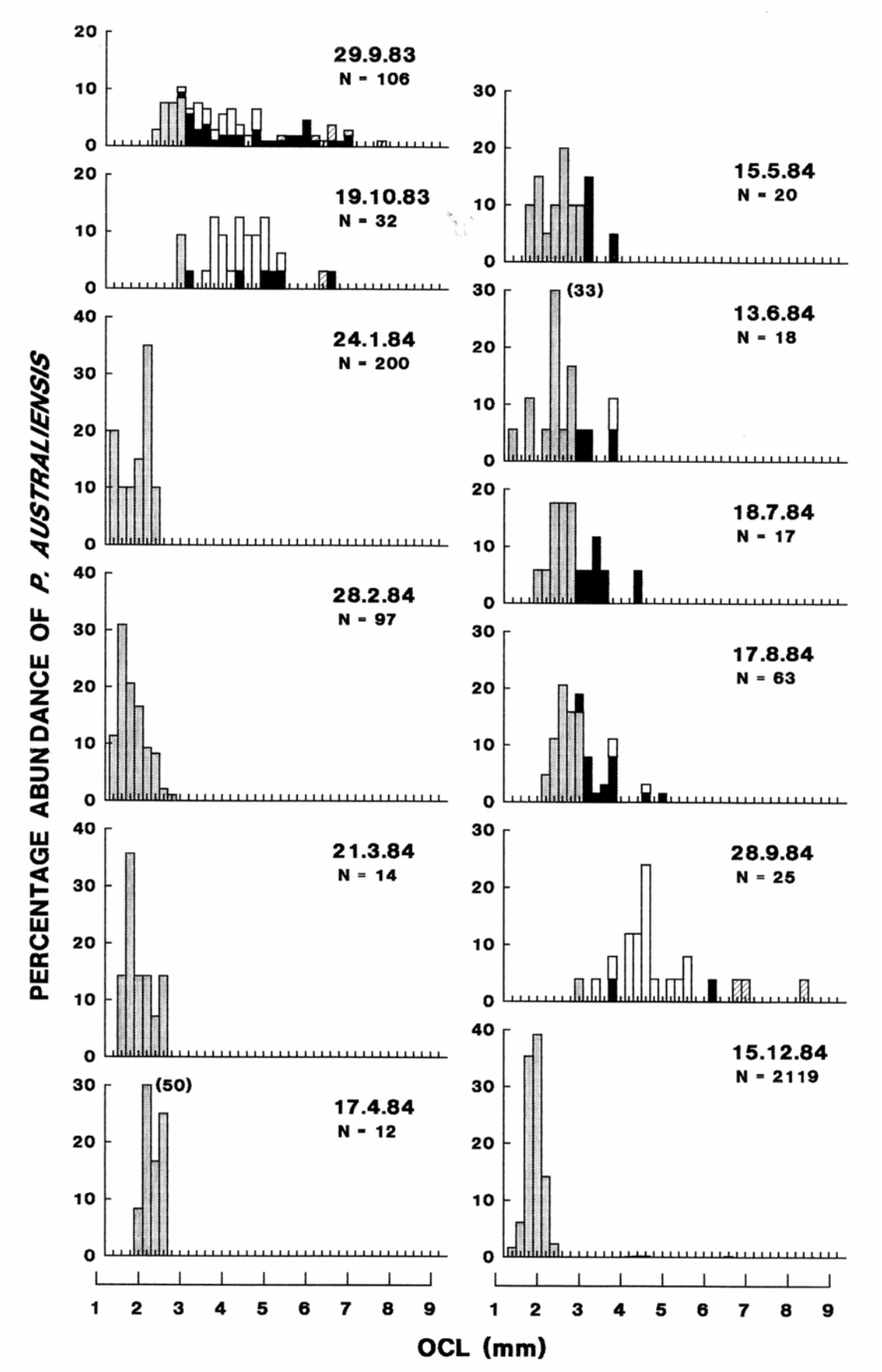
Fig. 4.4. *Paratya australiensis*. Seasonal changes in size frequency distributions in populations at JP over the quantitative sampling period, 1983-1984. Shading scheme as in Fig. 4.3


PERCENTAGE ABUNDANCE OF P. AUSTRALIENSIS
29.9.83
N = 106
19.10.83
N = 32
24.1.84
N = 200
28.2.84
N = 97
21.3.84
N = 14
17.4.84
N = 12
(50)
15.5.84
N = 20
13.6.84
N = 18
(33)
18.7.84
N = 17
17.8.84
N = 63
28.9.84
N = 25
15.12.84
N = 2119
OCL (mm)

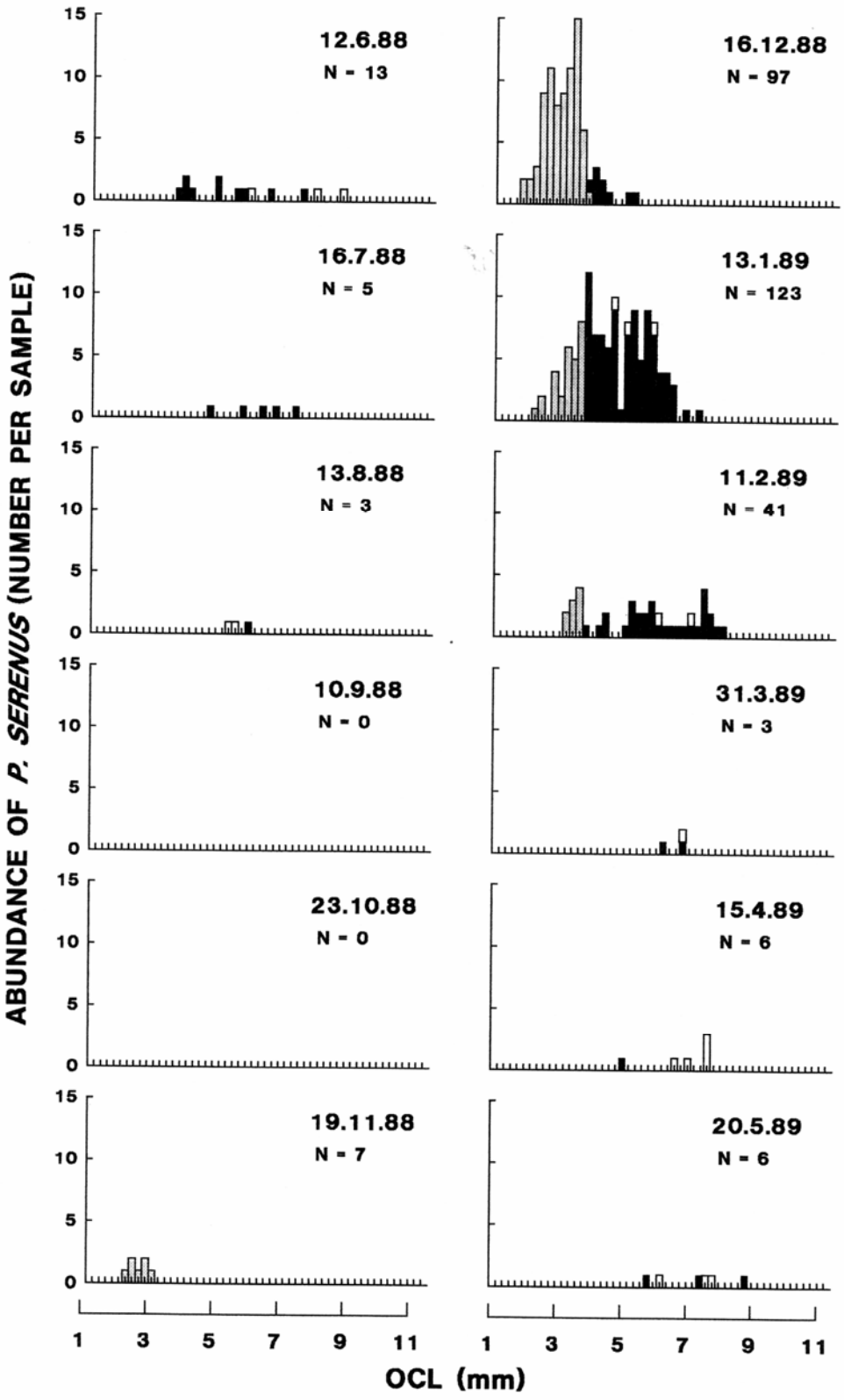


Fig. 4.5. *Palaemon serenus.* Seasonal changes in size frequency distributions in populations at HB over the quantitative sampling period, 1988-1989. Shading scheme as in Fig. 4.1

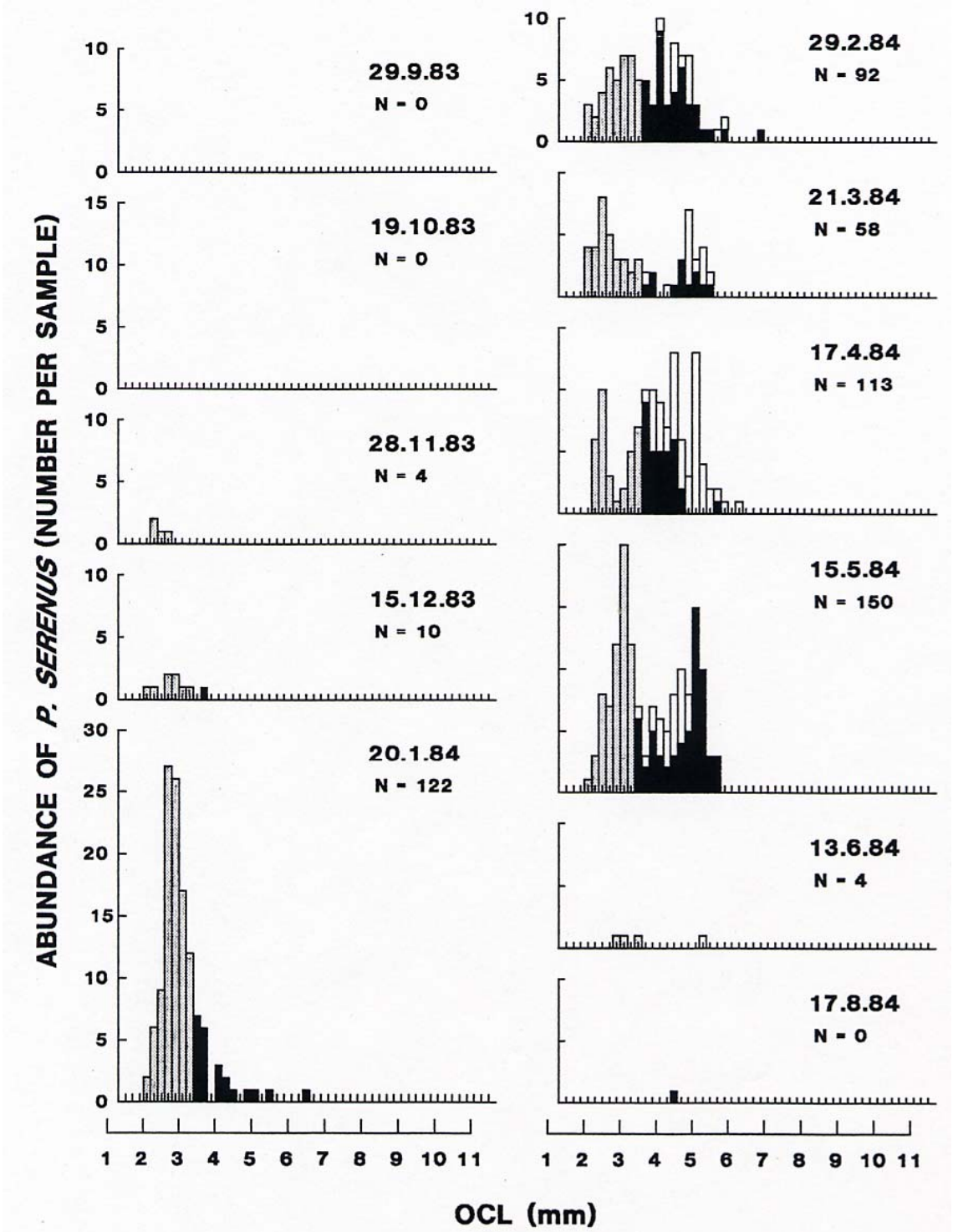
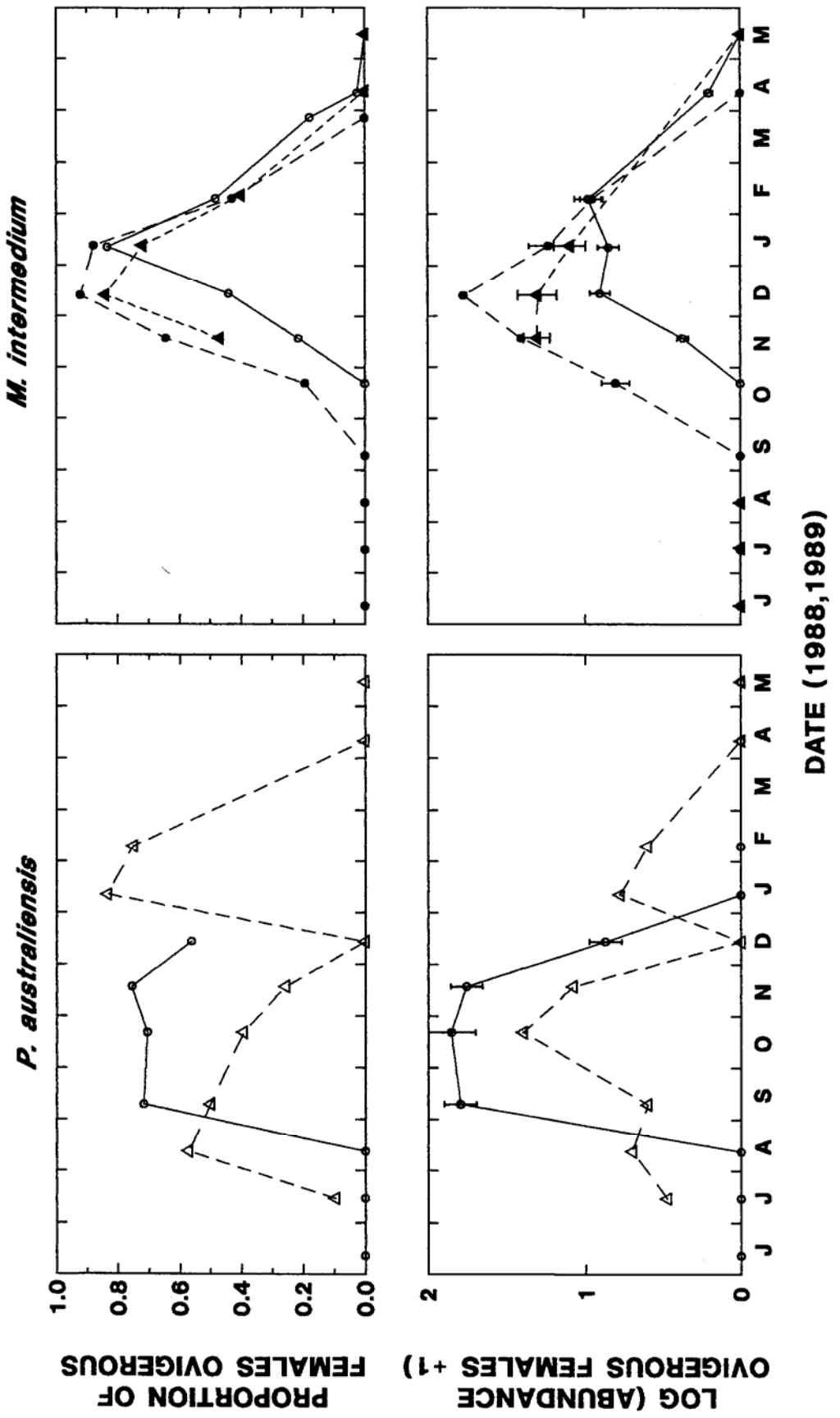


Fig. 4.6. *Palaemon serenus.* Seasonal changes in size frequency distributions in populations at HB over the qualitative sampling period, 1983-1984. Shading scheme as in Fig. 4.1


M. intermedium
P. australiensis
PROPORTION OF FEMALES OVIGEROUS
LOG (ABUNDANCE OVIGEROUS FEMALES +1)
DATE (1988,1989)
J J A S O N D J F M A M
1.0
0.8
0.6
0.4
0.2
0.0
2
1
0

less occurring by December. No mature females were collected from JP after 15 December 1988.

* * *

Ovigerous *M. intermedium* were collected in the estuary from October to March 1989, but at JP, the more upstream site where the two species were sympatric, onset and last occurrence of reproductive activity were later. Reproductive activity of *P. australiensis* in the estuary was restricted to September to December, but was more extended at TS above estuarine influence. Thus the period in which the two species were reproductively active at the same location was limited to November, when abundance of ovigerous *M. intermedium* was low, and December, when abundance of ovigerous *P. australiensis* was low (Fig. 4.7).

4.3.4. SEX RATIOS

M. intermedium

Sex ratios oscillated around 1:1 males:females over 1988 and 1989 at HB, RF and JP (Fig. 4.9) with significant deviations from 1:1 on six occasions at HB, five occasions at RF and once at JP (Table 4.1). Pooled, total and heterogeneity G-values were all significant at HB and RF. The pooled sex ratio at HB was 2090 males: 1891 females, and at RF was 805 males: 920 females. None of these summary G-values were significant at JP.

Initially, a three-way table of sex, all eleven sampling occasions, and only sites JP and HB was analysed. A log-linear model for a three-way interaction was fit after four iterations, with the Williams corrected G-value for goodness of fit (Sokal and Rohlf, 1981) significant ($G=54.7$, $P<0.001$). The only significant Freeman-Tukey deviates were for 16 July 1988 and the samples from December to February. Samples were taken at RF on all these occasions. Therefore a second three-way table was analysed using nine sampling occasions and all three sites (Table 4.2). The most striking deviations from expected occurred in the December, January and February samples, which coincided with a series of drops in sex ratio (Fig. 4.9):

- In December at JP, the sample of *M. intermedium* was dominated by large females (>7 mm OCL) with very few smaller individuals. In January, at this site, a cohort of recruits and another cohort of sub-adults, which had not been present previously, were present, thus balancing the sex ratio (Fig. 4.1).

←

Fig. 4.7. Proportion of females that were ovigerous and the absolute abundance of ovigerous females (in m^{-2}±SE for quantitative samples at HB, RF and JP, and number per standard effort at TS) over the quantitative sampling period, for *Paratya australiensis* and *Macrobrachium intermedium*.
Open triangles, TS; open circles JP; closed triangles, RF; closed circles, HB.

Table 4.1. *Macrobrachium intermedium*. Tests for deviation from a 1:1 sex ratio at HB, RF and JP, with tests for heterogeneity between sampling occasions. M, F, number of males and females respectively in each sample; G, G-statistic of Sokal and Rohlf (1981).

Date	HB				RF				JP			
	M	F	df	G	M	F	df	G	M	F	df	G
12 June 1988	158	136	1	1.648	94	124	1	4.142	64	68	1	0.121
16 July 1988	132	105	1	3.083	72	84	1	0.924	43	40	1	0.108
13 August 1988	164	107	1	12.079 *	146	158	1	0.474	63	67	1	0.123
10 September 1988	143	120	1	2.014					57	70	1	1.333
23 October 1988	74	99	1	3.625					39	40	1	0.013
19 November 1988	330	240	1	14.270 *	50	52	1	0.039	16	14	1	0.133
15 December 1988	205	203	1	0.010	53	50	1	0.087	8	24	1	8.372 *
14 January 1989	67	112	1	11.435 *	32	90	1	28.720	45	35	1	1.253
11 February 1989	54	157	1	52.495 *	38	58	1	4.197	49	64	1	1.997
31 March 1989	130	93	1	6.167 *					26	30	1	0.286
15 April 1989	255	237	1	0.659	66	93	1	4.607	123	110	1	0.726
20 May 1989	378	282	1	14.013 *	254	211	1	3.982	113	110	1	0.040
pooled			1	9.952 *			1	7.672			1	0.513
heterogeneity			11	111.54 *			8	39.500			11	13.993
total			12	121.50 *			9	47.172			12	14.506

- In January and February at RF (and HB), the same cohorts of juveniles and sub-adults occurred in both these sites the latter cohort was dominated by females. By March and April, the juvenile cohort had grown to sub-adult level, and its sex ratio was nearer 1:1 than the older, less numerous female-dominated cohort.

P. australiensis

The patterns of sex ratio over 1988 and 1989 at JP and TS are strikingly different in value, but similar in trend (Fig. 4.9). At JP, sex ratio was not significantly different from 1:1 except on 23 October 1988 and 15 December 1988 when females outnumbered males (Table 4.3). Pooled and total G-values were significant with more females overall, but heterogeneity was not significant in this case, showing deviations from 1:1 were generally of the same magnitude and in the same direction. At TS there were significantly more males than females on all occasions except 11 February 1989 and 15 April 1989 (Table 4.3).

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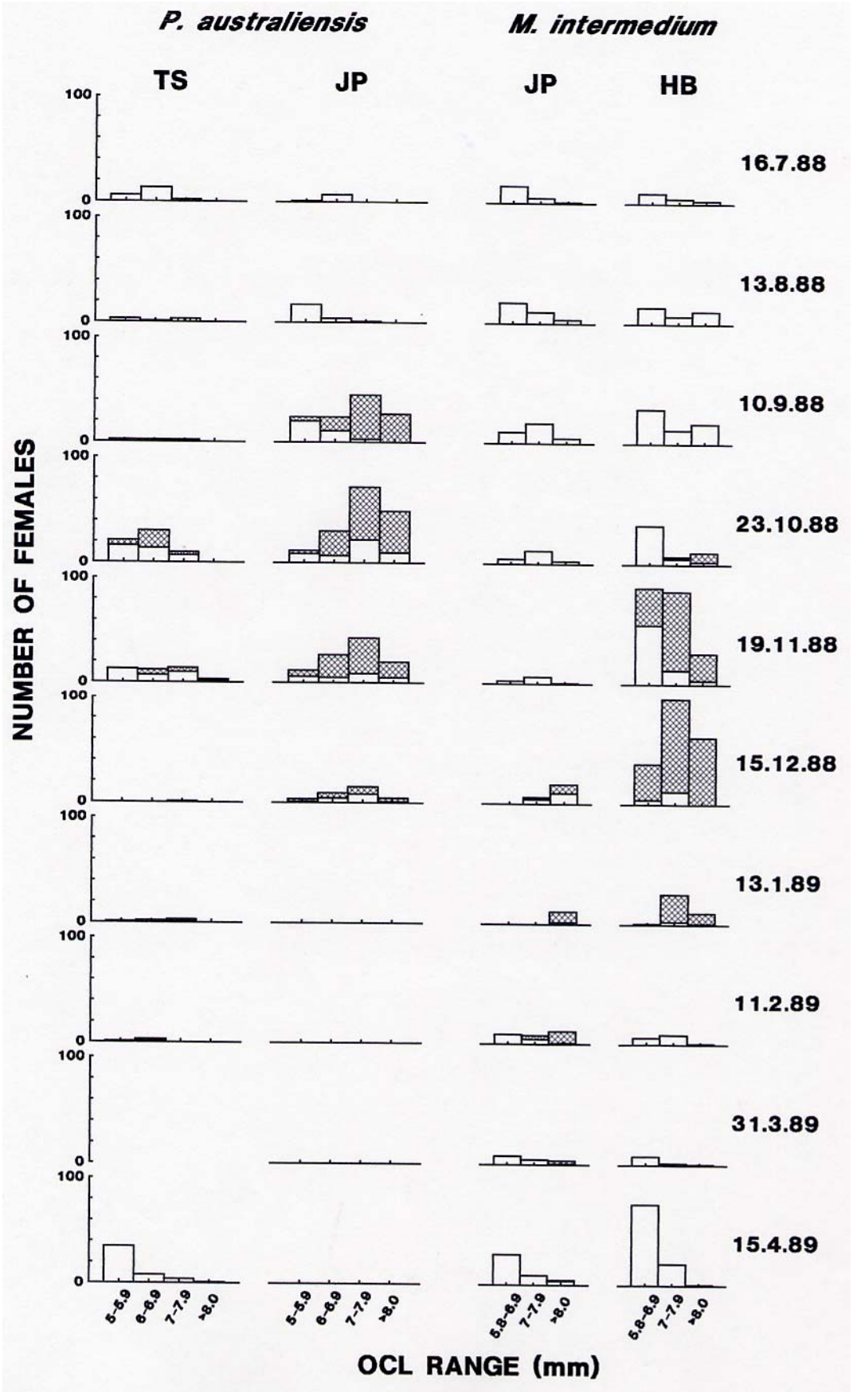
Fig. 4.8. Trends in abundance (total number collected in each sample) of mature females and their reproductive status:

- for *Paratya australiensis* at TS and JP; size classes are 5.0-5.9, 6.0-6.9, 7.0-7.9 and >8.0 mm OCL

-for *Macrobrachium intermedium* at JP and HB; size classes are 5.8-6.9, 7.0-7.9 and >8.0 OCL

Stippled, ovigerous females; open, non-ovigerous females.


P. australiensis
M. intermedium
TS
JP
JP
HB
16.7.88
13.8.88
10.9.88
23.10.88
19.11.88
15.12.88
13.1.89
11.2.89
31.3.89
15.4.89
NUMBER OF FEMALES
100
0
5-5.9
6-6.9
7-7.9
>8.0
5.5-6.9
7-7.9
>8.0
OCL RANGE (mm)

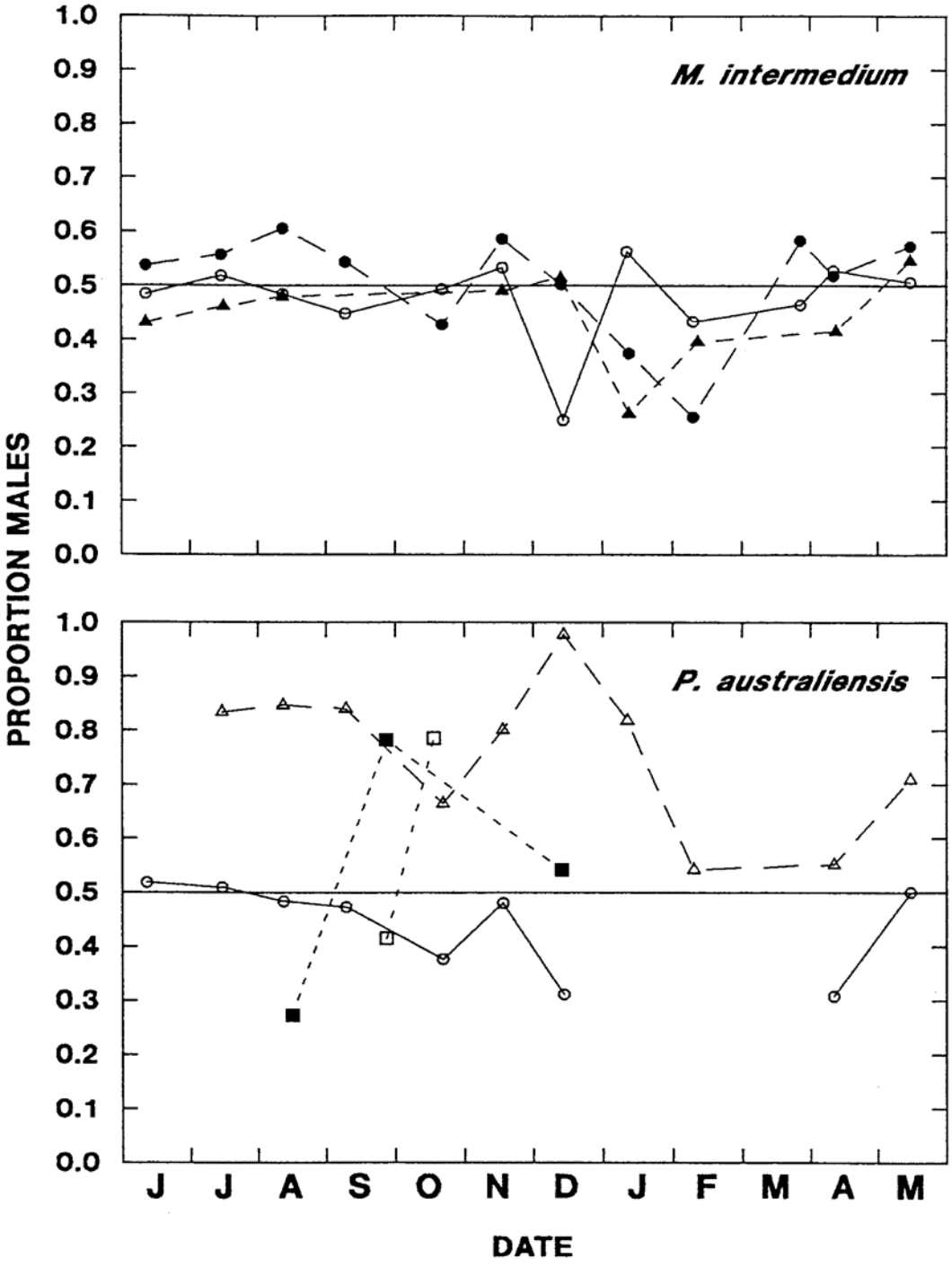


Fig 4.9. Sex ratios of *Macrobrachium intermedium* and *Paratya australiensis* expressed as the proportion of shrimps >3.5 mm OCL that were male. Closed circles, HB; closed triangles, RF; open circles, JP (1988, 1989 sampling period); open squares, JP in 1983; closed squares, JP in 1984; open triangles, TS

Table 4.2. *Macrobrachium intermedium*. Tests for independence of sex ratio, site and sampling occasion (three sites, HB, RF, and JP, and nine sampling occasions), after a model testing for a three-way interaction was found to be significant. Approximate criterion for a large Freeman-Tukey deviate was 1.067.

		Observed			Expected			Freeman-Tukey deviates		
Date	Sex	HB	RF	JP	HB	RF	JP	HB	RF	JP
12 June 1988	f	136	124	68	142.7	119.3	66.1	-0.543	0.451	0.266
	m	158	94	64	151.3	98.7	65.9	0.556	-0.456	-0.208
16 July 1988	f	105	84	40	108.6	81.1	39.3	-0.322	0.343	0.152
	m	132	72	43	128.4	74.9	43.7	0.336	-0.305	-0.070
13 August 1988	f	107	158	67	119.7	153.0	59.4	-1.164*	0.422	0.990
	m	164	146	63	151.3	151.0	70.6	1.027*	-0.390	-0.902
19 November 1988	f	233	52	14	236.8	49.2	13.1	-0.230	0.434	0.317
	m	330	50	16	326.2	52.8	16.9	0.222	-0.361	-0.168
15-16 Dec 1988	f	203	50	24	203.0	57.6	16.4	0.018	-0.999	1.736*
	m	205	53	8	205.0	45.4	15.6	0.017	1.116*	-2.132*
13-14 January 1989	f	112	90	35	107.5	80.3	49.2	0.454	1.076*	-2.149*
	m	67	32	45	71.5	41.7	30.8	-0.511	-1.551*	2.347*
11 February 1989	f	157	58	64	136.8	67.4	74.8	1.689*	-1.157*	-1.264*
	m	54	38	49	74.2	28.6	38.2	-2.496*	1.673*	1.669*
15 April 1989	f	237	93	110	237.4	86.6	116.0	-0.012	0.704	-0.540
	m	255	66	123	254.6	72.4	117.0	0.043	-0.741	0.569
20 May 1989	f	282	211	110	279.6	225.6	97.8	0.156	-0.968	1.218*
	m	378	254	113	380.4	239.4	125.2	-0.109	0.942	-1.092*

The log-linear model for three-way interaction between sex, the two sites and eight sampling occasions was fit after seven iterations, and the G-test for goodness of fit was significant (G=23.4, P=0.001). The trends of sex ratio were remarkably similar at the two sites in most months (Fig. 4.9), with only the 15 December 1988 producing highly significant Freeman-Tukey deviates (Table 4.4). In this month, sex ratio at JP dropped while it rose at TS: the total number of adult shrimps dropped markedly at both sites, but the drop in number of large females (>6.5 mm OCL) was more pronounced at TS (25 on 19 November 1988 to 1 on 15 December 1988) than at JP (62±2 to 8±1 m^{-2}).

The drop in sex ratio from September to October (Fig 4.7) was due to the arrival at both sites of many large females (Fig. 4.3). Numbers of this cohort declined at both sites from October to November and sex ratio correspondingly rose at both sites. The parallel rise in sex ratio at both sites from April to May 1989 (Fig. 4.9) is difficult to assess due to small numbers at JP. At TS there was a decline in the dominant female cohort relative to males between these two months (Fig. 4.3).

Table 4.3. *Paratya australiensis*. Tests for deviation from a 1:1 sex ratio at JP and TS, with tests for heterogeneity between sampling occasions. Conventions as in Table 4.1

	JP					TS				
Date	M	F	df	G		M	F	df	G	
12 June 1988	29	27	1	0.071						
16 July 1988	29	28	1	0.017		126	25	1	73.799	*
13 August 1988	58	62	1	0.133		72	13	1	45.113	*
10 September 1988	140	156	1	0.865		63	12	1	38.022	*
23 October 1988	109	180	1	17.622	*	137	69	1	22.873	*
19 November 1988	97	105	1	0.316		194	48	1	94.402	*
16 December 1988	14	31	1	6.584	*	45	1	1	54.134	*
13 January 1989	0	0				27	6	1	14.455	*
11 February 1989	0	0				13	11	1	0.167	
31 March 1989	0	0								
15 April 1989	4	9	1	1.973		80	65	1	1.555	
20 May 1989	5	5	1	0		22	9	1	5.624	*
pooled			1	12.823	*			1	272.67	*
heterogeneity			8	14.762				9	77.476	*
total			9	27.585	*			10	350.14	*

Table 4.4. *Paratya australiensis*. Tests for independence of sex ratio, site and sampling occasion (two sites, TS and JP, and eight sampling occasions), after a model testing for a three-way interaction was found to be significant. Approximate criterion for a large Freeman-Tukey deviate was 0.917.

		Expected		Observed		Freeman-Tukey deviates	
DATE	SEX	JP	TS	JP	TS	JP	TS
16 July 1988	f	28	25	27.540	25.459	0.133	-0.042
	m	29	126	29.460	125.543	-0.039	0.063
13 August 1988	f	62	13	59.895	15.108	0.301	-0.491
	m	58	72	60.105	69.892	-0.241	0.279
10 September 1988	f	156	12	153.762	14.247	0.200	-0.545
	m	140	63	142.237	60.754	-0.167	0.316
23 October 1988	f	180	69	189.060	59.937	-0.648	1.157*
	m	109	137	99.942	146.062	0.909*	-0.740
19 November 1988	f	105	48	106.136	46.866	-0.086	0.200
	m	97	194	95.864	195.136	0.141	-0.064
15 December 1988	f	31	1	23.306	8.694	1.518*	-3.567*
	m	14	45	21.693	37.306	-1.754*	1.234*
15 April 1988	f	9	65	10.188	63.803	-0.299	0.180
	m	4	80	2.812	81.192	0.736	-0.105
20 May 1988	f	5	9	6.113	7.886	-0.359	0.458
	m	5	22	3.887	23.114	0.618	-0.181

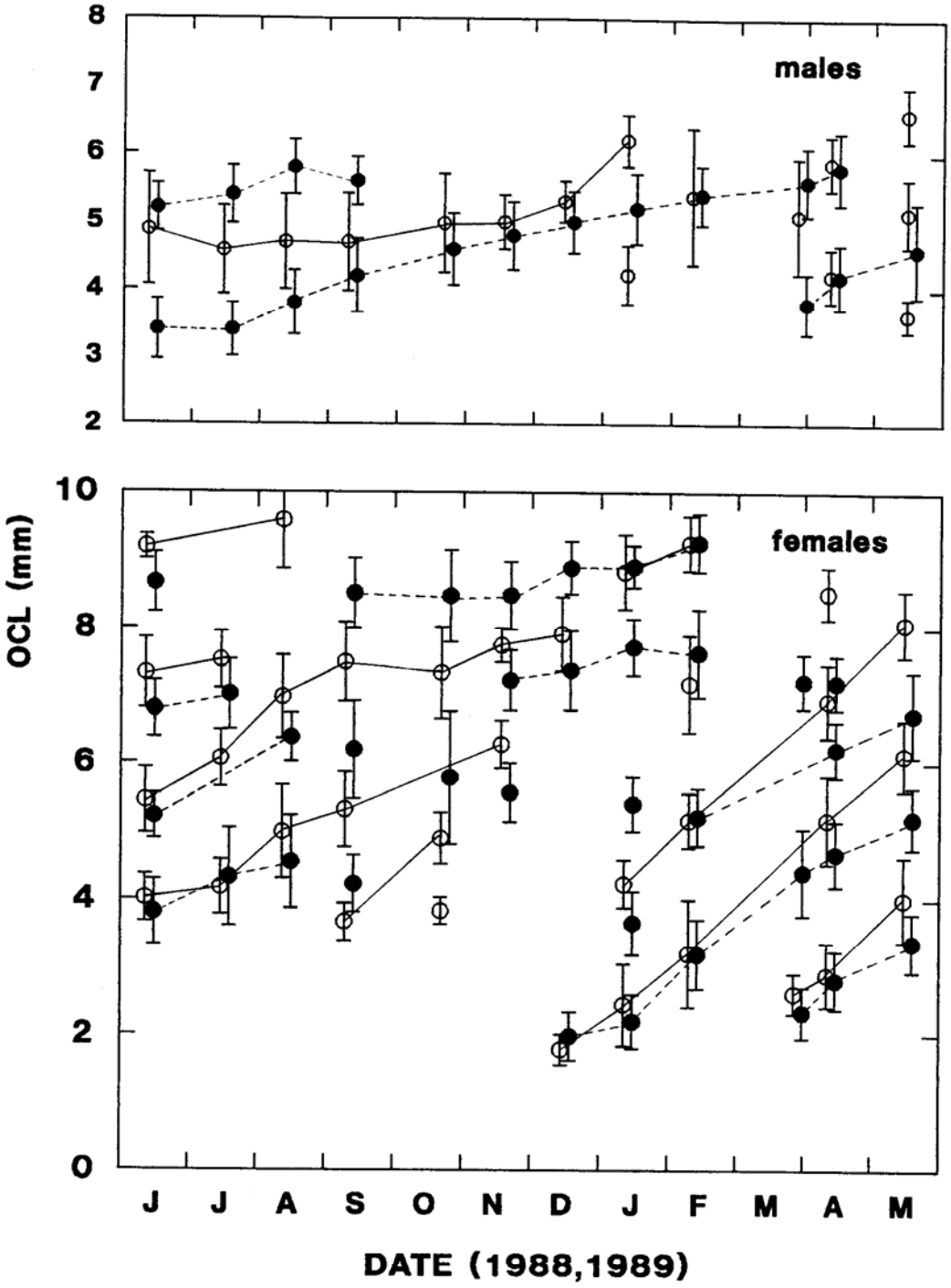


Fig. 4.10. *Macrobrachium intermedium.* Mean (± sd) OCL of male and female cohorts at two sites in the Hopkins River estuary, 1988-1989. Closed circles, HB; open circles, JP

In the qualitative samples of 1983 and 1984 at JP, numbers of post-juvenile shrimps were too low to calculate reliable sex ratios in most samples. However five cases in which N>10 are plotted in Fig. 4.9. Perhaps because of the small sample sizes, fluctuations in sex ratio in these samples were much wider than in the quantitative samples. Large numbers of large females on 29 September 1983 (Fig. 4.4) caused a low sex ratio (22 males: 31 females), although it was not significantly different from 1:1. Fewer large females were collected on 19 October 1983, while numbers of mature males remained the same, thus increasing the sex ratio to 22 males: 6 females (significantly different from 1:1). In September 1984, far fewer large females were collected than in the previous year (Fig. 4.4) resulting in a sex ratio of 18 males: 5 females, which was significantly different from 1:1. Sex ratios on 17 August 1984 and 15 December 1984 did not differ significantly from 1:1.

4.3.5. GROWTH

M. intermedium

Male and female cohorts identified from the quantitative samples at HB and JP over 1988 and 1989 are shown in Fig. 4.10. Two major cohorts of recruits were identified at both sites, one first appearing in November and another in March. A third cohort of sub-adults was first collected at both sites on 14 January 1989. It would seem that this cohort recruited to the estuary as sub-adults, rather than from the plankton as mean size at first occurrence was 3.7±0.5 mm OCL at HB and 4.2±0.4 mm OCL at JP. In June 1988, three female cohorts corresponding to a similar pattern of recruitment in the previous summer, and a larger cohort, probably adults in their second year, were discernible. After June 1988, the larger cohorts were difficult to distinguish at HB, while at JP, the two smaller cohorts could be followed to November and December, when they had reached a mean size of ≈6 and ≈8 mm OCL respectively.

Growth rates for females were about 0.5-0.7 mm OCL per month at both sites, possibly faster at JP, and growth rate decreased as size increased.

A cohort of males was followed at HB over the sampling period, which grew at a rate of ≈0.25 mm OCL per month (Fig. 4.10). A larger cohort, probably adults in their second year, was present in declining numbers from July to September. At JP the male size distribution showed a consistent median size between 4.5 and 5.8 mm OCL over most of the year. In January, April and May 1989, several cohorts were identified but no single cohort was observed to grow over the year.

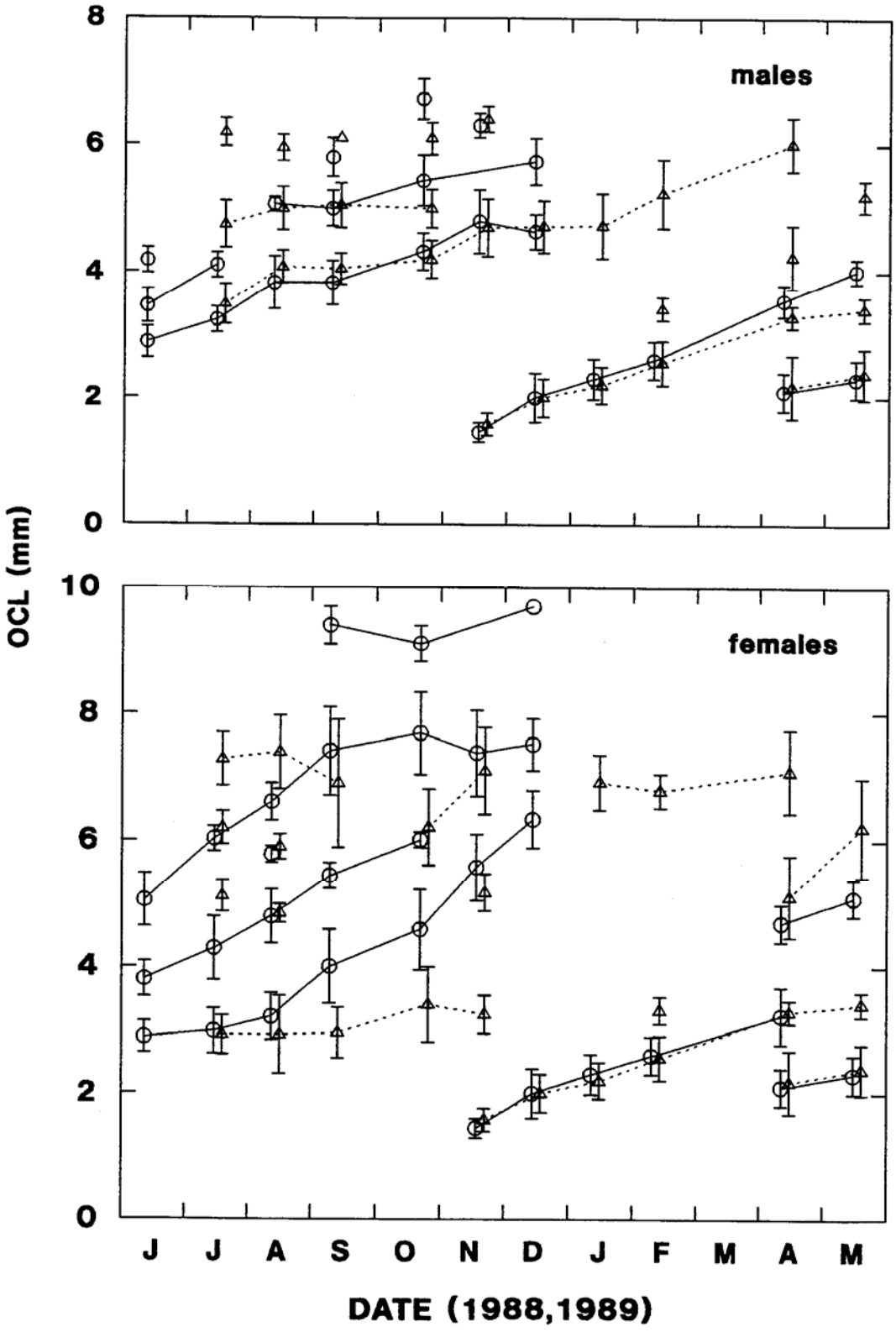


Fig. 4.11. *Paratya australiensis.* Mean (± sd) OCL of male and female cohorts at two sites in the Hopkins River estuary, 1988-1989. Circles, JP; triangles, TS

Table 4.5. *Paratya australiensis.* Mean (±sd) OCL in mm of juvenile cohorts identified at JP and TS during the 1983,1984 and 1988,1989 sampling periods

	1984	1984 (/1985)	1988	1988	1988/ 1989	1988/ 1989	1988/ 1989	1988/ 1989
	JP	JP	JP	TS	JP	TS	JP	TS
Month					First cohort		Second cohort	
November					1.5	1.6		
December		1.95			2.0	2.0		
January	1.8				2.3	2.2		
February	1.8				2.6	2.6		
March	1.1				2.7			
April	2.2				3.3	3.3	2.1	2.2
May	2.5					3.4	2.3	2.4
June	2.4		2.9	2.9				
July	2.7		3.0	2.9				
August	2.7		3.2	3.0				
September	2.6			3.4				
October				3.3				

P. australiensis

Recognition of cohorts was more reliable in *P. australiensis* with close agreement at both JP and TS in many cases (Fig. 4.11). Like *M. intermedium*, two distinct recruit cohorts were identified: one first appearing November 1988 and a second, less numerous cohort in April 1989. Both cohorts were present at both sites with growth rates of 0.3-0.4 mm OCL per month. Although the data from the qualitative samples of 1983-1984 is patchy, comparisons of cohorts show that recruitment timing and growth rates are comparable between years in the Hopkins River estuary (Table 4.5). No early recruit cohort was evident in November 1983, but the recruits of January 1984 were similar in size to the second cohort of recruits of 1989, first collected on 15 April 1989. Thus it would seem that, although not collected at either JP or TS until April, this cohort recruited from the plankton as early as January.

Many juveniles were collected at TS, LG, JP and RF on 19 November 1988, 15 December 1988 and 13-14 January 1989, and a few were collected at HB on these last two dates. Mean (±sd) OCL for the juvenile cohorts from each of these samples is shown in Fig 4.12. A two-way ANOVA was conducted on OCL with three levels of site (LG, JP and RF: HB was excluded due to the small number of juveniles collected there and the resulting heterogeneous variances) and three levels of sampling occasion. Both effects and the interaction term were significant with sampling occasion accounting for most of the variance. As it was of interest whether mean size of juveniles differed between seagrass meadows on a single occasion, nine planned comparisons were made: between nearest neighbouring meadows on each occasion (Table 4.6).

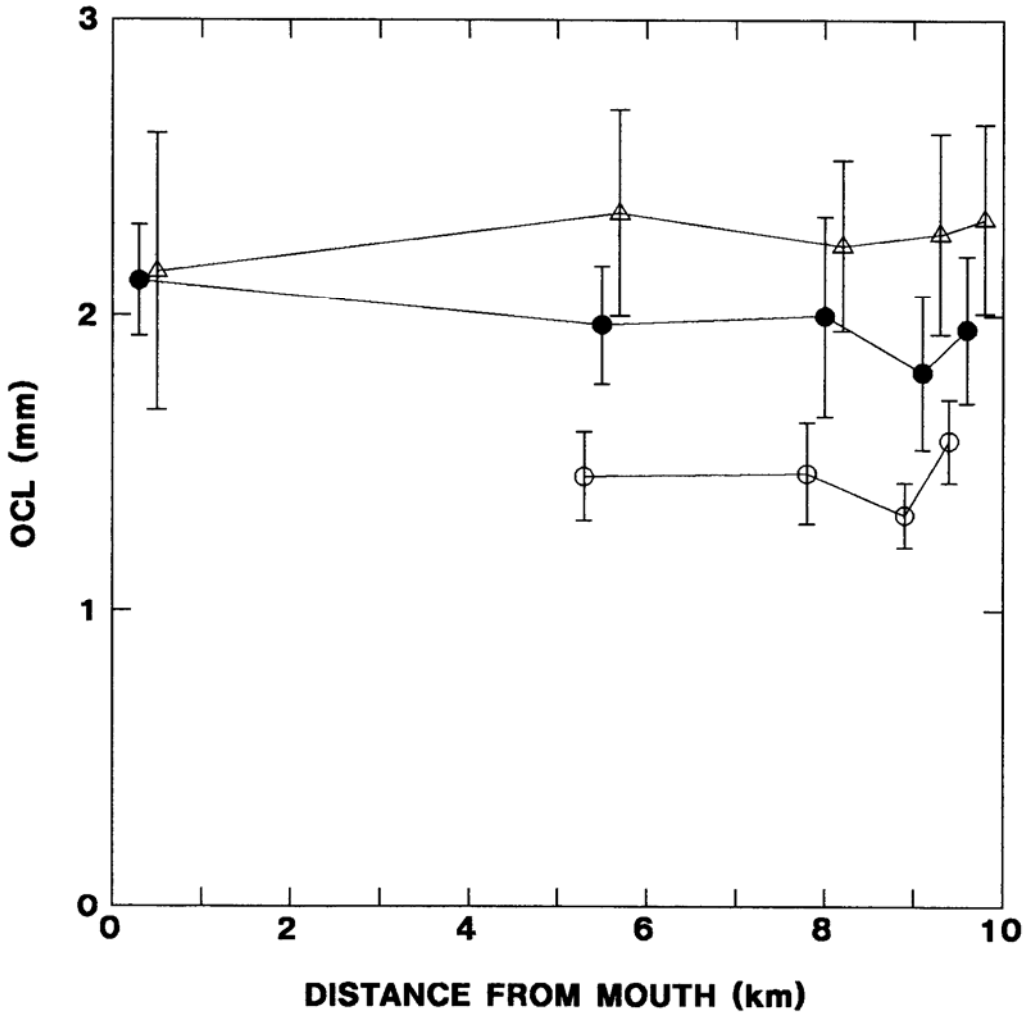


Fig. 4.12. *Paratya australiensis*. Mean (± sd) OCL of juveniles collected at HB, RF, JP, LG, and TS, plotted by distance upstream of the mouth of the estuary, on three sampling occasions. Open circles, 19 November 1988; closed circles, 15-16 December 1988; triangles, 13-14 January 1989

Table 4.6. *Paratya australiensis*. Planned single df comparisons of mean OCL measurements of juveniles at four sites on three sampling occasions

Date	Site	Mean	N	Comparison							
				TS vs LG			LG vs JP			JP vs RF		
				MS	P		MS	P		MS	P	
19 November 1988	TS	1.58	93	138.01	<0.001	*						
19 November 1988	LG	1.33	41				37.94	0.017	*			
19 November 1988	JP	1.47	35							0.32	0.826	
19 November 1988	RF	1.46	61									
16 December 1988	TS	1.96	99	105.11	<0.001	*						
16 December 1988	LG	1.81	106				115.95	<0.001	*			
15 December 1988	JP	2.00	50							2.08	0.576	
15 December 1988	RF	1.98	100									
14 January 1989	TS	2.33	99	6.32	0.331							
14 January 1989	LG	2.28	32				4.43	0.415				
13 January 1989	JP	2.24	151							52.84	0.005	*
14 January 1989	RF	2.26	62									
				error MS = 6.669, 917 df								

Mean size of juveniles was significantly greater at JP than at LG in both December and January, and was greater at RF than at JP in January (Table 4.6). There was thus a tendency for juveniles be larger nearer the mouth of the estuary. However the difference in mean size of juveniles was more striking between the *Ruppia* meadow at LG and the freshwater macrophytes in the rapids at TS, only 400 m upstream, where mean juvenile size was larger in November and December.

Three female cohorts were identified in June 1988 at JP and these cohorts were consistently present at this site until December, after which few adults remained (Figs 4.11, 4.3). These three cohorts probably correspond to three maxima of recruitment during the previous summer. All three cohorts grew an average of 0.4-0.5 mm OCL per month, until an OCL of ≈6.5 mm was reached, after which growth appeared to slow (Fig. 4.11). These three cohorts were not consistently identifiable at TS. Large females (>8 mm OCL) were present in small numbers in September, October and November, representing adults in their second year.

On 12 June 1988 two male cohorts were clearly present. These cohorts could usually be identified at both sites until December, after which they were present only at TS. Male growth rates were 0.30-0.35 mm OCL per month.

4.4. DISCUSSION

Breeding

Reproductive patterns of *M. intermedium* and *P. australiensis* in the Hopkins River estuary were distinct, both from each other and from the reproductive patterns of each species reported from other locations. In the estuary, breeding activity occurred earlier in *P. australiensis* than in *M. intermedium*. At JP, where the species co-occurred, breeding in *P. australiensis* was curtailed compared to locations upstream of the estuary. *M. intermedium* at JP breeding began later and continued breeding longer compared to *M. intermedium* at locations nearer the mouth of the estuary. *P. serenus* did not breed in the estuary.

Gray (1985) discussed the occurrence of latitudinal differences in breeding period and recruitment of *M. intermedium*. He attributed some trends to the more northerly and hence warmer climate of his Sydney study compared to the cooler Victorian and Tasmanian sites of Howard (1981) and Walker (1979). This was probably the case for the all-year-round occurrence of ovigerous females in Gray's study, in contrast to the spring-to-autumn occurrence of ovigerous females in Western Port, Tasmania and the Hopkins River estuary. However, differences in breeding patterns between the Hopkins and Western Port populations of *M. intermedium* (Howard, 1981) must be due to other causes, as the two sites are at approximately the same latitude. Ovigerous *M. intermedium* were collected in the Hopkins from October, but were collected as early as July in Western Port. The later onset of breeding activity in the Hopkins is likely to be due to its estuarine nature, with low salinities prior to October delaying the onset of reproductive activity. Such an interpretation is bolstered by the observation of later onset of breeding upstream at JP. No ovigerous females were found at JP until November (Fig. 4.7), when salinity over the meadows had reached 8-10 (Fig. 2.8). Energetic demands of osmoregulation at low salinities may preclude egg development in *M. intermedium* before November or December at JP. This may also explain the absence of ovigerous *P. serenus* from the estuary. *Crangon franciscorum* was similarly found unable to breed in the brackish waters of the San Francisco Bay delta (Siegfried, 1980).

Ovigerous *P. australiensis* were present in the estuary from September to December but were present upstream from July at least until February. (Ovigerous females have been caught as late as April in other years in the Hopkins River—see chapter 7.) This period of reproductive activity is considerably greater than recorded in Cardinia Creek, Victoria (September to January or February: Williams, 1977). Walker (1977), who did not collect samples from December to February, found no ovigerous females before October and none after February in Tasmania. Hancock (Griffith University, personal communication) found ovigerous females from August to February in the upland streams of southern Queensland. Nevertheless, breeding activity was briefer in the estuary than upstream (Figs. 4.7, 4.8). The later first occurrence of ovigerous females in the estuary is likely to be due to the small number of large female *P. australiensis* in

the estuary prior to September, rather than being due to females remaining non-reproductive in the estuary (Fig. 4.8). Similarly, the earlier cessation of breeding activity in the estuary was due to the complete disappearance of adult *P. australiensis* from the estuary between December 1988 and January 1989. The importance of physiological tolerance to rising salinity and the possibility of competitive displacement by *M. intermedium* as potential causes of this disappearance were discussed in Chapter 3.

Differing periods of reproductive activity in different sections of the estuary were probably due to physiological responses of resident females to differing salinity conditions in *M. intermedium*. While female *M. intermedium* in the lower estuary began breeding as early as October, those in the upper estuary delayed breeding until November or December when salinity rose to ~10. In contrast, the differing periods of reproductive activity in *P. australiensis* between the estuary and upstream were due to females migrating into and out of the estuary. Migration of large females into the estuary was associated with the period directly after peak discharge, rather than changes in salinity over the meadows of the estuary. Change in flow conditions is therefore a likely cue for migration downstream. The cue for migration out of the estuary is likely to be salinity over the meadow at JP rising above ~10. Migration is discussed further below and is pursued further in Chapter 7.

In both *M. intermedium* and *P. australiensis*, larger females were the first to breed. In both cases these females were in their second year, and it was two months until the majority of smaller females (in their first year) became ovigerous. This phenomenon of a progressive change in the size of ovigerous females through a breeding season is common among carideans (Höglund, 1943; Forster, 1951; Wood, 1967; Alon and Stancyk, 1982; Baden and Pihl, 1984; Gray, 1985).

The analysis of population dynamics of *P. australiensis* has not proved, but has strengthened the case for Williams' (1977) conjecture that each female is capable of producing a number of broods in each breeding season. Williams (1977) noted female *P. australiensis* in the laboratory producing two successive broods, and also observed contemporaneous ovarian development. Breeding activity in the Hopkins River has been shown to persist for over six months, and the period required for fertilised eggs to hatch is of the order of a month (Walsh, 1993; Chapter 5 of this study). It is therefore likely that at least three broods could be produced by a female in her second year.

Recruitment

First recruitment of *M. intermedium* in the Hopkins (December) was later than in Western Port (November), but recruitment probably occurred earlier in coastal waters adjacent to the Hopkins. Three peaks in recruitment in the Hopkins probably corresponded to three stages of breeding activity:

- the first cohort (present as sub-adults in the estuary from January) as a result of an initial burst of breeding activity in adjacent coastal waters in late spring;
- the second cohort (first present in December) as result of peak breeding activity in the lower part of the estuary (RF and HB) in November and December (Fig. 4.7);
- the third cohort (first present in March) possibly as a result of a peak in breeding activity at JP while breeding activity was still high in the lower sections of the estuary in January and February.

Patterns of recruitment in *M. intermedium* were similar throughout the estuary, but the abundance of all three cohorts decreased at upstream sites. It is probable that a similar pattern of recruitment occurred in 1988, because three female cohorts of corresponding size were present in June 1988 (Fig. 4.10). However a comparison of May 1989 and June 1988 distributions (Fig. 4.1) shows that the last cohort, which probably recruited in January or February, was dominant in 1988, while the earlier cohort, which recruited in December, was the dominant cohort in 1989. The decreased importance of later recruitment to the estuary in 1989 may have been due to the extended period of closure the estuary went through from January to March 1989. Sill formation at the mouth of the estuary may have prevented later summer migration of breeding adults or juveniles from coastal waters, which would have been possible in 1988 when the mouth did not close. This speculation could be confirmed by comparison of population structure over more breeding seasons in the Hopkins River estuary.

Walker (1979) and Howard (1981) both found *M. intermedium* juveniles only between spring and autumn, and with only one major peak of recruitment, while Gray (1985) found juveniles present all year round with two or three peaks of recruitment, usually in spring and then late summer-autumn. In the Hopkins, *M. intermedium* juveniles were present only from summer to autumn, but it appears juveniles recruited to adjacent coastal waters in spring, subsequently migrating into the estuary in summer. Such recruitment to inshore coastal areas followed by migration into estuaries has been documented for carideans by Emmerson (1986) and commonly in penaeids (e.g. Staples and Vance, 1987).

Recruitment was more intense in *P. australiensis* than in *M. intermedium,* but for a shorter period. The abundance of ovigerous females was no greater than that of *M. intermedium* at HB, and indeed, averaged over the entire estuary, there were far fewer ovigerous *P. australiensis* than *M. intermedium*. Average brood size of *P. australiensis* females in the Hopkins River estuary was ≈400-800 (calculated from Walsh, 1993), and for *M. intermedium* (in Western Port, but presumably not very different from the Hopkins population) ≈50-450 (calculated from Howard, 1981). Although *P. australiensis* produces more offspring in each brood than *M. intermedium*, the difference is not sufficient to explain the observation that the abundance of *P. australiensis* recruits was over a factor of ten greater than in *M. intermedium*. More synchronous spawning in *P. australiensis* may have caused higher juvenile densities, or it may

be due to larval behaviour resulting in concentrated occurrences of late stage larvae. The observed differences in recruitment intensity between species are investigated in relation to larval distribution and abundance in chapter 6.

Two peaks of recruitment were discernible in *P. australiensis* at both JP and TS. The second recruitment peak was less intense than the first, particularly at JP, where only very few individuals of the second cohort were collected. It was more numerous upstream of the estuary at TS, suggesting this second episode of recruitment originated outside the estuary. This phenomenon of two recruitment peaks was observed in one of the two populations studied by Walker (1972), but not in the Cardinia Creek population studied by Williams (1977). The tendency for *P. australiensis* juveniles to be larger nearer the mouth of the estuary (Table 4.6, Fig. 4.12) suggests earlier recruitment to the more downstream sites. Evidence supporting the contention is presented in Chapter 6, where recruitment processes in *P. australiensis* within and upstream of the estuary will be discussed further.

Post-larval migration

Post-larval migration into and out of the estuary, and between meadows within the estuary appeared to be an important determinant of both distributions and population structure of the three epibenthic caridean species of the Hopkins River estuary. Large numbers of ovigerous *P. australiensis* migrated into the estuary from upstream in September and October, soon after the annual flood. *P. serenus* adults and juveniles migrated into the lower part of the estuary during summer, but no reproductive activity was detected in this species. Although juveniles of both *P. australiensis* and *M. intermedium* recruited to the seagrass meadows directly from planktonic larvae in the estuary in large numbers, migration of juveniles of both species is also likely. The migration of a cohort of juvenile *M. intermedium* into the estuary from adjacent coastal waters in summer was discussed above.

The rapid decline in numbers of juvenile *P. australiensis* throughout the estuary from December to January must be due to either mortality or emigration. The larger size of juveniles just above the estuary at TS than at the nearby estuarine site LG (Table 4.6, Fig. 4.12) could be explained by migration out of the estuary to TS by some newly settled juveniles from sites nearer the mouth of the estuary, while recruits continued to settle at LG. If this were the case, many of the juveniles at TS on 19 November, which were similar in size to juveniles at JP and RF (Fig. 4.12), would have settled at sites in the lower estuary one to a few weeks earlier, while the majority of juveniles at LG would have been more recent recruits. This conjecture is considered again in Chapter 6, and the broader question of juvenile *P. australiensis* emigration from the estuary is considered further in Chapters 6 and 7.

Migration within the estuary is also evident from the occurrence of both *P. australiensis* and *M. intermedium* adults at the ephemeral *Ruppia* meadow at LG in summer of 1988-1989, when, prior to the growth of this meadow, the nearest seagrass meadow was JP. Migration of adults of

several caridean species on this scale was reported by Sogard (1989). It is thus apparent that, for motile epibenthic fauna such as the carideans under study, post-larval migration is at least as important as larval distribution in determining adult distribution on a between-meadow scale within an estuary.

The observed variations in sex ratio of *P. australiensis* may have been the result of migration on a larger scale than that between meadows within the estuary. The decline in male:female sex ratio observed in October 1988, and the subsequent rise in November (Fig. 4.9) was caused by an influx and subsequent decline in numbers of large females at JP and TS. Because the trend of sex ratios is consistent between the two sites, it is likely that, if the changes in sex ratio are caused by migration of specific parts of the population, migration is at a greater scale than the distance between the two sites. That is, large females migrate from and to sections of the river further upstream of the estuary than TS. The consistently larger proportion of males at TS than at JP suggests that, if males also migrated to the estuary from upstream, they were more likely to remain at the upper edge of the estuary at TS than to invade the seagrass meadows of the estuary. Alternatively, the larger proportion of males at TS could be indicative of female depletion from sites further upstream, from which large females have migrated to the estuary to spawn. Differing degrees of migration between the sexes have been suggested to explain temporal variation in other carideans such as *Palaemon pacificus* (Emmerson, 1986) and *Palaemonetes pugio* (Alon and Stancyk, 1982). Migration of adult *P. australiensis* is investigated further in Chapter 7.

Growth

Females of both species grew faster and to a greater maximum length than males. This trend of larger, faster growing females has been recorded consistently for *M. intermedium* (Walker, 1979; Howard, 1981; Gray, 1991b), and also for other palaemonids such as *Palaemonetes pugio* (Welsh, 1975; Alon and Stancyk, 1982), *Palaemon squilla* (Höglund, 1943), and *Palaemon serratus* (Forster, 1951), and atyids such as *Caridina nilotica* (Hart, 1981). *C. simoni* (de Silva, 1988a),and *C. pristis* (de Silva, 1988b). Faster growth in females than males is recorded commonly in the Caridea, and has been discussed by Walker (1979) and Howard (1981). Howard proposed that males tend to be larger than females in species in which male territoriality is exhibited. If territoriality is not favoured by natural selection, then smaller males may be selected because they would be less vulnerable to predation while maintaining high reproductive output. Female reproductive output is more dependent on body size, and the most adaptive female size would be more dependent on the trade-off between increased reproductive output and increased risk of predation.

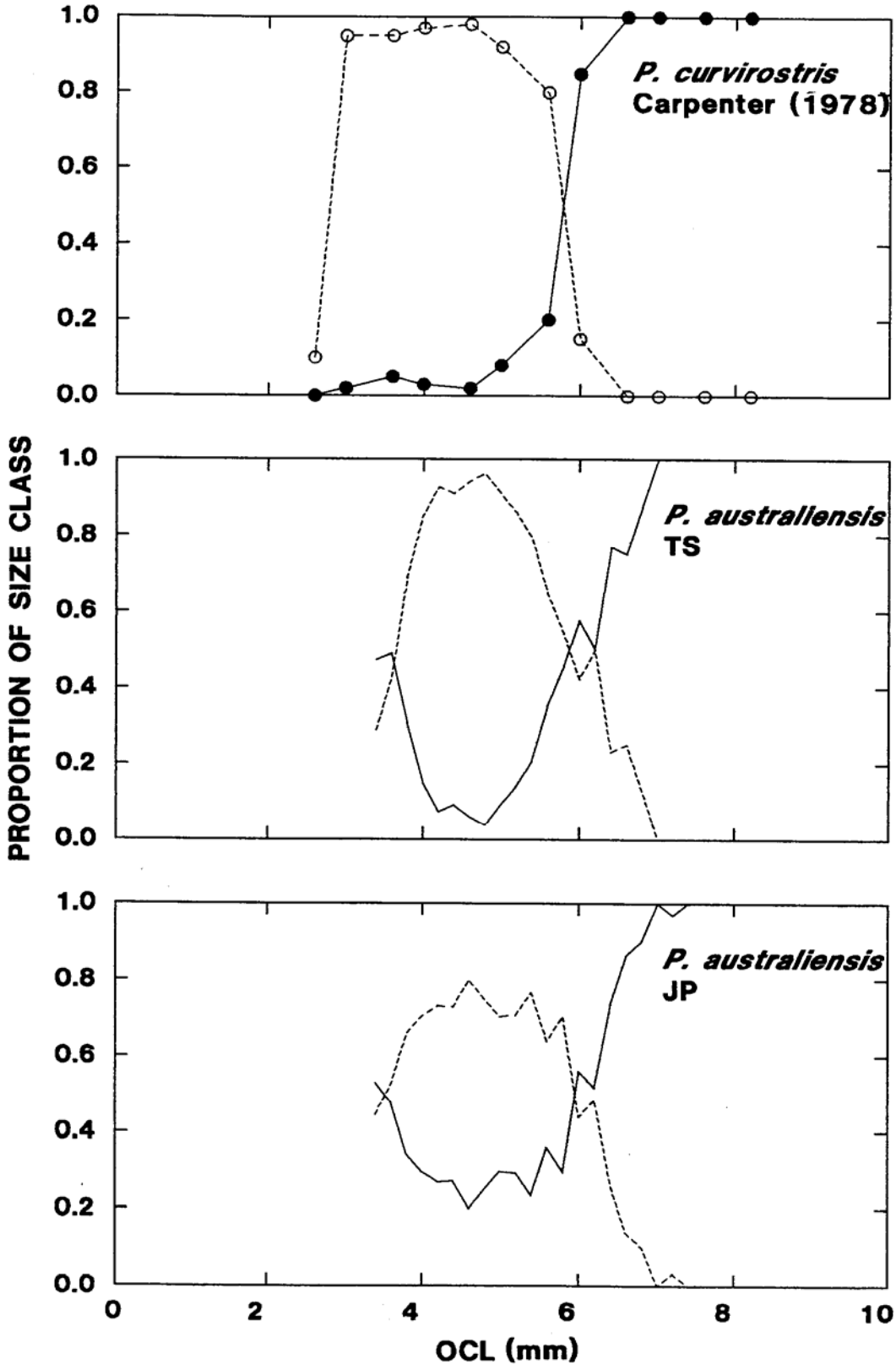
Table 4.7. Growth rates of *Macrobrachium intermedium* estimated in four studies, calculated to a common unit. OCL measurements were derived from total lengths in Walker's (1979) study using the regression equations of Howard (1981) listed in section 4.3.1.

Study	Location	Sex	Growth rate (mm OCL.month^{-1})		
			Summer	Winter	Annual
Walker (1979)	SE Tasmania	Juveniles	0.95-1.00		
		Males	≈0.20	≈0.10	0.10-0.17
		Females	≈0.45	≈0.10	0.14-0.27
Howard (1981)	Western Port, Victoria	Males	0.21-0.25	0.13-0.21	0.17-0.23
		Females	0.37-0.43	0.27-0.60	≈0.56
Gray (1991a)	Port Hacking, NSW	Juveniles	≈0.5		
		Males			≈0.5
		Females			≈0.7
This study	Hopkins River estuary	Males			≈0.25
		Females			0.5-0.7

Table 4.7 shows the reported growth rates from all studies of *M. intermedium* recalculated to a common unit. A male growth rate of ≈0.25 mm OCL per month in *M. intermedium* is comparable to the rate of Western Port populations (Howard, 1981), but higher than that of Tasmanian populations (Walker, 1979) and lower than that of Port Hacking populations (Gray, 1991a). The range of female growth rates of 0.5-0.7 mm OCL per month spans the rates reported by Gray (1991b) and Howard (1981), but is greater than that reported by Walker (1979). These variations in growth rate appear to have a latitudinal component, probably due to variation in temperature. Seasonal variation in growth was observed in Tasmania and in males in Western Port, with slower growth in winter. This variation might not be attributable solely to temperature variation, as growth tended to slow as size increased, and Howard (1981) suggested greater availability of food may speed growth in summer. Seasonal growth patterns were not determined in the current study due to the shortness of the sampling program, nor in Gray's (1991a) study. However some growth was recorded in all studies in winter, in contrast to studies of palaemonids in the high latitudes of the northern hemisphere, which showed virtually no growth in winter with all growth occurring in summer (Höglund, 1943; Forster, 1951).

→

Fig. 4.13. Size specific sex ratios of *Paratya curvirostris* from New Zealand as described by Carpenter (1978), and of *P. australiensis* from JP and TS. All *P. australiensis* collected in 1988-1989 were pooled for each site, and sex ratio was calculated for groups of 2 mm OCL intervals. Open circles, dashed lines, male; closed circles, solid lines, female


P. curvirostris
Carpenter (1978)
P. australiensis
TS
P. australiensis
JP
PROPORTION OF SIZE CLASS
OCL (mm)
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
10

Carideans commonly exhibit reduced growth after the onset of maturity (e.g. Hart, 1981; Dudgeon, 1985). Dudgeon (1985) presumed such reduction in growth in *Neocaridina serrata* was the result of the diversion of energy from somatic growth into gamete production. This also appeared to be the case for both *M. intermedium* and *P. australiensis*, but attaining adult size did not immediately result in the reduction in growth rate. For instance the cohort of female *P. australiensis* beginning at 5.2-5.5 mm OCL in June 1988 (Fig. 4.11) grew steadily until September, attaining a mean OCL of >7 mm, after which growth was reduced. The reduction in growth rate coincided with the onset of the breeding season, rather than the onset of sexual maturity.

Sex

Wenner (1972) described a number of relationship patterns between sex ratio and size in marine Crustacea, characteristic of differing life history patterns. Carpenter (1978) found *Paratya curvirostris* to exhibit a curve identical to the theoretical 'Wenner' curve for protandrous species (Fig. 4.13). There was very little overlap in size ranges of males and females in *P. curvirostris*. When a similar curve is plotted for *P. australiensis* caught at JP and TS over 1988-1989 (Fig. 4.13), overlap in size ranges of the sexes is evident. Thus this species is not protandrous (at least not obligatorily). However the shape of the Wenner curve for *P. australiensis* is of the 'anomalous' pattern observed in the amphipod *Neohaustorius biarticulatus*, the brachyuran *Emerita analoga*, and the harpacticoid copepod *Asellopsis intermedia* (Wenner, 1972). A similar pattern was observed in *M. intermedium*. Wenner explored a number of explanations for this pattern of size specific sex-ratios, which are relevant to the population dynamics of *P. australiensis* and *M. intermedium*:

-differential longevity: this does not appear to be the case in either *M. intermedium* or *P. australiensis*, in which both sexes appear capable of surviving into their second year. Gray (1985) suggested that *M. intermedium* in New South Wales was capable of survival into a third year because of the presence of large individuals up to 6.8 mm OCL in males and 9.8 mm OCL in females. It is possible that the large females collected in both *M. intermedium* and *P. australiensis* were 2+ years old.

-differential growth rates: this has been shown to be the case in both *M. intermedium* and *P. australiensis* (Figs. 4.10, 4.11). Such different growth rates in the sexes is sufficient to explain the observed pattern of sex ratio-size distributions in both species.

-differential migration: this could explain the differences between Wenner curves for *P. australiensis* at JP and TS. The very small proportion of females at TS with OCL 4-5 mm OCL is possibly a result of a greater level of migration into the estuary by females.

-sex reversal: Wenner (1972) discussed a theoretical means by which such an anomalous curve could be achieved by a double sex reversal in a portion of the population. Such a possibility for *P. australiensis* has not been disproved by the current work. The observed Wenner curve indicates that *P. australiensis* is not completely protandrous in the manner of *P. curvirostris*,

and the most parsimonious explanation for the observed curve is the faster growth rate exhibited by females.

* * *

The work of Bell (Bell and Westoby, 1986a, 1986c; Bell et al., 1988) on fish and decapods in seagrass meadows of New South Wales concentrated on the importance of larval settlement in determining epifaunal abundance within seagrass meadows. Bell and Westoby (1986c) constructed a model to account for variability in abundance of decapods and fish, of which a central hypothesis was that individuals do not leave a seagrass meadow once they have settled. Analysis of the population structure of the three epifaunal caridean shrimp species of the Hopkins River estuary has shown this not to be the case, with post-larval migration, both between seagrass meadows, and into and out of the estuary, being a significant factor in determining their abundance and distributions. Bell et al. (1988) concluded that differences in abundances of fish and decapods between seagrass meadows were most likely due to variation in distribution and availability of competent larvae. The potential for post-larval migration between meadows was considered less important. In contrast, Sogard (1989), working in a New Jersey, USA estuary, found settled juveniles and adults of both fish and decapods to be important colonisers of artificial seagrass meadows. She proposed that life history differences between epifauna of New South Wales and New Jersey may increase the importance of planktonic larvae in dispersal. The most abundant species in New Jersey meadows have reduced planktonic larval development or direct development, while most of the common species in New South Wales have extended planktonic larval stages.

The epifaunal caridean shrimps of the Hopkins River estuary all have extended larval development (Williamson, 1972; Fincham and Figueras, 1986; Walsh, 1993: Chapter 5 of this study), and yet both direct recruitment from planktonic larvae, and post-larval migration appear important determinants of distribution of *M. intermedium* and *P. australiensis* in the seagrass meadows of the estuary. The occurrence of *P. serenus* appears to be solely due to post-larval migration. The importance of post-larval migration may be enhanced in the Hopkins due to wide seasonal variations in salinity, making the seagrass meadows sub-optimal habitat for part of the year, but optimal habitat with abundant food and cover for some of the year.

Recruitment from planktonic larvae is also an important determinant of juvenile distributions in *M. intermedium* and *P. australiensis* in the seagrass meadows. The biology of the larvae of all three caridean species is considered in the following chapters.

5. LARVAL DEVELOPMENT OF THE ESTUARINE CARIDEANS OF THE HOPKINS RIVER, REARED IN THE LABORATORY

5.1. INTRODUCTION

To identify the larvae of the carideans of the Hopkins River estuary, and to assess the distribution, abundance, and age structure of larval populations, descriptions of larval stages of each species were required. Of the three species under investigation, the larval development of only *M. intermedium* has been described prior to this study (Williamson, 1972). Williamson (1972) did not rear this species to metamorphosis, but only to stage VIII of an estimated ten stages. He did not monitor the number of ecdyses during development, but assigned the eight stages from a mass culture. Development of palaemonid larval stages I-IV is usually regular (sensu Gore, 1985) with minimal phenotypic variation, but later stages exhibit more variation as moulting, growth, and morphogenesis become less synchronous (Fincham and Figueras, 1986). Significant geographical variation in duration, number and morphology of larval instars been reported for *Palaemonetes vulgaris* (Sandifer, 1973; Knowlton, 1974), *Palaemon elegans* (Fincham, 1977), and *Palaemon paucidens* (Nishino, 1984, cited in Fincham and Figueras, 1986). Because such variation is common within palaemonid species it was necessary to rear larvae of *M. intermedium* in the laboratory to compare development of southern Victorian populations with the specimens from central New South Wales described by Williamson (1972). Although no ovigerous females of *P. serenus* were recorded in the Hopkins River estuary (see Chapter 4) it is possible that larvae released in adjacent coastal waters were transported into the estuary. It was thus important to rear larvae of this species to allow differentiation of field-collected larvae of the two palaemonid species.

Both intrinsic and extrinsic variation in larval development patterns have been reported within atyid and palaemonid species. Variation in the number of instars to metamorphosis and overall larval duration under constant environmental conditions has been described in many species with marine or estuarine larval phases—e.g. *Atya innocous* (Hunte, 1979b), *Micratya poeyi* (Hunte, 1979a), *Macrobrachium equidens* (Nguyen, 1976), *Palaemonetes vulgaris* and *P. pugio* (Broad, 1957).

The larval development of the atyid *P. australiensis* is of greatest interest as, before this study, no description of laboratory-reared larval development existed for any species of *Paratya*—although Yokoya (1931) assigned ten larval stages to *P. compressa* based on larvae collected from a land-locked freshwater pond. The planktonic nature of *P. australiensis* larvae has been noted as problematic in light of the riverine habit of the species (Williams, 1977). The current

study has shown *P. australiensis* to complete larval development in both estuaries and riverine pools well upstream of estuarine influence in south-eastern Australia (Walsh, 1993, and see chapters 6 and 7 of this study). Estuarine development of larvae has been speculated upon for other species of *Paratya*: *P. curvirostris* (Ch'ng, 1973; Carpenter, 1983) and *P. compressa* (Shokita, 1979). The latter species has also been shown to complete larval development in land-locked fresh waters (Yokoya, 1931).

Descriptions of larval development in a number of other atyid genera exist, showing a diversity of development types within the family. Benzie (1982) reviewed the range of development among *Caridina* species, from direct development in *C. singhalensis* (Benzie and de Silva, 1983), *C. brevirostris* (Shokita, 1973), and *C. denticulata* (Shokita, 1976), through abbreviated development of 1 day in *C. mccullochi* (Benzie, 1982), to development of intermediate durations in freshwater of 12 days in *C. nilotica* (Glaister, 1976) and 26 days in *C. weberi* (Chinnaya, 1974). Hayashi and Hamano (1984) reared the upland-stream dweller, *C. japonica*, from egg to juvenile in 24-38 days at a salinity of 16.9. Shokita (1979) reported estuarine larval development and subsequent upstream migration of juveniles for this species. Extended larval development has been recorded for three Atlantic atyid species. *Atya scabra* developed for 53 days at an optimal salinity of 18 (Abrunhosa and Moura, 1988), *Micratya poeyi* developed for 53-74 days at an optimal salinity of 32 (Hunte, 1979a), and *A. innocous* developed for 76-119 days at an optimal salinity of 30 (Hunte, 1979b). Hunte (1978) postulated that *M. poeyi* and *A. innocous* undergo larval development in marine conditions and migrate upstream as juveniles. This life history pattern has subsequently been confirmed for *A. innocous* (Felgenhauer and Abele, 1983).

Shokita (1981) and Hayashi and Hamano (1984) divided the Atyidae into three groups based on egg size with 'small egg' species generally exhibiting extended development and 'large egg' species exhibiting abbreviated or direct development. The range of development types observed within the Atyidae corresponds to a range of ecological requirements for recruitment —from direct developers which usually complete their entire life cycle in upland streams to extended developers which tend to utilise marine or estuarine environments for larval development. The genus *Paratya* appears to exhibit characteristics intermediate to these two extremes: its larval development is not confined to estuarine development, but can also occur in upstream riverine environments. Thus *Paratya* is in an interesting evolutionary position, as its larval development spans the two distinct developmental strategies of complete in-stream development and amphidromous estuarine development. The description of the larval development of *P. australiensis* allows a clearer identification of a sequence of larval development types across the Atyidae.

This chapter: describes the complete larval development of *P. australiensis* reared in the laboratory (published as Walsh, 1993). It also provides data on the duration of larval

development, the number of ecdyses to metamorphosis, and differentiation of the laboratory-reared larvae of the palaemonids *M. intermedium* and *P. serenus*. Finally this chapter records the effect of different rearing salinities on the development and survival of each species.

5.2. METHODS

M. intermedium and P. serenus

On 28 December 1988, three ovigerous *M. intermedium* were collected from the *Zostera* meadow at HB in water of salinity of 30.5-32 at 23.5°C, and four ovigerous *P. serenus* were collected from a *Zostera* meadow north of Griffith Island at the mouth of the Moyne River, 25 km west of the Hopkins River mouth, in water of salinity 35.5 at 23.5°C. All specimens were placed in small aerated aquaria in sea water (salinity 35.6). Temperature varied between 18.5 and 22.5°C during the development period. For each species, on hatching, three groups of over 100 larvae were removed to small aquaria containing sea water. Distilled water was added slowly to two of the aquaria so that salinity was lowered to 25 over four hours. This process was continued into one aquarium for another five hours until a salinity of 15 was reached. One hundred active larvae at each salinity (35.5—hereafter referred to as the 35 treatment—, 25 and 15) were then transferred individually to numbered 50 mL plastic beakers. A further fifty larvae of each species were maintained in sea water in small aquaria and were used for dissection and drawing. Water and food was changed at least every second day. Larvae in all treatments were fed freshly hatched *Artemia salina* nauplii at a density of 1-2 mL^{-1} for the first two weeks rising to ≈4 mL^{-1} thereafter. The larvae in the 50 mL beakers were checked daily (occasionally every second day) for survival and exuviae to determine stage duration.

The effect of rearing salinity on the proportion of larvae surviving to metamorphosis was tested by a 3×2 test of independence using the G-statistic (Sokal and Rohlf, 1981) for each species. Three levels of salinity were tabulated against larval fate (death or survival to metamorphosis). If a significant result was achieved 2×2 tests were conducted comparing survival rates at salinity 15 and 25, and 25 and 35. For these planned comparisons, a Dunn-Sidák correction of the critical value of α was made (Sokal and Rohlf, 1981), so that significance was accepted at $P<0.025$.

The effects of rearing salinity on duration of larval development and the number of ecdyses to metamorphosis were tested by two one-way ANOVAs, with three levels of salinity: one on larval duration and the other on number of ecdyses for all larvae that survived to metamorphosis. Heterogeneity of variances and the number of outliers were reduced by log transformations. Differences between means were tested using Tukey's unplanned multiple comparison test. Sample sizes were unequal due to the differing survival of larvae in each

treatment. Because Tukey's test is sensitive to unequal sample sizes, significance was only accepted at $P<0.01$

P. serenus larvae for whole animal drawings were anaesthetised in a few drops of ethanol. Drawings were made with the aid of a camera lucida. Gross morphology drawings and measurements were made using a dissecting (×8-×40) microscope and ocular grid.

P. australiensis

P. australiensis larvae were reared from adults collected at two locations: one estuarine and one fresh water. Two ovigerous females were collected from the *Zostera* meadow at JP on 24 November 1989 in water of salinity 1.9, and two were collected on 20 December 1989 from a ribbon-weed (*Vallisneria spiralis*) bed in Lake Purrumbete at the head of the Curdies River (see section 7.2) in water of salinity 0.5. Specimens were placed in small aerated aquaria in water from their natural habitat. Temperature varied between 18.5 and 22.5°C during the developmental period. After the eggs hatched, the females were preserved in 2% formaldehyde.

In initial rearing trials larvae, regardless of their origin, did not survive beyond stage III in salinities of 0.75 or 5, but survival to metamorphosis was high in salinity of 15. This may have been a result of the non-viability of the food source (*Artemia*) in fresh water, rather than a reflection on the physiological tolerance of *P. australiensis*. Descriptions are based on larvae from both habitats reared at 15. The larvae were separated on hatching and sea water was gradually (over 1 h) added to their habitat water to raise salinity to 15.

Fifty individuals from each brood (two hundred in total) were reared individually in 50 mL plastic beakers. The remaining larvae were maintained separately in groups of about twenty in 500 mL glass beakers. In all treatments, water was changed and an excess of *Artemia* cysts, decapsulated after Sorgeloos et al. (1986), was added every 2-3 days. The larvae were checked daily (occasionally every second day) for survival and exuviae to determine stage duration.

Larvae for dissection were preserved in 2% formaldehyde and dissected in glycerol. Appendages were mounted in Gurr's Aquamount. At least five larvae of each stage were dissected. Drawings were made with the aid of a camera lucida. Gross morphology drawings and measurements were made as for *P. serenus*. Appendages were drawn using a compound microscope with phase contrast lighting.

The morphological terminology used follows that of Williamson (1969), and the terminology of developmental types, including 'mark-time moult' and 'skipped stage', follows that of Gore (1985). Slides of dissections and representative specimens of each stage and of the female parents have been lodged in the Museum of Victoria (NMV Reg. Nos. J25311-J25374).

Because of the lack of success in finding a suitable food source for *P. australiensis* larvae at the low salinities in which they are known to grow naturally (Walsh, 1993, and see chapters 6 and 7 of this study), experiments comparing larval development at a wide range of salinities were not conducted for this species. However viability of larvae was investigated at salinities approaching sea water. Twenty larvae from JP were reared in individual 50 mL beakers at salinity 28.8, and also at 34.5, using the individual rearing and monitoring procedures described above. A salinity tolerance experiment was conducted on early stage larvae at 20.5± 0.3°C in the same manner as described for adults and juveniles in section 3.2.2. Experimental larvae were taken from ovigerous females collected from TS on 3 and 8 January 1992, and kept in large holding tanks in tap water to which $CaCO_3$ had been added to approximate Hopkins River water. Larvae released on the nights of 9 and 10 January 1992 were placed into treatment containers—600 mL glass beakers—on 11 January 1992 with an excess of decapsulated *Artemia* cysts. Twenty larvae were placed in each of five randomised replicate beakers at each of five experimental salinities (27.7, 30.7, 33.8, 36.9, and 39.7) and a control of 12.5 (salinity at which maximum survival was expected). Survivors were counted after 96 hours. Fifty percent lethal salinities (LC_{50}) were calculated using logistic regression (Finney, 1978; Steinberg and Colla, 1991) as described in section 3.2.1.1.

5.3. RESULTS

5.3.1. LARVAL MORPHOLOGY AND DEVELOPMENT

5.3.1.1. *M. INTERMEDIUM*

In the laboratory zoeal development of *M. intermedium* lasted between 17 and 49 days, and involved 6-11 ecdyses. Larval stages were identified corresponding to all those denoted by Williamson (1972), although development after stage V was often rapid with metamorphosis sometimes being achieved after two further ecdyses.

5.3.1.2. *P. SERENUS*

In the laboratory, zoeal development of *P. serenus* lasted between 27 and 62 days, and involved 8-15 ecdyses. Stages I-IV involved regular development lasting 11-18 days. Thereafter a variable number of ecdyses occurred at variable intervals—often with little morphological change after an ecdysis. This work does not describe the complete larval development of *P. serenus*, and stages have not been denoted to particular morphological traits beyond stage IV. Stages I-IV correspond to the key for larvae of the sub-family Palaemoninae constructed by Fincham and Figueras (1986). The attributes described below are intended only to allow differentiation between this species and *M. intermedium*.

Stage I (Fig. 5.1a)

Total length 2.1-2.3 mm. Ten marginal setae on scaphocerite (12 in *M. intermedium*). Ratio of telson width: width of abdominal segment 3, 1.35-1.65 (1.75-2.00 in *M. intermedium*). In fresh specimens, *P. serenus* larvae are more heavily pigmented than *M. intermedium*, with prominent chromatophores on: anterior part of eyes; ventrally at the base of second antennae; at the bases of rostrum and maxillipeds; and ventrally, laterally and dorsally on abdominal segments.

Stage II (Fig. 5.1b)

Total length 2.5-2.6 mm. Fourteen marginal setae on scaphocerite (15 in *M. intermedium*). Ratio of telson width: width of abdominal segment 3, 1.2-1.5 (1.7-1.8 in *M. intermedium*).

Stage III (Fig. 5.1c)

Total length 2.8-2.9 mm. Eighteen marginal setae on scaphocerite (17 in *M. intermedium*). Ratio of telson width: width of abdominal segment 3, 0.75-0.95 (0.9-1.0 in *M. intermedium*). This last value is similar in both species due to the tendency for the telson to be narrower in stage III *M. intermedium* than in *P. serenus*. *P. serenus* remains distinguishable from *M. intermedium* by its stouter abdomen, with the width of segment 3 measuring 0.45-0.50 mm (0.40-0.45 mm in *M. intermedium*).

Later stages of *P. serenus* were similarly distinguishable from *M. intermedium* by their wider, less elongate abdomen.

5.3.1.3. *P. AUSTRALIENSIS*

Females of *P. australiensis* carried eggs for at least 25 days at 18-22.5°C. In the laboratory, hatching usually took place at night and zoeal development lasted between 28 and 45 days. Larvae generally swam near the bottom of the beakers with tails pointing upwards. They swam tail first, powered by the exopods of the maxillipeds. On metamorphosis, the endopods of the pereiopods were used to anchor to the bottom or side of the container, and movement was of the adult form.

Larval development involved 7-12 ecdyses, with eight distinct stages being recognised. Stages I-IV involved regular development lasting 12-16 days. Stages V-VIII were more irregular, particularly in larvae from JP, with delayed development commonly manifesting as 'mark-time' moults. In one specimen from Lake Purrumbete, stage VIII was skipped and a juvenile developed from stage VII. Ten larvae from Lake Purrumbete and six from JP metamorphosed in the individual rearing beakers. Losses from the initial two hundred larvae were due to both mortality and the taking of specimens at each stage for dissection and drawing. Allowing for loss of specimens for drawing, the proportion of larvae surviving to metamorphosis was similar in larvae from the two locations (Fig. 5.2). One-way ANOVAs

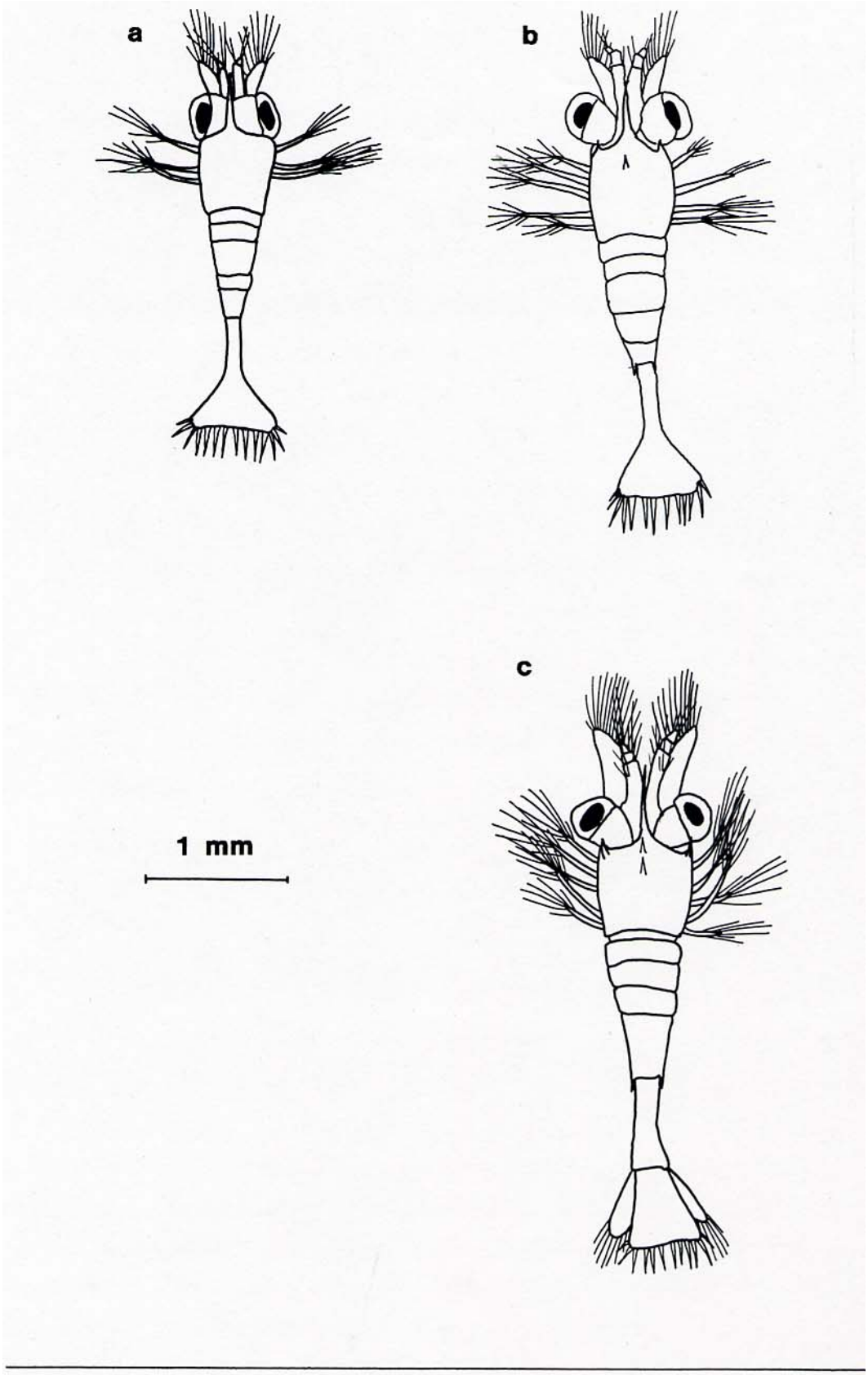


Fig. 5.1. Dorsal views of whole *Palaemon serenus* larvae . (a) stage I (b) stage II (c) stage III

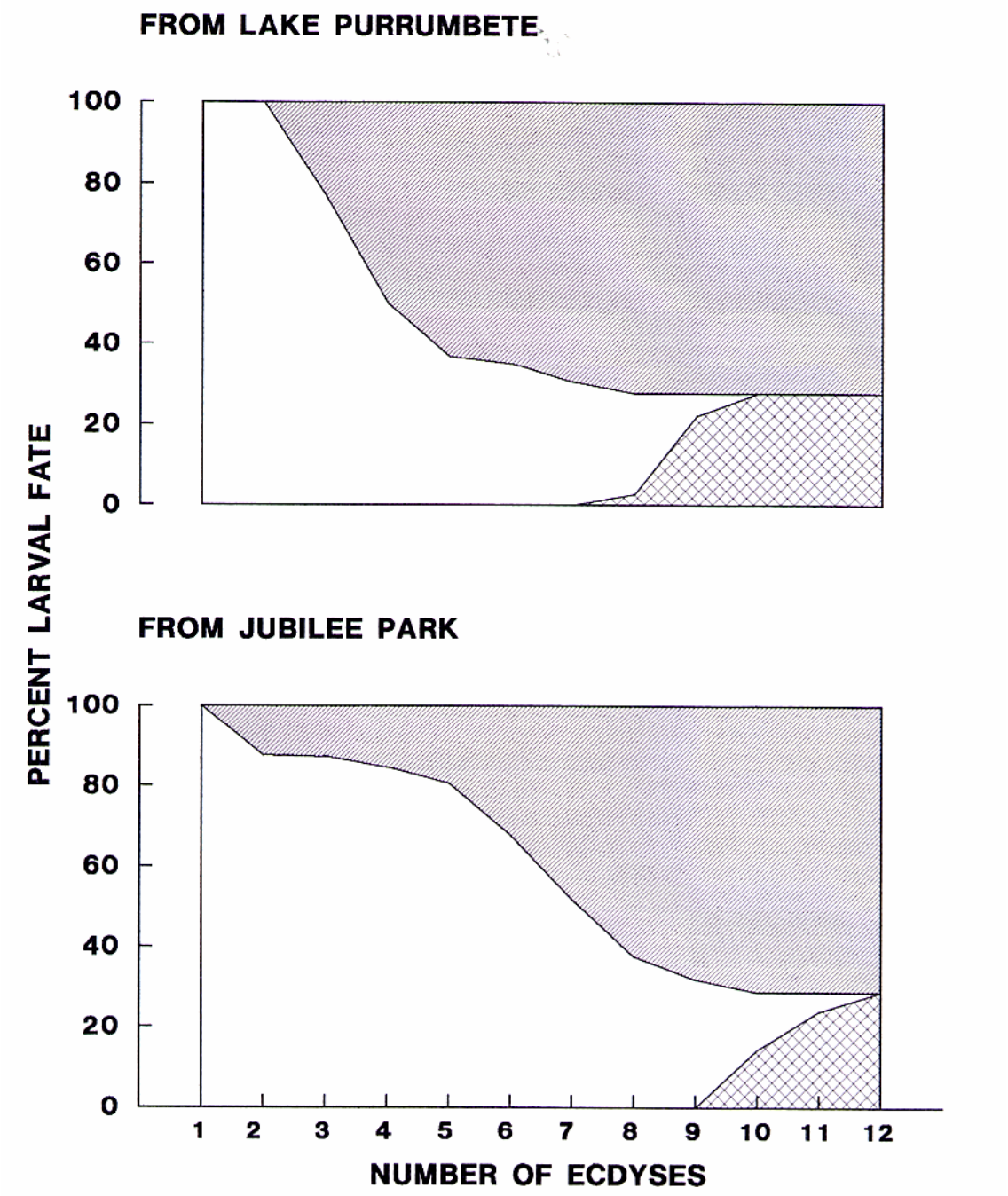


Fig. 5.2. *Paratya australiensis* larvae reared in the laboratory from females collected at two locations: Lake Purrumbete and Jubilee Park, showing proportion of individuals after each ecdysis that had died (grey), remained larvae (unshaded) or achieved metamorphosis (cross-hatched)

were conducted to compare firstly the number of ecdyses to metamorphosis, and secondly the duration of larval development, between larvae from the two locations. The mean number of ecdyses to metamorphosis (±SD) in larvae from JP (9.7 ± 0.8) was greater than those from Lake Purrumbete (8.1 ± 0.6) ($F=20.6$, $P<0.001$). Despite fewer ecdyses, the mean (±SD) duration of larval development in larvae from JP (36.8 ± 3.8 days) was not significantly greater than in those from Lake Purrumbete (33.7 ± 3.7 days) ($F=2.6$, $P=0.13$). The power of the second analysis to detect an effect of the size of the difference between the two means (with $\alpha=0.05$) was 0.78 for a sample size of six and 0.88 for a sample size of ten. The difference in number of ecdyses between larvae from the two locations was manifested in mark-time moults in later stages in larvae from JP, and no differences in morphology were discerned between larvae derived from Lake Purrumbete and those from the Hopkins River estuary.

DESCRIPTION OF STAGES

Stage I (Fig. 5.3a)

Duration of stage: 3 (occasionally 4) days.

Carapace (Fig. 5.3a)—Rostrum straight, directed forward. Suborbital margin angular, but not a well developed spine. Well developed pterygostomial spine. Eyes sessile.

Abdomen (Fig. 5.3a)—Six segments, distal segment fused with telson.

Tail (Fig. 5.4a)—Telson indented midposteriorly; bearing 7+7 plumose setae, with 2 hairs in median incision. Setae 4-6 (from centre) longest, outermost setae shortest.

First antenna (Fig. 5.5a)—Peduncle 2-segmented, bearing a long, stout, plumose median flagellum, and an unsegmented lateral flagellum bearing a short, plumose seta and a long, naked seta subterminally, and 3 terminal aesthetes.

Second antenna (Fig. 5.5b)—Peduncle with a naked seta at distal edge ventral to flagellum. Scaphocerite with 4 segments, bearing 11 plumose setae: first segment with 2 laterally and 3 medially; second and third segments each with 1 medially; forth segment with 4 terminally and a small laterodistal spine. Flagellum bearing a long, plumose seta and a short, naked seta distally.

Mandibles (Fig. 5.5c)—Left molar process with 4-6 marginal teeth, a lateral plumose seta, and an irregular array of teeth proximally. Lacinia mobilis irregular. Four or five teeth on incisor process with a conical tooth and a spinose tooth at base. Right molar process with 4-6 marginal teeth. Lacinia mobilis conical, 1 spine in spine row. Three to five teeth on incisor process.

First maxilla (Fig. 5.5d)—Exopod with 3 stout plumose setae. Endopod with 2 terminal plumose setae, and subterminally, a plumose seta and a seta with 2 plumes and 7 or 8 distally

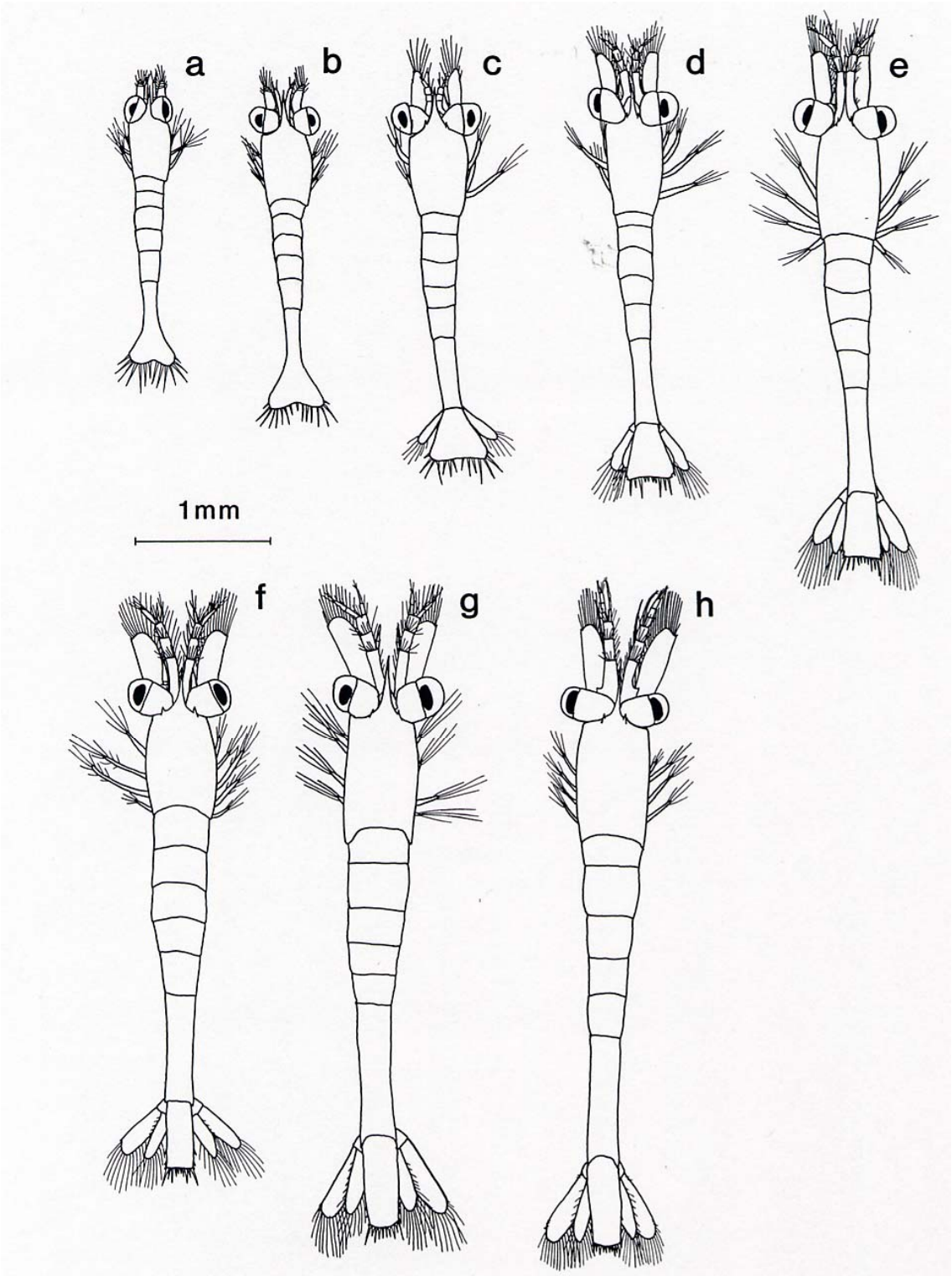


Fig. 5.3. Dorsal views of whole larvae of *Paratya australiensis*. (a) stage I (b) stage II (c) stage III (d) stage IV (e) stage V (f) stage VI (g) stage VII (h) stage VIII

directed bristles. Basal endite with a large spine with a ring of bristles, and 2 spines and 4 setae along distal edge. Coxal endite with 4 stout, plumose setae terminally, a plumose seta laterally, and 1 naked and 1 plumose seta medially.

Second maxilla (Fig. 5.5e)—Five plumose setae on margins of scaphognathite. Endopod unsegmented, lateral margin bearing fine hairs; median margin with 5 lobes, bearing 3,2,1,1,2 plumose setae moving from proximal lobe to distal margin. Basal endite: distal and proximal lobes both with 2 terminal and 1 sub-terminal plumose setae. Coxal endite: distal lobe with 2 terminal and 2 subterminal plumose setae, proximal lobe with 9 plumose setae.

First maxilliped (Fig. 5.5f)—Biramous. Exopod with a small terminal segment bearing 2 long, plumose setae. Proximal segment bears 2 long, natatory plumose setae distally and often a pair of short plumose setae proximally. Endopod 4-segmented, length ratios moving distally 1:1:2:1, carrying 3,1,1,4 setae respectively. All setae plumose on median margin, except setae of distal segment; 1 plumose and 2 naked terminally, and 1 short, naked laterally. Basis with 10-12 plumose setae, and coxa with 4-6 plumose setae. Endopod:exopod length ratio 1:2.

Second maxilliped (Fig. 5.5g)—Exopod as in first maxilliped. Endopod 4-segmented, length ratios 1:1:2:1, carrying 3,1,2,5 setae respectively. Setae on 3 proximal segments plumose and median. Distal segment bearing 1 seta with few short bristles and 3 naked setae terminally, and a short, naked seta laterally. Basis and coxa with 9 and 2 plumose setae respectively. Endopod:exopod length ratio 1:2.

Third maxilliped (Fig. 5.5h)—Exopod as in other maxillipeds. Endopod 4-segmented, length ratios 1:1:3:1, carrying 2,1,2,4 setae respectively. Setae on 3 proximal segments sparsely plumose and median. Distal segment bearing 2 setae with short bristles and 1 naked seta terminally, and a short naked seta medially. Protopod with 4 sparsely plumose setae. Endopod:exopod length ratio 0.8:1.

Stage II (Fig. 5.3b)

Duration of stage: 3-4 days

Carapace (Figs. 5.3b, 5.4b$_1$)—Eyes stalked, supraorbital spine. Otherwise as in stage I.

Abdomen (Fig. 5.3b)—As in stage I.

Tail (Fig. 5.4b)—Posterior margin of telson bearing 8+8 plumose setae. Median incision less pronounced than in stage I.

First antenna (Fig. 5.6a)—Peduncle 2-segmented. Distal segment with 2 short plumose setae distally, dorsal to lateral flagellum. Median flagellum a long stout plumose seta. Lateral flagellum consisting of a single segment with 4 aesthetes and a long naked seta terminally.

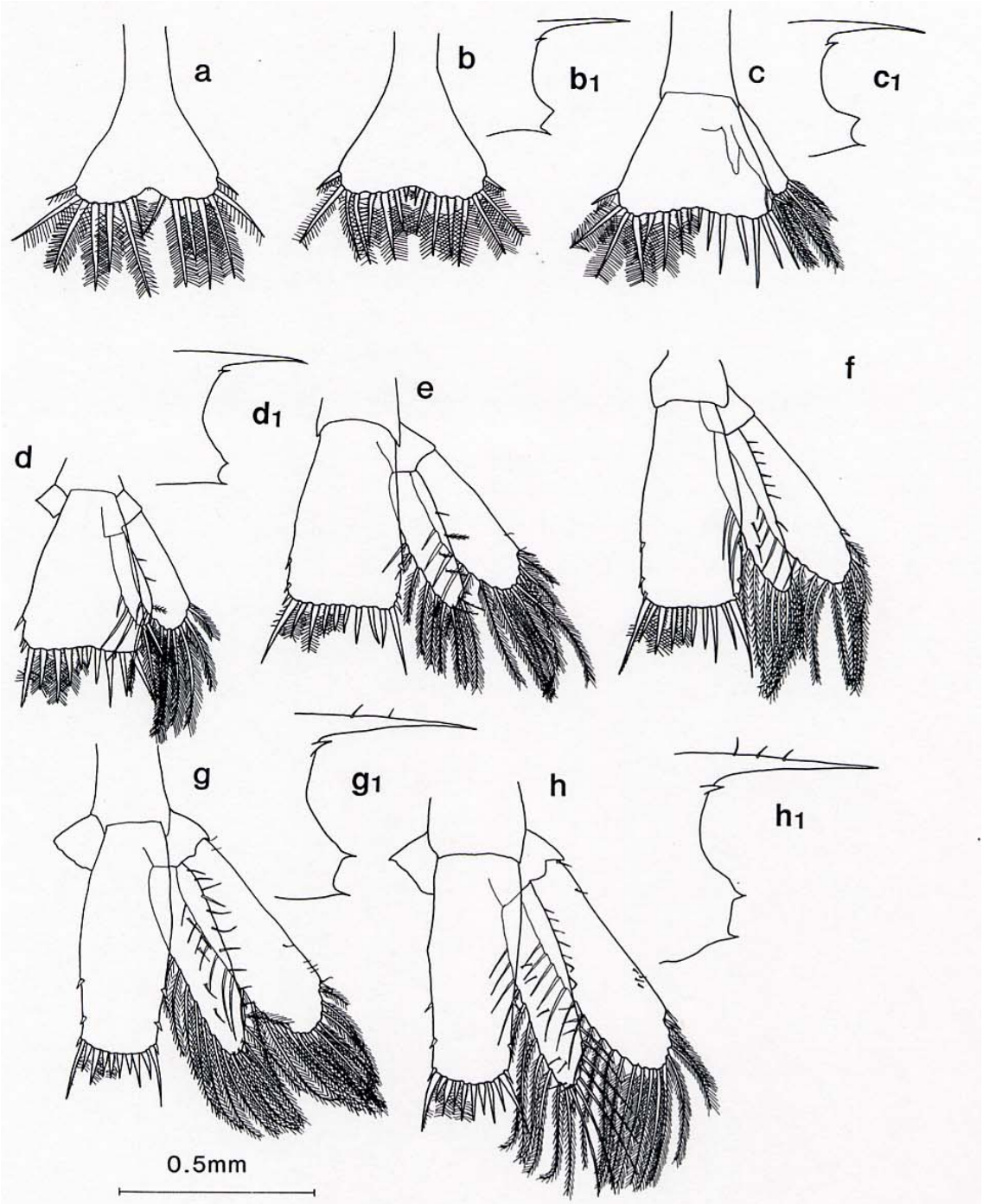


Fig. 5.4. Details of tail and lateral view of anterior portion of carapace of *Paratya australiensis* larvae. (a) stage I; b, b_1) stage II c, c_1) stage III; d, d_1) stage IV (e) stage V (f) stage VI; g, g_1) stage VII; h,h_1) stage VIII

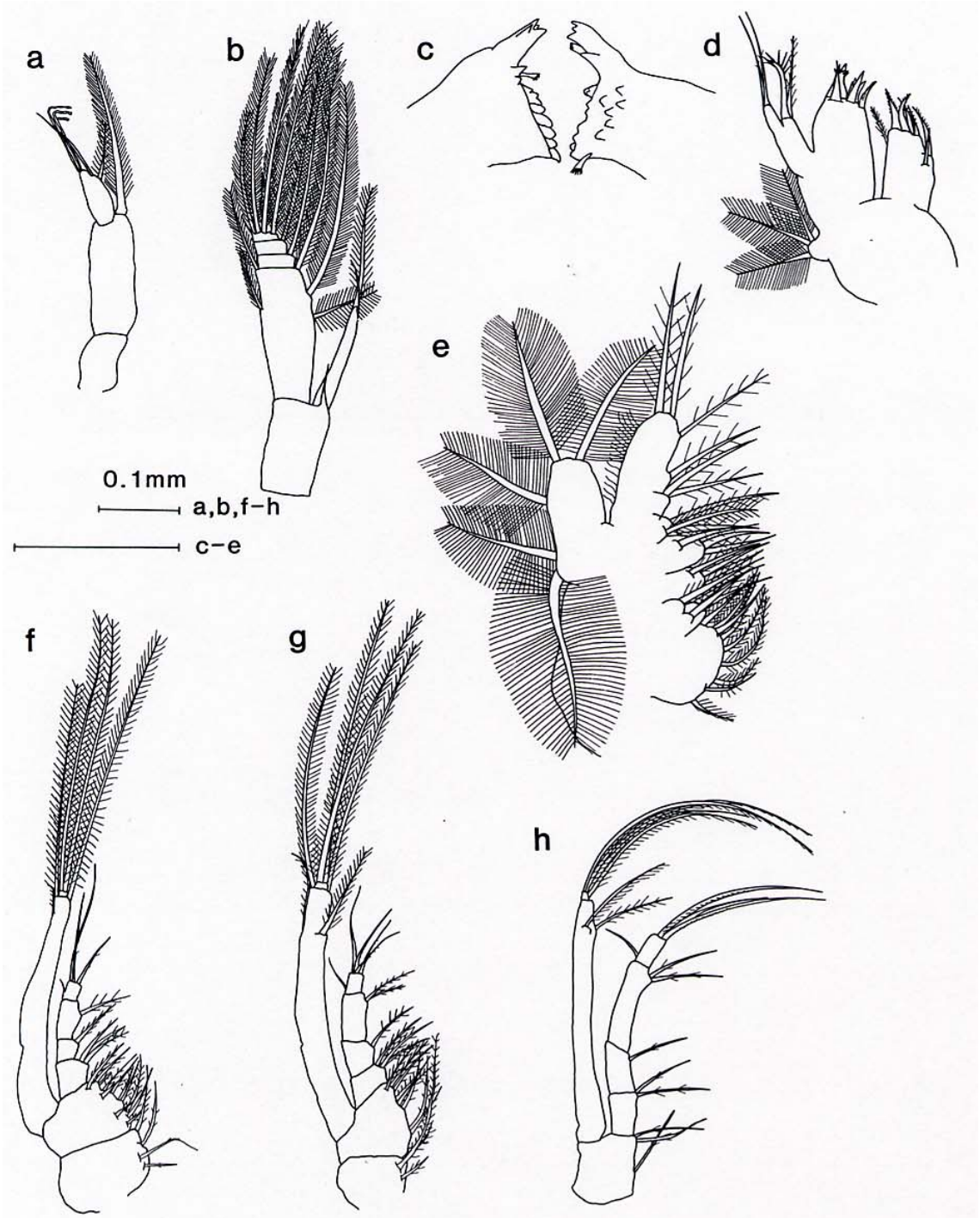


Fig. 5.5. *Paratya australiensis*, stage I. (a) first antenna (b) second antenna (c) mandibles (d) first maxilla; e) second maxilla (f) first maxilliped (g) second maxilliped; h) third maxilliped

Second antenna (Fig. 5.6b)—As in stage I, but the 2 or 3 proximal segments of scaphocerite sometimes fused.

Mandibles (Fig. 5.6c)—Left molar process as in stage I, but without a lateral plumose seta. Two spines in spine row. Incisor process with 4-6 teeth, and a basal spinose tooth. Right molar process with 5 or 6 ridges. Lacinia mobilis 2-toothed with 2 spines in spine row. Incisor process with 4-6 teeth.

First maxilla (Fig. 5.6d)—Exopod and endopod as in stage I. Basal endite with 7 or 8 terminal spines and 1 subterminal spine. Coxal endite with 4 or 5 stout, sparsely plumose setae terminally, 1 naked seta medially and 1 plumose seta laterally.

Second maxilla (Fig. 5.6e)—Scaphognathite and endopod as in stage I. Basal endite: distal and proximal lobes each with 4 plumose setae. Coxal endite: distal lobe as in stage I, proximal lobe with 10 plumose setae.

First maxilliped (Fig. 5.6f)—Exopod as in stage I. Endopod as in stage I except all 3 terminal setae of distal segment sparsely plumose. Basis with 13-16 plumose setae, and coxa with 5-8 plumose setae.

Second maxilliped (Fig. 5.6g)—Endopod consisting of 5 segments of sub-equal length bearing 4,1,0,2,4 or 5 setae. All setae plumose on median edge, except for 1 lateral plumose seta on segment 1, and 3 or 4 terminal, sparsely plumose setae, and 1 naked lateral seta on distal segment. Otherwise as in stage I.

Third maxilliped (Fig. 5.6h)—Endopod 5-segmented, length ratios 1:1:1:1:0.5 carrying 2,1 or 2,0,2,4 setae respectively. All setae plumose on median edge, except 1 lateral plumose seta sometimes occurring on segment 2, and setae of distal segment arranged as in stage I. Otherwise as in stage I.

First cheliped (Fig. 5.6i)—Well-developed biramous bud.

Second cheliped—Absent or small uniramous bud.

Stage III (Fig. 5.3c)

Duration of stage: 3-4 days

Carapace (Figs. 5.3c, 5.4c$_1$)—Supraorbital spine, suborbital angle more spine like, pterygostomial spine.

Abdomen (Fig. 5.3c)—Six segments, last distinct from telson.

Tail (Fig. 5.4c)—Outer uropod well developed with 6 plumose setae. Inner uropod rudimentary, occasionally with 1 or 2 setae terminally. Telson with 8+8 plumose setae, median indentation less pronounced than in stage II.

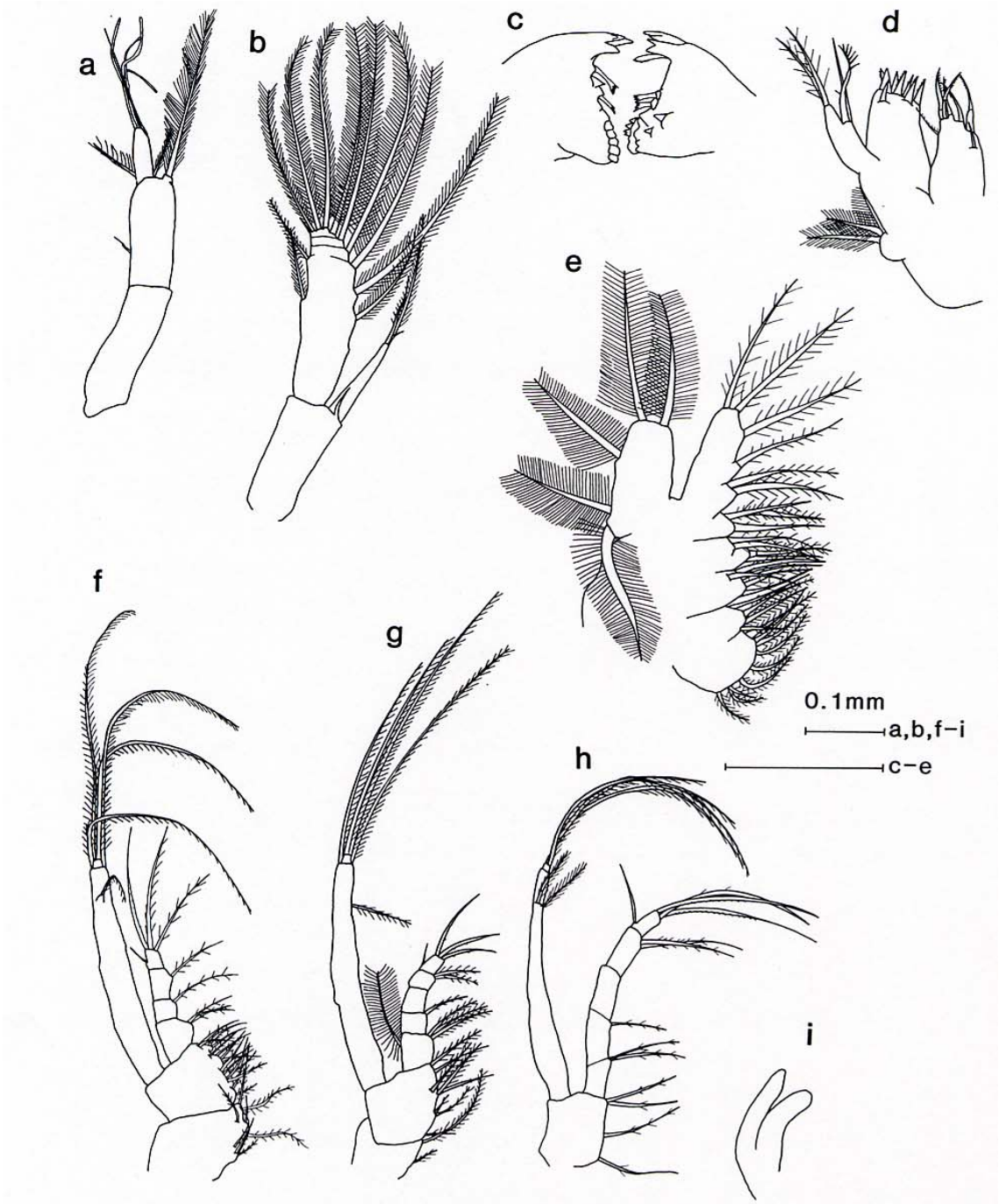


Fig. 5.6. *Paratya australiensis*, stage II. (a) first antenna (b) second antenna (c) mandibles (d) first maxilla (e) second maxilla (f) first maxilliped (g) second maxilliped (h) third maxilliped (i) first cheliped

First antenna (Fig. 5.7a)—Peduncle 3-segmented. Proximal segment with stylocerite forming a lateral bulge bearing 1 plumose seta. This segment bears 1 median and 2 lateral plumose setae. Segment 2 with 1 median plumose seta proximally and, at distal margin, 1 median, 1 lateral and 1 dorsal plumose setae. Segment 3 with 2 plumose setae along distal margin ventrally and 3-4 plumose setae dorsally. Median flagellum consisting of a single segment with a long, stout plumose seta distally. Lateral flagellum unsegmented with a subterminal plumose seta, and 1 plumose seta and 1 aesthete terminally.

Second antenna (Fig. 5.7b)—Scaphocerite 2 or 3-segmented, bearing 11-13 plumose setae: two small plumose setae laterally and 9-11 setae medially to laterodistal spine. Flagellum bearing 2 naked setae distally.

Mandibles (Fig. 5.7c)—Left molar process with 6-12 fine marginal teeth, with an irregular array of teeth proximally. Irregular lacinia mobilis with 2 spines in spine row, with a spinose tooth more laterally. Incisor process with 4-7 teeth. Right molar process with 6 or 7 ridges. Lacinia mobilis 3- or 4-toothed with 2 spines in spine row. Incisor process as in stage II.

First maxilla (Fig. 5.7d)—Exopod and endopod as in stage II. Basal endite with 8 or 9 terminal spines and 1 subterminal spine. Coxal endite with 5 terminal plumose setae, a stout, plumose seta and a naked seta medially, and a small plumose seta laterally.

Second maxilla (Fig. 5.7e)—Scaphognathite bearing 6 or 7 plumose setae. Endopod as in stage II. Basal endite: distal lobe with 5 or 6 plumose setae, proximal lobe with 5 plumose setae. Coxal endite: distal and proximal lobes with 4 and 11 plumose setae respectively.

First maxilliped (Fig. 5.7f)—Hairs on lateral margin of proximal 3 endopod segments. Basis with 17-20 plumose setae and coxa with 5 or 6 plumose setae. Otherwise as in stage II.

Second maxilliped (Fig. 5.7g)—Endopod as in stage II, except second segment sometimes bearing a plumose seta laterally. Otherwise as in stage II.

Third maxilliped (Fig. 5.7h)—As in stage II, but second segment always bearing a plumose seta laterally and third segment occasionally bearing a plumose seta laterally.

First cheliped (Fig. 5.7i)—In some specimens, well-developed biramous buds. In most specimens, a segmented biramous appendage with exopod as in maxillipeds. Endopod 5-segmented, length ratios 1:1:1:1:0.5, carrying 2,0,0,2,3 naked or sparsely plumose setae respectively. Protopod with 0 or 1 setae.

Second cheliped (Fig. 5.7j)—Well-developed biramous bud.

Third Pereiopod—Absent or small uniramous bud.

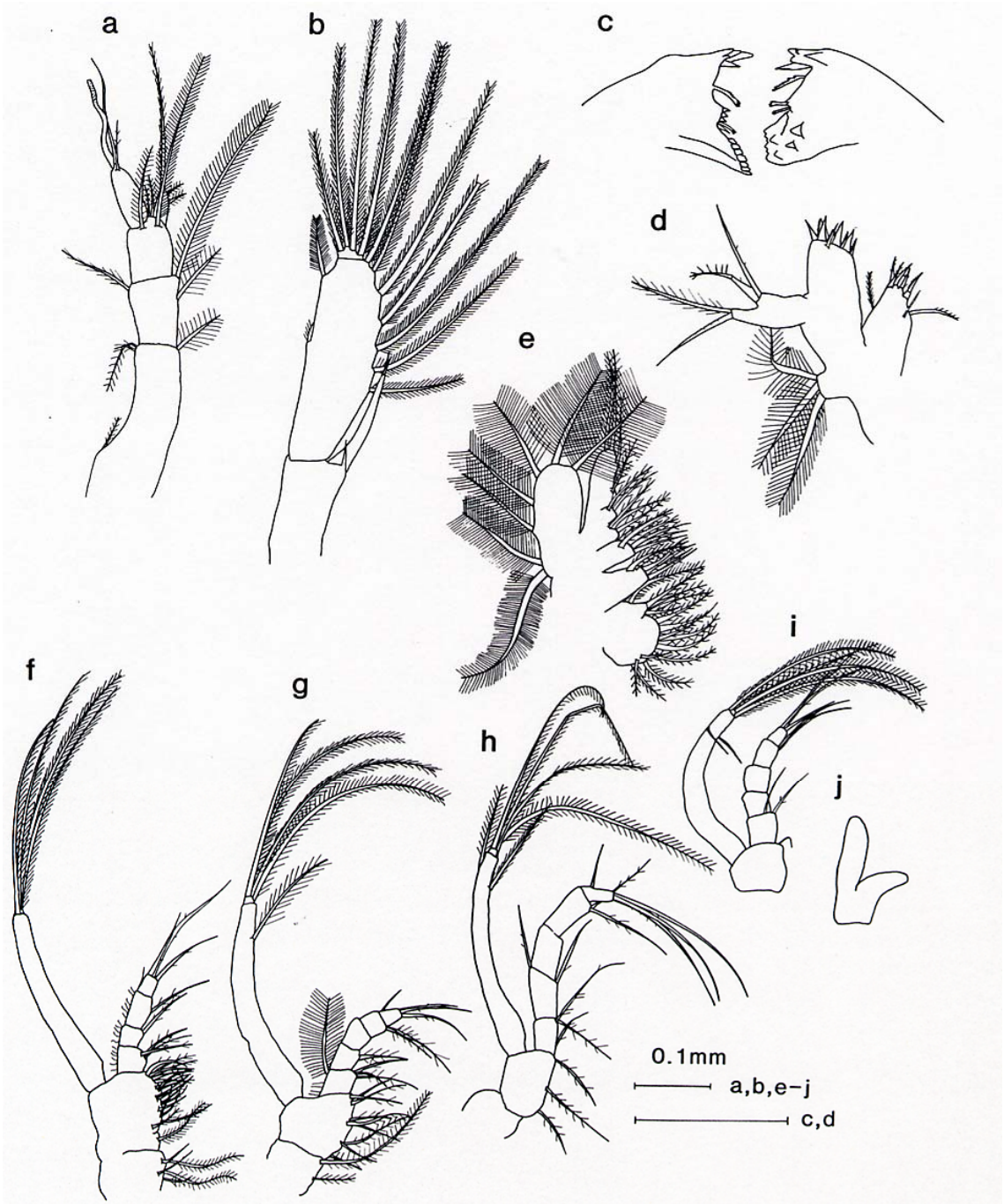


Fig. 5.7. *Paratya australiensis*, stage III. (a) first antenna (b) second antenna (c) mandibles (d) first maxilla (e) second maxilla (f) first maxilliped (g) second maxilliped (h) third maxilliped (i) first cheliped (j) second cheliped

Stage IV (Fig. 5.3d)

Duration of stage: 3-5 days

Carapace (Figs. 5.3d, 5.4d$_1$)—As in stage III, but with a suborbital spine.

Abdomen (Fig. 5.3d)—As in stage III.

Tail (Fig. 5.4d)—Outer uropod with laterodistal spine and 9 or 10 marginal plumose setae medially, often with 1 or 2 fine setae on ventral surface. Inner uropod with 6 or 7 plumose setae around distal and median margins, with 2 or 3 fine setae on lateral margin. Telson broadening posteriorly, with slight median indentation. Five plus five plumose setae along distal margin with 2 spines at posterior corners and 1 on lateral margin.

First antenna (Fig. 5.8a)—Stylocerite as in stage III. Proximal segment bearing a spine ventrally, 1 or 2 setae on median margin, 3 or 4 setae at laterodistal margin, and 2 setae on dorsodistal margin. Second segment with 2 setae on median margin, 2 setae at laterodistal margin, and 2 setae on dorsodistal margin. At distal edge of third segment, 4 setae ventrally,4 dorsally, and one naked seta laterally (all other setae being plumose). Median flagellum as in stage III. Lateral flagellum as in stage III, but 2 aesthetes terminally.

Second antenna (Fig. 5.8b)—Scaphocerite unsegmented, bearing a small plumose seta on midlateral margin, and 13 or 14 plumose setae medially to laterodistal spine. Flagellum as in stage III.

Mandibles (Fig. 5.8c)—Left molar process with 3 or 4 rows of fine teeth with an irregular array of teeth proximally. Lacinia mobilis irregular with 3 spines in spine row. Incisor process as in stage III. Right molar process with 7-9 ridges. Lacinia mobilis 3- or 4-toothed. Four spines in spine row. Incisor process as in stage III.

First maxilla (Fig. 5.8d)—As in stage III, but basal endite with 10 terminal spines and coxal endite with 6 terminal plumose setae.

Second maxilla (Fig. 5.8e)—Scaphognathite with 8 plumose setae. Proximal lobe of coxal endite with 14 setae. Otherwise as in stage III.

First maxilliped (Fig. 5.8f)—Basis with 19-21 plumose setae and coxa with 7 or 8 plumose setae. Otherwise as in stage III.

Second maxilliped (Fig. 5.8g)—Lateral plumose seta always present on second segment of endopod. Third segment with 0 or 1 lateral plumose setae, and fifth segment with 4 or 5 terminal plumose setae. Otherwise as in stage III.

Third maxilliped (Fig. 5.8h)—As in stage III.

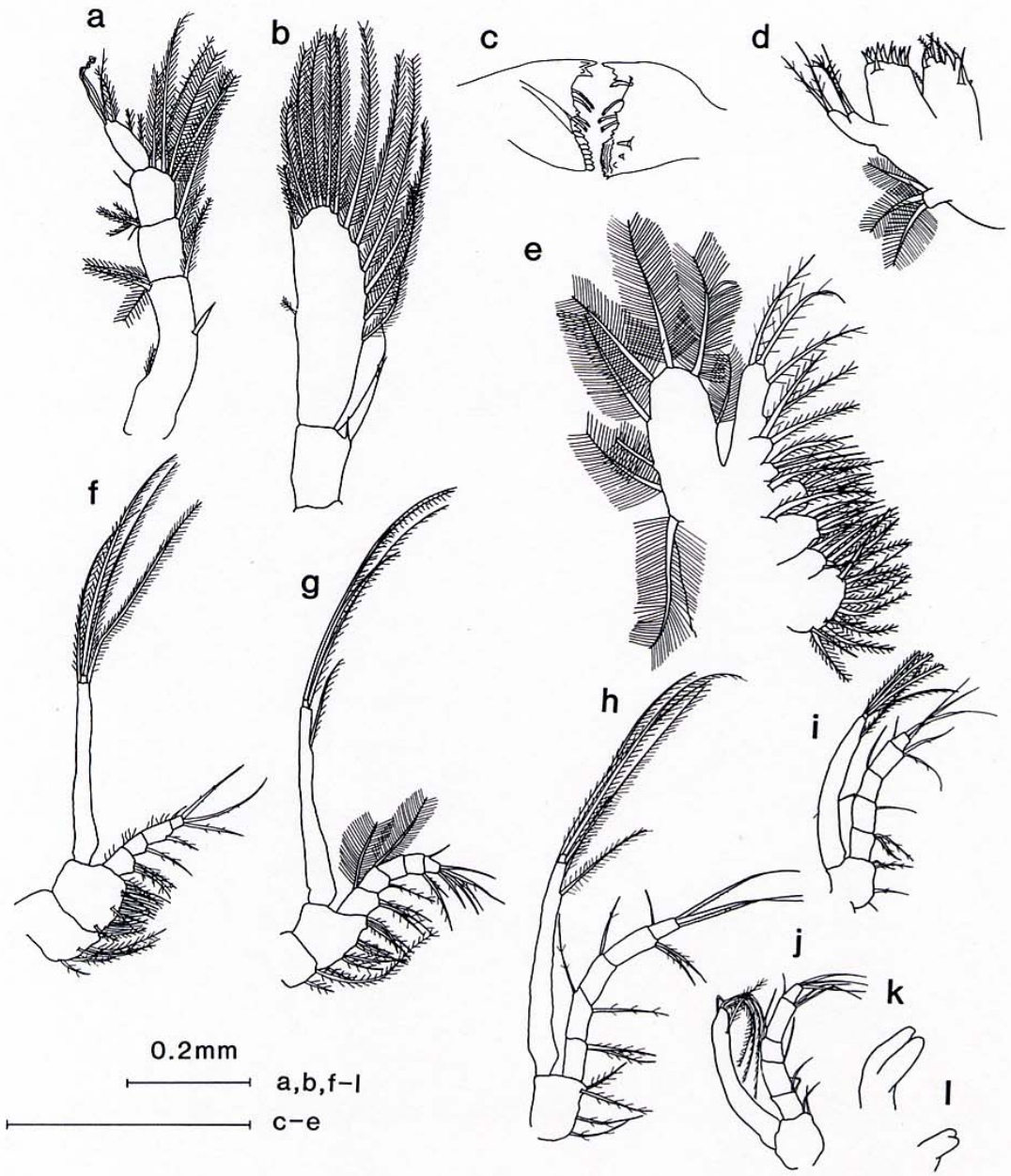


Fig. 5.8. *Paratya australiensis*, stage IV. (a) first antenna, latero-ventral view (b) second antenna (c) mandibles (d) first maxilla (e) second maxilla (f) first maxilliped (g) second maxilliped (h) third maxilliped (i) first cheliped (j) second cheliped (k) third pereiopod (l) fourth pereiopod

First cheliped (Fig. 5.8i)—Exopod as in maxillipeds, but proximal pair of setae always present. Setae of endopod naked or sparsely plumose, arranged thus: segment 1, 2 medially; segment 2, 1 medially and 0 or 1 laterally; segment 3, 0 or 1 medially and 1 laterally; segment 4, 2 medially; segment 5, 3 terminally and 1 laterally. Protopod with 2-4 setae.

Second cheliped (Fig. 5.8j)—Exopod as in first pereiopod. Endopod 5-segmented. Naked setae arranged thus: segment 1, 0-2 medially; segment 2, 0 or 1 medially; segment 3, 0 or 1 laterally; segment 4, 1 or 2 medially; segment 5, 2 or 3 terminally and 1 laterally. Protopod with 1-4 naked setae.

Third pereiopod (Fig. 5.8k)—Well developed biramous bud.

Fourth pereiopod (Fig. 5.8l)—Small uni- or biramous bud.

Stage V (Fig. 5.3e)

Duration of stage: 3-4 (occasionally 5-6) days

(occasionally maintained through a mark-time moult).

Carapace (Fig. 5.3e)—As in stage IV.

Abdomen (Fig. 5.3e)—As in stage IV.

Tail (Fig. 5.4e)—Outer uropod with 1 or 2 fine setae and a spine laterodistally, and 12-14 marginal plumose setae medially, with 1 or 2 fine setae on ventral surface. Inner uropod with 8-11 plumose setae around distal and median margins, with 3-6 fine setae on lateral margin, and 1 or 2 setae on dorsal surface. Telson broadening slightly posteriorly, with no median indentation. Five plus five plumose setae along distal margin with 1 spine at posterior corner and 2 on lateral margin.

First antenna (Fig. 5.9a)—Stylocerite as in stage IV, but bearing 2 setae. First segment with a ventral spine, 3 setae on median margin and 2 or 3 setae dorsodistally, and 2 or 3 laterodistally. 4 or 5 setae along dorsal side of distal margin. Second segment as in stage IV. Third segment as in stage IV, but 5 setae ventrodistally. Median flagellum as in stage IV. Lateral flagellum as in stage IV, but with 2 or 3 terminal aesthetes.

Second antenna (Fig. 5.9b)—Scaphocerite with a small naked seta midlaterally, a laterodistal spine, and 15 or 16 plumose setae. Flagellum bearing 1-3 naked setae terminally.

Mandibles (Fig. 5.9c)—Left molar process with 4 or 5 rows of fine teeth with an irregular array of 8-10 teeth proximally. Lacinia mobilis and spine row as in stage IV. Incisor process as in stage IV. Right molar process with 10-12 ridges. Lacinia mobilis irregular. Four or five spines in spine row. Incisor process as in stage IV.

Fig. 5.9. *Paratya australiensis*, stage V. (a) first antenna, latero-ventral view (b) second antenna (c) mandibles (d) first maxilla (e) second maxilla (f) first maxilliped (g) second maxilliped (h) third maxilliped (i) first cheliped (j) second cheliped (k) third pereiopod (l) fourth pereiopod (m)fifth pereiopod

First maxilla (Fig. 5.9d)—Exopod reduced to a small lump. Endopod as in stage IV. Basal endite with 10 or 11 terminal spines and 1 subterminal spine. Coxal endite with 6 plumose setae distally, 2 plumose setae and 1 naked seta laterally, and 1 plumose seta medially.

Second maxilla (Fig. 5.9e)—Scaphognathite with 11-14 plumose setae along margin. Endopod as in stage IV, but distal lobe with 1 or 2 plumose setae. Basal endite: distal lobe as in stage IV, proximal lobe with 6 or 7 plumose setae. Coxal endite as in stage IV.

First maxilliped (Fig. 5.9f)—Proximal segment of endopod with 4 plumose setae. Basis bearing 20-24 plumose setae. Otherwise as in stage IV.

Second maxilliped (Fig. 5.9g)—As in stage IV, but third segment of endopod always with a plumose seta laterally, and 0 or 1 naked setae laterally.

Third maxilliped (Fig. 5.9h)—As in stage IV, but segment ratios of endopod 0.5:1:1:1:0.5, third segment with 1 naked seta medially. Basis and coxa with 4 and 1 plumose setae respectively.

Chelipeds (Fig. 5.9i, j)—Exopods as in stage IV, but with an additional pair of setae proximally. Plumose setae arranged on endopods thus: segment 1, 2 median; segment 2, 1 medially, 1 laterally; segment 3, 1 medially on first cheliped, 1 laterally; segment 4, 2 medially; segment 5, 3 terminally and 1 naked laterally. Protopod with 2-4 median plumose setae.

Third pereiopod (Fig. 5.9k)—In some specimens endopod and exopod single segments each with 2 terminal setae; setae plumose on exopod, naked on endopod. In most cases, exopod as in maxillipeds, and endopod 4-segmented with setae arranged thus: segment 1, 2 naked medially; segment 2, 0 or 1 naked laterally; segment 3, 2 plumose medially: segment 4, 2 naked and 1 plumose terminally, and 1 naked laterally. Protopod with 0 or 1 naked setae.

Fourth pereiopod (Fig. 5.9l)—Exopod a single segment with 0-2 terminal setae. Endopod a single segment without setae. Protopod without setae.

Fifth pereiopod (Fig. 5.9m)—Simple biramous bud.

Stage VI (Fig. 5.3f)

Duration of stage: 3-7 days (occasionally maintained through a mark-time moult).

Carapace (Fig. 5.3f)—As in stage V.

Abdomen (Fig. 5.3f)—As in stage V.

Tail (Fig. 5.4f)—Outer uropod with 1 or 2 fine setae and a spine laterodistally, and 15-18 marginal plumose setae medially, with 3-5 fine setae on ventral surface. Inner uropod with 10-15 plumose setae around distal and median margins, with 6 or 7 fine setae on lateral margin, and 2-5 setae on dorsal surface. Telson elongate, broadest at one third of length from posterior margin. Spinal arrangement as in stage V.

First Antenna (Fig. 5.10a)—Stylocerite a pronounced lateral projection bearing 3 or 4 plumose setae. First segment with a ventral spine, 4 or 5 setae on median margin and 2 or 3 setae dorsally. At distal margin, 9 or 10 plumose setae along dorsal side. Second segment as in stage V, but occasionally with a third median seta. Third segment as in stage V, but 6 setae ventrodistally. Median flagellum 1- or 2-segmented, bearing a long plumose seta, and a short naked seta. Lateral flagellum 1- or 2-segmented bearing 2 terminal plumose setae and 3 subterminal aesthetes.

Second antenna (Fig. 5.10b) —Scaphocerite with 0 or 1 small naked seta midlaterally, a laterodistal spine and 17-19 plumose setae. Flagellum 2-segmented, bearing 1-4 naked setae terminally.

Mandibles (Fig. 5.10c)—Left molar process as in stage V. Lacinia mobilis irregular with 4 or 5 spines in spine row. Incisor process as in stage V. Right molar process as in stage V. Lacinia mobilis irregular. Six or seven spines in spine row. Incisor process as in stage V.

First maxilla (Fig. 5.10d)—As in stage V, but basal endite with 11 terminal spines and 1 subterminal spine.

Second maxilla (Fig. 5.10e)—Scaphognathite with 18-21 plumose setae along margin, proximal edge elongated to form a lobe. Endopod as in stage V. Basal endite: distal and proximal lobes each with 6 or 7 plumose setae. Coxal endite: distal lobe with 4 or 5 plumose setae, proximal lobe with 14-16 plumose setae. Otherwise as in stage V.

First maxilliped (Fig. 5.10f)—As in stage V.

Second maxilliped (Fig. 5.10g)—As in stage V.

Third maxilliped (Fig. 5.10h)—Endopod as in stage V but 1 median plumose seta on segment 3; 0 or 1 naked setae on segment 4; 0 or 1 lateral naked setae on segment 5. Otherwise as in stage V.

Chelipeds (Fig. 5.10i, j)—As in stage V, but first cheliped with a lateral naked seta on segment 4, and 4 terminal setae on segment 5. Protopods bearing 4 or 5 plumose setae.

Pereiopods (Fig. 5.10k, l, m)—Third and fourth pairs: exopods as in maxillipeds. Endopods 5-segmented, bearing 1 or 2,1,0,2 median plumose setae on 4 proximal segments, with 3 naked or sparsely plumose setae terminally, and 1 naked seta laterally on distal segment. Protopod with 1-3 naked or sparsely plumose setae. The fourth pereiopod in some specimens: unsegmented exopod with 2 terminal plumose setae and unsegmented endopod with 2 or 3 terminal naked setae. Fifth pereiopod with unsegmented exopod and endopod each bearing 0-2 terminal setae.

Pleopods (Fig. 5.10n, o)—Well developed biramous buds.

Stage VII (Fig. 5.3g)

Duration of stage: 3-5 days (often maintained through a 'mark-time' moult).

Carapace (Fig. 5.3g, 5.4g$_1$)—As in stage VI, but with 2 fine setae on dorsal edge of rostrum.

Abdomen (Fig. 5.3f)—As in stage VI.

Tail (Fig. 5.4g)—Outer uropod with 2 or 3 fine setae lateroproximally, 4 or 5 fine setae and a spine laterodistally, 17-23 marginal plumose setae, and 5 or 6 fine setae on ventral surface. Inner uropod with 13-16 plumose setae around distal and median margins, with 10 fine setae on lateral margin, and 7-9 fine setae on dorsal surface. Telson elongate, rectangular to ellipsoid. Spinal arrangement as in stage VI.

First Antenna (Fig. 5.11a)—Stylocerite an angular projection bearing 4 or 5 plumose setae. First segment as in stage VI, but with 4 or 5 setae on median margin. Second segment with 2 or 3 setae along median margin and 6 or 7 setae dorsodistally. Third segment as in stage VI. Median flagellum 2-segmented, bearing a long plumose seta, and 3 short naked setae terminally. Lateral flagellum 2-segmented with distal segment bearing 1 naked and 2 plumose setae terminally and 3 subterminal aesthetes.

Second antenna (Fig. 5.11b)—Scaphocerite with a laterodistal spine and 17-19 plumose setae. Flagellum 4-segmented, distal segment bearing 4 naked setae terminally. Scaphocerite and flagellum lengths sub-equal.

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Fig. 5.10. *Paratya australiensis*, stage VI. (a) first antenna, ventral view (b) second antenna (c) mandibles (d) first maxilla (e) second maxilla (f) first maxilliped (g) second maxilliped (h) third maxilliped (i) first cheliped (j) second cheliped (k) third pereiopod (l) fourth pereiopod (m) fifth pereiopod (n) first pleopod (o) fourth pleopod


a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
0.2mm
a,b,f–o
e
c,d

Mandibles (Fig. 5.11c)—Left molar process 6-8 ridges of fine teeth with an irregular array of 8-13 teeth behind. Lacinia mobilis irregular, with 5 or 6 spines in spine row. Incisor process as in stage VI. Right mandible as in stage VI.

First maxilla (Fig. 5.11d)—As in stage VI, but basal endite with 13 terminal spines and 1 subterminal spine, and coxal endite with a second median naked seta .

Second maxilla (Fig. 5.11e)—Scaphognathite with 20-24 plumose setae along margin. Endopod as in stage VI. Basal endite: distal lobe with 6 or 7 plumose setae, proximal lobe with 7 or 8 plumose setae. Coxal endite: distal lobe with 5 plumose setae, proximal lobe with 16 plumose setae..

First maxilliped (Fig. 5.11f)—As in stage VI, but first segment occasionally bearing a lateral plumose seta.

Second maxilliped (Fig. 5.11g)—As in stage VI, but fourth segment bearing a lateral naked seta.

Third maxilliped (Fig. 5.11h)—As in stage VI, but fourth segment bearing a median naked seta subterminally.

Chelipeds (Fig. 5.11i, j)—As in stage VI, but fifth segment bearing 4 terminal setae, and no lateral seta. Mediodistal edge of fourth segment expanded distally to form rudimentary chelae.

Pereiopods (Fig. 5.11k, l, m)—Third and fourth pairs: exopods as in maxillipeds, and endopods 5-segmented. Segment 1 bearing 1 or 2 median setae: segment 2 with 1 median and 1 lateral seta; segment 3 with 1 median and 0 or 1 lateral setae; segment 4 with 2 median and 0-2 lateral plumose setae; segment 5 with 3 or 4 naked or sparsely plumose setae terminally. Protopod with 3-5 naked or sparsely plumose setae. Fifth pereiopod: 1-segmented exopod bearing 2 naked and 4 plumose terminal setae. Five-segmented endopod. Segment 1 with 1-3 median setae; segment 2 with 0 or 1 lateral setae; segment 3 with 0 or 1 lateral and 1 median setae; segment 4 with 1 or 2 median setae; segment 5 with 3 terminal setae. Protopod with 0 or 1 setae.

Pleopods (Fig. 5.11n, o)—Exopods with 0-4 naked setae terminally. Endopod of first pleopod reduced. In others, endopod with 0-2 naked terminal setae.

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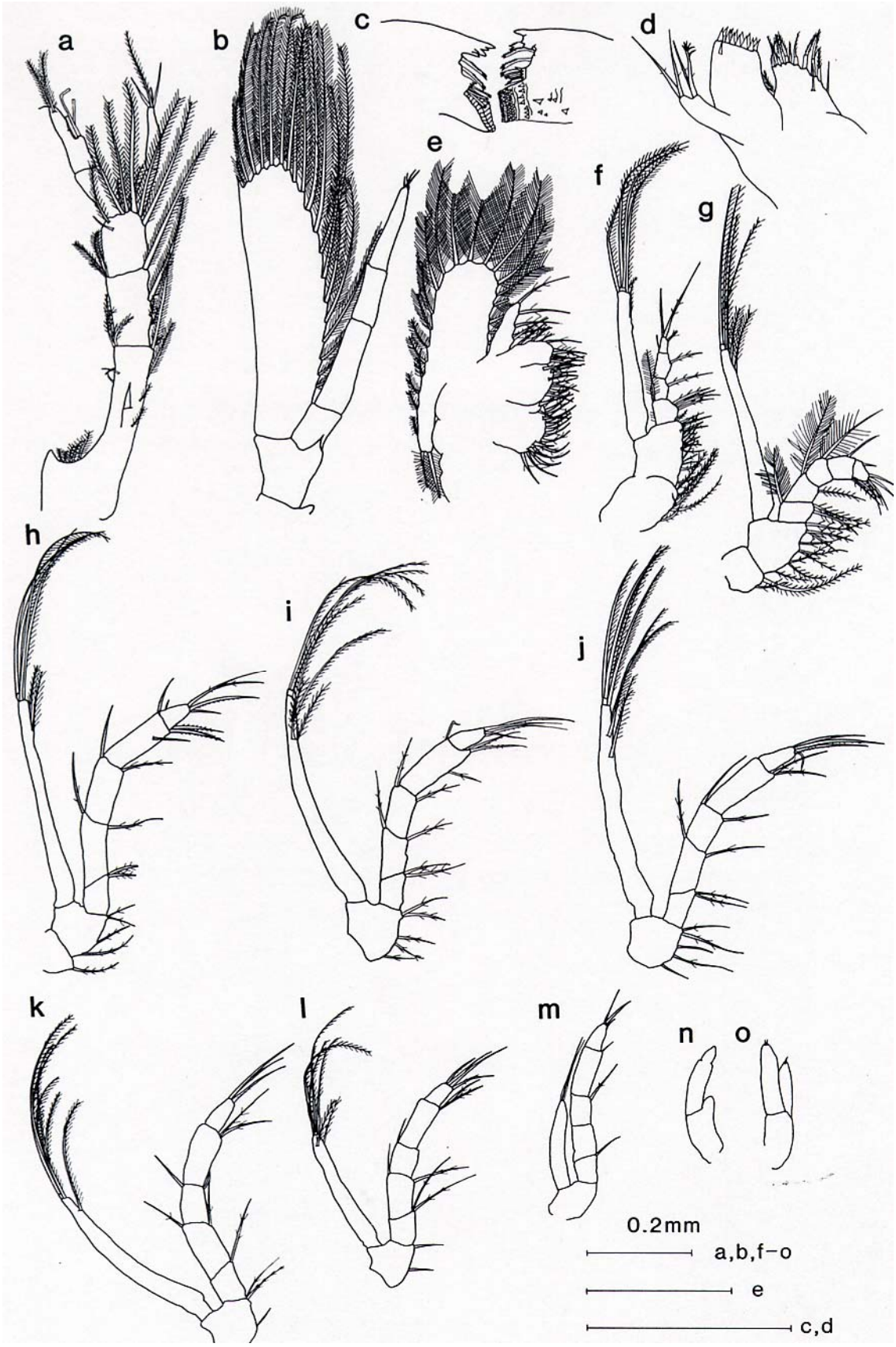
Fig. 5.11. *Paratya australiensis*, stage VII. (a) first antenna, ventral view (b) second antenna (c) mandibles (d) first maxilla (e) second maxilla (f) first maxilliped (g) second maxilliped (h) third maxilliped (i) first cheliped (j) second cheliped (k) third pereiopod (l) fourth pereiopod (m) fifth pereiopod (n) first pleopod (o) fourth pleopod


a
b
c
d
e
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g
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k
l
m
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o
0.2mm
a,b,f–o
e
c,d

Stage VIII (Fig. 5.3h)

Duration of stage: 3-5 days (occasionally maintained through a mark-time moult, and occasionally skipped with a juvenile developing directly from stage VII).

Carapace (Figs. 5.3h, 5.4h$_1$)—As in stage VII, but with 3 fine setae on dorsal edge of rostrum.

Abdomen (Fig. 5.3h)—As in stage VII.

Tail (Fig. 5.4h)—Outer uropod with 2 or 3 fine setae lateroproximally, 4 or 5 fine setae midlaterally and a fine seta and a spine laterodistally; 21-26 marginal plumose setae medially, with 5 or 6 fine setae on ventral surface. Inner uropod with 17 or 18 plumose setae around distal and median margins, with 8-10 fine setae on lateral margin, and 7-9 fine setae on dorsal surface. Telson elongate and rectangular. Spinal arrangement as in stage VII.

First Antenna (as in Fig. 5.12a) —Stylocerite sharply pointed bearing 9 or 10 plumose setae. First segment as in stage VII but with 5 or 6 setae on median margin and 7 or 8 dorsally. Second segment with 3 plumose setae along median margin and 7 or 8 setae along dorsodistal edge. Third segment as in stage VII. Median flagellum 2- to 4-segmented, bearing 3 terminal naked seta. Lateral flagellum 2- to 4-segmented. Second or proximal segment with 1 or 2 aesthetes, and 0 or 1 naked seta medio-distally. Next segment with 2 or 3 aesthetes medially, and 1 plumose seta distally. Distal segment bearing 3 subterminal naked setae.

Second antenna (as in Fig. 5.12b)—Peduncle 2-segmented; 1 bearing scaphocerite, 1 bearing flagellum and, in some specimens, ventral spine. Scaphocerite with laterodistal spine and 19-21 plumose setae. Flagellum 8-10-segmented, distal segment bearing 4 naked setae terminally, and a naked seta at distal edge of some segments. Scaphocerite: flagellum length ratio, 0.6-0.8.

Mandibles (as in Fig. 5.12c)—Left molar process as in stage VII. Six or seven spines in spine row. Incisor process with 6-8 teeth. Right molar process with 12-16 ridges. Six to eight spines in spine row. Incisor process as in stage VII.

First maxilla (as in Fig. 5.12d)—Endopod as in stage VII, or more palp-like with a naked seta terminally, and a plumose and a naked seta subterminally. Basal endite with 13 terminal spines, 2 subterminal spines, and 1 naked seta medially. Coxal endite with 12 plumose setae along distal edge, 1 naked seta subterminally and 2 plumose setae laterally.

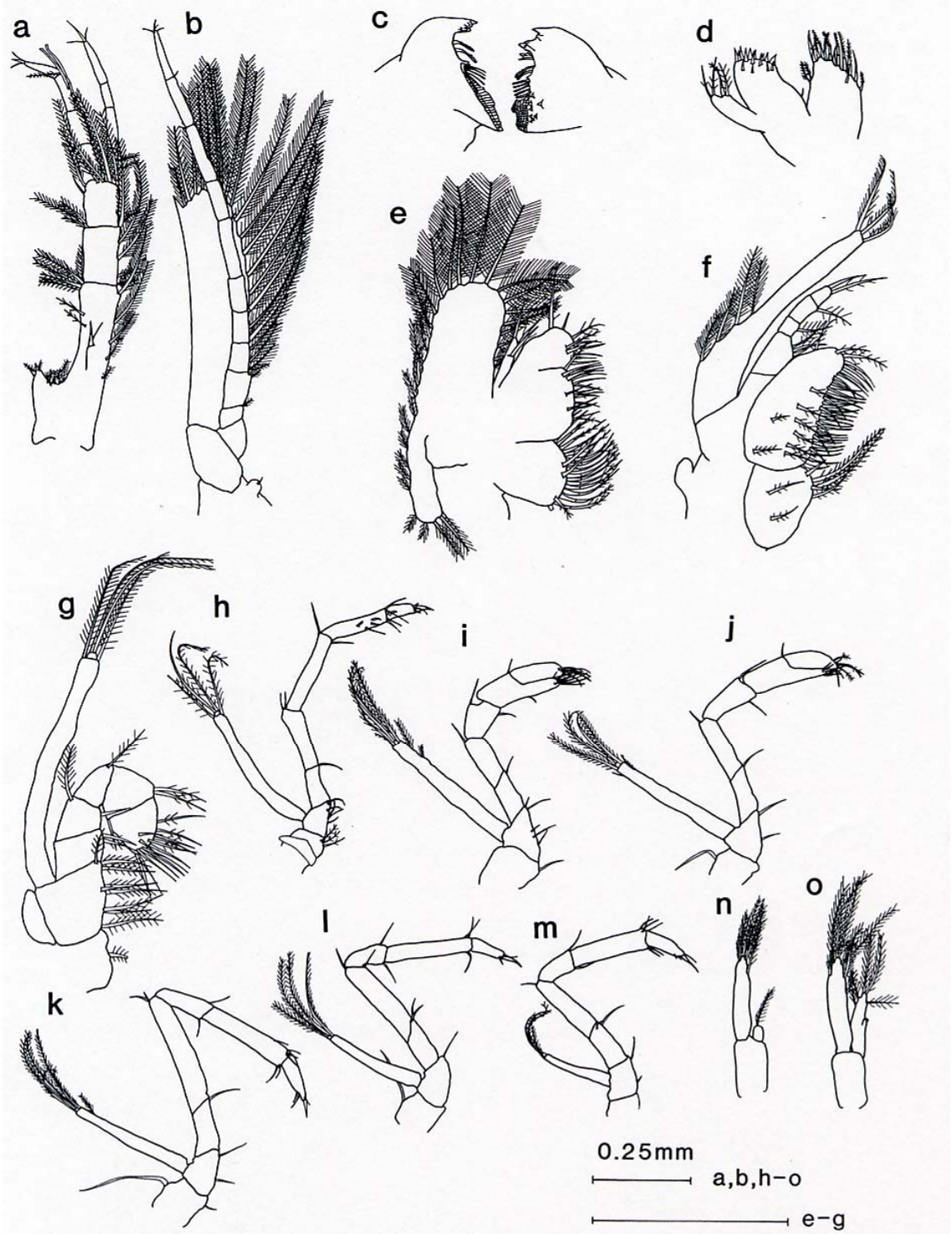

Fig. 5.12. *Paratya australiensis*, juvenile after seventh molt (a) first antenna, ventral view (b) second antenna (c) mandibles (d) first maxilla (e) second maxilla (f) first maxilliped (g) second maxilliped (h) third maxilliped (i) first cheliped (j) second cheliped (k) third pereiopod (l) fourth pereiopod (m) fifth pereiopod (n) first pleopod (o) Fourth pleopod

Second maxilla (as in Fig. 5.12e)—Scaphognathite with 22-31 plumose setae along margin. Endopod obscured by basal endite, with 4 or 5 lobes. Distal 3 segments bearing 1 plumose seta each. Proximal 1 or 2 lobes bearing 2 or 3 setae. Basal endite: distal lobe with 1 naked and 1 plumose seta directed anteriorly and 6-8 plumose setae medially. Proximal lobe with 10-17 plumose setae. Coxal endite: distal lobe with 5 plumose setae, obscured by basal endite. Proximal lobe with 20 plumose setae.

First maxilliped—Exopod as in stage VII. Endopod: proximal segment expanded bearing 3 or 4 plumose setae medially and 0 or 1 laterally. Segments 2 and 3 each bearing 1 plumose median seta Distal segment bearing 2 or 3 terminal setae. Basis expanded with 26-30 marginal plumose setae and 4-8 plumose setae on ventral surface. Coxa expanded with 7 or 8 plumose setae.

Second maxilliped—Exopod as in stage VII. Distal 2 segments of endopod dilated and directed posteriorly. Proximal 3 segments as in stage VII, but lateral seta of first segment sometimes absent. Fourth segment with 1 or 2 naked setae medially and 1 or 2 plumose setae laterally. Distal segment with 7-11 setae around terminal margin. Basis and coxa as in stage VII.

Third maxilliped—Exopod as in stage VII. Segment 1, 2-4 median setae; segment 2, 0 or 1 median and 1 or 2 lateral setae; segment 3, 1 or 2 median and 1 or 2 lateral setae; segment 4, 4 setae along midlength, of which 2 or 3 spinelike and, at distal edge, 1 or 2 setae medially and 1 or 2 laterally; segment 5, 1 spine-like seta proximally and a spine and 3 setae terminally. Basis with 4 or 5 setae and coxa with 1-3 setae.

Chelipeds—Exopod as in stage VII. Endopod almost fully formed, with dactylus and propodus distinct. Ischium with 1 or 2 median setae. Merus with 0 or 1 median and 1 lateral seta. Carpus with 1 median and 1 lateral seta. Propodus with 1 lateral and 1 or 2 median setae. Distal ends of propodus and dactylus with 3-7 and 4-7 setae respectively. Basis with 5 median setae on first cheliped, and 2-4 on second. Coxa with 1 or 2 median setae on first cheliped, and 1 median and 1 lateral seta on second cheliped.

Pereiopods—As in third and fourth pairs of stage VII, but with 1 or 2 setae laterally on merus and carpus, and with 2-4 setae laterally on propodus. Dactylus with 1 spine and 2 or 3 setae terminally. Basis with 1-4 setae. Coxa with 0 or 1 median and 1 large lateral seta in third and fourth periopods. No setae on coxa of fifth pereiopod.

Pleopods (as in Fig. 5.12n, o)—Exopods with 3 or 4 pairs of plumose setae. Endopod of first pleopod reduced with a terminal plumose seta. In others, endopod with 2 or 3 pairs of plumose setae, appendix interna with 2 hooks.

Juvenile

The appendages of a juvenile after 7 ecdyses are illustrated in Fig. 5.12. The antennae, mandibles and maxillae of this specimen (Fig. 5.12a-e) were of the form of a stage VIII larva. The maxillipeds (Fig. 5.12f-h) were more specialized feeding appendages with reduced exopods. In particular, the exopod of the first maxilliped (Fig. 5.12f) was a single segment, expanded at the base, with 3 terminal and 4 lateral plumose setae. The ratios of exopod: endopod lengths for the chelipeds were 0.7 (Fig. 5.12i,j) and for pereiopods 3, 4 and 5, were 0.3, 0.3, and 0.25 respectively (Fig. 5.12k-m). Juveniles metamorphosing after stage VIII had a longer flagellum on the second antenna than those metamorphosing after stage VII.

5.3.2. EFFECT OF SALINITY ON LARVAL DEVELOPMENT

5.3.2.1. *M. INTERMEDIUM*

The proportion of *M. intermedium* larvae surviving to metamorphosis was significantly affected by rearing salinity (G=6.25, P=0.044). Ninety-two percent, 99% and 93% of larvae survived to metamorphosis at salinities of 15, 25, and 35 respectively. Survival at 25 was significantly higher than at 15 (G=5.62, P=0.018), but was not significantly higher than at 35 (G=4.34, P=0.037 NS). Most deaths at 15 occurred before stage IV was reached, while no deaths occurred at 35 until after the fifth ecdysis (Fig. 5.13).

Mean (± SD) number of ecdyses to metamorphosis for *M. intermedium* in the laboratory was 7.3 ± 0.8 at salinity 15, 7.1 ± 0.8 at 25, 8.0 ± 1.0 at 35 (Fig. 5.14). The number of ecdyses was significantly greater at 35 than at 15 or 25 (F=51.8, P<0.001; Tukey's test, P<0.001 for both comparisons), but no difference was detected between larvae reared at 15 and those at 25 (P<0.089). Larval development lasted a mean (± SD) of 26.3 ± 4.9 days at salinity 15, 23.2 ± 3.3 days at 25, and 29.9 ± 5.4 days at 35 (Fig. 5.14). There were significant differences between all of these means (F=51.8, P<0.001; Tukey's test, P<0.001 for all comparisons). The distributions of log-transformed larval duration at salinities 15 and 35 both included a number of high outliers (Fig. 5.14), with several individuals taking greater than forty days to reach metamorphosis. Removal of these outliers did not alter the results of the analyses. Fig. 5.13 shows that over 60% of all individuals in the 15 and 25 treatments had achieved metamorphosis by the eighth ecdysis, while in the 35 treatment less than 40%had.

Thus *M. intermedium* larvae developed in fewer ecdyses at lower salinities than in sea water, but at the lowest salinity, 15, they took longer to develop than at the intermediate salinity, 25. In seawater, there were more ecdyses and larval development took longer than in either of the lower salinities. Mortality in salinity 15, which was significantly higher than in the intermediate salinity or in seawater, was greatest in the earlier stages. In contrast, most mortality occurred in later stages in sea water.

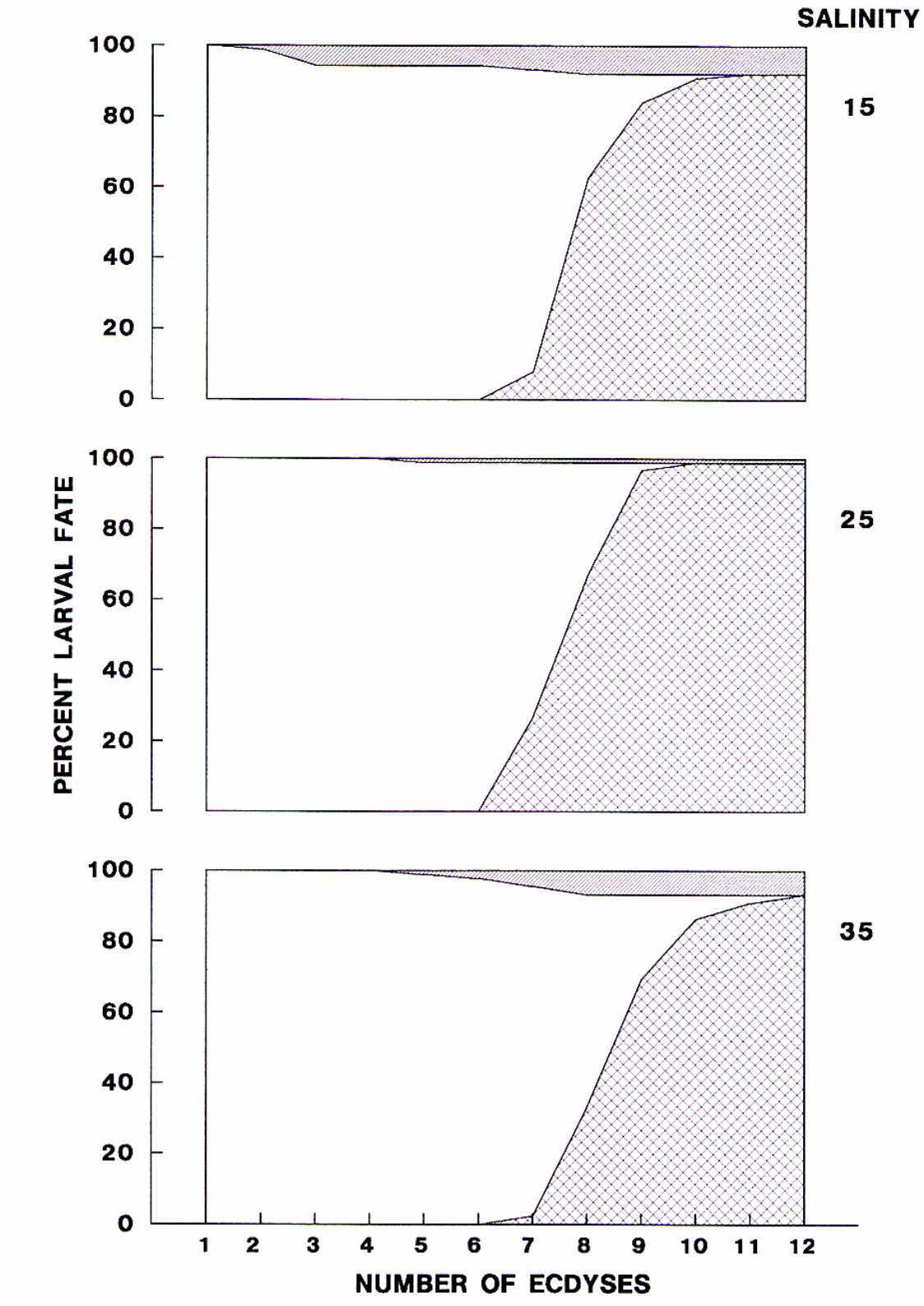

Fig. 5.13. *Macrobrachium intermedium* larvae reared in the laboratory under three salinity conditions—15, 25 and 35—, showing proportion of individuals after each ecdysis that had died (grey), remained larvae (unshaded) or achieved metamorphosis (cross-hatched)

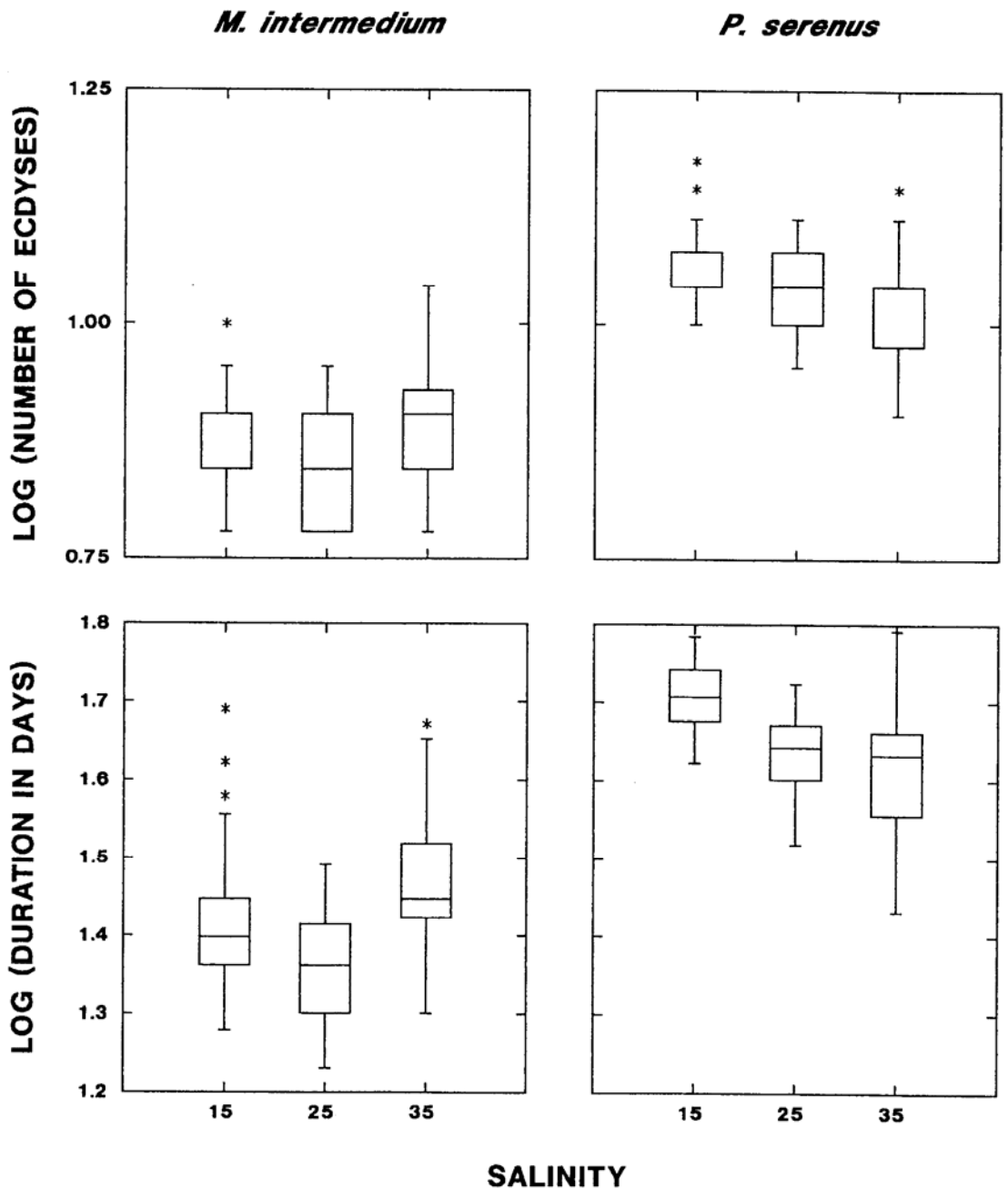

Fig. 5.14. Box plots of number of ecdyses to metamorphosis and duration of larval development in days (both log-transformed) for *Macrobrachium intermedium* and *Palaemon serenus* in the laboratory under three salinity conditions —15, 25, and 35. Box-plot conventions are those of Wilkinson (1990).

5.3.2.2. *P. SERENUS*

The proportion of *P. serenus* larvae surviving to metamorphosis was significantly affected by rearing salinity (G=45.10, P<0.001). Sixteen percent, 47% and 62% of larvae survived to metamorphosis at salinities of 15, 25, and 35 respectively. Survival was higher at 25 than at 15 (G=20.9, P<0.001), but was not significantly higher at 35 than at 25 (G=4.46, P=0.035 NS). The mortality rate in salinity 15 was relatively constant from moult to moult, although many individuals died between the sixth and seventh ecdyses. In contrast, most deaths occurred after the tenth ecdysis in salinities 25 and 35 (Fig. 5.15).

Mean (± SD) number of ecdyses to metamorphosis for *P. serenus* in the laboratory was 11.9 ± 1.4 at salinity 15, 11.0 ± 1.2 at 25, 10.5 ± 1.4 at 35 (Fig. 5.14). The number of ecdyses was significantly greater at 15 than at 35, but the number at 25 was not significantly from that at either 15 or 35 (F=6.4, P=0.002: Tukey's test, 15 vs 35, P=0.002; 25 vs 35, P=0.19 NS; 15 vs 25, P=0.08 NS). Larval development lasted a mean (± SD) of 51.3 ± 5.2 days at salinity 15, 43.6 ± 5.4 days at 25, and 42.0 ± 7.2 days at 35 (Fig. 5.14). Development at 15 took significantly longer at 15 than at either 25 or 35, which were not significantly different (F=11.9, P<0.001: Tukey's test, 15 vs 25, P=0.001; 15 vs 35, P<0.001; 25 vs 35, P=0.32).

Thus *P. serenus* larvae developed in more ecdyses and took longer to reach metamorphosis at salinity 15 than at 25 or 35. Mortality at higher salinities was low until about the tenth ecdysis, after which mortality rate increased, more dramatically at the intermediate salinity (Fig. 5.15). In contrast, mortality at 15, which was significantly greater than at the higher salinities, was reasonably constant through all stages.

5.3.2.3. *P. AUSTRALIENSIS*

At a salinity of 28.8 all *P. australiensis* larvae from JP died between six and fifteen days after hatching (mean ± SD: 10.5 ± 3.5 days). Nineteen percent died after two ecdyses, 50% after three ecdyses, and 31% after four ecdyses. At a salinity of 34.5 all larvae died between three and eleven days after hatching (mean ± SD: 6.9 ± 3.1 days). Nineteen percent died after one ecdysis, 50% after two ecdyses, and 31% after three ecdyses.

The 96 h LC_{50} for early stage *P. australiensis* larvae at 20.3-20.8°C was a salinity of 36.7 with 95% fiducial limits of 36.1 and 37.4.

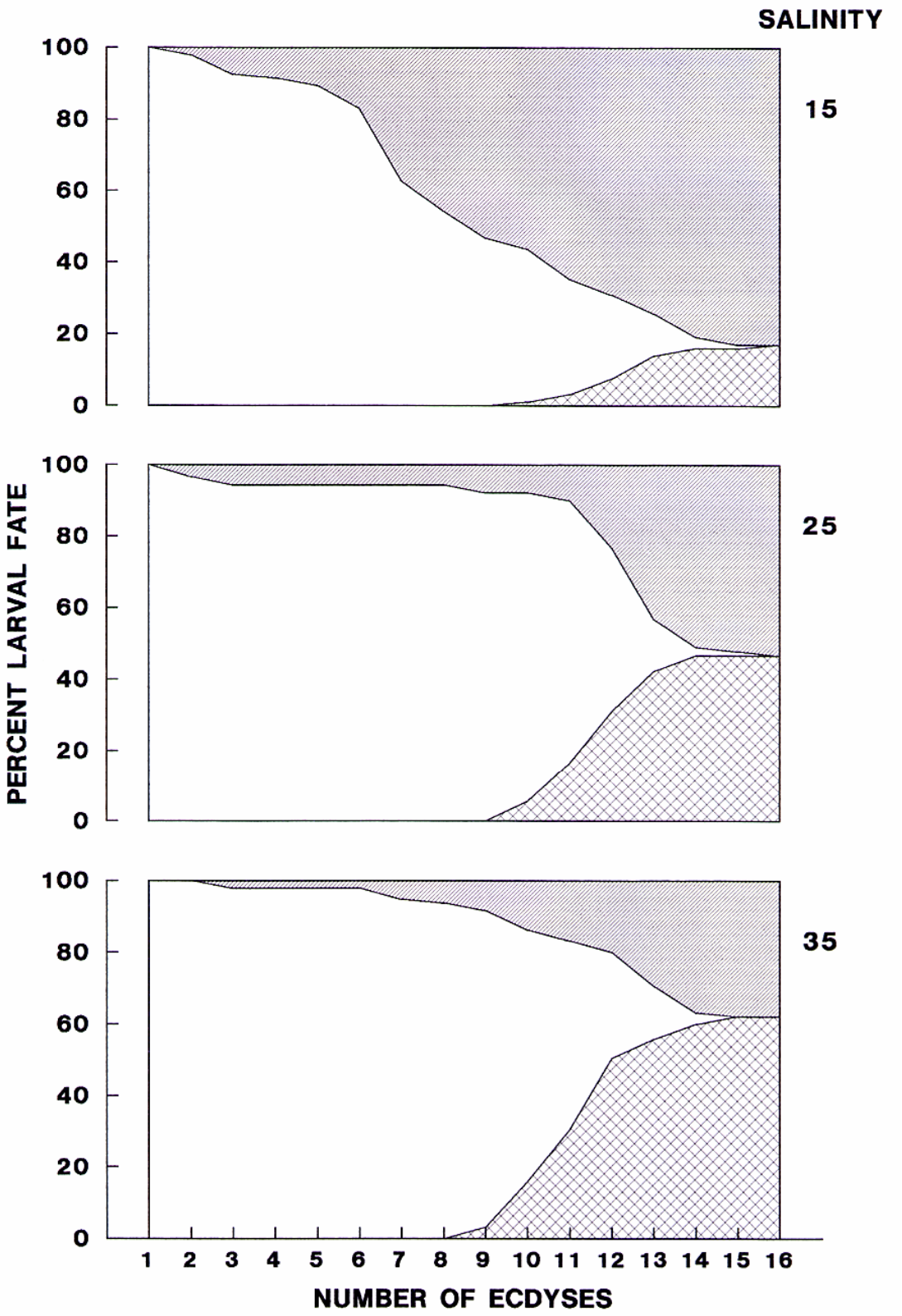

Fig. 5.15. *Palaemon serenus* reared in the laboratory under three salinity conditions—15, 25 and 35. Proportion of individuals after each ecdysis that had died (grey), remained larvae (unshaded) or achieved metamorphosis (cross-hatched)

5.4. DISCUSSION

5.4.1. LARVAL MORPHOLOGY AND DEVELOPMENT

M. intermedium

Although eight larval stages of *M. intermedium* were observed which corresponded to the descriptions by Williamson (1972), some larvae in all salinities metamorphosed after as few as six ecdyses. Williamson, using larvae from shrimp collected in a marine location at Cronulla on the central New South Wales coast, did not rear larvae to metamorphosis and did not monitor moulting history of each individual. Consequently, a direct comparison of larval development is tenuous. Williamson identified eight stages from an estimated ten, whereas the mean number of ecdyses in larvae from the Hopkins River estuary reared in seawater was eight. It would appear that *M. intermedium* larvae from the Hopkins River estuary undergo a less extended development than larvae from New South Wales. Geographic variation in larval development has been recorded in several palaemonid species (Sandifer, 1973; Knowlton, 1974; Fincham, 1979; Nishino, 1984, cited in Fincham and Figueras, 1986), but Fincham (1977) cautioned that the number of moults to metamorphosis may vary from study to study due to laboratory water quality, particularly temperature. Williamson (1972) reared *M. intermedium* larvae at 18°C while in this study, temperature ranged from 18.5-22.5°C, and Williamson's reporting of more stages may have been a function of lower rearing temperature. Nevertheless, the morphology and staging of the Hopkins River estuary larvae were similar enough to the stages described by Williamson (1972) that his morphological criteria can be used in the identification of stages.

P. australiensis

Stages I-IV in the larval development of *P. australiensis* correspond to moult stages and have been denoted by tail characteristics in a sequence typical of those reported for other atyids (eg. Hunte, 1979a, 1979b; Benzie, 1982; Salman, 1987a). Beyond stage IV, development is irregular and the morphology of the tail is not reliable as an indicator of developmental stage. Stages V-VIII have been denoted by pereiopod, pleopod and antennal development.

This pattern of regular development until stage IV and irregular development thereafter differs from that described for *Caridina* spp. All species described to date exhibit regular morphological change with each ecdysis through all stages of larval development (Hayashi and Hamano, 1984; Salman, 1987a; and see Benzie, 1982 for a review of other species). Larval development in *P. australiensis* appears to be more similar to the extended development
reported for *Micratya poeyi* and *Atya innocous* (Hunte, 1979a, 1979b), which produce

morphologically distinct stages at each moult up to stage IV or V, and thereafter undergo a large number of moults before metamorphosis, with less marked changes at each moult.

The recognition of eight stages in the development of *P. australiensis* was based on the morphological change observed at each moult in larvae that developed via the shortest series of moults. An eighth stage was included, despite a precocious metamorphosis directly from stage VII, because of the frequent occurrence of a distinct eighth zoeal stage. Juveniles derived from stage VII shared some characteristics with stage VIII zoeae, such as antennal and maxillary morphology, but their maxillipedal and pereiopodal exopods were reduced and not used for locomotion. The neotenous retention of pereiopodal exopods in *Paratya* results in a metamorphosis characterised by a gradual change in the morphology of the exopods. Juveniles are recognizable by their more specialized feeding appendages, and in live specimens, by a change in their posture and locomotion. Thus Yokoya (1931), who did not describe the movement of the late stages of *P. compressa*, may have included post-larval stages in his description of the larval development of this species. As Ch'ng (1973) noted, stages IX and X of Yokoya's description have degenerated maxillipedal exopods and well developed pleopods. Thus it may be more realistic to consider Yokoya's stage IX and X as post-larval stages.

The retention in juveniles of *P. australiensis* of the distal lobe of the coxal endite of the second maxilla is of interest. Benzie (1982) suggested that the loss of this feature on metamorphosis might be characteristic of the Atyidae. This appears not to be the case. Although the lobe is retained in *P. australiensis*, it is obscured by the proximal lobe of the basal endite, and so it is possible that it may have been overlooked in previous studies. It was not included beyond stage VIII in *P. compressa* by Yokoya (1931).

The exopod of the first maxilla is retained as a lobe bearing three plumose setae until stage IV in *P. australiensis* (Fig. 8d). Williamson (1982) stated that this feature only occurred in some Caridea to stage III, adding that its interpretation as an exopod was questionable. Yokoya (1931) did not include this lobe at all in illustrations of *P. compressa*. Ch'ng (1973), in a study of the first three larval stages of *P. curvirostris*, also depicted a 'fourth' stage larva with a lobe on the first maxilla similar to *P. australiensis*. This 'fourth' stage was more like a stage III larva and may have been the result of a 'mark-time moult' due to lack of suitable nutrition. However, it is possible that the persistence of this lobe in *Paratya* to the fourth stage may be characteristic of the genus.

Variation in the number of larval instars to metamorphosis between populations of *P. australiensis* (Fig. 5.1) suggests genetic differentiation of populations, despite neither significant difference in larval duration, nor morphological differences in larval stages being apparent. Larvae from the lacustrine environment of Lake Purrumbete tended to undergo fewer ecdyses after stage IV, while larvae from the Hopkins River estuary tended to undergo

mark-time moults more frequently during the later stages of development. Because survival to metamorphosis was quite low in the laboratory (≈30%) it is likely that the larvae were under stress, and it is possible that larvae from the estuary tended to respond to stress by extending larval period by mark-time moults, while the Purrumbete population tended to increase the intermoult period between later stages. An intrinsically variable number of instars, as observed in larvae from both populations, suggests potential plasticity of developmental patterns in varying environmental conditions. It would be of great interest to develop a technique of larval rearing in low salinities to study the effect of changes in salinity and temperature on developmental patterns in larvae from the two populations.

It is normal to include discussion of egg and larval size in a treatment of larval development, but these features have been found to be highly variable between populations of *P. australiensis* (Walsh, 1993). Variation in fecundity, egg size and larval size between natural populations is considered in Chapter 7, separate from the above laboratory-based studies. Further discussion of the range of atyid larval development is presented there.

5.4.2. SALINITY AND LARVAL DEVELOPMENT

All three caridean species of Hopkins River estuary exhibited considerable euryhalinity in the larval phase. Both *P. serenus* and *M. intermedium* developed to metamorphosis in salinities ranging from as low as 15 to as high as seawater. While *P. australiensis* was not successfully reared in the laboratory at a salinity below 15, collection of all larval stages of this species in freshwater habitats (Walsh, 1993; Chapter 7 of this study; M. Hancock, Griffith University, personal communication) suggests strongly that this species can metamorphose successfully in salinities from <1 to at least 15. In addition, *P. australiensis* larvae survived in seawater for at least several days, the 96 h LC_{50} at around 20.5°C being 36.7—well above the salinity of seawater. It is noteworthy that this value is well above values of the same statistic for juvenile and adult *P. australiensis*: 21.4 and 22.9, respectively (Table 3.2).

M. intermedium is the most euryhaline species of the three, with survival to metamorphosis at 15 so high that metamorphosis would probably be possible at much lower salinities. However survival was maximal at salinities of 25 and 35, while larval development was more rapid and number of ecdyses to metamorphosis was lower at 25 than at 35. It thus appears that, of the three test salinities, 25 is optimal for rapid growth to metamorphosis at temperatures in the range of 18.5-22.5°C. It is of interest that, at 35, both larval duration was longer and the number of larval instars was greater, while at 15, although larval duration was longer, the number of larval instars was not greater than at 25. Intrinsic variability of larval instars probably has strong adaptive importance (Gore, 1985). Reduction of instar number in salinities less than seawater reflects an ability to put more energy into growth between ecdyses

at salinity 25, while an increase in intermoult period at 15 is possibly an indication of stress impeding the moulting process. The experimental temperatures of 18.5-22.5°C approximate summer conditions in the Hopkins River estuary (Figs. 2.8, 2.9), but are higher than conditions likely to be experienced by larvae in adjacent coastal waters. To gain a complete picture of the optimal conditions for growth of *M. intermedium* larvae, further trials should be conducted at temperatures approximating natural marine conditions, particularly in light of the importance of temperature reported for other palaemonids (e.g. Sandifer, 1973; Rochanaburanon and Williamson, 1976; Lee and Fielder, 1981).

P. serenus did not show a similar reduction in larval instars at decreased salinities. Survival and larval duration were not significantly different between 25 and 35, although a linear trend was evident in each of larval duration (increasing) , number of instars (increasing) and survival (decreasing) from 35 through 25 to 15 (Figs. 5.14, 5.15). It thus appears that, of the salinities tested, 35 is the optimal for larval development of this species.

Previous studies of palaemonid larval development have usually shown temperature to have a more important effect on larval duration and instar number than salinity. In *Palaemonetes vulgaris*, *Palaemon elegans*, and *Macrobrachium australiense*, although temperature affected the number of days to metamorphosis and, in the case of the first two species, the number of ecdyses, no effect of salinity was detected (Sandifer, 1973; Rochanaburanon and Williamson, 1976; Lee and Fielder, 1981). Salinity was found to affect the larval duration in *Macrobrachium amazonicum* (Moreira et al., 1986), but the number of ecdyses to metamorphosis was not monitored. The finding of salinity affecting the number of ecdyses in *M. intermedium* and *P. serenus* is the first such result for palaemonid shrimps, but the importance of salinity relative to temperature can not be assessed from this work.

All three Hopkins River estuary caridean species have tolerances which might allow complete larval development in an estuarine environment. The relative values of optimal salinities for larval development correspond to estuarine distributions and physiological tolerances in adults and juveniles of the three species (Chapters 2 and 3), with a gradation from the most freshwater *P. australiensis*, through the intermediate *M. intermedium*, to the most marine *P. serenus*. Of the three species, M. intermedium is the most euryhaline in both the adult and larval phases.

6. TEMPORAL AND SPATIAL PATTERNS OF LARVAL DISTRIBUTION IN THE CARIDEAN SHRIMPS OF THE HOPKINS ESTUARY

6.1. INTRODUCTION

The hydrodynamics of the Hopkins River estuary is an important determinant of the adult and juvenile distribution and abundance of all three caridean species under investigation (Chapter 3). Hydrological patterns in the estuary have been shown to be also of prime importance in structuring the zooplankton community (Newton, 1994). This chapter, which investigates caridean larval ecology, therefore focuses on the relationship between larval distribution and abundance, and the hydrodynamics of the estuary. Two scales of investigation are pursued: variation in larval abundance in relation to seasonal hydrological patterns, and variation in larval distribution in relation to tidal fluctuations. Chapter 4 identified recruitment from planktonic larvae as a potentially important determinant of juvenile distributions in *M. intermedium* and *P. australiensis*. This chapter also investigates the relationship between larval distributions and juvenile recruitment patterns in each species.

Although many studies have investigated decapod larval distribution and behaviour in estuaries (e.g. Chaloupka, 1978; Cronin and Forward, 1982; Dittel and Epifanio, 1990; and see review by McConaugha, 1988), few studies have concentrated on caridean larvae (Sandifer, 1973; Thorne et al., 1979: Paula, 1989). The emphasis in most studies has been larval retention in or displacement from estuaries, either by behaviour of larvae in relation to two-layered circulation (e.g. Cronin and Forward, 1982; Dittel and Epifanio, 1990), or by timing of larval release to coincide with tidal cycles (e.g. Christy and Stancyk, 1982; Paula, 1989).

Newton (1994) conducted a wide-ranging study of position maintenance in members of the zooplankton community of the Hopkins River estuary. Newton erected a number of behavioural models to explain the observed distribution patterns of the many taxa of the community. To the shrimp larvae of the Hopkins River estuary (treated as a single taxon), she attributed a model of avoiding the outward-flowing surface layer, and instead using the open water column below the halocline at slack tides and the bottom boundary layer at other times. Similar behaviour has been suggested for other carideans. Three estuarine caridean species in the York River estuary, eastern USA occurred most commonly in the deep saline layer (Sandifer, 1975). *Macrobrachium novaehollandiae* in the Brisbane River estuary, Queensland used the bottom boundary layer to avoid downstream displacement (Thorne et al., 1979).

Another of Newton's (1994) models of position maintenance in estuaries involved migration from the water column during strong ebb and/or flood tides into littoral vegetation, where the current is reduced. Such a mechanism has been observed in post-larval penaeid prawns (Xiao et al., 1988), but not in any decapod larvae. Newton (1994) attributed a variation of this strategy, which she termed an 'ontogenetic strategy', to shrimp larvae of thei Hopkins River estuary. This referred to the change in ecological habit at metamorphosis, resulting in the preference of post-larval stages for the littoral seagrass meadow habitat.

A strategy, independent of larval behaviour, that may be employed by ovigerous adults to avoid displacement of larvae is to time larval release to coincide with periods when the potential for export is minimised due to hydrological factors. Such a strategy is more relevant to meroplankters such as decapod larvae, than to holoplankton, which were the emphasis of Newton's (1994) work. On a seasonal scale, timing of larval release is particularly important in an estuary such as the Hopkins, in which freshwater input is the dominant determinant of hydrodynamics, and in which the mouth can be closed for part of each year.

Recruitment of juvenile *M. intermedium* in early 1989 was maximal during the extended period when the mouth of the estuary was closed. While the abundance and distribution of larvae of this species in relation to annual hydrological cycles are therefore of interest, behavioural mechanisms to avoid (or enhance) larval export from the estuary were not easily investigated. *P. australiensis*, on the other hand, recruited to the estuary while discharge was declining from the annual August and September floods. Therefore, larval development in this species most likely occurred in the estuary during a period of nett outward flow. An investigation of larval distribution and behaviour in *P. australiensis* is of interest to determine the means by which larvae avoid displacement from the estuary.

This chapter reports on two surveys of larval distributions in the Hopkins River estuary, conducted over two years. In addition, the ichthyoplankton samples of Newton's (1994) study have been re-analysed to identify individual caridean species. From these surveys, the temporal and spatial trends in distribution and abundance of caridean larvae are described, and related to the hydrological cycle, and to the patterns of juvenile abundance reported in Chapter 4. This work should clarify the importance of recruitment from the larvae in determining juvenile and adult distributions in the estuary. In addition, diurnal patterns of vertical distribution in *P. australiensis* are investigated and a model of larval behaviour is developed to explain the observed patterns. Two diurnal surveys, spanning a total of three tidal and diurnal cycles, investigated the vertical migration patterns of *P. australiensis*. Some preliminary surveys of *P. australiensis* larval distribution at sites above estuarine influence are also presented.

6.2. METHODS

6.2.1. SURVEYS OF LARVAL ABUNDANCE

A preliminary survey of larval abundance in the Hopkins River estuary was conducted over eight months from September 1988 until April 1989, sampling at monthly intervals (see appendix 1 for sampling dates). Sampling for larvae in this period was always conducted within two days of the quantitative sampling program in the seagrass meadows (see Chapters 2 and 4). Samples were collected at or adjacent to the four meadows, LG, JP, RF and HB, using a demersal tow with a 350 μm mesh (Fig. 6.1). This mesh size was large enough to allow the escape of stage I and possibly stage II *P. australiensis* larvae, but was adequate for the capture of later stage larvae and juveniles and all stages of *M. intermedium*, allowing at least a preliminary understanding of larval distributions. The net was towed from a long line (>20 m) behind a boat at a depth set by adjustment of the buoyancy float. A calibrated 'General Oceanics' flow meter (model 2035 Mk III) was suspended in the centre of the mouth of the net. An estimate of volume filtered was made from the meter. Sample volumes ranged from 1 to 2 m^3, except for some tows through seagrass, which were smaller (as small as 0.3 m^3) due to fouling of the net.

Before sampling, a profile of salinity, temperature and dissolved oxygen measurements was conducted at the deepest point at each site using a 'Yeo-Kal' salinometer (Model 602 Mk III) and a Yellow Springs Instrument dissolved oxygen meter (Model 57).

To test possible mechanisms of avoidance of downstream displacement by *P. australiensis* larvae, sampling was designed to test the hypotheses that:

1. Larvae concentrated in fringing eelgrass meadows where presumably flow is decreased.
2. Larvae concentrated in the salt wedge where nett water movement is nil or upstream.

Three samples were taken at each site:

1. Midstream near the surface, at 0.3-0.7 m depth: always above the halocline if present.
   Midstream samples were collected as follows:
   LG, over the deep hole (≈12 m) immediately below TS (Figs. 2.1, 2.3);
   JP, over the deep hole (≈12 m) adjacent to the diving board (Figs. 2.1, 2.4);.
   RF, in the channel (≈4 m) west of the meadow parallel to the cliff (Figs. 2.1, 2.5);.
   HB, in the channel (≈3 m) north of the bridge on the western side of the estuary (Fig. 2.1).
2. Midstream at a mid water depth. When a halocline was present, the sample was taken from 0.5-3 m below the halocline.
3. Over fringing mudflats or seagrass meadows if present, at 0.1-0.6 m depth. Fringe samples were collected as follows:

LG, over the mudflat on which the ephemeral *Ruppia* meadow grew from November to January (Figs. 2.1, 2.3).

JP, in the unvegetated backwater channel behind the island from which meadow 2 extended (Figs. 2.1, 2.4).

RF, at the outer section of the meadow (Figs. 2.1, 2,5)

HB, from 17 September 1988 until 15 January 1989 over the meadow on the east side of the estuary north of the bridge (Fig. 2.1), and from 13 February 1989 until 16 April 1989 from the deeper north section of the meadow south of the bridge (Figs. 2.1, 2.6)

A second more intensive survey was conducted in the estuary from July 1989 until January 1990 in order to concentrate on the occurrence of *P. australiensis* (see appendix 1 for sampling dates). Samples were collected from midstream at LG, JP and HB as described above using Clarke-Bumpus samplers (Clarke and Bumpus, 1940) with 120 μm mesh, which was fine enough to capture all caridean larval stages. The samplers were fitted with calibrated flow meters which were used to estimate the volume filtered. Three replicate tows were taken at each depth at each site.

Depths sampled depended on the physical properties of the water column. A sample at 0.5 m and one or more deeper samples were always taken after a profile of salinity, temperature and dissolved oxygen was measured as described above. The positions of the deeper samples were determined by the presence of a halocline and the levels of dissolved oxygen. At HB, samples were taken at one or two depths below the halocline. At JP and TS, three samples were taken below the halocline: one just below it, and two deeper. If a layer of the deeper water was anoxic (reading <2 $mg.L^{-1}$), a single sample was taken in that layer and was assumed to be representative, and a sample was taken just above the anoxic layer. If the deeper water was not anoxic, samples were taken at regular depths: usually at 3, 6, and 9 m.

Clarke-Bumpus samples were also collected at JP on 29 October 1991 and at TS on 4 December 1991. In order to relate the timing of larval occurrence in the estuary to that upstream, a series of Clarke-Bumpus samples was collected in the pool below the confluence of the Hopkins River and the Mount Emu Creek (MH; see Fig. 1.1) from November 1991 to April 1992 (see Appendix 1 for sampling dates). On each occasion, three replicate samples were taken at three depths—1, 3, and 5 m. A profile of conductivity, salinity, temperature and

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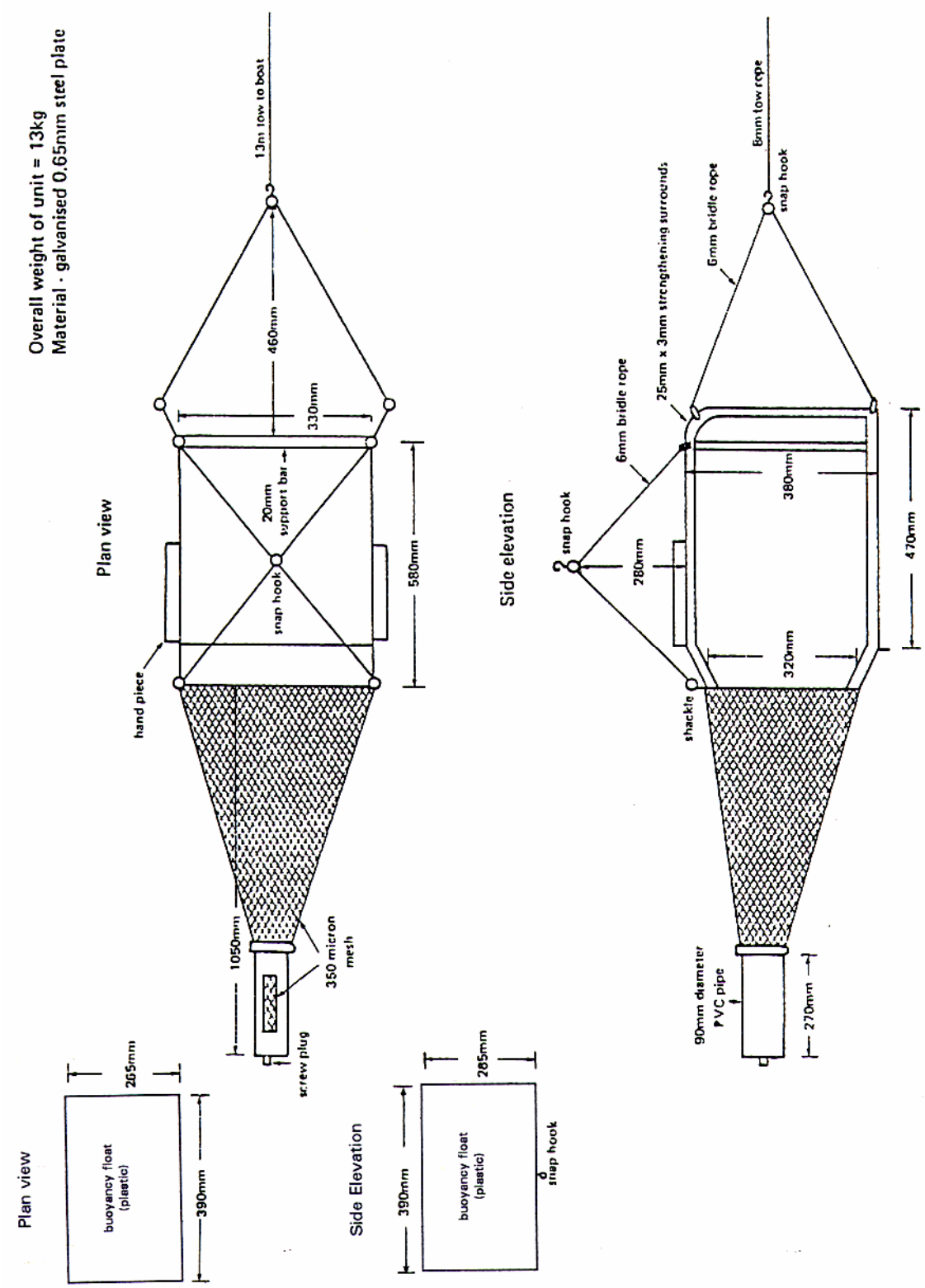
Fig. 6.1. Design of demersal tow used to sample shrimp larvae in Hopkins River estuary from September 1988 to April 1989. Depth was adjusted by varying the length of the line between the buoyancy float and the top snap hook. Samples at 0.5 m depth were achieved by wedging the float beneath the top snap hook.


Overall weight of unit = 13kg
Material - galvanised 0.65mm steel plate
Plan view
13m tow to boat
460mm
330mm
20mm support bar
snap hook
hand piece
580mm
1050mm
350 micron mesh
screw plug
Side elevation
snap hook
6mm bridle rope
25mm x 3mm strengthening surrounds
6mm bridle rope
6mm tow rope
snap hook
280mm
380mm
320mm
shackle
470mm
90mm diameter PVC pipe
270mm
Plan view
buoyancy float (plastic)
265mm
390mm
Side Elevation
390mm
buoyancy float (plastic)
285mm
snap hook

dissolved oxygen was taken prior to sampling using a Yellow Springs Instruments salinity and conductivity meter (Model 33) and dissolved oxygen meter (Model 57).

In addition the caridean larvae from icthyoplankton samples collected by G. Newton, Deakin University, in 1984 and 1985 were identified and counted. These samples were collected using a 0.5 m diameter conical plankton net with 250 μm mesh towed obliquely from bottom to surface over ≈3 minutes. Volume filtered was estimated using a calibrated flow meter in the mouth of the net, each sample averaging ≈10-20 m^{-3}. Samples analysed were collected monthly from February 1984 to February 1985 (see Appendix 1 for sample dates) from locations that approximated the sampling locations used in this study.

All plankton was preserved in 2% formaldehyde. In the laboratory all shrimp larvae were identified, staged and counted using a dissecting microscope (×8-×40). *P. australiensis* was staged according to Walsh (1993) and *M. intermedium* according to Williamson (1972). Any juvenile or adult shrimp were identified and measured.

In comparing densities of larvae collected at specific depths by Clarke-Bumpus samplers, heterogeneity of variance was corrected by log (x+1)-transformations. Means and their standard errors were calculated from the transformed values and were then untransformed for expression in the text.

To estimate mean abundance at each site, Clarke-Bumpus samples were treated as stratified samples in which a sample at each depth was assumed representative of a stratum, the size of each stratum was determined by the physical properties of the water column: if the fresh water layer above the halocline was 1.5 m deep then the 0.5 m sample was assumed representative of that 1.5 m stratum; if the anoxic layer was 7 m in extent, from 5-12 m deep, then the sample taken in that stratum was assumed representative; if there was no abrupt change in salinity or dissolved oxygen, depth ranges were divided evenly. The weight applied to each depth range was based on the volume of that stratum (Table 6.1). For JP and TS, the volumes of strata were calculated by integrating between contours on maps drafted by J. Sherwood (Deakin University, personal communication). Volumes for MH were calculated in a similar manner from a survey conducted by the author. Because RF and HB were more channel-like nd not characterised by a distinct deep pool like the other three sites, weight for each stratum at these sites was based on cross-sectional area from depth profiles. The weighted mean density and its standard error for a whole site were calculated using the arithmetic mean densities from each depth (Elliott, 1977; Snedecor and Cochran, 1980). A weighted mean density was similarly estimated for demersal tow samples, but a mean of midstream surface and fringing tows was assumed representative of the mean density above the halocline and the single deep sample was considered representative of the mean density below the halocline (except in depth ranges with <2mg.L^{-1} dissolved oxygen, in which it was assumed no shrimp

Table 6.1. Weights (W) used in estimating mean density of larvae at five sites in the Hopkins River: cross-sectional area (A) in m^2 and the proportion of total area (W) of strata in the channels at HB and RF; volumes (V) in $10^3 \times m^3$ and proportions of total volume (W) of strata in the pools at JP, TS and MH. Volumes were calculated for JP and TS from contour maps constructed by J. Sherwood (Deakin University, personal communication).

Depth	HB		RF		JP		TS		MH	
range (m)	A	W	A	W	V	W	V	W	V	W
0-1	113	0.38	82	0.44	52.0	0.31	55.1	0.29	19.0	0.67
1-2	89	0.30	58	0.31	31.8	0.19	44.5	0.23		
2-3	67	0.23	37	0.19	22.8	0.13	33.7	0.18	6.4	0.23
3-4	25	0.08	11	0.06	18.2	0.11	21.6	0.11		
4-5					14.1	0.08	12.47	0..07	2.5	0.09
5-6					10.2	0.06	6.94	0.04		
6-8					13.0	0.08	8.6	0.05	0.4	0.01
8-10					6.4	0.04	5.5	0.03		
10-12(+)					1.9	0.01	2.3	0.01		
Total	293		188		170.4		193.9		28.4	

larvae were present). The density from the oblique icthyoplankton tows was treated as mean density for the site.

6.2.2. DIURNAL SURVEYS OF VERTICAL DISTRIBUTION OF *P. AUSTRALIENSIS*

Two surveys to detect diurnal changes in abundance of *P. australiensis* larvae in the estuarine environment were conducted:

- -a 30 hour survey at KH in the Hopkins River estuary on 15-16 November 1990 (Fig. 2.1);
- -a 44 hour survey at a site in the U-shaped channel 2 km upstream from the mouth of the Fitzroy River estuary on 10-12 November 1991 (see section 7.2 for a description of the Fitzroy River). This site was chosen because the Hopkins River estuary supported only very low densities of *P. australiensis* larvae in the spring of 1991.

In both surveys, plankton samples were collected from an anchored boat at a fixed station (4.5 m deep at KH and 3 m deep at the Fitzroy) using a 'Davey' impeller pump. The pump drew water at 145 $L.min^{-1}$ through an inlet hose of 6 cm diameter which was hung vertically from the boat during collection. The inlet head consisted of an enclosed chamber between two horizontal plates to draw water from a narrow depth range. The pumped water was passed through a mesh of 120 μm. In the first survey this mesh was stretched across a sieve into which the water was pumped, but as this technique resulted in considerable mechanical

damage to the shrimp larvae, in the second survey, pumped water was filtered through a partly submerged plankton net with 120 μm mesh. A pump was used to collect larvae for the study of vertical migration rather than nets to allow collection from near the bottom and to allow rapid collection from a series of closely separated depths.

To assess the precision of the technique in the collection of *P. australiensis*, a number of comparisons of the pumping technique and Clarke-Bumpus net tows was undertaken. An initial trial at 1500 h, 23 November 1989 at JP, in which three consecutive 3 min pump sample units were taken at 1.5 m depth in turbid water, followed by three Clarke-Bumpus tows at the same depth, showed the effect of local depletion with continuous pumping (Fig. 6.2). Numbers of larvae collected in the third pump replicate , were consistently lower than in the first and second replicates in all larval stages. All stages except I and II showed a decline in numbers from replicate 1 to 2, suggesting lesser avoidance ability in earlier stages. These trends were not apparent in the tow sample. A two-way ANOVA was performed comparing the log(x+1)-transformed density of each stage in the first pump replicate with the three tow replicates (two factors: collection technique and larval stage). Density of each stage in the first pump replicate was significantly lower than mean density from the tow samples ($P=0.001$). Consequently, a single 3 min tow (0.44 m^3) at each depth was considered small enough to avoid problems of local depletion, while being large enough to collect larval stages at moderately low densities. Although the interaction between stage and technique was not significant, it was low ($P=0.093$). Thus it should not be concluded that the two techniques sample all stages equally effectively.

A second trial was conducted at KH on 15 and 16 November 1989 at 1600 h. On each day a single pump sample was taken at two depths either side of the halocline—1 and 1.5 m—followed by a Clarke-Bumpus tow at the same depths. Both sampling techniques collected small numbers of larvae at 1 m, and much greater numbers at 1.5 m deep (Fig. 6.3). The fact such a difference in densities can be detected over a distance of 0.5 m indicates the pumping technique collects from an adequately narrow depth range. An ANOVA to compare the numbers collected by the two techniques from this trial would ideally include the effects of depth, larval stage and sampling technique. However, because the numbers collected in the 1 m samples were so small (0-2 individuals of each stage per sample), interactions between the unreplicated effect of sampling occasion, and one or all of depth, larval stage and sampling technique would be likely if the 1 m samples were included in an ANOVA of these effects. Interpretation of such an ANOVA would be dubious (Underwood, 1981). With log(x+1)-transformed data from only the 1.5 m samples (and therefore no depth effect), Tukey's test for non-additivity did not show an interaction between sampling occasion (day) and either technique ($P=0.17$) or larval stage ($P=0.12$). Thus an ANOVA was conducted for the 1.5 m samples (two levels of day, two levels of sampling technique and eight levels of larval stage),

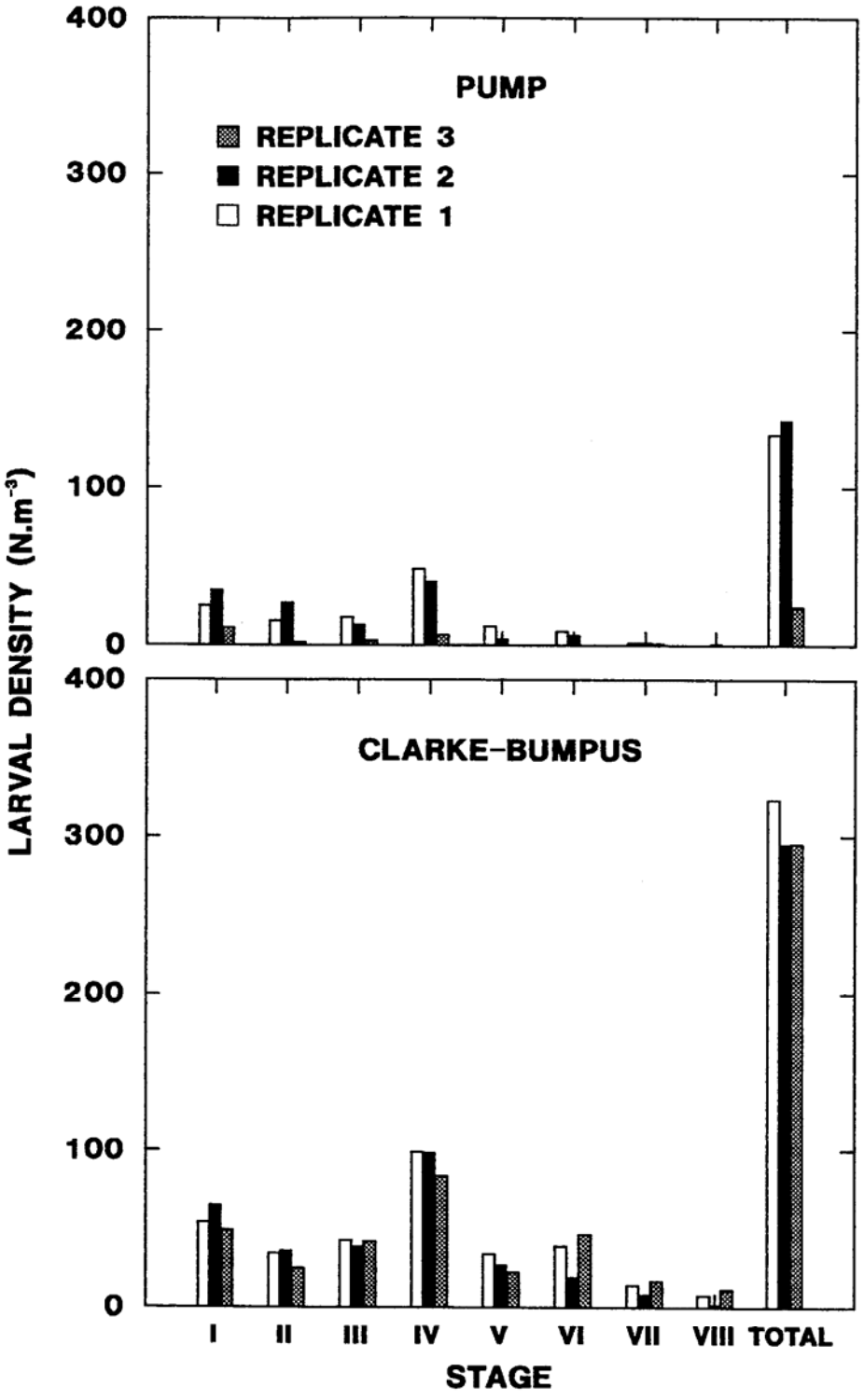


Fig. 6.2. Comparison of larval sampling techniques. Density of larval stages of *Paratya australiensis* per m^3 of water filtered in three replicate pumping efforts and three replicate Clarke-Bumpus net tows from 1.5 m depth, just below the halocline, at JP at ≈1500 h on 23 November 1989

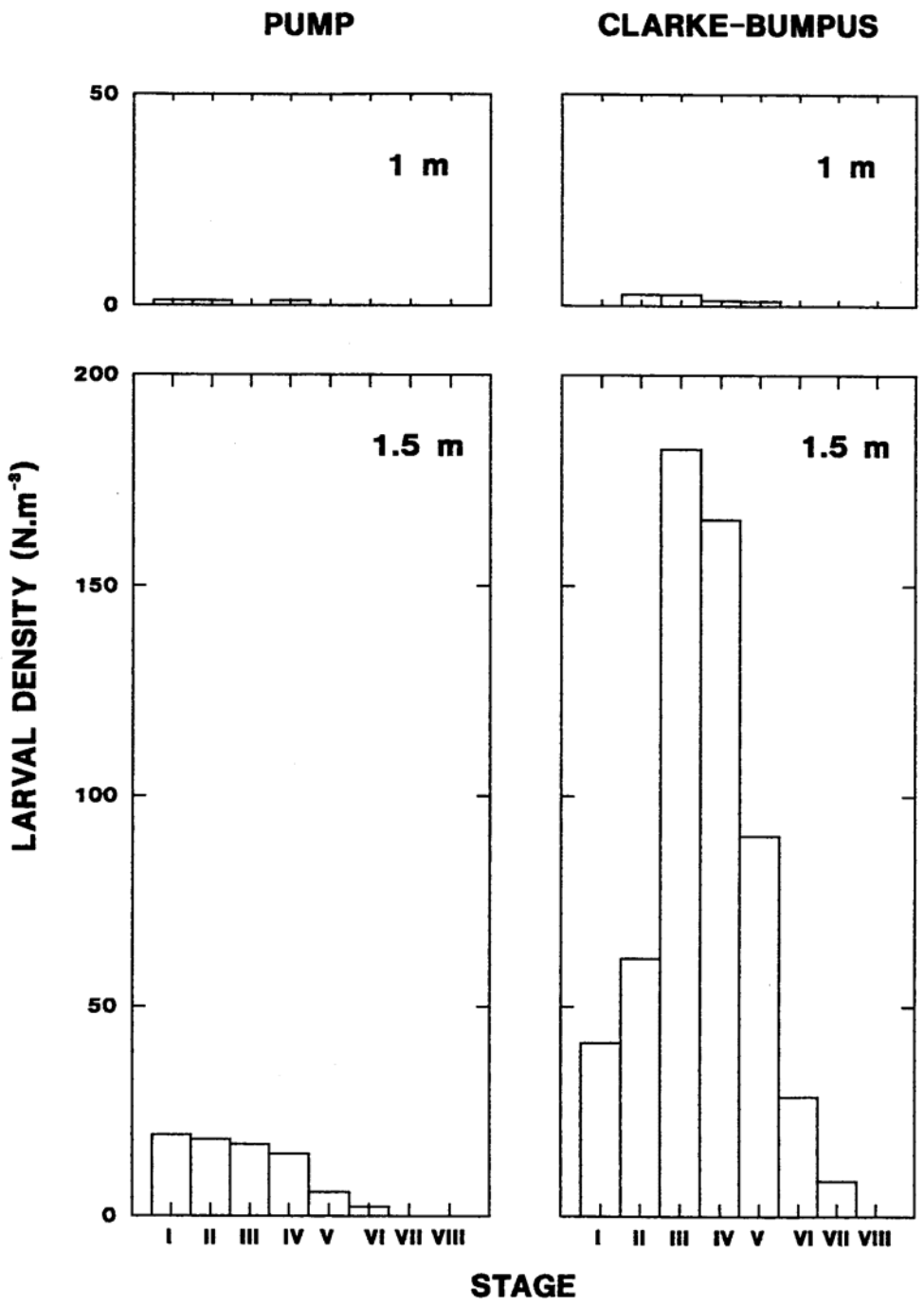


Fig. 6.3. Comparison of larval sampling techniques: pump versus Clarke-Bumpus net. Mean densities of each larval stage of *Paratya australiensis* at two depths either side of the halocline (1 and 1.5 m) at KH at ≈1600 h on 15 and 16 November 1990

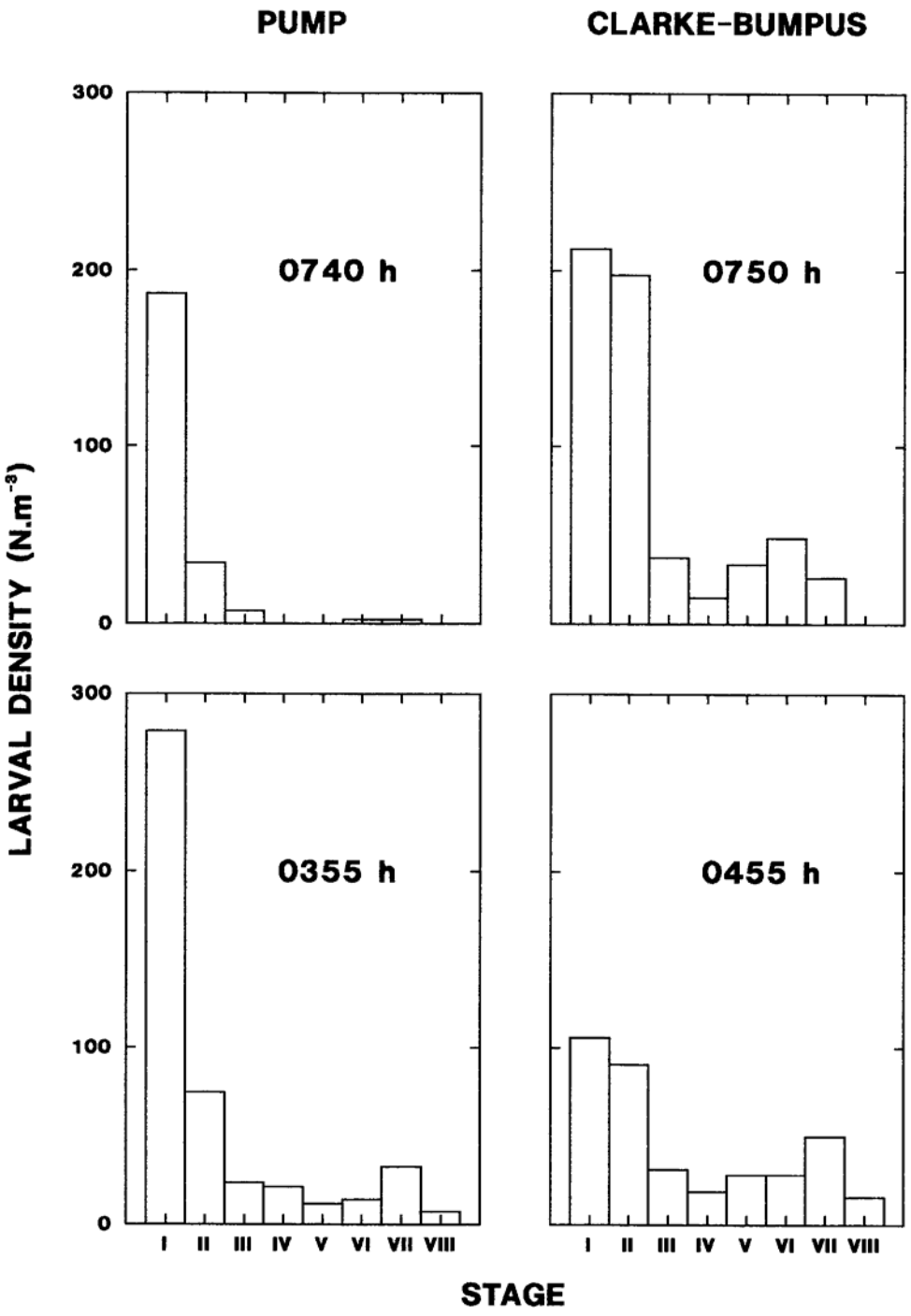


Fig. 6.4. Comparison of larval sampling techniques: pump versus Clarke-Bumpus net. Densities of each larval stage of *Paratya australiensis* at 1.5 m depth in the Fitzroy River estuary at two times (day and night) on 12 November 1991

showing the two techniques to be significantly different ($P<0.001$). Although the interaction between technique and larval stage was not significant ($P=0.056$), this probability level is too low to conclude that the two techniques sample all larval stages equally effectively. Indeed Fig. 6.3 suggests the pump is relatively less efficient at collecting late stage larvae than the Clarke-Bumpus sampler. Thus the pumping system is significantly less efficient than Clarke-Bumpus tows, probably more so for the later stages than the earlier stages. The differences observed at KH were greater than observed at JP (Figs. 6.2, 6.3) which may have been due to the water being less turbid at KH and thus increasing the effect of visually stimulated avoidance. This effect will have serious consequences on the relative efficiency of day and night samples, so a third comparison trial was conducted on 12 November 1991 at the Fitzroy River estuary. A sample was taken during both day and night with each sampling technique at 1.5 m depth, just below the halocline. At night, stages II and greater were collected with comparable efficiency using either method, while during the day the efficiency of the pump in collecting these stages was greatly reduced (Fig. 6.4). Stage I larvae were collected with comparable efficiency during the day, but at night were collected more efficiently by the pump. Thus caution must be exercised when interpreting the catches of the pump. Differing densities day and night mean comparisons of absolute densities cannot be made confidently, and relative abundance should be used. Differences in the efficiency of the technique in capturing different larval stages between day and night required light conditions to be constant during each sample and for light to penetrate to the bottom sample depth so that the potential for visually stimulated avoidance was consistent throughout the water column. This was not the case in one sample (Hopkins, 2020 h 15 November) which spanned twilight into night. This sample was excluded from consideration.

At each location, sampling was conducted every two hours: in the Hopkins at KH from 1000 h 15 November 1990 to 1400 h 16 November 1990, and at the Fitzroy from 1700 h 10 November 1991 to 1100 h 12 November 1991. For each sample, the following procedure was followed:

1 A salinity, temperature and dissolved oxygen profile was taken at 0.5 m intervals using a 'Yeokal' salinometer (Model 602 Mk III) and a Yellow Springs Instruments dissolved oxygen meter (Model 57);
2 Water velocity was measured at 0.5 or 1 m intervals (depending on flow conditions) using a 'General Oceanics' flow meter (Model 2035 Mk III) fitted with a low speed rotor. At depths at which flow was detected, the direction was checked by a lightly weighted, open-ended, plastic box with a surface area of ≈ 0.04 m^{-2} lowered on fine fishing line;
3 Ambient and underwater light intensity were measured using a Kahl Scientific Instrument underwater irradiometer (Model 286WA310) at 0.5 m intervals;
4 A series of three-minute pump samples was taken at 0.5 m intervals (nine samples in 4.5 m at KH, and six in 3 m at the Fitzroy), beginning at 0.5 m depth. In the Hopkins,

pump samples were collected before the above steps (1, 2 and 3), but in the Fitzroy, pump samples were collected last. All plankton collected was preserved and analysed as in section 6.2.1.

During each survey the tidal level of each estuary was continually measured using a tide gauge fixed to the jetty at Deakin University (Fig. 2.1) for the survey at KH and fixed to the jetty at the boatramp ≈500 m downstream of the sampling site at the Fitzroy river. In both cases, this data was calibrated against water level measured against a benchmark at the sampling location before and after each two-hourly sampling procedure.

In most cases the depth distribution of *P. australiensis* was unimodal, and to aid analysis of variation in depth, mean depth and standard deviation were calculated from the number of larvae collected at each depth. Because the two locations varied in total depth and depth to halocline, mean depths were expressed as depth below the halocline, where the halocline was defined as the 5 isohale

In order to compare diurnal changes in vertical distribution in the estuaries to diurnal changes in distribution in the absence of tidal influence, day and night samples were taken in the deep pool at MH, upstream of the Hopkins River estuary (Fig. 1.1) on 19 December 1991. Clarke-Bumpus samples of 0.35-0.65 m^{-3} volume were taken at 1, 3, and 5 m depth. Three replicates were taken at each depth during the day (1600-1700 h) and at night (2230-2330 h). Day and night distributions were compared by a two-way ANOVA, with three levels of depth and two levels of time using log (x+1)-transformed densities. Three planned comparisons were made, comparing day and night density at each depth.

6.3. RESULTS

6.3.1. SEASONAL PATTERNS OF LARVAL DISTRIBUTION AND ABUNDANCE

6.3.1.1. *P. AUSTRALIENSIS*

High densities of *P. australiensis* larvae were recorded throughout the length of the Hopkins River estuary 6-10 weeks after peak discharge in three separate years (Fig 6.5). Mean densities were highest in each year at TS—6.7×10^3 m^{-3} on 8 December 1984, 1.5×10^3 m^{-3} on 21 November 1988, 7.3×10^2 m^{-3} on 24 November 1989—with usually lower densities at downstream sites, although a density of 1.3×10^3 m^{-3} was recorded on 24 October 1988 at HB. In 1984 peak densities were collected at all sites on 8 November (except at HB where a few more individuals were caught on 17 December). However in the other years there was a tendency for peak densities to be recorded at downstream sites before densities had peaked at upstream sites. In 1988 peak densities occurred at HB and RF on 24 October, but peak densities were recorded upstream at JP and TS a month later on 21 November. In 1989 peak density was recorded at HB on 10 November, and upstream at TS on 24 November, while high densities were recorded at JP on both those occasions. In 1989, the only year in which data was obtained beyond the minimum discharge period in the estuary, a small number of *P. australiensis* larvae persisted in estuarine sites at least until May: usually only one or two individuals were collected per sample. The increased density of larvae on 21 January 1985 at TS (Fig. 6.5) was not reflected in densities downstream, and no similar resurgence in densities at the end of summer was observed in other years, including in February and March 1984, which are not shown in Fig. 6.5. Other than in 1985 at TS, the sharpness of the peaks in density in the estuary (<1 month) is in contrast to the extended period of high larval density at the upstream riverine site (MH) from December to February (Fig. 6.5)

Thus almost all *P. australiensis* larvae which occurred in the estuary did so over a one to two month period, soon after peak river discharge (usually in November), with densities at downstream estuarine locations usually peaking before upstream estuarine locations. In contrast larval densities in deep riverine pools upstream, which were comparable to densities recorded in the estuary, did not peak until river discharge had dropped further (in December), after which high densities were maintained until after the low flow period

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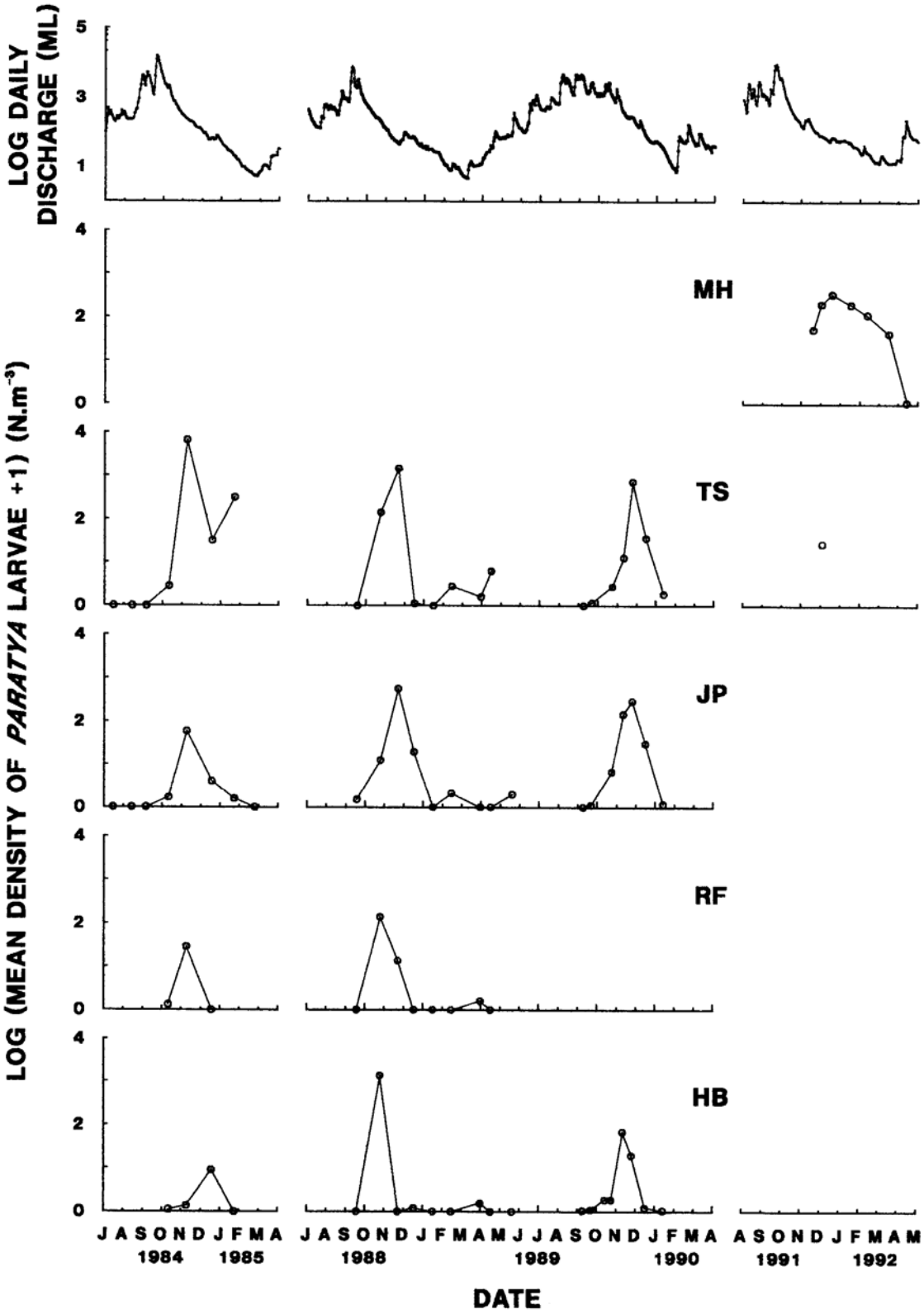
Fig. 6.5. Mean densities of *Paratya australiensis* larvae at four sites in the Hopkins River estuary and one site 20 km upstream of the estuary over four sampling periods: 1984-1985, Oblique tows collected by G. Newton (Deakin University, personal communication); 1988-1989, demersal tow samples; 1989-1990 and 1991-1992, Clarke-Bumpus tows. Daily discharge in ML at the Hopkins Falls gauging station (Fig. 1.1) for the same periods is also indicated (data from the Rural Water Corporation, Victoria).


LOG DAILY DISCHARGE (ML)
5
3
1
LOG (MEAN DENSITY OF PARATYA LARVAE +1) (N.m-3)
MH
TS
JP
RF
HB
4
2
0
J A S O N D J F M A
1984
1985
J A S O N D J F M A M J J A S O N D J F M A
1988
1989
1990
A S O N D J F M A M
1991
1992
DATE

The demersal tows over the fringing meadows and mudflats consistently produced densities of *P. australiensis* larvae comparable to those collected from surface waters midstream (Fig. 6.6). However on occasions when large numbers of *P. australiensis* were collected (i.e. 23 October 1988 at all sites and 21 November 1988 at JP and TS), the majority of larvae were found in the deep sample collected below the halocline. On such occasions, the deep sample contained one to two orders of magnitude more individuals than the corresponding freshwater surface samples. More larvae were collected from surface waters than from below the halocline on 23 November 1988 at RF, but in this case salinity above the 1 m deep halocline was 15-18, and was 28-32 below (Fig. 6.6). More detailed data showing depth distributions in the midstream were collected in Clarke-Bumpus samples taken the following year (Fig. 6.7). The salinity profiles for 10 November 1989 show the salt wedge had intruded as far as JP but not to TS. Small numbers of first stage larvae occurred at TS: 1, 19, 21, 14 m^{-3} at 0.5, 3, 6, and 9 m respectively. At JP mean densities at 0.5, 1.5, 5, 8 m were 13, 160, 229, and 230 m^{-3} respectively. In both cases, density in the surface layer was significantly less than in deeper water, but larvae were by far most abundant in the saline layer at JP. By 24 November 1989, dissolved oxygen had been reduced to $\leq$2 $mg.L^{-1}$ in deeper parts of the salt wedge. The depth distribution of *P. australiensis* larvae at both sites was characterised by very high densities in depths below the halocline, but above the depth at which dissolved oxygen was $\leq$2 $mg.L^{-1}$. Thus at TS mean densities at 3 and 6 m were 3553 and 176 m^{-3} respectively, while only 2 at 0.5 m and 8 at 9 m. At JP mean densities at 1 and 3 m were 919 and 128 m^{-3} respectively, while only 3 at 0.5 m and 2 at 8 m respectively. Overall densities of *P. australiensis* larvae had decreased for subsequent sampling occasions, but at JP similar relative depth distributions were evident. At TS dissolved oxygen did not continue to decline over the sampling period, possibly due to the gradual increase in salinity representing a continuing influx of more oxygenated, more saline water over the basalt barrier at JP (Figs. 2.1, 2.3). On 15 December 1989 at TS there were 146 larvae m^{-3} at 1.5 m, and 45 larvae m^{-3} at 6 m, but only 1 m^{-3} at 3 m (Fig.6.7). This low larval density at 3 m was possibly due to avoidance of an extremely dense occurrence of hydromedusae at this depth, rather than a response to physical conditions. By 12 January 1990 mean densities were less than 3 larvae m^{-3} at all depths at all estuarine sites.

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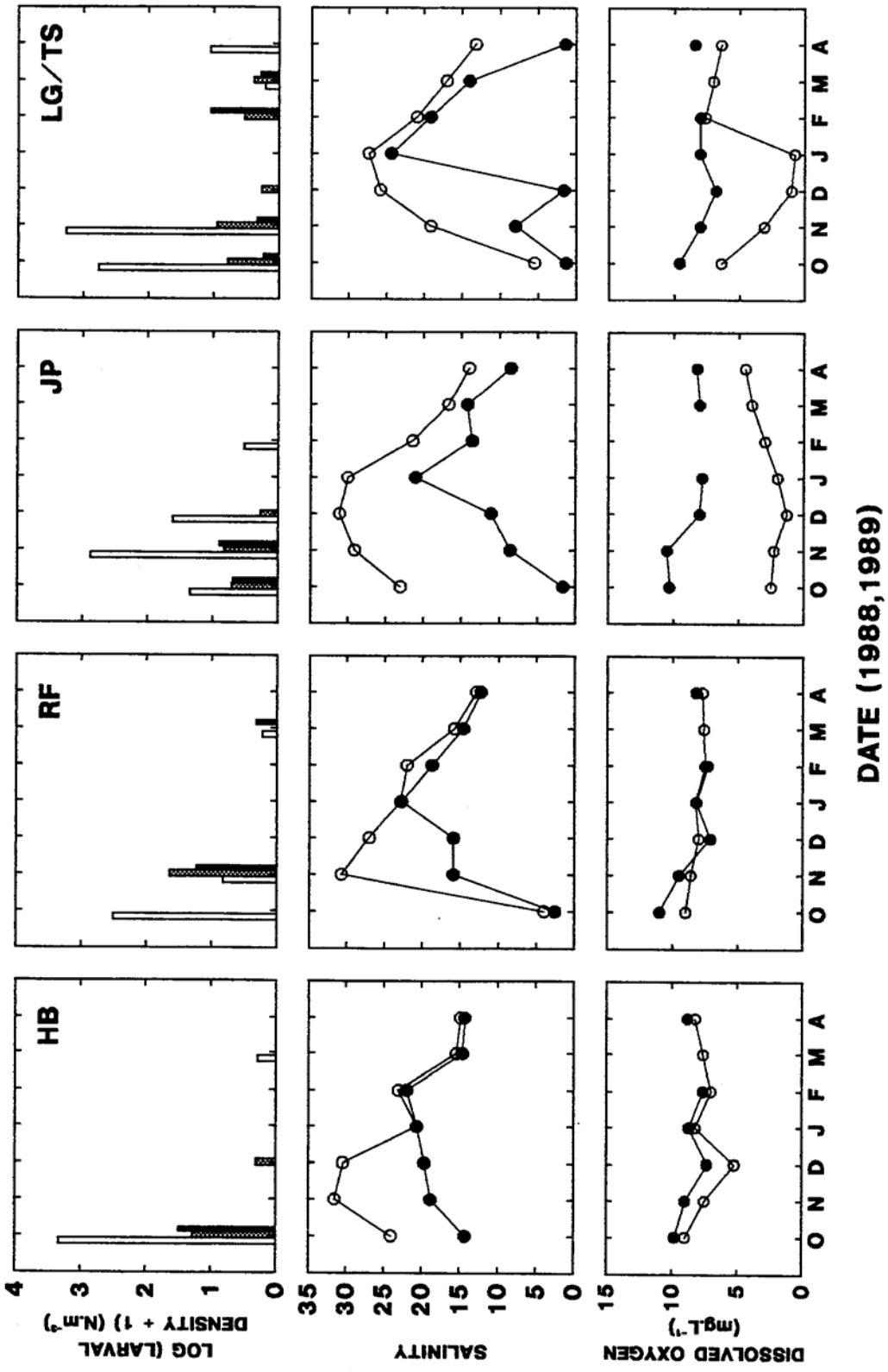
Fig 6.6. Densities of *Paratya australiensis* larvae collected in the demersal tow from October 1988 to April 1989 from three habitats at four locations in the Hopkins River estuary. Open bars, midstream below the halocline; grey bars, midstream surface (≈0.5 m deep); black bars, surface over fringing seagrass meadows (RF and HB) or mudflat (JP) or both (LG/TS). Salinity and dissolved oxygen at the depth of the surface sample (closed circles) and the deep sample (open circles) are also shown.


HB
RF
JP
LG/TS
LOG (LARVAL DENSITY + 1) (N.m⁻³)
SALINITY
DISSOLVED OXYGEN (mg.L⁻¹)
O N D J F M A
DATE (1988,1989)

Thus *P. australiensis* larvae were most abundant in the Hopkins River estuary below the halocline in the salt wedge soon after the wedge's first intrusion into each section of the estuary. As dissolved oxygen levels decreased in the salt wedge, larval densities concentrated in the upper section of the wedge where dissolved oxygen remained greater than ≈2 $mg.L^{-1}$. Despite oxygen levels greater than this level at TS, densities of larvae were very low by 12 January 1990.

Fig. 6.5 shows peak densities occurring at downstream sites before densities had peaked at upstream sites in 1988-1989 and 1989-1990, suggesting retention of larvae may begin earlier downstream. This interpretation is supported by stage-frequency distributions. In all years sampled, on a single sampling occasion, the modal stage and/or the oldest stage present at more downstream sites was older than at more upstream sites. The stage-density distributions of *P. australiensis* larvae at TS, JP and HB on the four sampling occasions of maximum abundance in 1989 (Fig. 6.8) illustrate this trend. On 10 November 1989 stage II larvae dominated the distribution at HB, with larvae as old as stage VI being present. At JP stage I larvae occurred in large numbers with a few stage II larvae and a very few stage III-V larvae, suggesting that larvae had only recently begun to be retained at this site in large numbers. On the same occasion, a small number of stage I larvae occurred at TS, suggesting that little retention of larvae had occurred at this site. Fourteen days later, the dominant stages at HB were V-VI, while they were IV-V at JP and II at TS. This progression of stages corresponds to a growth through four stages at HB and JP in the fourteen days between 10 and 23 November 1989, which falls within the range of growth rate observed in the laboratory, where stages I-IV lasted twelve to seventeen days (see section 5.3.1.3).

Using a growth rate of three to four days per stage, it is possible to back-calculate from the oldest stage present at each site on 10 November 1989, and estimate that the time of first retention of larvae was between 21 and 26 November at HB, between 2 and 7 November at JP, and shortly after 10 November at TS. Each of these events corresponds to the progression of the salt wedge into the estuary, illustrated schematically in Fig. 2.2. On 23 October 1989 the salt wedge had intruded as far as Kinnears Hut. This corresponds to the approximate time at which larvae are estimated to have first been retained at the lower end of the estuary. Small numbers of stage I and II larvae were collected at HB on this occasion, suggesting that large numbers of larvae were not retained until shortly after. It is possible that the wedge may have receded after 23 October 1989: daily discharge of the Hopkins River at Hopkins Falls dropped steadily from 1914 ML on 19 October to 1022 ML on 26 October, but a pulse of 2542 ML on 28 October may have been enough to at least partly flush the wedge from the estuary. It is probable that most larvae would have been retained after the pulse event of 28 October which

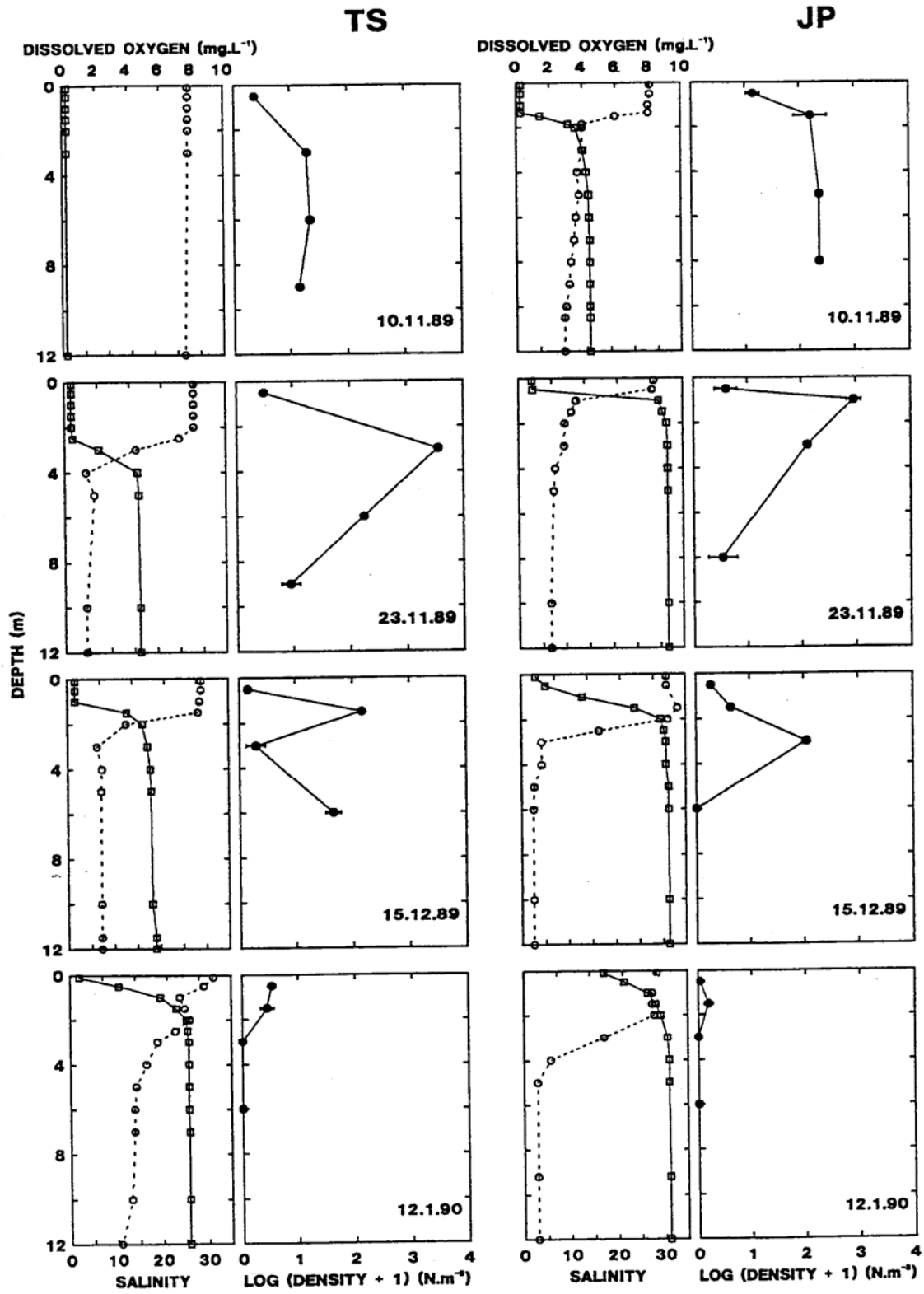


Fig. 6.7. Depth profiles of dissolved oxygen (open circles, dotted lines) and salinity (open squares, solid line) and mean (± SE) density of *Paratya australiensis* larvae at four depths in the deep pools below TS and JP on four consecutive sampling occasions

Table 6.2. Mean densities of *Paratya australiensis* larval stages, arranged so assumed cohorts are placed together (connected by common underlines), on three consecutive sampling occasions at HB, JP, and TS with ratios of density on each occasion to density of the same cohort on the previous occasion.
A standardised proportional change between consecutive stages (PS) was calculated by assuming constant change in density from stage to stage

SITE	10 Nov 1989		23 Nov 1989			15 Dec 1989			
	Stage	Density (D1)	Stage	Density (D2)	D2/D1	Stage	Density (D3)	D3/D2	PS
HB	I	7.1	V	4.3	0.61				**0.88**
	II	32.2	VI	4.4	0.14				**0.61**
	III	18.7	VII	2.7	0.14				**0.62**
	IV	5.5	VIII	0.7	0.13				**0.60**
JP			I	39.2		VII	3.2	0.08	**0.70**
			II	38.7		VIII	4.4	0.11	**0.73**
			III	23.5					
			IV	53.5					
	I	113	V	67	0.59				**0.88**
	II	12.4	VI	48.7	3.93				**1.41**
	III	0.27	VII	15.9	59				**2.77**
	IV	0.07	VIII	6.1	87				**3.06**
TS			I	187		VII	0.40	0.002	**0.42**
			II	235		VIII	0.58	0.002	**0.42**

corresponds to the large numbers of stage II and III larvae collected at HB thirteen days later on 10 November. The speculated first retention of larvae at JP corresponds to the first intrusion of the salt wedge past KH prior to 10 November, and the speculated first retention of larvae at TS corresponds to the first intrusion of the salt wedge past JP prior to 24 November (Fig. 2.2).

Assuming a progression through four stages during the period 10-23 November, and through seven stages during the period 23 November - 15 December, an estimate of survival/migration at each site can be made by comparing densities of corresponding stage classes (Table 6.2). In this table, stages, I, II, III and IV on 10 Novemeber are assumed to belong to the same cohort as stages V, VI, VII, and VIII respectively on 23 November. Similarly, stages I and II on 23 November correspond to stages VII and VIII respectively on 15 Decemeber. By assuming a constant change in density over each period, a standardised proportional change per stage can be calculated in each case. Changes in density for II-VI, III-VII, and IV-VIII were all consistent at HB, with about a 40% loss (60% survival) between consecutive stages (Table 6.2). Change for I-IV was less (12% loss between consecutive stages), possibly due to a

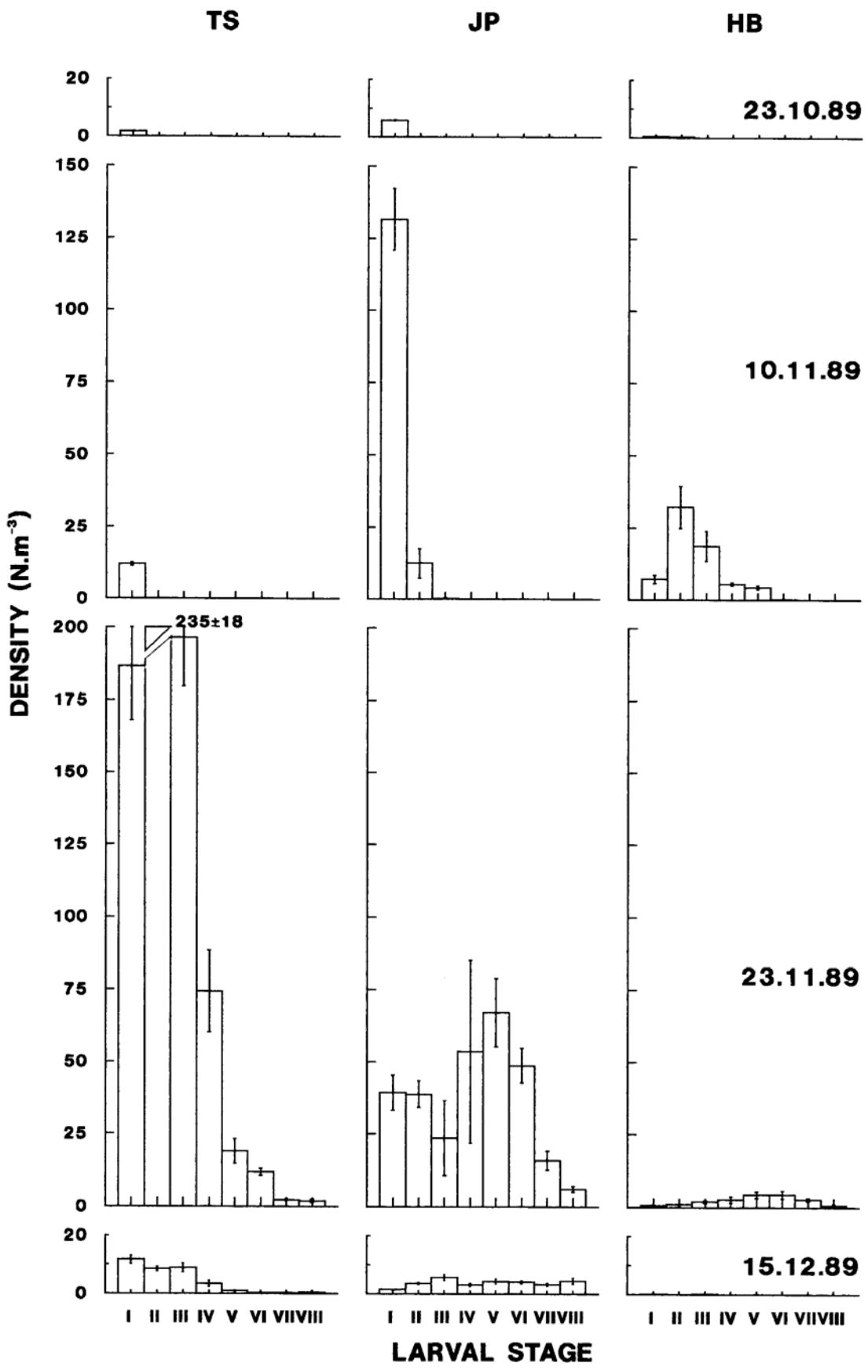


Fig. 6.8. Density of each larval stage of *Paratya australiensis* at three locations in the Hopkins River estuary on four occasions from October to December 1989

further influx of stage I larvae soon after the 10 November sample (see Fig. 6.8). The relatively constant decline in larval densities at HB suggests a constant rate of mortality or emigration from this site from 10 to 23 November. This is in contrast to the trend at JP over the same period where there were increases in density for II-VI, III-VII, and IV-VIII (Table 6.2). These increases in density indicate immigration of larvae at stages later than stage I to this site (or the less likely possibility of some larvae developing from I to VIII in fourteen days). A similar situation was evident at TS where stages VI-VIII were present on 23 November, but the corresponding stages were not present on 10 November. Immigration of these later stage larvae at JP and TS was most probably from downstream. Larvae, which were most abundant in the deep saline layer, probably moved upstream with the salt wedge as it intruded upstream during this period. The hypothesis of upstream migration is supported by the observation that increases in densities of later stage larvae were recorded only at upstream sites.

Despite this apparent immigration of later stage larvae from downstream, the dominant stages at each site were those that had begun as stage I at that site (e.g. JP on 10 November and TS on 23 November—Fig. 6.8). These larvae were presumably released upstream of and near the site in question. The importance of the site of release being near the site of stage I larval retention is underlined by the Clarke-Bumpus sample taken on 29 October 1991at JP, soon after the salt wedge had intruded to this site. In this season, very little seagrass, and consequently very few adult carideans, were present in the estuary. Two Clarke-Bumpus tows, 0.5 m and 1.0 m below the halocline, each collected ≈8 *P. australiensis* larvae m^{-3}: all of which were stage III or less. Thus although there was a large pool of adult *P. australiensis* upstream of the estuary, only very few larvae occurred in the estuary when very few adults occurred there. Recruitment therefore tended to be autochthonous.

Once discharge declines to a level at which the salt-wedge has become established at TS, it appears that deep pools upstream become stable enough for larvae to be retained in them, and retention of larvae in such upstream pools is maintained over the entire low flow period. Only stage I larvae were collected on 19 November 1991 at MH, suggesting little retention of larvae at this upstream site at a time when larvae were likely to be retained in the estuary. Thirteen days later, on 2 December, larvae as old as stage VI were collected from MH, with stages I and II dominating, suggesting a high level of on-going recruitment and some retention

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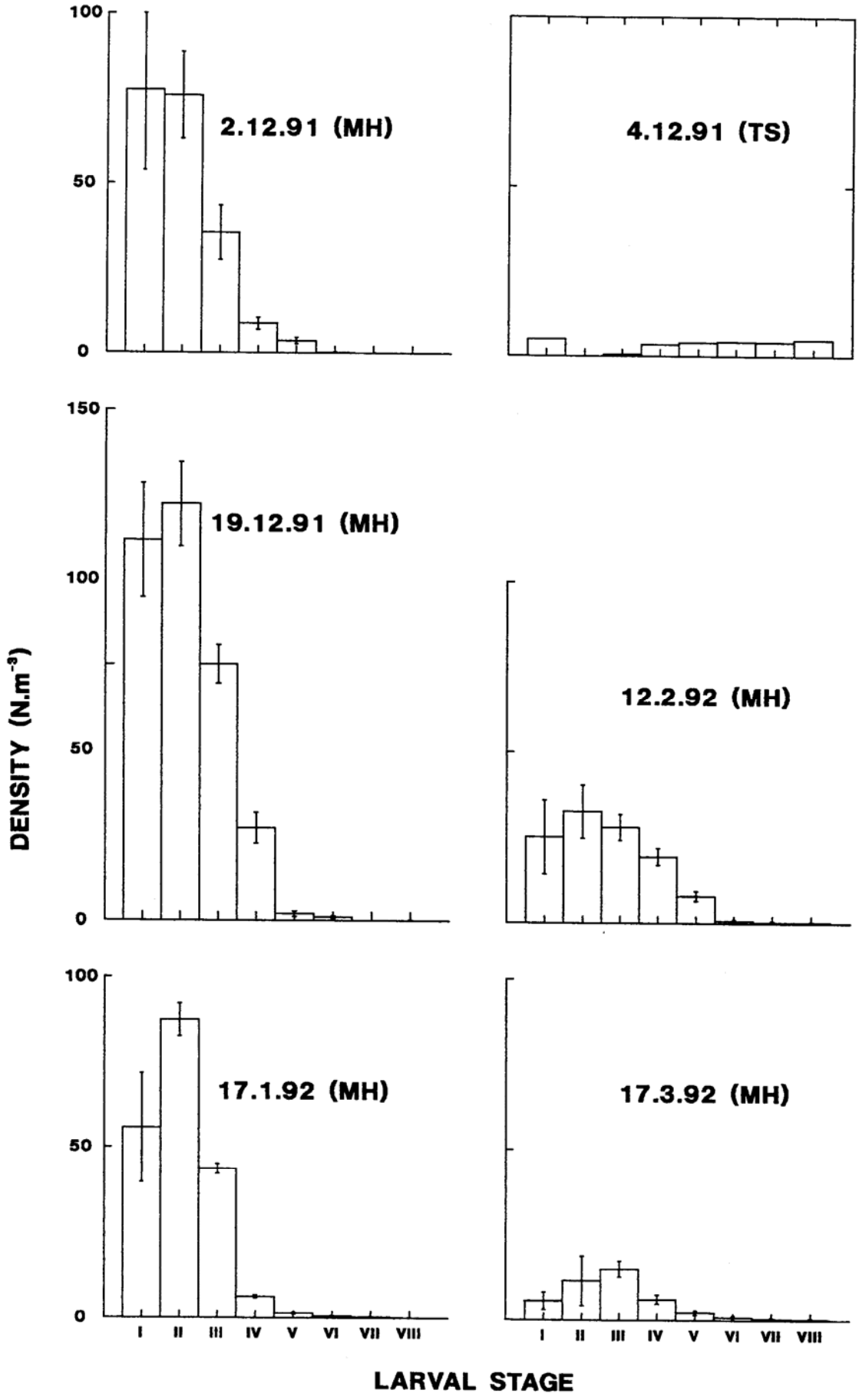
Fig. 6.9. Mean density (±SE) of larval stages of *Paratya australiensis* on five occasions from December 1991 to March 1992 at an upstream riverine pool (MH) and on 4 December 1991 at an estuarine pool (TS).


2.12.91 (MH)
4.12.91 (TS)
19.12.91 (MH)
12.2.92 (MH)
17.1.92 (MH)
17.3.92 (MH)
DENSITY (N.m-3)
LARVAL STAGE
I II III IV V VI VII VIII
0
50
100
150

of larvae (Fig. 6.9). At around the same time (4 December) few stage I larvae occurred in the estuary at TS. The population of *P. australiensis* larvae there was dominated by later stage larvae (Fig. 6.9), suggesting that peak larval densities and peak arrival of stage I larvae at TS had passed. The extended period of high densities of larvae at MH over the summer of 1991-1992 (Fig. 6.5) is in contrast to the brief peaks of larval recruitment in the estuary (Fig. 6.5). In addition, the dominance of early stage larvae at MH from December until February (Fig. 6.9) is in contrast to the dominance of a single corhort at each estuarine site (Fig. 6.8)

Because of this extended period of recruitment of stage I larvae to the pool at MH over summer, it was not possible to follow cohorts as it was at estuarine sites where there was a distinct pulse of recruitment. Very few late stage larvae were collected at MH on any sampling occasion, despite peak densities of early stage larvae similar to those found in the estuary (cf. Figs. 6.8, 6.9). Such a lack of later stage larvae suggests either a high mortality rate within the pool or a high emigration rate downstream. Mortality may also be increased by the action of being washed downstream. Emigration with little mortality is unlikely to be the main factor in all years as a high migration rate of larvae from upstream pools would result in large numbers of late stage larvae occurring at TS over the summer period. This was not the case in 1984, 1989 or in 1990. However, the late increase in density at TS on 21 January 1985 (Fig. 6.5) was composed of a larval population dominated by stages III and IV.

It is improbable that the deeper water of the pool at MH was retained over the summer of 1991/1992, like the deep saline water in the pools of the estuary. On all but one occasion, dissolved oxygen in the deepest part of pool was >80% that of the surface water (Fig. 6.10d). Discharge following the lowest dissolved oxygen record was as low as or lower than at any earlier occasion when larvae were present in the pool (Fig. 6.5), and yet there was enough circulation in the pool between 12 February and 17 March to replenish lost oxygen in the deeper water. Thus the pool appears not to be as stable a body of water as the salt wedge of the estuary, in which anoxia is reached soon after intrusion (Fig. 6.7). The greater circulation may explain the lack of larval retention in the pool at MH.

Sampling of larvae in the deepest 3 m of the pool was not possible using the Clarke-Bumpus sampler, but it is apparent from samples at 1, 3, and 5 m that larvae occurred most commonly deeper than 1 m (Fig. 6.10a). Larval densities were higher at 5 m than at 3 m in February and March, but were comparable at the two depths in December and January.

In summary these results allow construction of a usual series of larval recruitment events following the annual flood of the Hopkins River. Prior to discharge declining sufficiently to allow intrusion of a salt-wedge into the estuary, *P. australiensis* larvae are likely to be lost from the river. High densities of stage I larvae were retained at the head of the wedge, but arrival of stage I larvae at each site decreased after the head of the wedge had moved further upstream. This suggests that most larvae found in the estuary were released upstream of and

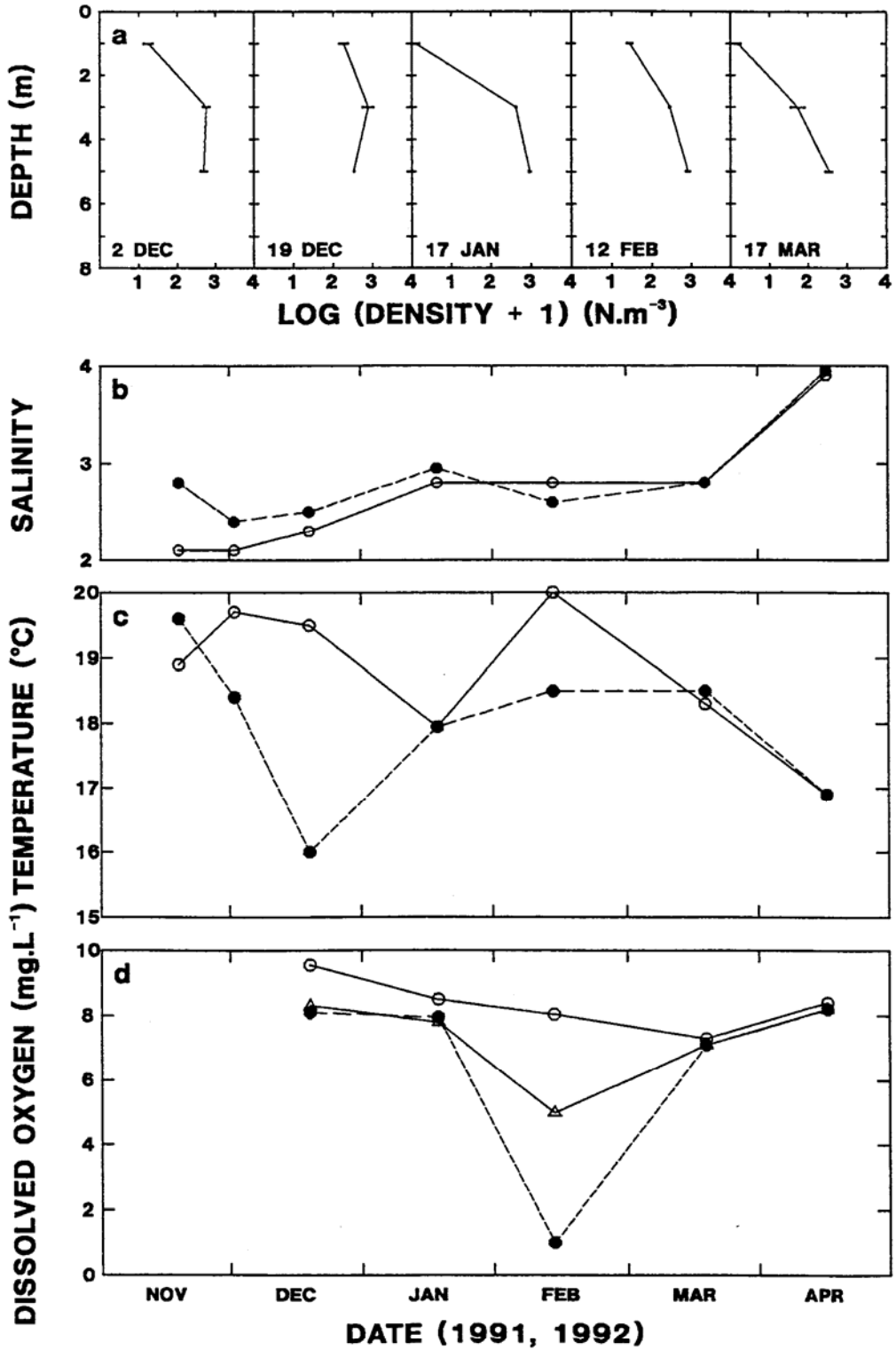


Fig. 6.10. *Paratya australiensis* at MH. (a) Mean (±SE) larval densities at three depths on five occasions (b) surface (open circles) and bottom (8 m, closed circles) salinity from 19 November 1991 to 14 April 1992 (c) surface and bottom temperature (d) dissolved oxyygen at surface, bottom and 5 m (triangles)

near the advancing wedge. However some upstream migration of later stage larvae with the advancing wedge is probable. The intrusion of the salt-wedge allows a series of pulse larval recruitment events in the estuary with relatively high survival rates (0.4-0.7 per stage). After the wedge has stabilised in the estuary, stage I larvae are retained and develop in deep riverine pools upstream of the estuary. Upstream recruitment continues for several months until the first increase in discharge after the low flow period. A high level of recruitment upstream persists for several months over summer, but it is possible that survival, or at least retention, to metamorphosis is lower than in the estuary.

6.3.1.2. *M. INTERMEDIUM* AND *P. SERENUS*

M. intermedium

Larval densities of *M. intermedium* reached maxima comparable to those of *P. australiensis* at JP, RF and TS in 1988/1989, but not until one to two months later: in December and January (Fig. 6.11). *M. intermedium* larvae were first collected in October at the more downstream sites RF and HB, and reached peak densities of >500 m^{-3} at all sites except TS, where only small numbers were collected. Although such high densities were collected only on one occasion at each site, *M. intermedium* larvae were present throughout the estuary in densities of >5 m^{-3} until April at JP, RF and HB, and were still present at HB in May 1989. This is in contrast to the occurrence of *P. australiensis* larvae, which after December, were represented by only an occasional larva until as late as May 1989. In the following season, *M. intermedium* larvae were collected from 16 November 1989 at HB and from 24 November at JP and TS until sampling was discontinued in January 1989. Over this period, larval densities did not exceed 3.6 m^{-3} at HB, 1.2 m^{-3} at JP and 0.7 m^{-3} at TS.

M. intermedium larvae showed no consistent tendency to occur in greater densities within the salt wedge, in fringing meadows, or in midstream surface waters (Fig. 6.12). Concentration of larvae in deeper water was not necessarily linked to the presence of a halocline and high dissolved oxygen levels, as was the case with *P. australiensis*. Larvae predominated below the sharp halocline at HB on 24 October and 21 November 1988, but not in similar conditions at HB on 17 December, nor at RF on 21 November 1988. *M. intermedium* larvae were most abundant at times when surface salinity was >10.

Stage-frequency distributions for *M. intermedium* larvae at JP, RF and HB were dominated by stage I larvae in 1988/1989 (Fig. 6.13), suggesting an extended period of larval recruitment throughout the downstream majority of the estuary. Large numbers of stage VIII larvae at RF

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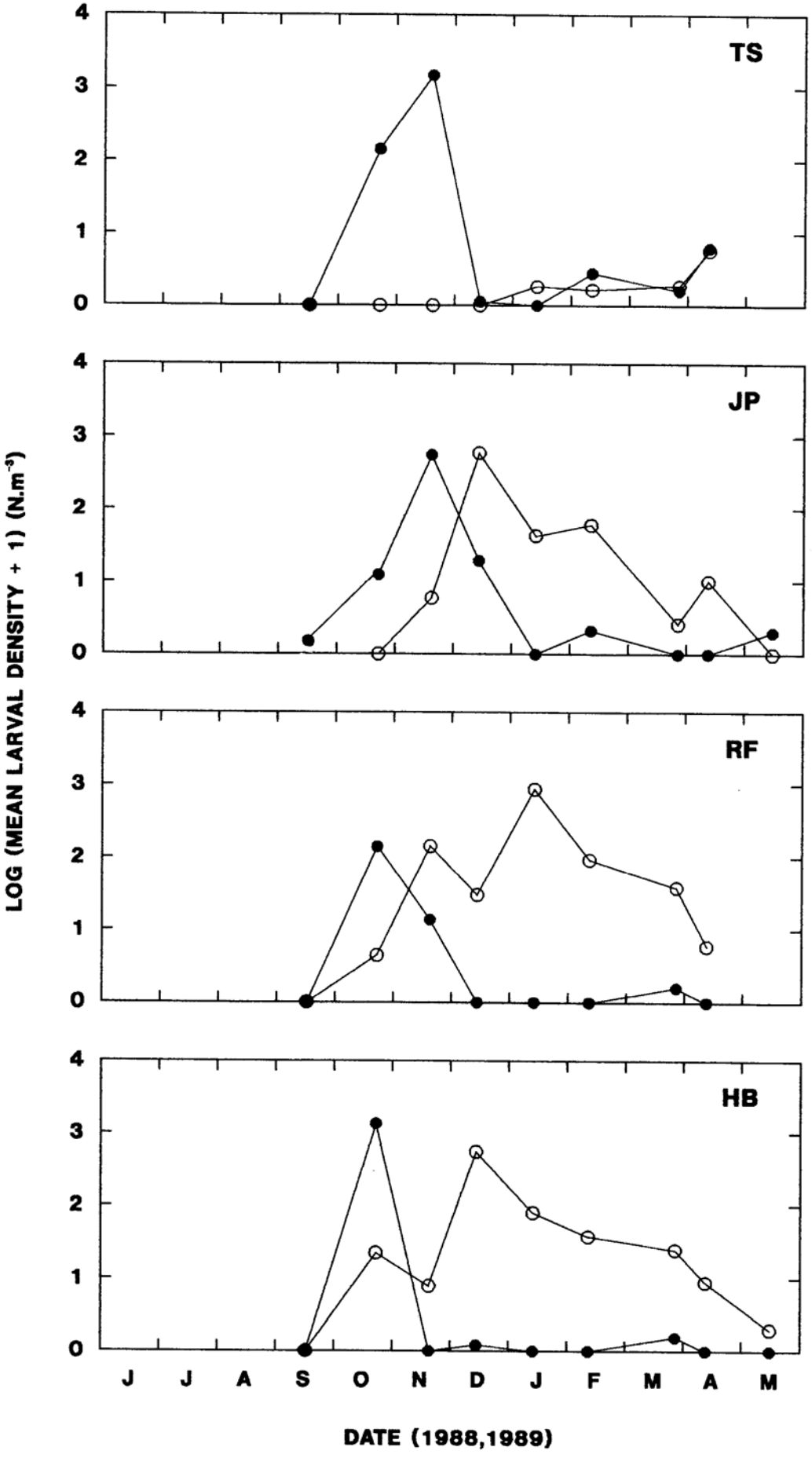
Fig. 6.11. Mean densities of larvae of two caridean shrimp species collected in the demersal tow at four sites in the Hopkins River estuary from September 1988 to April/May 1989.
closed circles, *Paratya australiensis;* open circles, *Macrobrachium intermedium*.


TS
JP
RF
HB
LOG (MEAN LARVAL DENSITY + 1) (N.m-3)
0
1
2
3
4
J J A S O N D J F M A M
DATE (1988,1989)

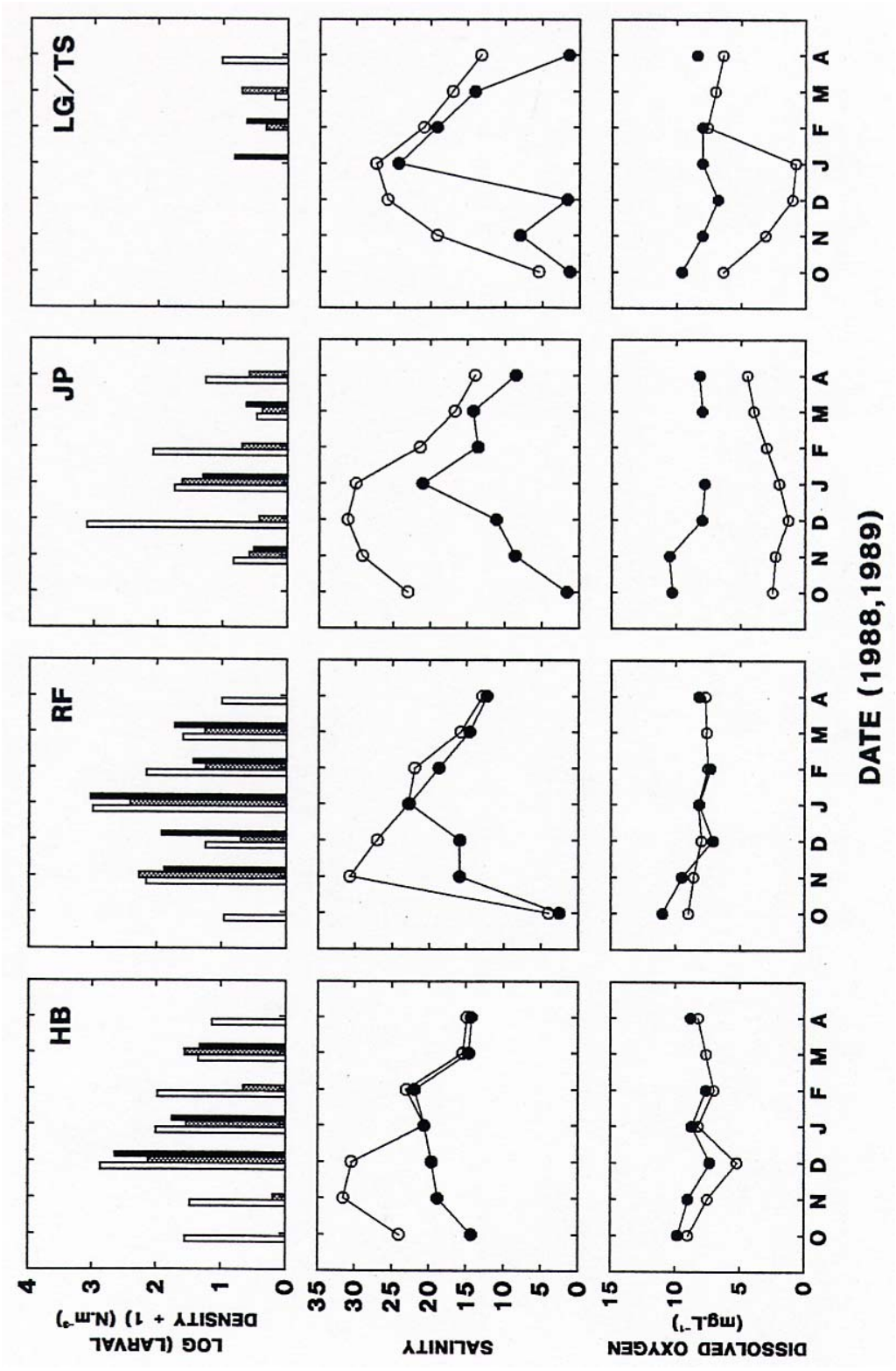


Fig. 6.12. Densities of *Macrobrachium intermedium* larvae collected in the demersal tow from October 1988 to April 1989 from three habitats at four locations in the Hopkins River estuary. Open bars, midstream below the halocline; grey bars, midstream surface (≈0.5 m deep); black bars, surface over fringing seagrass meadows (RF and HB) or mudflat (JP) or both (LG/TS). Salinity and dissolved oxygen at the depth of the surface sample (closed circles) and the deep sample (closed circles) are also shown.

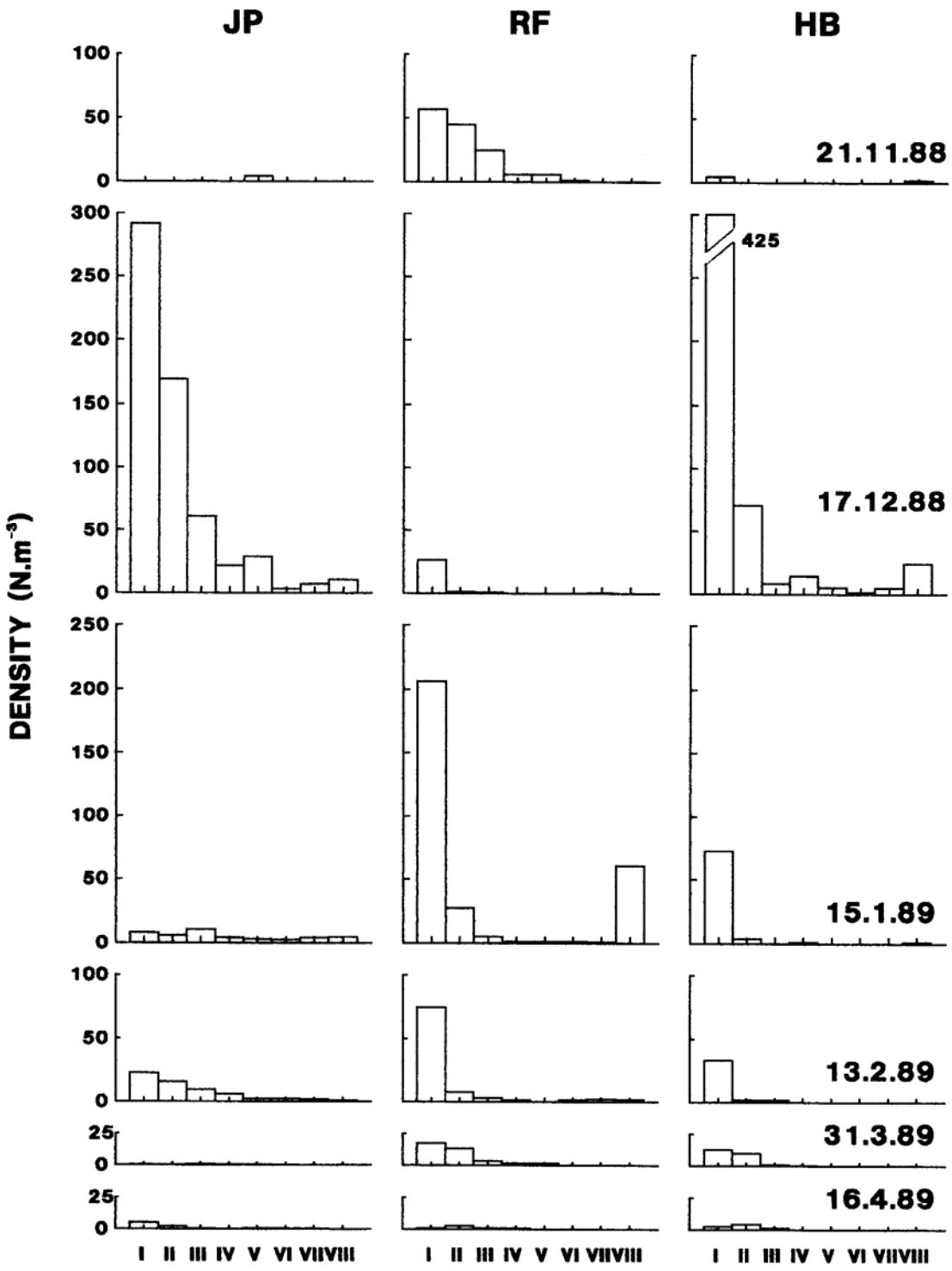


Fig. 6.13. Density of each larval stage of *Macrobrachium intermedium* at three locations in the Hopkins River estuary from November 1988 to April 1989

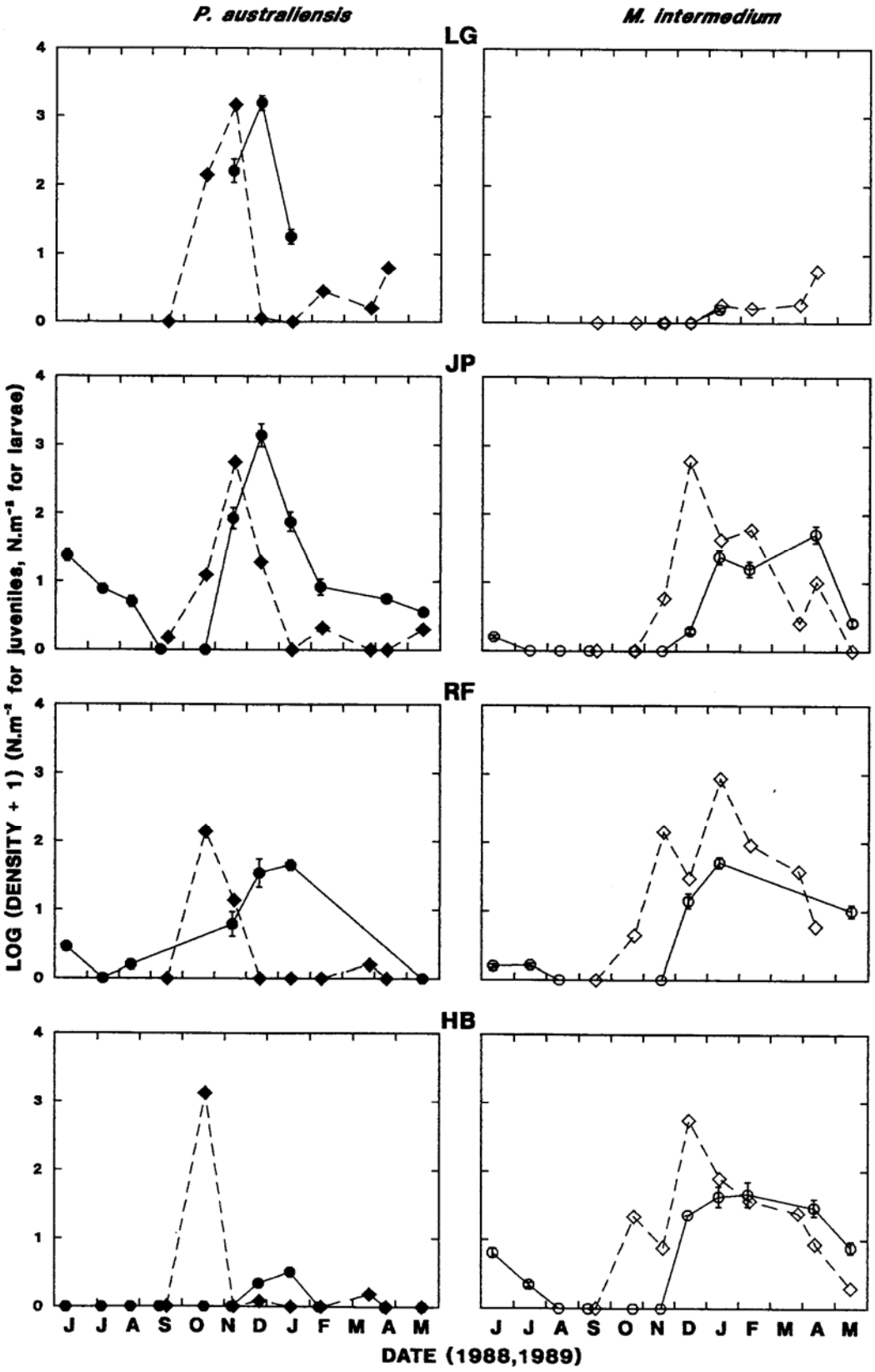


Fig. 6.14. Mean densities of *Paratya australiensis* (closed points) and *Macrobrachium intermedium* (open points) at four sites in the Hopkins River estuary from June 1988 to May 1989. Diamonds, dashed line, mean densities of larvae collected with the demersal tow; circles, solid lines, mean densities (±SE) of juveniles collected with core sampler (see chapter 2)

on 15 January 1989 and at HB on 17 December 1988 were primarily collected over the fringing meadows, in association with large numbers of juveniles. Peak densities of stage I larvae at each location were followed by an extended period of juvenile occurrence in the seagrass meadows (Fig. 6.14). Peak densities of larvae of *P. australiensis* and *M. intermedium* were comparable in 1988/1989 (Fig. 6.11). In contrast, juveniles of the two species showed marked differences in density trends along the estuary. Peak density of juvenile *P. australiensis* at JP was much higher than *M. intermedium*, while at RF, juveniles of both species occurred in similar densities, and at HB, *M. intermedium* juveniles were more numerous (Fig.6.14).

P. serenus

Larvae of *P. serenus* were rare in the estuary. Only one individual was collected: a stage I larva from below the halocline at HB on 31 March 1989.

6.3.2. DIURNAL PATTERNS OF VERTICAL DISTRIBUTION IN *P. AUSTRALIENSIS* LARVAE

6.3.2.1. VERTICAL DISTRIBUTION PATTERNS IN ESTUARIES

The tidal patterns observed in the Hopkins and Fitzroy rivers during the vertical distribution surveys were similar. Tidal amplitude in the Hopkins on 15-16 November was 0.35 m, and in the Fitzroy was 0.37 m on 10-11 November and 0.22 m on 11-12 November (Fig. 6.15a). Flood tides caused a rapid increase in estuary level during the night over 5-6 h, with ebb tides lasting the remainder of the day. The small semi-diurnal rise predicted for each afternoon in adjacent coastal waters (Department of Defence, 1990; 1991) was not recorded other than as a slowing of the ebb.

In the Hopkins estuary, no flow was recorded below the halocline, while in the Fitzroy, an upstream flow was recorded in the mid-depths of the salt wedge on two occasions, around high tide (Fig. 6.15c). In the Fitzroy, the fresh layer was shallower (0.7-1.2 m) and flowed out at a greater rate than in the Hopkins. It was recorded flowing upstream soon after low tide on 11 November 1991 (Fig. 6.15b,c). The fresh layer of the Hopkins was 1-1.5 m deep during the sampling period, which allowed two flow measurements in this layer. The flow rate at 1 m was usually greater than at 0.5 m, but on three occasions—at high tide and at the semi-diurnal slowing of the afternoon ebb—flow was detected at 0.5 m, but not at 1 m (Fig. 6.15c). In both rivers, the fresh layer bulged around low tide, and then narrowed again as the layer below the halocline deepened with the flood tide (Fig. 6.15b).

In short, the salt wedge of each river showed no flow (or, on two occasions, some upstream flow), while the fresh layer varied from downward flow during ebb tide to no flow (or small upstream flow) during flood tides. In such a flow regime, the minimum distributional requirement for a plankter to avoid downstream displacement would be to avoid the fresh layer in periods when it is flowing downstream. Fig. 6.15e shows the proportion of larvae

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Fig. 6.15. Surveys of vertical distribution in *Paratya australiensis* larvae in the Hopkins River estuary, 15 and 16 November 1990, and in the Fitzroy River estuary, 10-12 November 1991. (a) Tidal variation in estuary above an arbitrary benchmark. Solid line, from tide gauge; dashed line, from benchmark at sampling site (b) variation in height of estuary surface (upper line) and halocline (salinity=5, lower line) above estuary bottom (c) flow rates of fresh layer (0.5 m, circles; 1 m, upright triangles) and salt wedge (1.5 m, inverted triangles; no flow detected in the Hopkins). Positive values indicate downstream flow. (d) Log (x+1) transformed irradiance at 3 m depth (e) variation in the proportion of larvae in the fresh layer (0.5 m, circles; 1 m, triangles) (f) variation in mean (±SE) depth below the halocline (salinity=5) of larvae. Means are connected by a spline curve (Wilkinson, 1990). Asterisks indicate means based on diffuse or bimodal distributions (see Figs. 6.16, 6.17). Vertical lines through all graphs indicate sunrise and sunset.

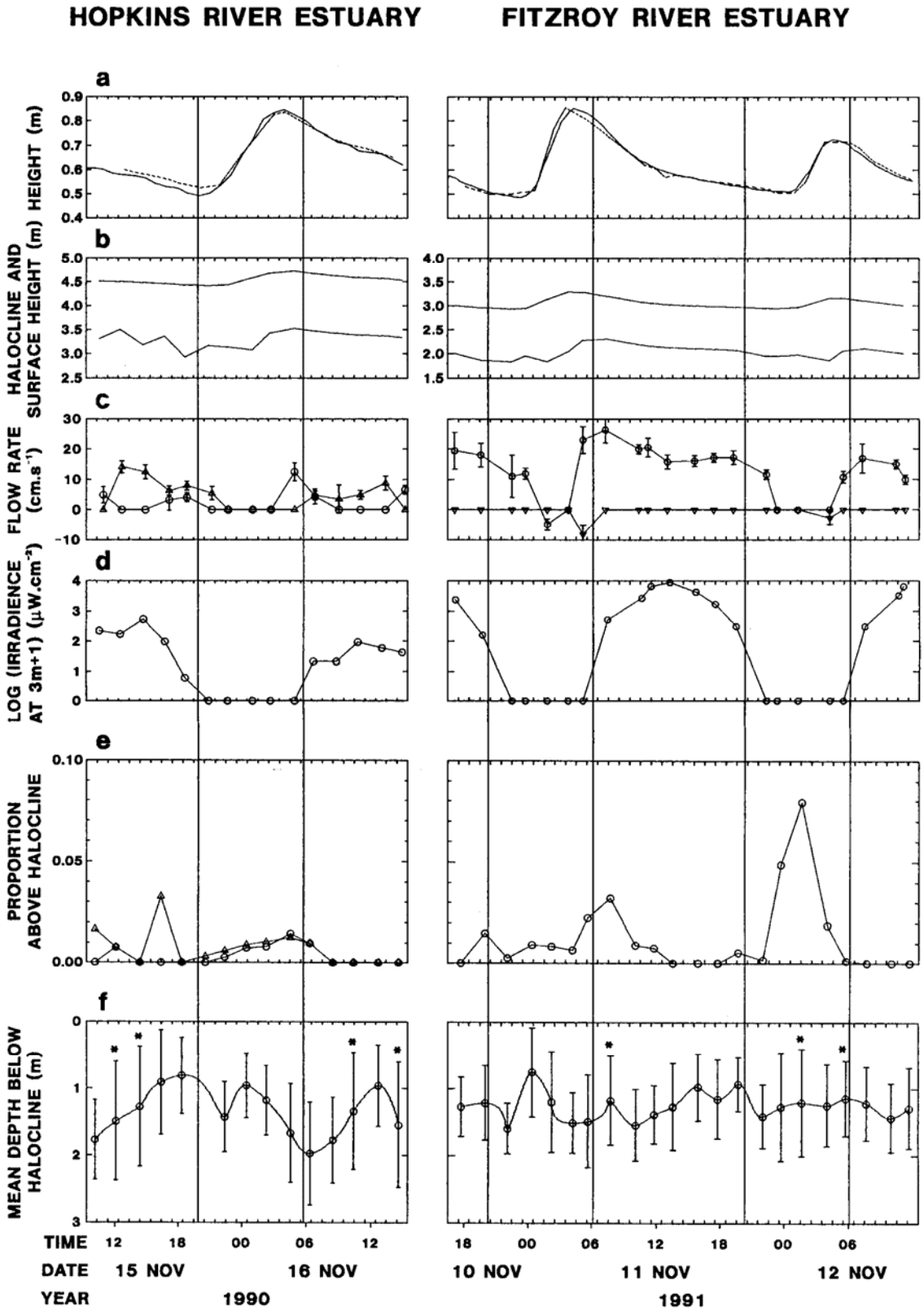
HOPKINS RIVER ESTUARY
FITZROY RIVER ESTUARY
a
b
c
d
e
f
HEIGHT (m)
HALOCLINE AND SURFACE HEIGHT (m)
FLOW RATE (cm.s⁻¹)
LOG (IRRADIENCE AT 3m+1) (μW.cm⁻²)
PROPORTION ABOVE HALOCLINE
MEAN DEPTH BELOW HALOCLINE (m)
TIME
DATE
YEAR
15 NOV
16 NOV
10 NOV
11 NOV
12 NOV
1990
1991

Table 6.3. Number of *Paratya australiensis* larvae in the fresh layer above the halocline (N), and that number as a percentage of larvae from all depths sampled (%) in (a) fifteen samples in the Hopkins River estuary and (b) twenty-two samples in the Fitzroy River estuary, under varying flow conditions n=number of samples in which the flow conditions prevailed; numbers in brackets are results if a sample taken at high tide is not included (see text).

(a) Hopkins River (two depths sampled above the halocline)

	0.5 m				1 m			
	Flow detected (n=6)		No flow detected (n=9)		Flow detected (n=9)		No flow detected (n=6)	
Depth (m)	N	%.	N	%	N	%	N	%
0.5	23(2)	1.1%(0.3)	36	0.5%	4	0.2%	55	0.7%
1	24(6)	1.2%(1.1)	54	0.7%	8	0.4%	70	0.9%
sum	47(8)	2.3%(1.5)	90	1.2%	12	0.6%	125	1.6%
All depths	2013(565)		7626		1957		7682	

(b) Fitzroy River (0.5 m only above the halocline)

	Upstream flow detected (n=1)		Downstream flow detected (n=4)		No flow detected (n=17)	
	N	%	N	%	N	%
0.5	2	0.8%	27	0.5%	139	4.0%
	240		5767		3515	

collected in the freshwater layer in each sample. In the Hopkins River, the proportions at 0.5 m and at 1 m were similar on all but two occasions (1000 h and 1615 h 15 November), when sample size was small (<120). There was a sustained increase in the proportion at both depths in the fresh layer during the flood tide, when flow at 0.5 m was not detectable (Fig. 6.15a, c, e). In the Fitzroy, a similar but more pronounced increase was observed on the second flood tide when the fresh layer was stationary. However, on the previous morning of 11 November (0530 and 0730 h) the proportion of larvae in the fresh layer of the Fitzroy increased *after* high tide, coinciding with high downstream surface flows (Fig. 6.15a, c, e).

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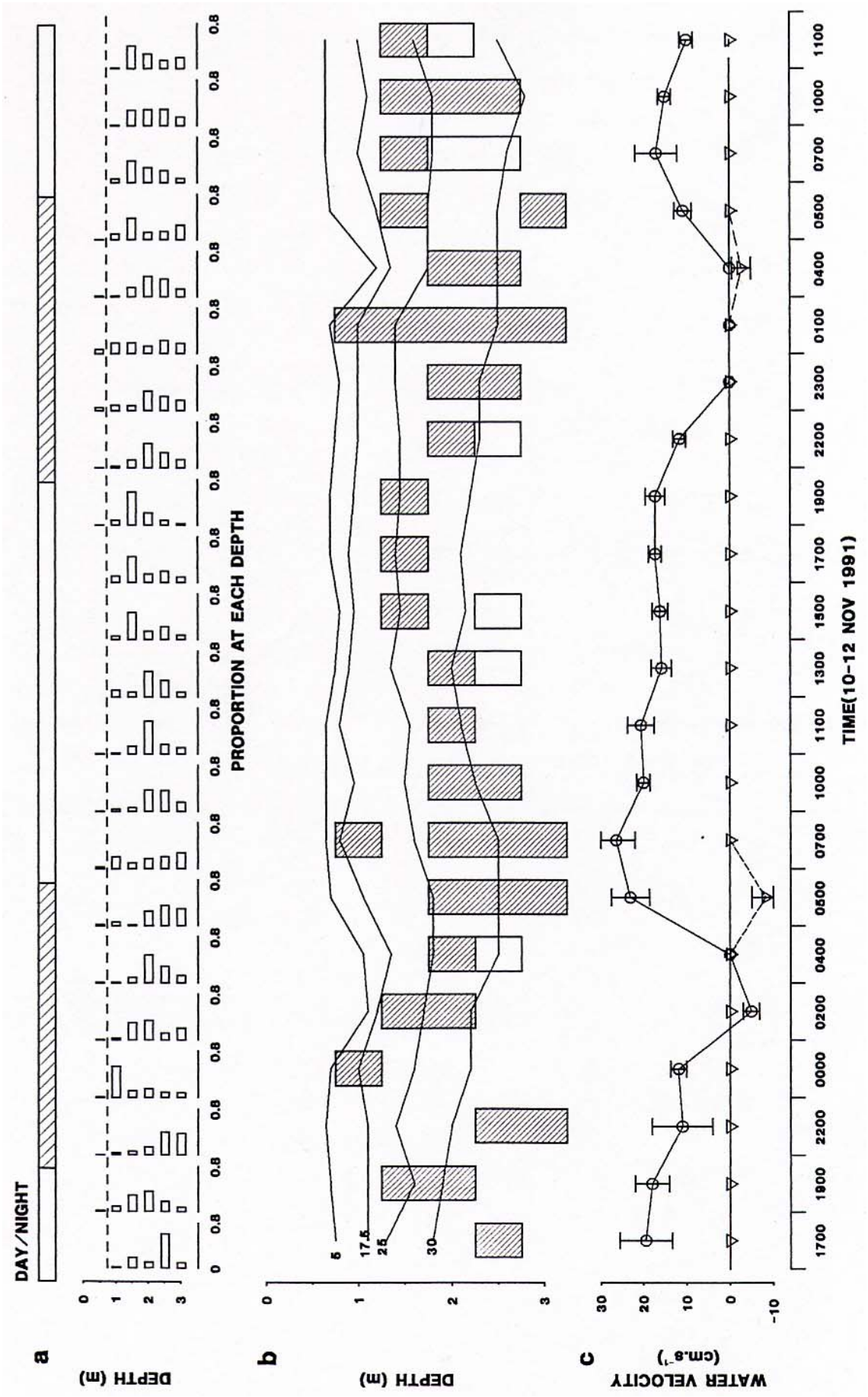
Fig. 6.16. (a) Proportion of *Paratya australiensis* larvae in each of six depths in twenty-two samples from the Fitzroy River estuary over 44 h, 10-12 November 1991. Dashed line indicates level of halocline, which was between the 0.5 m and 1 m samples. Bar indicates periods of day (open) and night (hatched). (b) Salinity contours varying with depth and sample. Dominant (shaded) and sub-dominant (open) modes in the depth distributions of larvae are superimposed. (c) Flow rates of water in fresh layer (0.5 m, circles), and in salt wedge (1.5 m, triangles), measured 10-15 min before each sample


a
DAY/NIGHT
DEPTH (m)
PROPORTION AT EACH DEPTH
b
DEPTH (m)
5
17.5
25
30
c
WATER VELOCITY
(cm.s⁻¹)
TIME(10-12 NOV 1991)

This unexpected result is considered below. Despite the inconsistency of trend, the proportion of larvae in the fresh layer was less overall when flow was detected in the fresh layer (Table 6.3). This trend was most apparent in the Fitzroy. In the Hopkins, flow at 1 m was associated with lower proportions of larvae above the halocline, but such an association was not apparent for flow at 0.5 m (Table 6.3a). However, almost all the larvae collected in the fresh layer in the 'flow-detected-at-0.5m' category were from the 0415 h 16 November sample at high tide. In this sample, 0.5 and 1 m were sampled 30 min before flow rates were measured, and as the sample was taken around high tide, it is likely that there was no flow at 0.5 m when the sample was taken. If this sample is not included in the calculation of proportion of larvae in the fresh layer, the percentage collected from 0.5 m (above depth of no flow) is 0.3%.

Thus, on no occasion was more than 0.6% of larvae collected in depths with a downstream flow. This may also be interpreted as larvae spending 0.6% or less of their time to metamorphosis in water flowing downstream. Assuming a larval development period of 37 days (the mean duration of development for larvae from the estuary, reared in the laboratory: see section 5.3.1.3), this equates to a maximum of 5.3 h. If the remainder of development time is spent in the salt wedge with nett upstream movement, it is likely that horizontal position will be maintained or the larva will move upstream.

The depth distributions of stages I, II, III-IV, and V-VIII are presented in Appendix 3. In almost all cases, the distributions of all stages were similar, with most discrepancies occurring in samples with small N. The only recurring difference between stages was for late-stage larvae in some small day-time samples in the Fitzroy River to occur more commonly at 3 m depth (bottom). The small numbers of late-stage larvae in these samples result in them having little effect if all stages are pooled (Fig. 6.16).

Figs. 6.16a and 6.17a show the vertical distributions of *P. australiensis* larvae (all stages pooled) in all samples from each survey. Most distributions were unimodal, and the modal depth varied considerably during both surveys: between 1 and 2.5-3 m in the Fitzroy, and between 1 and 3-4 m in the Hopkins (Fig. 6.16c). Such movement of a single depth mode is suggestive of synchronous migration of the larval population (Pearre, 1979). However, seven samples showed no clear mode, suggesting some asynchrony. The two most bimodal distributions (Fitzroy, 0730 h 11 November, and 0530 h 12 November) were the first samples after upstream flow had been detected in the salt wedge. The other diffuse distributions were: Fitzroy, 0130 h 12 November, at low tide, and Hopkins, 1200 h and 1415 h, 15 November, and 1000 h and 1420 h, 16 November, all during the slowing of the day-time ebb. At 0530 h, the salt wedge was recorded flowing upstream while the fresh layer flowed out(Fig. 6.15c), and this may have resulted in increased turbulence around the halocline.

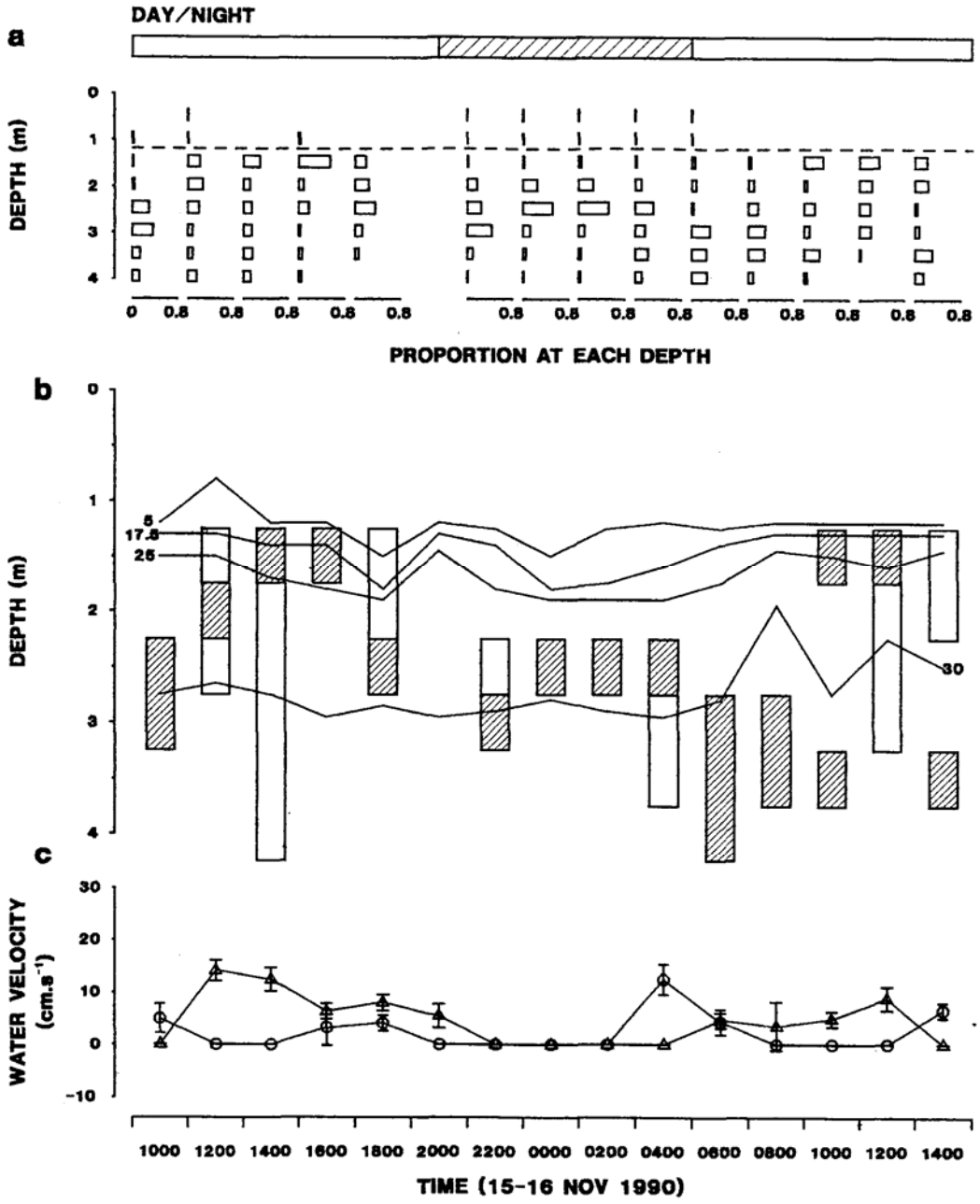


Fig. 6.17. (a) Proportion of *Paratya australiensis* larvae in each of eight depths in fourteen samples from KH in the Hopkins River estuary over 30 h, 15-16 November 1990. Dashed line indicates level of halocline which was between the 1 m and 1.5 m samples. Bar indicates periods of day (open) and night (hatched). (b) Salinity contours and dominant depth modes for larvae as in Fig. 6.16b (c) Flow rates of water in fresh layer (0.5 m, triangles; 1 m, circles), measured 10-15 min after each sample

Changes in flow were associated with changes in salinity conditions in the salt wedge (Figs. 6.16b, 6.17b). The maximum salinity recorded during the survey was a little over 30 (31 in the Hopkins, 32 in the Fitzroy). Although the surface salinity in both estuaries was ≈2, the halocline was narrower in the Hopkins (see salinity contours in Figs. 6.16b and 6.17b). In both estuaries, on most occasions, larvae were most abundant in salinities between 17.5 and 30. Several samples had peak abundances of larvae in depths below salinity of 30, while only two samples were dominated solely by larvae in the 0.5 m nearest the fresh layer. No clear association between variation in salinity-depth distribution and larval depth distribution was evident, although in the Fitzroy there was a tendency for deeper modes when the 30 isohale was deeper.

The change in distributional structure (from umimodal to diffuse and bimodal) around tidal events and the variation in the proportion of larvae in the fresh layer with flow conditions (Table 6.3) are suggestive of vertical migration in response to tidal conditions. However, because the tidal and diurnal cycles were nearly synchronous during these surveys, it is difficult to separate their influences. This survey, spanning three day-night cycles and three tidal cycles, was not long enough to allow firm association of migration patterns with physical cycles. However, some preliminary hypotheses can be erected from the observed patterns in mean depth (Fig. 6.15f).

Variation in mean depth of ≈1 m was observed in the Hopkins and in the first tidal cycle in the Fitzroy, but mean depth varied less in the second half of the Fitzroy survey. Tidal amplitude was one third less on this third tidal cycle, suggesting the magnitude of tidal fluctuations may influence the magnitude of migration. Generally mean depth decreased (i.e. upward movement) during the day from an early morning maximum, and increased (i.e. downward movement) around dusk. There was a sharp decrease in mean depth (upward movement) in the early night, shortly after low tide, in the Hopkins and in the Fitzroy on the night of 10-11 November, but not on the following night, when mean depth varied little. On the two earlier nights, the night-time minimum (mean depth nearest the surface) was followed by a steady increase in mean depth until soon after dawn. This downward movement appeared to continue through high tide and changing flow patterns in the surface layer. The steady downward movement is not apparent from the mean depths in the Fitzroy on the morning of 11 November (Fig. 6.15f). However, this statistic is misleading for a bimodal distribution: the 0730 h sample shows a relatively small mean depth, but most larvae were in the deepest metre of the water column at this time, with a second mode just below the halocline (Fig. 6.16). This is the second of the two samples discussed earlier which showed heightened proportions of larvae in the downstream-flowing fresh layer. This bimodal distribution of larvae may have been a result of turbulence around the halocline due to opposing flows in the fresh layer and the salt wedge detected at 0510 h (Fig. 6.15c). A hypothetical model of larval behaviour to explain such a distribution is constructed in the discussion (Section 6.4).

These trends in mean depth point to the importance of both diurnal and tidal cycles in shaping diurnal patterns of vertical distribution in *P. australiensis*. The post-dusk maximum in mean depth appears to be associated with the diurnal cycle as it was observed on all three nights, irrespective of the timing and magnitude of low tide. The rapid upward movement, which followed it on the two nights with the largest tidal amplitudes, is likely to be associated with the flood tide. However, on both occasions when the upward movement was observed, the minimum depth was reached, and downward movement began before high tide, and continued beyond high tide. The steady upward movement during the day began at dawn, and appeared independent of tidal conditions.

Upstream flow of the salt wedge was observed on only two occasions, only at 1.5 m, in the top metre of the salt wedge. On both these occasions, the majority of *P. australiensis* larvae were collected from 2 m or deeper (Fig. 6.16). More observations are required, but this suggests that vertical migration patterns do not maximise or assist upstream displacement. It is suggestive of avoidance of flow irrespective of its direction.

In summary, it is likely that horizontal position in salt wedge estuaries is maintained by *P. australiensis* larvae by persistence in the salt wedge, which has no (or upstream) nett flow. Migrations into the fresh layer when flowing downstream were uncommon, but diurnal vertical migrations were evident within the salt wedge. Some variation in mean depth appeared tidally influenced, but the overall pattern of vertical distribution appears to be associated with the diurnal cycle. No evidence was found of upstream displacement being enhanced by vertical migration patterns.

6.3.2.2. VERTICAL DISTRIBUTION IN A RIVERINE POOL

The mean densities of *P. australiensis* larvae at three depths, day and night, in the pool at MH are presented in Fig. 6.18. All stages showed similar depth distributions. In the day samples, larvae of all stages were most abundant at 3 m, the intermediate depth, and least abundant nearest the surface, at 1 m. In the night samples, all stages showed a trend to greater abundance with depth.

Larvae of stages II, III-IV, and V-VIII were less numerous at night than in the day at 1 m, and more numerous at night than in the day at 5 m (all $P<0.01$). Stage I larval densities were not significantly different between day and night at these depths ($P=0.099$ at 1 m, and $P=1.000$ at 5 m). At 3 m, densities of all stages were greater during the day than at night ($P<0.01$ in all cases).

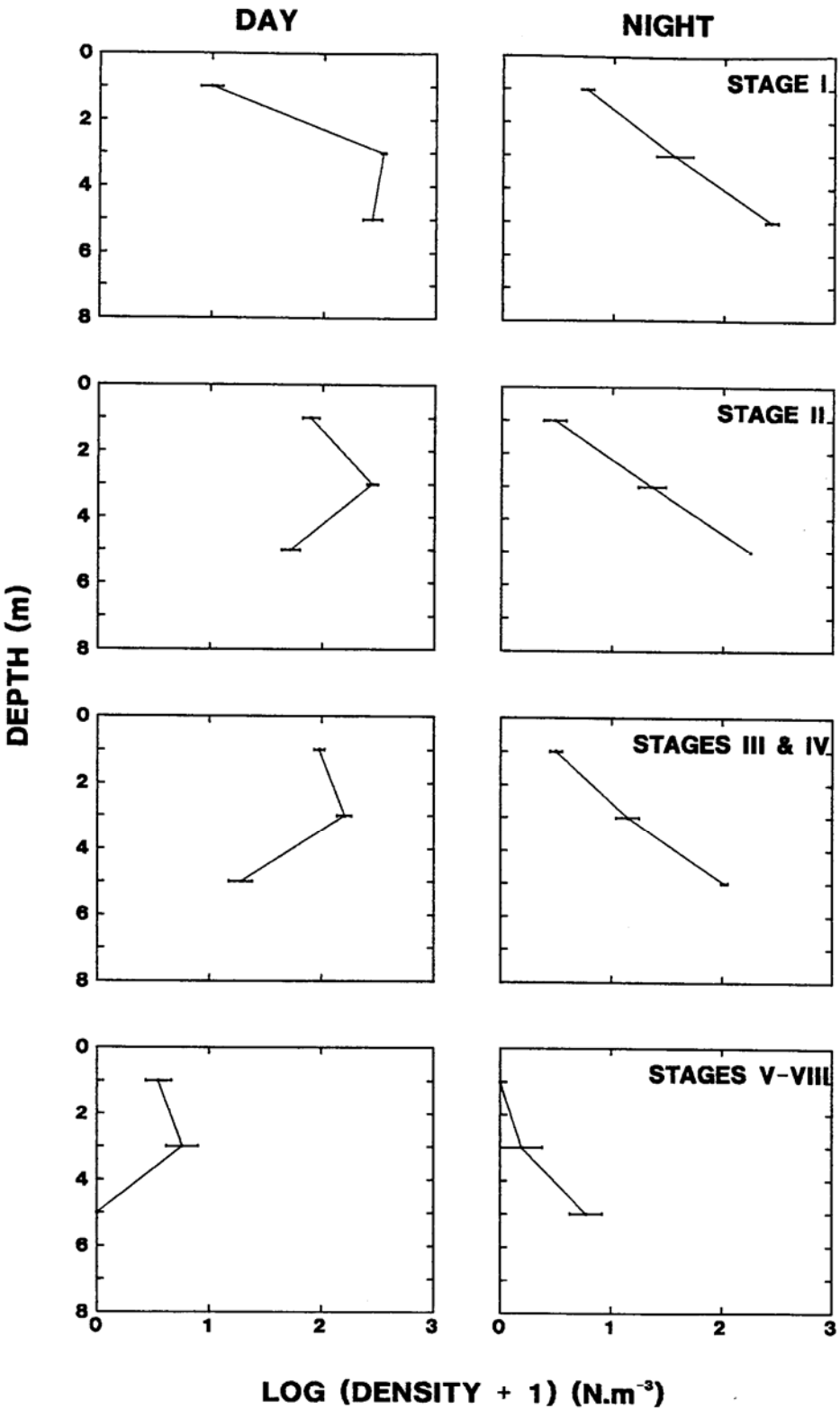


Fig. 6.18. Mean (±SE) density of four stage groupings of *Paratya australiensis* larvae at three depths in the 8 m deep pool at MH, 19 December 1991 at 1600-1700 h (day) and 2230-2330 h (night)

Because only the 3 m sample differed between day and night in stage I larvae, it is not possible to interpret the result in terms of vertical migration. The stage I larvae that were present at 3 m during the day but not collected at night may have moved up to between 1 and 3 m, or to an unsampled lower depth.

The trends for all later stages suggest there was a downward migration between the day, 4-5 h before sunset (1600-1700 h), and the night, 1.5-2.5 h after sunset (2230-2330 h). Such a trend is consistent with patterns observed in the estuary of an upward movement during the day and downward movement at dusk. It does not show the rapid post-dusk rise that was associated with flood tides in the estuaries. These observations point to the importance of the diurnal cycle in vertical migration of *P. australiensis* larvae in the absence of a tidal cycle.

6.4. DISCUSSION

6.4.1 SEASONAL VARIATION IN LARVAL DISTRIBUTION

The high densities of larval *P. australiensis* and *M. intermedium* reported in this study are consistent with the densities reported by Newton (1994). She found the zooplankton community of the Hopkins River estuary to be highly diverse and abundant among Australian estuaries. The sill at the mouth of the estuary was considered a likely explanation for the richness of the community, because it limits both tidal action and the immigration of marine invaders. In the context of epibenthic fauna with meroplanktonic larvae, the sill allows immigration of adult and juvenile forms into the estuary, as has been proposed in Chapter 4 for *M. intermedium* and *P. serenus*, but reduces the chance of larval export. Larval export is reduced because the sill prevents outflow of the salt wedge with tidal fluctuations. The wedge is only flushed from the estuary under conditions of high river discharge. The hydrodynamics of the estuary is therefore more influenced by patterns of river flow than by tidal fluctuation, which may account for a freshwater species such as *P. australiensis* being such an abundant member of the zooplankton community. Newton (1994) found the hydrological cycle to be of prime importance in structuring the zooplankton community and determining abundance of particular taxa. Such influences are particularly important to the occurrence of the meroplanktonic larvae of caridean shrimps, which are produced at particular times of the year in association with particular phases of the hydrological cycle.

P. australiensis

For a species known to complete its life cycle in fresh inland waters (Williams, 1977; Walsh, 1993), *P. australiensis* is remarkably well adapted for larval development and juvenile recruitment in the estuarine environment. Timing of larval production in relation to the

hydrological cycle and the vertical distribution patterns of larvae contributed to high larval densities in the Hopkins River estuary in all years studied in which seagrass meadows were widespread. The high densities of later stage larvae in the saline water below the halocline provide strong evidence of *P. australiensis* larvae actively using the hydrodynamics of these estuaries to avoid further downstream displacement during development. This conclusion is at odds with previous speculation that any estuarine occurrence of this species is the incidental result of floods washing individuals downstream of their preferred habitat (Walker, 1972).

The majority of mature females in the lower reaches of the river were ovigerous soon after the annual sharp peak in discharge and in the remaining months of 1988 (Figs. 2.8, 4.5). During this time, large numbers of ovigerous females migrated into the estuary, and upon discharge declining enough to allow intrusion of a salt wedge into the estuary, large numbers of early stage *P. australiensis* larvae occurred in the plankton of the estuary. No evidence was gathered of larvae being released maximally to coincide with spring tides, but such tidally-timed behaviour has been reported in other carideans (Paula, 1989). If larvae were maximally released during spring tides at the critical discharge during the post-flood decline in river discharge (Fig. 6.5), then the probability of larvae being released into the intruding salt wedge would be high. This proposition warrants further study and is considered again in Chapter 7.

P. australiensis larvae showed a striking preference for the deep saline layer of the newly stratified estuary (Figs. 6.6, 6.7), and although they were shown to migrate vertically during the course of each day, a very small proportion of their entire larval development period was spent in water flowing downstream. Such behaviour would allow the maintenance of position in the estuary, if not a nett upstream movement during development. Larval behaviour is considered in more detail in the next section.

It was surprising to find *P. australiensis* larvae occurring most commonly between salinities of 20 and 30 in both vertical migration surveys (Fig. 6.16, 6.17). Larval rearing was not attempted in the laboratory between salinities of 15 and 28.8 (see Section 5.3.2.3). Of the salinities trialed, rearing was most successful at 15. Although larvae were viable for up to sixteen days at 28.8, no larvae were successfully reared at this salinity. It is possible that larvae could have been more successfully reared at salinities in the low 20s. Nevertheless it is apparent that *P. australiensis* larvae in the Hopkins and the Fitzroy estuaries spent a significant part of their developmental time in salinities that were sub-optimal in the laboratory. Perhaps development in the laboratory could be enhanced by varying salinity diurnally.

By linking dominant larval cohorts (Fig. 6.5), a developmental period was extrapolated for estuarine larvae consistent with developmental period in the laboratory at salinity 15 (Section 5.3.1.3). Larval duration was longer than the period that the salt wedge remained oxygenated in 1989. Thus, for the cohort released just prior to 10 November 1989 when the salt wedge reached JP, larval habitat became restricted to a narrow layer in the second half of the larval

Table 6.4. Number of days taken for daily discharge at Hopkins Falls to drop from 2000 ML to 300 ML, in seven years. (Data from the Rural Water Corporation, Victoria)

Year	1984	1985	1987	1988	1989	1990	1991	mean
Days	25	30	62	29	37	19	21	31.9

developmental period. This narrow layer, just below the halocline, supported high densities of a diverse planktonic community. During this period when available habitat for larvae was reduced, low levels of stage I larval recruitment were still evident, on 23 November and 15 December 1989 (Fig. 6.8). The declining early stage larval densities over this period corresponded to the decline in ovigerous females at JP observed over the same period of the previous year (Fig. 4.5). Thus, the decline in larval numbers in the estuary may not have been due to the estuary becoming a less suitable larval habitat, but due to processes determining adult mortality or migration from the estuary.

However, if the decline in larval density were caused solely by factors driving *P. australiensis* adults from the estuary, then it would be expected that higher densities of larvae be maintained throughout the low flow period at TS. At this site, ovigerous females could release larvae into the estuary from the freshwater environment of TS. In all years sampled, early stage larval numbers declined at TS in line with other estuarine sites, while upstream pools such as MH maintained high stage I larval densities. Thus it is possible that migration out of the estuary by large females is driven not just by their physiological tolerances as salinities rose, but also by the decline in value of the estuary as larval habitat.

Sherwood (1985) estimated the minimum discharge required to flush the salt wedge from the Hopkins River estuary at 4000 ML.day^{-1}. The salt wedge reintruded 6 km into the estuary as far as KH, allowing retention of *P. australiensis* larvae, between 19 and 26 November 1989, when daily discharge had dropped to between ≈2000 and ≈1000 ML. A similar discharge-wedge relationship was observed in 1984 (G. Newton, Deakin University, personal communication). Larvae were retained upstream of the estuary at MH after late November 1991, when daily discharge had dropped to below ≈300 ML. The utilisation of the estuary by *P. australiensis* larvae, thus permits an extension of the potential breeding season each year of 20-60 days (Table 6.4). On average, the period in which larvae are retained in the salt wedge of the estuary, but not in pools further upstream, is about the same as the duration of larval development in the laboratory, and a little longer than the incubation period (see Chapter 5). The length of time between broods has not been investigated, but it is likely that the utilisation of estuaries permits females in the lower section of the river to produce an extra brood each season. In light of the apparent higher survival of larvae in the estuary, the first

estuarine brood of the season could constitute a large part of the total fecundity of each *P. australiensis* female.

The nature of the planktonic communities of the estuary and the upstream pools differed remarkably. The first estuarine samples in which *P. australiensis* was abundant each year (e.g. 23 October 1989) were dominated by *P. australiensis*, with small numbers of copepods, oligochaetes, and fish and brachyuran larvae. Blooms of rotifers were common in the Hopkins River estuary, soon after peak discharge in 1983 and 1984, and the period of early intrusion of the salt wedge into the estuary coincided with rapid expansion of estuarine copepod populations, and the occurrence of high densities of nauplii (Newton, 1994). Rotifers and copepod nauplii may also have been present in large numbers during the current study, but missed due to the large mesh sizes used. Later estuarine samples, particularly those from the narrow layer above the anoxic salt wedge, were extremely densely populated by a diverse group of organisms, usually dominated by copepods. In contrast to the estuarine samples, most of the samples from MH were dominated by *P. australiensis* larvae, with very small numbers of cladocerans, chironomids, and fish larvae The trophic ecology of *P. australiensis* larvae has not been investigated, but it is probable that they select food on a basis of size, with small nauplii of copepods, around the size of decapsulated *Artemia* cysts, being the most likely source. Further work is required on the trophic ecology of *P. australiensis*, in particular the availability of food for larvae and the abundance of predators in estuarine and upstream environments. It is likely the highly productive estuarine environment would be richer in food for larvae than upstream, which may account for higher apparent survival rates in the estuary. The importance of food availability to larval and adult *P. australiensis* in riverine and estuarine locations is considered further in Chapter 7.

Larval and juvenile densities of *P. australiensis* corresponded closely (with a month's lag) at both JP and LG in 1988-1989 (Fig. 6.14). Thus juvenile densities in the upper estuary were probably determined by availability of larvae in nearby midstream waters. No such close association of larval and juvenile numbers was evident at the lower sites. Low densities of juveniles were present at RF and HB two and three months after sharp peaks in larval numbers, but no corresponding sharp peak in juvenile numbers was evident at either site.

The complete lack of juveniles or larvae at HB in November 1988, following the October peak in larval density may have been caused by a number of circumstances: high mortality either due to predation or flushing from the estuary; migration upstream as larvae with the intruding salt wedge; or migration upstream immediately upon settlement as juveniles. High mortality due to predation is an unlikely cause because analysis of larval cohorts at HB, JP and TS in the following year (Table 6.2) suggested that larval survival at the downstream site was comparable with the upstream sites. Larvae having been flushed from HB is also unlikely because a similar drop in larval numbers was not observed upstream. Upstream migration as

larvae or juveniles is the most likely explanation. Indeed, the decline in numbers of juveniles at JP and LG almost exactly parallelling the decline in numbers of larvae in the previous month strongly suggests constant migration from the site upon settlement. Such speculation is consistent with the findings of Chapter 4, which pointed to the importance of post-larval migration in determining distributions of shrimp populations in the seagrass meadows of the estuary.

Thus larval abundance of *P. australiensis* is not a good indicator of juvenile abundance in the seagrass meadows of the lower estuary,. However, given a one-month lage component, it may be quite a good indicator of juvenile abundance in the upper estuary. From December to January, numbers of juveniles in the seagrass meadows dropped dramatically, in line with the drop in larval numbers in the estuary. It is evident that most juveniles either migrate out of the estuary upstream or die soon after settlement. If migration is the more important factor, larval abundances will prove a useful indicator of juvenile numbers exported from the estuary to the river, but not a good indicator of adult abundance in the estuarine seagrass meadows. In the present study, no quantitative samples of jueniles or adults were taken at any sites upstream of the estuary. Therefore this hypothesis cannot be tested using the available data. However, the evidence of larger juveniles at TS than at LG (Fig. 4.13) is consistent with early recruits to the lower estuary migrating upstream to TS while recruitment continued later at LG. Migration is considered again in Chapter 7.

M. intermedium

The peak of *P. australiensis* larval abundance in late spring coincided with the peak for crustacean meroplankton in general reported by Newton (1994). In contrast, the later, more prolonged peak in abundance of *M. intermedium* coincided with the late autumn peak in total zooplankton (Newton, 1994). Greater abundances of zooplankton would presumably make a greater food supply available for the larvae. Food size requirements of *P. australiensis* appeared to be smaller than for *M. intermedium*. In the laboratory, *P. australiensis* were only able to be reared on decapsulated *Artemia* cysts. Hatched *Artemia* nauplii were too large, particularly for early larval stages of *P. australiensis*. In contrast, *M. intermedium* larvae of all stages preyed successfully on several stages of *Artemia* nauplii. The differing periods of larval occurrence in *P. australiensis* and *M. intermedium* could therefore be associated with food availability. *P. australiensis* larvae were present when high densities of small copepod nauplii and rotifers were present in the estuary, and *M. intermedium* larvae when the total zooplankton community was at its peak abundance and diversity, with larger plankters more common.

M. intermedium did not occur consistently or as predominantly in the salt wedge as *P. australiensis*. This does not necessarily mean that *M. intermedium* was more vulnerable to displacement from the estuary. In October at RF and HB, in November at HB and JP and in

December at JP and HB, *M. intermedium* larvae did occur in greater numbers in the salt wedge. In subsequent months in which *M. intermedium* was present in the estuary, the mouth of the estuary was closed for all but a few days (Fig. 2.8), meaning that *M. intermedium* was not in danger of downstream displacement.

Given the closed nature of the estuary during that period, lack of later stage larvae in the estuary (Fig. 6.13) is striking. In conditions of no flow, horizontal migration of any magnitude is unlikely and the massive decrease from stage I to later stage larvae is most likely due to mortality. Although Fig. 6.14 should be interpreted with caution because of different scales for larval and juvenile densities, a comparison of the relative abundances of juveniles and larvae in *P. australiensis* and those in *M. intermedium* is instructive. Although peak larval densities at JP, RF and HB were comparable in both species, juvenile densities did not reflect larval densities at any site as strongly as *P. australiensis* did at JP. At JP, where *P. australiensis* juveniles were present in greater numbers (in m^{-2}) than larvae had been in the previous month (in m^{-3}), *M. intermedium* juveniles were more than an order of magnitude less abundant than larvae had been in the previous month. This suggests that a smaller proportion of *M. intermedium* larvae than *P. australiensis* survive to metamorphose in the seagrass meadows of the estuary. Emigration is an unlikely explanation, particularly given the conclusion of Chapter 4 that juveniles immigrated from adjacent coastal waters in December, just prior to the mouth closing in January. The later period of larval occurrence in *M. intermedium*, later than in *P. australiensis*, is characterised by increased diversity and abundance in the planktonic community of the estuary (Newton, 1994). It is possible that predators with a preference for larger prey were more prevalent at this time, and *M. intermedium* larvae would be more prone to predation by their greater size alone.

Larval abundance was a good indicator of juvenile abundance in all seagrass meadows of the estuary. The ability to track individual cohorts of *M. intermedium* from juvenile stage to adult stage in each meadow of the estuary, suggests emigration is a less important factor in determining abundance of this species than appeared to be the case for *P. australiensis*.

6.4.2 A BEHAVIOURAL MODEL FOR *P. AUSTRALIENSIS* LARVAE

Newton (1994) conducted three surveys of vertical distribution of zooplankton in the Hopkins River estuary in early December 1983, 1984, and 1985. She did not distinguish species of shrimp larvae, treating them as a single taxon. Because of the timing of her surveys and because shrimps were more abundant at JP than HB in her studies, it is probable that her samples were dominated by *P. australiensis*. However it is likely that small numbers of *M. intermedium*, an unidentified pandalid/hippolytid species, and the thalassinid *Callianassa* sp. were present. (The last two species were present in small numbers both in the plankton samples of the current study and in Newton's study.) So, although the shrimp larvae trends

reported by Newton (1994) are likely to be dominated by the abundance of *P. australiensis*, caution should be exercised in applying her observations to the behaviour of the one species.

Newton (1994) attributed the behaviour of shrimp larvae in her study to a variation of her 'avoidance of the surface layer' hypothesis, whereby larvae spend almost all their time in the salt wedge, utilising the water column mainly during slack tides, and using the bottom layer at other times, in the manner of *Macrobrachium novaehollandiae* (Thorne et al., 1979). While the results of this study confirm the predominance of *P. australiensis* in the salt wedge, they do not point to *P. australiensis* using the boundary layer in such a consistent way. *P. australiensis* was found in deep water at high salinities during the vertical distribution studies, but only on a few occasions was the dominant mode in the bottom depths. It should, however, be noted that there was a tendency for later stage larvae to occur at the bottom depth more commonly than early stage larvae (Appendix 3), suggesting a greater affinity to a benthic habit towards the end of larval development. In samples from JP and TS when dissolved oxygen levels became low, no *P. australiensis* larvae were found in depths that were anoxic (Fig. 6.7). A similar result was reported by Newton (1994) at JP, suggesting *P. australiensis* larvae are capable of completely planktonic existence, without resort to a bottom boundary layer. Persistence in the deep saline layer of estuaries, without migration between the two layers is possibly a common strategy by which carideans maintain position in estuaries. Sandifer (1975) found three caridean species dependent upon the York River estuary in the eastern USA most commonly in the deeper saline layer where nett transport was upstream.

Sulkin (1990) stressed the importance of laboratory experiments to detect orientation responses to environmental stimuli, which can help to explain observed distributions. No such experiments on *P. australiensis* larvae have been reported here, but their behaviour was observed in the laboratory while rearing them, and certain hypotheses can be erected from the observed field distributions pointing to worthwhile further behavioural research. *P. australiensis* larvae in the laboratory generally swam with tails pointing upwards. Locomotory movement of the exopods of the maxillipeds propelled the larvae backwards and upwards. Without swimming movement, the larvae tended to sink. Thus locomotory movement was required to achieve upward movement, while downward movement could be achieved by passive sinking, or possibly by complementary locomotory movement. Such a scheme is consistent with the situation for brachyuran larvae (Sulkin, 1984).

The observed vertical distribution patterns for *P. australiensis* could be explained by a simple model of behavioural responses to environmental conditions.

1. Response to flow: positive geotaxis.

P. australiensis was consistently found below a layer of fresh, flowing water, both in the estuary and upstream in the deep pool at MH. More larvae were found in the fresh layer above the halocline when flow in that layer stopped. On both occasions when upstream flow

was detected in the saline layer of the Fitzroy River, most larvae were found at depths lower than at which flow was detected, even though salinity at these levels was >25. It appears likely that flow stimulates positive geotaxis regardless of salinity. This is in contrast to the behaviour of the freshwater *Macrobrachium acanthurus*, which maintained a lower position in a flowing water column in fresh water than in saline water (Hughes and Richard, 1973). They interpreted the freshwater flow as simulating an ebb tide, and saline flow as simulating a flood tide.

The deduction that larvae move upstream with the intruding salt wedge from stage-frequency distributions is at odds with the avoidance of flow independent of direction or salinity. It is possible the nature of upstream flow of the wedge is a complex turbulent flow which is difficult to avoid. The single behavioural trait of positive geotaxis in response to flow is sufficient to explain the almost exclusive occurrence of *P. australiensis* larvae below the halocline in the estuary or in deeper water in upstream pools after discharge has dropped below the level at which the salt wedge had become established at TS. The apparent vertical migrations observed within the salt wedge can only be explained by other behavioural responses.

2. Responses to light, salinity, and hydrostatic pressure.

Observations of different diurnal patterns of variation in vertical distribution in both the estuary, under tidal influence, and upstream at MH, above tidal influence, suggest both tidal and diurnal effects are important in determining vertical migration. Diurnal vertical movement may result from responses to light intensity, as is commonly found among zooplankters (Forward, 1988). Pearre (1979) proposed a model for vertical migration to explain the imprecise correlation between light regime and observed migration patterns in many data sets. He proposed hunger or satiation as a mediator in deciding how long a plankter will remain at the surface or the depth of abundant food. Thus, the downward movement of the mode of larval distribution at night observed at MH, and the downward movement in the latter part of the night observed in the estuaries, may be due to sinking after early night feeding in waters near the surface. The diurnal investigation at MH was preliminary, and a more intensive study of diurnal migration at such a site, away from tidal influence, is required.

The influence of tides on the extent of the rapid rise in mean position of *P. australiensis* larvae associated with the two large incoming tides may be due to changes in hydrostatic pressure. Small changes in pressure as low as of ≈1-2 kPa can trigger behavioural responses in many marine animals. In many zooplankters, an increase in pressure induces negative geotaxis. (Knight-Jones and Morgan, 1966; Morgan, 1984). Changes in pressure as a result of depth changes of 0.3-0.4 m (≈ 3-4 kPa), as occurred on the first two nights sampled, exceed the pressure response thresholds known for many crustaceans (Knight-Jones and Morgan,

1966; Morgan, 1984), while the rise of 0.2 m on the third night may have been insufficient to trigger such a response.

Pearre (1979) explored possible relationships between observed population movements and individual movements, cautioning against equating the two. Increased migration on the flood tide resulting in more bimodal or diffuse distributions at high tide as observed in this study, is consistent with Newton's (1994) observation of most shrimp near the halocline at tidal changes. No such trend was found at low tide, although they tended to be higher in the late afternoon, soon before low tide.

The distributions of *P. australiensis* observed in the vertical distribution surveys could be explained by the following model of individual behaviour:

> Individuals actively push into the vicinity of the halocline, possibly on a feeding foray, and then sink. There is a tendency to migrate more on the flood tide and more as the afternoon goes by, so that peak numbers are found near the halocline in the late afternoon, and on an incoming tide. The flood tide migrations could be in response to increased hydrostatic pressure, while the late afternoon migrations could be mediated primarily by hunger. When the salt wedge flows upstream, the response is unclear, due to bimodal distributions. Perhaps some larvae in the vicinity of the halocline get caught in the turbulence associated with opposing flows and remain around the halocline, while others are able to migrate down in response to the flow in the wedge.

Testing of this model requires further field and laboratory investigations as recommended by Sulkin (1990). Controlled laboratory experiments to test the response of *P. australiensis* larvae to varying hydrostatic pressure, to light and to flow under a number of salinity conditions would allow separation of the various stimuli the larvae are subject to simultaneously in the field. Cronin and Forward (1982) recommend sampling for the detection of vertical migration to extend over a large number of tidal cycles in order to provide 'sufficient data for useful analysis'. The difficulty in studying *P. australiensis* larvae in estuaries is the small window of opportunity afforded by their brief period of abundant occurrence in estuaries. The period of late November and early December, which is the only suitable time for such a study, is characterised by tides with a small semi-diurnal component, and a nocturnal flood. Sampling for a large number of tidal cycles in the estuary would require intensive sampling for a large number of days, and then the effect of tides and the diurnal cycle would remain confounded. However, an intensive diurnal survey of vertical distribution over several days at an upstream site, in the absence of tidal influence, would be valuable to compare the patterns of vertical migration observed in the estuary in this study.

However the issue of vertical migration within the salt wedge, or below the layer of flowing water in the pool at MH, is distinct from the major finding of this chapter for *P. australiensis* larvae: that horizontal location is maintained within the estuary, or nett upstream movement is

achieved by persistence in the salt wedge for almost the entire period of larval development. This is apparently achieved by positive geotaxis in response to flow. Retention within the estuary results in high levels of juvenile recruitment to the seagrass meadows of the estuary.

7. THE OCCURRENCE OF *P. AUSTRALIENSIS* IN SOUTHERN AUSTRALIAN ESTUARIES WITH DEMOGRAPHIC COMPARISONS BETWEEN ESTUARINE AND RIVERINE ENVIRONMENTS

7.1. INTRODUCTION

The discovery of *P. australiensis* as a significant element of an estuarine seagrass community is the first such finding for any atyid species. Both Walker (1972) and Williams (1977), despite their efforts in rivers of Tasmania and southern Queensland respectively, found no significant penetration of *P. australiensis* into reaches under marine influence. This study has shown *P. australiensis* to occur in the Hopkins River estuary throughout the year, but in largest numbers in the months following the annual peak in river discharge. With this knowledge of the importance of the hydrological cycle to the abundance of *P. australiensis* in one estuary, it was possible plan a survey of other estuaries of the region at a time at which the presence of *P. australiensis* was most likely. Such a survey would determine if the Hopkins River estuary is unique in its support of *P. australiensis*, or if *P. australiensis* is also prevalent in other estuaries. The characteristics of estuaries that support *P. australiensis* could also be identified. This chapter firstly describes a survey of estuaries from Adelaide to west Gippsland, an area covering the south-western portion of the expansive distribution of this species (Fig. 1.2).

Estuarine occurrence of *P. australiensis* has broader implications for the population biology and biogeography of this and other *Paratya* species. The production of some larvae during floods (Chapter 6) and the ability of larvae to survive for some time in marine conditions (Chapter 5) suggests a small level of gene flow between catchments is not impossible. Gene flow within catchments is likely to be more common, given the extended nature of larval development.

Kingston (1993) assessed the genetic divergence of P. australiensis populations within a catchment in the Connondale Ranges of south-eastern Queensland. He concluded that observed patterns of genetic divergence were most likely due to the dominance of downstream gene flow, possibly combined with populations disturbances in headwaters. He showed existing models for estimating gene flow to be inadequate for populations inhabiting river systems. Some of his speculations on gene flow were hampered by lack of information on the nature and extent of migrations in *P. australiensis*. The extended larval development of P. australiensis probably results in at least some downstream displacement of larvae from riverine pools (see Chapter 6), while upstream migration of post-larval *P. australiensis* has not been reported. Mass upstream migrations of carideans from juvenile habitats downstream have been reported in a number of freshwater palaemonid species (Ibrahim, 1962; Raman, 1965; Lee and Fielder, 1979), and in

Atya innocuous (Felgenhauer and Abele, 1983), and have been surmised for aother atyid species (e.g. Smith, 1987).

In light of complete larval development occurring in both upstream locations and in estuaries of south-western Victoria, and of phenotypic variation in life-history traits between riverine and estuarine populations (Walsh, 1993), the genetic divergence of populations in south-western Victorian catchments is of interest. This chapter reports on three studies aimed at describing genetic divergence between estuarine and riverine populations of *P. australiensis*, and identifying potential movement within a catchment:

(a) a survey to ascertain how far upstream *P. australiensis* occurs in the Hopkins River;
(b) field experiments designed to detect migration in the river;
(c) a preliminary study of allozyme variation between riverine and estuarine populations of *P. australiensis* in the Hopkins River and two other catchments.

Finally, this chapter reports on the nature of phenotypic variation of reproductive traits within and between estuarine and riverine populations, within and between catchments. The size of eggs of *Paratya australiensis* varies widely between localities (Roux, 1926; Walker, 1972; Williams and Smith, 1979; Walsh, 1993). Neither Walker (1972) nor Williams and Smith (1979) detected any geographic or temporal patterns in variation in egg size, although the two locations with the smallest eggs in Walker's (1972) study were the only ones near or within areas of permanent tidal influence. In the Hopkins River, *P. australiensis* produced larger eggs at upstream, riverine locations than in estuarine locations (Walsh, 1993). Williams and Smith (1979) also found wide geographic variation in the number of eggs per brood of *P. australiensis*, but ascribed no pattern to the variation. In the Hopkins River, variation in brood size complemented variation in egg size: in estuarine environments, eggs were smaller and broods were larger than in upstream environments (Walsh, 1993).

Such a trend suggests a trade-off between fecundity and investment per offspring. The negative relationship between fecundity and egg size is central to theoretical models of reproductive allocation (e.g. Vance, 1973a; 1973b; Christiansen and Fenchel, 1979), which have generally sought to explain variation in reproductive patterns between species. A few studies have investigated reproductive trade-offs within species (Lawlor, 1976; Mashiko, 1982; 1992; Skadsheim, 1984; Willows, 1987; Clarke, 1993b). *P. australiensis*, which shows a clear variation in reproductive patterns between environments, is possibly a useful subject to help unravel the complex inter-relationships between phenotypic plasticity in response to environment and genetic variation.

7.2. DESCRIPTION OF THE RIVERS AND ESTUARIES SAMPLED

Rivers of the Adelaide region and the Fleurieu Peninsula (Fig. 7.1)

The Adelaide Hills range is drained by a number of small rivers. The most northerly in which *P. australiensis* has been recorded is the River Torrens (Williams and Smith, 1979). The Torrens, the Onkaparinga and several smaller rivers drain westerly into Gulf St. Vincent. The rivers of this area have very low flows from December to May (Fig 7.2a, b) and usually dry up to a series of pools over this period. The estuary of the Onkaparinga is a wide channel at least 5 km upstream to beyond Old Noarlunga. There is a strong tidal influence at Old Noarlunga. On 3 December 1990, surface salinity at this site was 31.0, while at 1m, on the bottom of the channel, salinity was 32.8 (Fig. 7.3a). *Zostera* was common in the channel. The mouths of the other rivers on the peninsula were closed during the sampling period.

On 3 December 1990, the Bungala River terminated in a lagoon at Yankalilla Bay. Estuarine influence extended 1.5 km upstream in a 1 m deep channel fringed by *Phragmites australis*. Surface salinity for almost the entire length of the estuary was greater than 20, but at the upper limit, where the channel constricted and shallowed, a 10-20 cm layer of salinity <5 overlay a more saline layer (Fig. 7.3b).

The Inman and the Hindmarsh Rivers flow to the south-east of the Fleurieu Peninsula into Encounter Bay. Both river mouths were blocked by low sandbars. Neither estuary supported *Zostera* beds, but there were large amounts of drift marine algae near the seaward ends. The upper sections of both estuaries were fringed by *Melaleuca* scrub and *Phragmites australis*.

The Inman estuary was greater than 2 km long with surface salinity of 30 near the mouth. At 2 km upstream of the mouth, a 10-20 cm layer of low salinity overlay a deeper saline layer (Fig. 7.3c).

The Hindmarsh estuary was also greater than 2 km long, with surface salinity at 17-25 throughout its length. Salinity rose steadily with depth (Fig. 7.3d).

The Finnis and Bremer Rivers also flow south-easterly from the Adelaide Hills, but drain into Lake Alexandrina, part of the Murray River estuary complex. No estuarine components of these rivers were found above the lake. The Murray River estuary complex was not sampled.

South-east region of South Australia (Fig. 7.1)

This region is drained by a system of engineered drains. The discharge patterns of these drains are similar to those of the rivers of the Adelaide region (Fig. 7.2 c-e). The outlets of these drains to the Southern Ocean do not form large estuaries, and regions of mixing are dynamic and are generally less than 500 m long.

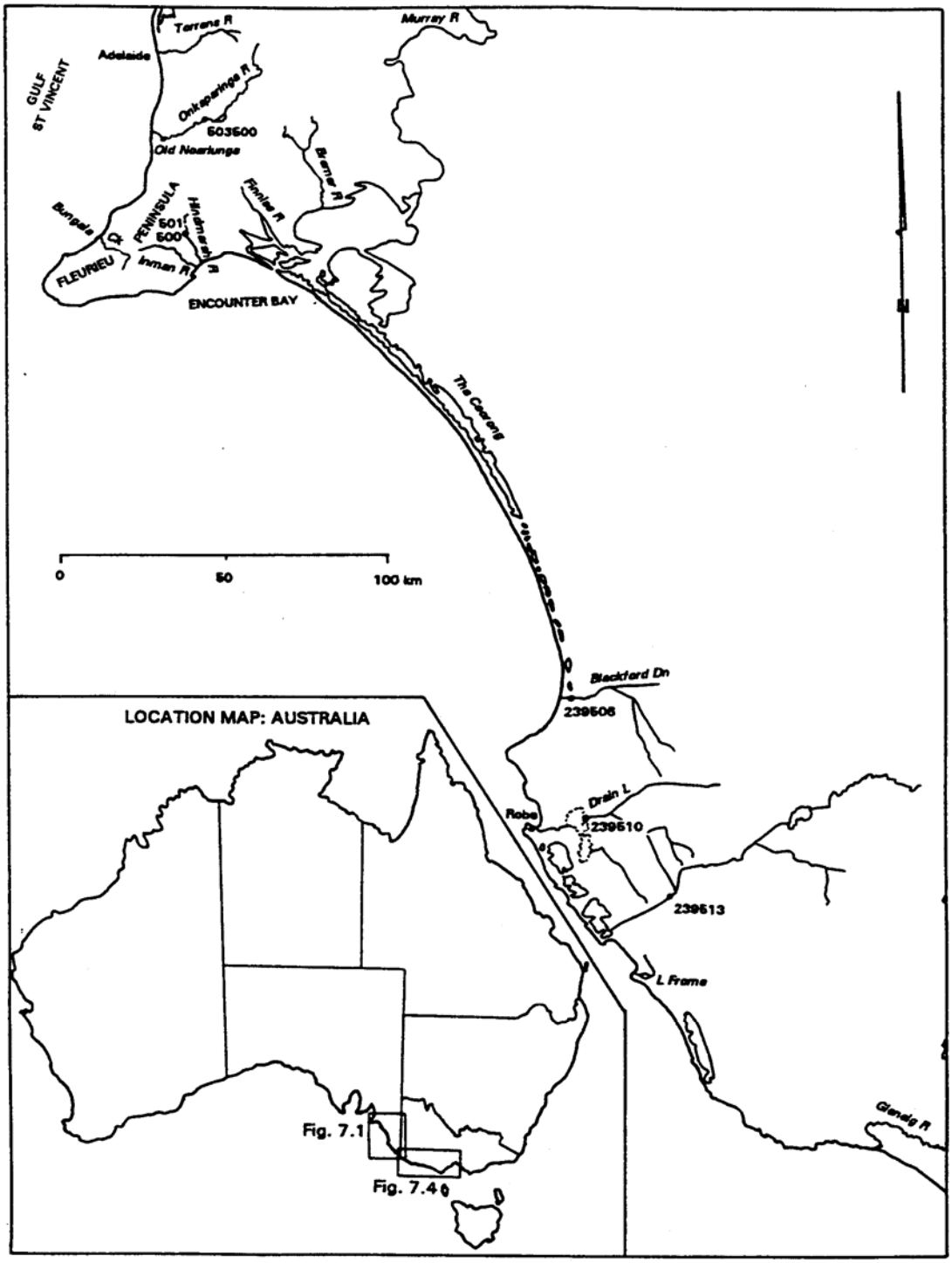


Fig. 7.1. Location of southern Australian rivers (from Adelaide to the South Australian-Victorian border), the estuaries of which were sampled for *Paratya australiensis* (Six-digit numbers refer to gauging stations used in Fig. 7.2.)

The salinity of the Blackwood Drain discharge was 14.4 at its mouth (Fig. 7.3e). Sea water was prevented from pushing up the channel by a barrage at the beach. However, large deposits of drift algae above the barrage suggested some marine influence.

Drain L enters a lagoon at Robe before discharging into the sea. Discharge salinity was 10 and a slight degree of stratification was evident (Fig. 7.3f). The lagoon supported stands of *Ulva* and large deposits of drift marine algae.

The outlet from lake Frome, which is the outlet of the Reedy Creek/Mt Hope catchment, forms a short fast flowing, dynamic estuary where some unstable stratification occurs (Fig. 7.3f). Discharge water had salinity of 14.8. Very little vegetation grows in this channel.

Glenelg River (Fig. 7.4): The Glenelg River rises in the west of the Gariwerd Range (the Grampians), with a catchment covering an area of 12 660 km^2 with a mean annual flow of 725 000 ML (Department of Water Resources Victoria, 1989b). Flow is strongly seasonal, with two thirds of average annual flow occurring from August to October (Fig. 7.2f). The Glenelg River estuary is a drowned river valley contained by canyon walls for much of its 80 km length. A sandbar at the mouth leads to a deep U-shaped channel ranging from 8 m deep just upstream of the bar, to 4 m deep at the head of the estuary (Sherwood and Backhouse, 1982). The estuary forms a highly stable salt wedge.

Collections were taken at Saunders Landing, 46 km upstream of the mouth. In the centre of the channel in 4.8 m, the halocline was at 1.5m (Fig. 7.3h). The steep sided estuary supports very few stands of seagrass, but bands of *Phragmites australis* are common.

Surry River (Fig 7.4): The Surry River rises in the lowland forest north of Portland and flows into Portland Harbour. Its seasonal pattern of discharge is similar to that of the Fitzroy, although total discharge is less (Fig 7.2g). The Surry River estuary is about 3 km long and supports stands of *Zostera.* Collections were made at the Princes Highway bridge, 1.5 km upstream of the mouth.

Fitzroy River (Fig. 7.4): The Fitzroy River rises in the same forests as the Surry River and flows south-eastward into Portland harbour east of the Surry. Its tributary, Darlot Creek, drains the swamps of Lake Condah. The catchment extends approximately 50 km from north to south and 55 km from west to east. The seasonal pattern of stream flow is similar to that of the Hopkins River, although peak monthly discharge is about one third of the Hopkins (Fig. 7.2h).

The Fitzroy River estuary extends for at least 4.5 km running parallel to the primary coastal dune. The shallow mouth leads to a wide shallow section (0.5-1.5 m deep) which extends for 1.5 km upstream. The estuary further upstream is a U-shaped channel 2-4 m deep and 25-40 m

wide. The upper half of the shallow coastal section and the fringes of the deeper channel support stands of *Zostera.*

Hopkins River: see Section 2.2.

Curdies River (Fig. 7.5): The Curdies River rises in the volcanic plains south of Camperdown, originating from Lake Purrumbete—elevation 137 m. The stream flow exhibits strong seasonal variation with a minimum in March (Fig. 7.2j). Near Timboon (station 235201) the mean annual flow is 140 830 ML. Dipnet samples were taken from Lake Purrumbete in a mixed *Vallisneria spiralis* and *Myriophyllum sp.* bed in the inlet south of Hoses Rocks on the west side of the lake.

The Curdies River estuary is at least 15 km long, a deep U-shaped channel for most of its length upstream of the wide, shallow Curdies Inlet. Dipnet samples were collected from just upstream of the Curdievale bridge 12.5 km upstream of the mouth. At this point the U-shaped channel was approximately 6 m deep, and the east bank supported a stand of *Potamogeton crispus* in 2 m of water from November 1991 to February 1992. During the flood this site was inaccessible, so a site 3 km downstream at Dances Lane was sampled through fringing grasses and *Phragmites australis*.

Gellibrand River (Fig. 7.5): The Gellibrand drains the western end of the Otways Ranges, which have an elevation of about 500m along the main ridge. Rainfall is considerably higher in the Otways (about 2000 mm per year on the main ridge) than on the volcanic plains to the west (Department of Water Resources Victoria, 1989b). The pattern of stream flow in the Gellibrand is less seasonal than the Curdies (Fig. 7.2k). Mean annual flow in the lower reaches (station 235224) is 298 185 ML.

The estuary is 10.7 km long and forms a highly stratified salt wedge (Fig 7.3m). It is a barrier estuary in the final stages of infilling (Sherwood, 1985). The generally U-shaped channel,

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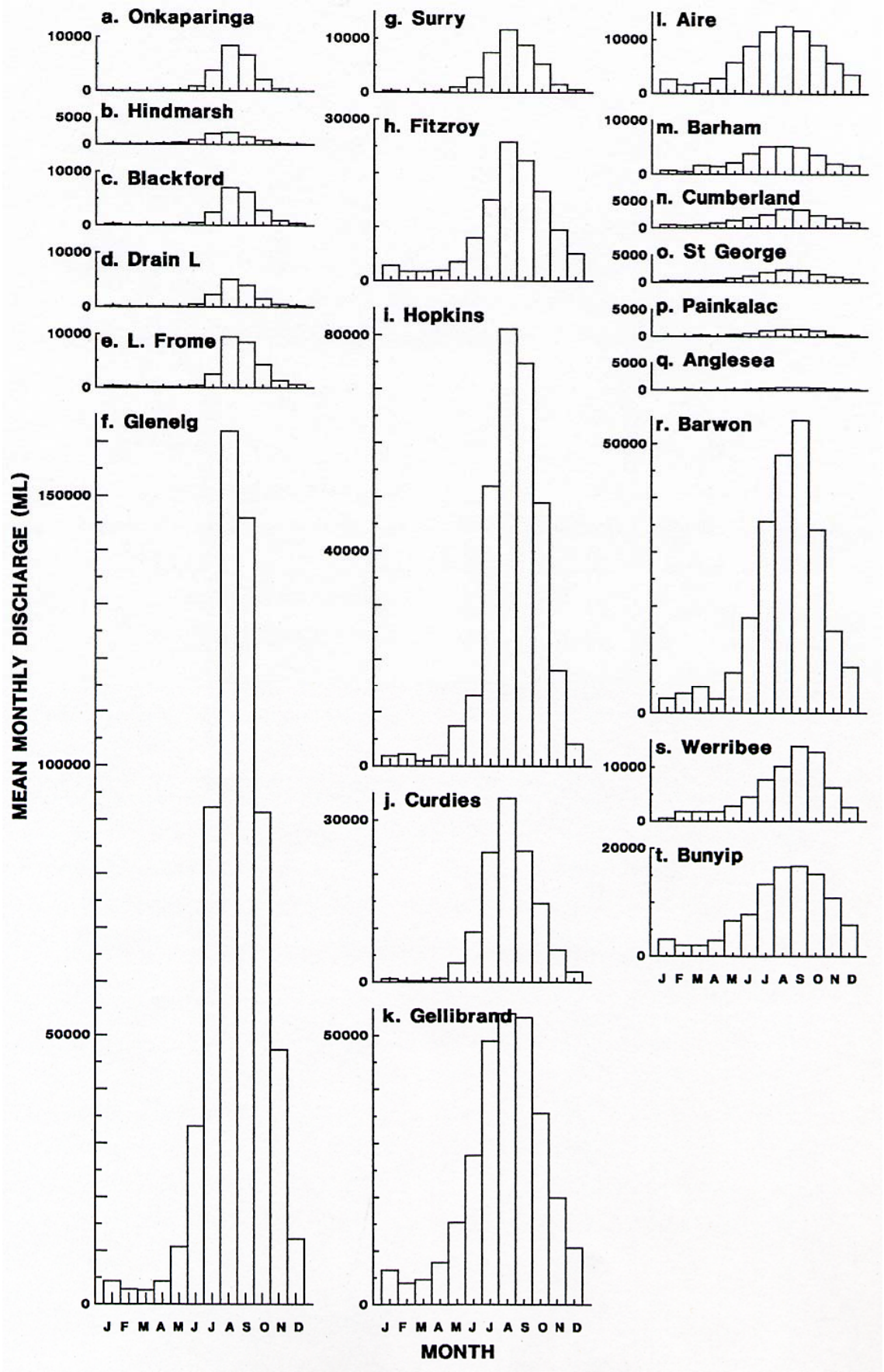
Fig. 7.2 Mean monthly discharges (ML) for rivers surveyed for *P. australiensis*. Gauging stations from which the data are derived are indicated on the appropriate maps (Figs. 2.1, 2.9 and 2.10). (a) Onkaparinga - Gauging station 503500 (b) Hindmarsh - 501500 (c) Blackford Drain - 239506 (d) Drain L - 239510 (e) Lake Frome outlet - 239513 (f) Glenelg - 238206 (g) Surry - 237207 (h) Fitzroy - sum of 237202 and 237205 (i) Hopkins - 236209 (j) Curdies - 235203 (k) Gellibrand - 235224 (l) Aire - 235219 (m) Barham - sum of 235221 and 235233 (n) Cumberland - 235216 (o) St. George - 235226 (p) Painkalac - 235232 (q) Anglesea - 235222 (r) Barwon 233200 (s) Werribee - 231204 (t) Bunyip - 228213.
Data from (a - e) Engineering and Water Supply Department, South Australia, (f - t) Rural Water Commission Victoria (1990).


a. Onkaparinga
b. Hindmarsh
c. Blackford
d. Drain L
e. L. Frome
f. Glenelg
g. Surry
h. Fitzroy
i. Hopkins
j. Curdies
k. Gellibrand
l. Aire
m. Barham
n. Cumberland
o. St George
p. Painkalac
q. Anglesea
r. Barwon
s. Werribee
t. Bunyip
MEAN MONTHLY DISCHARGE (ML)
MONTH
J F M A M J J A S O N D

which is fringed by *Phragmites australis*, *Triglochin procera*, grasses and some patches of *Melaleuca* scrub, meanders through extensive wetlands. There are few submerged weeds—some *Ruppia maritima*. Samples for the south coast survey were taken at a site 4 km upstream of the mouth.

Samples for demographic comparisons of *P. australiensis* populations (section 7.3.2) were taken from three sites:

(i) an estuarine site around the Princetown bridge, 1.2 km upstream of mouth;

(ii) a riverine site below the bridge on the River Road 26 km upstream of mouth (elevation ≈10 m), along the steep sided banks of the river among *Eucalyptus camaldulensis* snags and *Triglochin procera*;

(iii) a second riverine site upstream of the Kennedy's Creek Road bridge 34 km upstream of mouth (elevation ≈19 m), amongst *Potamogeton crispus* and *Triglochin procera* in a 1 m deep channel.

Aire River (Fig 7.5): The Aire River flows south from the main range of the Otways draining into the Southern Ocean west of Cape Otway. This river, and all the rivers that rise in the Otways, tend to show less markedly seasonal patterns of discharge than the rivers west of the Otways (Fig. 7.2). The Aire River estuary is similar to that of the Gellibrand, being a barrier estuary in the final stages of infilling, surrounded by extensive wetlands. At least 6.5 km long, it forms a stable salt wedge. On 7 December 1990, although there was a considerable outward flow, a deep saline layer was detected 6 km upstream of the mouth (Fig. 7.3n). Little submerged weed grew in the steep-sided channel of the estuary, but some minor stands of *Juncus sp* occurred at the edges, among inundated terrestrial grasses.

Smaller rivers of the Otway range (Fig 7.5)

West of Cape Otway, many small streams flow south-east from the Otway range, draining into Bass Strait. With the exception of the Barham River in the west and the Painkalac Creek and the Anglesea River in the east, the high gradient streams of this coast do not form

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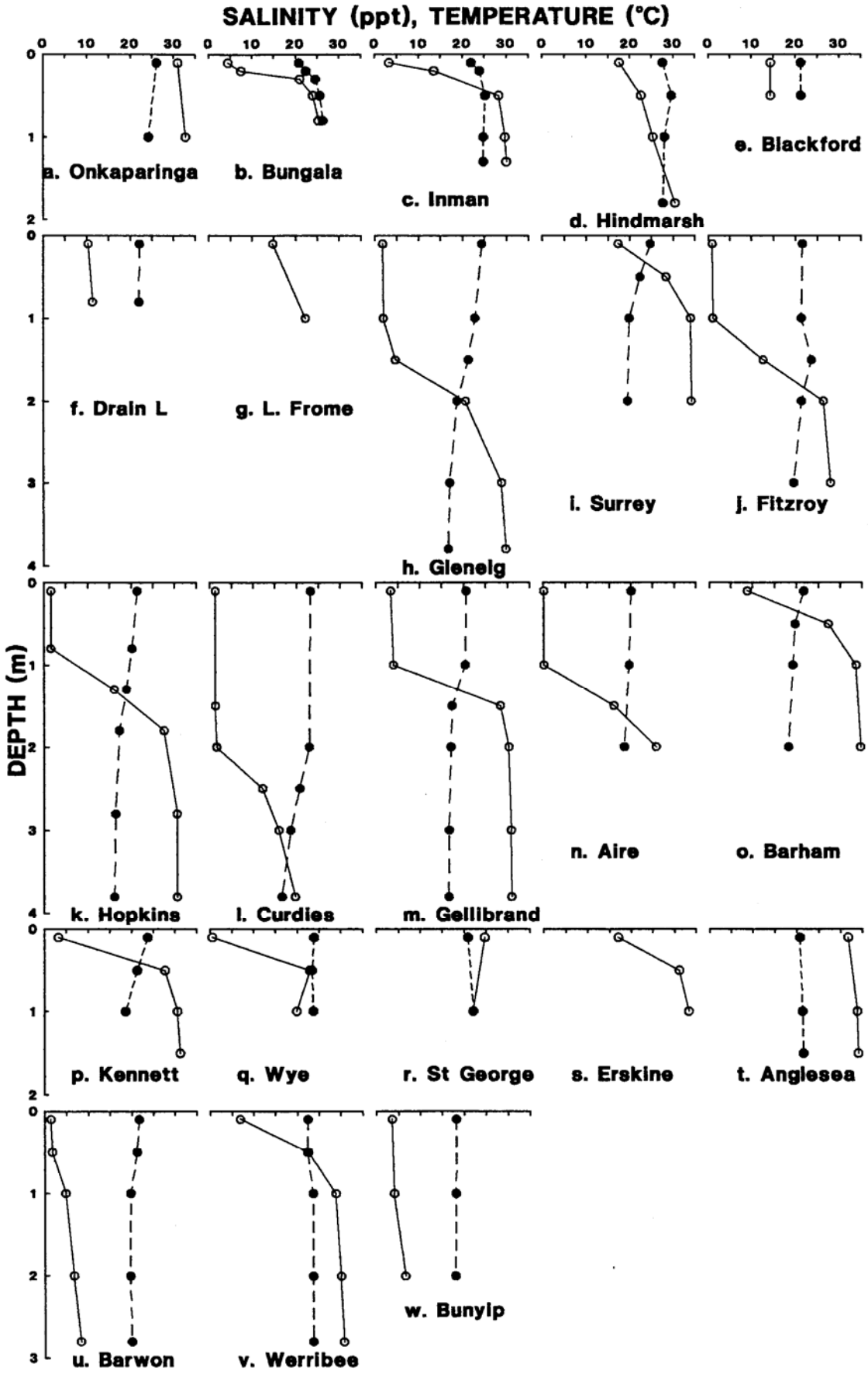
Fig. 7.3 Salinity (open circles, solid lines) and temperature (closed circles, dashed lines) profiles at locations sampled in the survey of estuaries 2-9 December 1990. Arrows indicate depths at which plankton samples were taken. Numbers in brackets indicate distance in km from the mouth and from the upstream limit of the estuary where known. (a) Onkaparinga (8,>1) (b) Bungala (1.5, 0) (c) Inman (2, ?) (d) Hindmarsh (2, ?) (e) Blackford drain at outlet (0, 0) (f) Drain L (0.5, 0) (g) Lake Frome outlet (0.1, 0.1) (h) Glenelg (46,34) (i) Surry (1.5, 1.5) (j) Fitzroy (1.5, 3) (k) Hopkins (6.5,3) (l) Curdies (12.5, >3.5) (m) Gellibrand (4, 7) (n) Aire (6, >0.5) (o) Barham (1, ?) (p) Kennett (0.2, <1) (q) Wye (0.2, <1) (r) St. George (0.3, <1) (s) Erskine (0.2, 0.4) (t) Anglesea (3, 0) (u) Barwon (14, 1.5) (v) Werribee (8, >2) (w) Bunyip (2, >1)


SALINITY (ppt), TEMPERATURE (°C)
DEPTH (m)
a. Onkaparinga
b. Bungala
c. Inman
d. Hindmarsh
e. Blackford
f. Drain L
g. L. Frome
h. Glenelg
i. Surrey
j. Fitzroy
k. Hopkins
l. Curdies
m. Gellibrand
n. Aire
o. Barham
p. Kennett
q. Wye
r. St George
s. Erskine
t. Anglesea
u. Barwon
v. Werribee
w. Bunyip

extensive estuaries. The streams of this coast have smaller discharges than the streams west of Cape Otway, but are similar in their seasonal discharge patterns (Fig. 7.2).

The Barham River estuary was sampled upstream of the Great Ocean Road bridge, where it was fringed by *Phragmites australis*. A salt wedge was evident (Fig. 7.3o).

At Skenes Creek, a high sandbar prevented any sea water intrusion into the small impoundment above the beach. Upstream of the Great Ocean Road bridge, salinity was 0.1, and the river was fringed by *Phragmites australis*.

Kennett and Wye Rivers exhibited short stretches of tidal influence above their beaches. In both cases, stratification was evident at the Great Ocean Road bridges (Fig. 7.3p,q), and both rivers were fringed by *Phragmites australis*.

The Cumberland River was fresh (salinity 0.1) to its outlet at the surf zone, where plankton samples were collected. Upstream, near the ford in the caravan park, collections were made through the fringing *Phragmites australis*.

The lower reaches of the St George River showed greater marine influence, with no freshwater layer just upstream of the Great Ocean Road bridge. Estuarine influence extends for ≈2 km upstream. On 7 December 1990, the estuary was fringed by blackberry (*Rubus sp*), burrs (*Acaena sp*) and *Juncus sp*. On 20 February 1993, at a lower tide, stands of *Zostera* were evident in the U-shaped channel.

The Erskine River estuary is a well-defined inlet approximately 600 m long. Marine intrusion further upstream is prevented by a barrage 50 m upstream of the Great Ocean Road bridge. The estuary is fringed by *Phragmites australis* in some shallow areas, but for much of its length it is steep sided with terrestrial vegetation overhanging its bare, mud walls. Samples were taken in the estuary just upstream of the footbridge near the mouth of the river where stratification was evident (Fig. 7.3s).

Painkalac Creek forms an inlet surrounded by extensive wetland about 3 km long. Samples were taken just upstream of the Great Ocean Road bridge where salinity was 31 from the surface to the bottom (1 m). *Phragmites australis* grew littorally, and *Ruppia* and *Zostera* grew sub-littorally.

The 2.5 km long Anglesea River estuary is truncated at its upper end by a culvert. The U-shaped channel is approximately 1.5 m deep for most of its length. *Zostera* grew sub-littorally up to 500 m upstream of the mouth, while further upstream, the channel was fringed by diverse wetland vegetation. Samples were collected at the upstream limit of the estuary and through the *Zostera* meadows near the mouth. On 8 December 1990, an algal bloom was evident in the estuary. Marine influence was strong to the upstream limit (Fig. 7.3t).

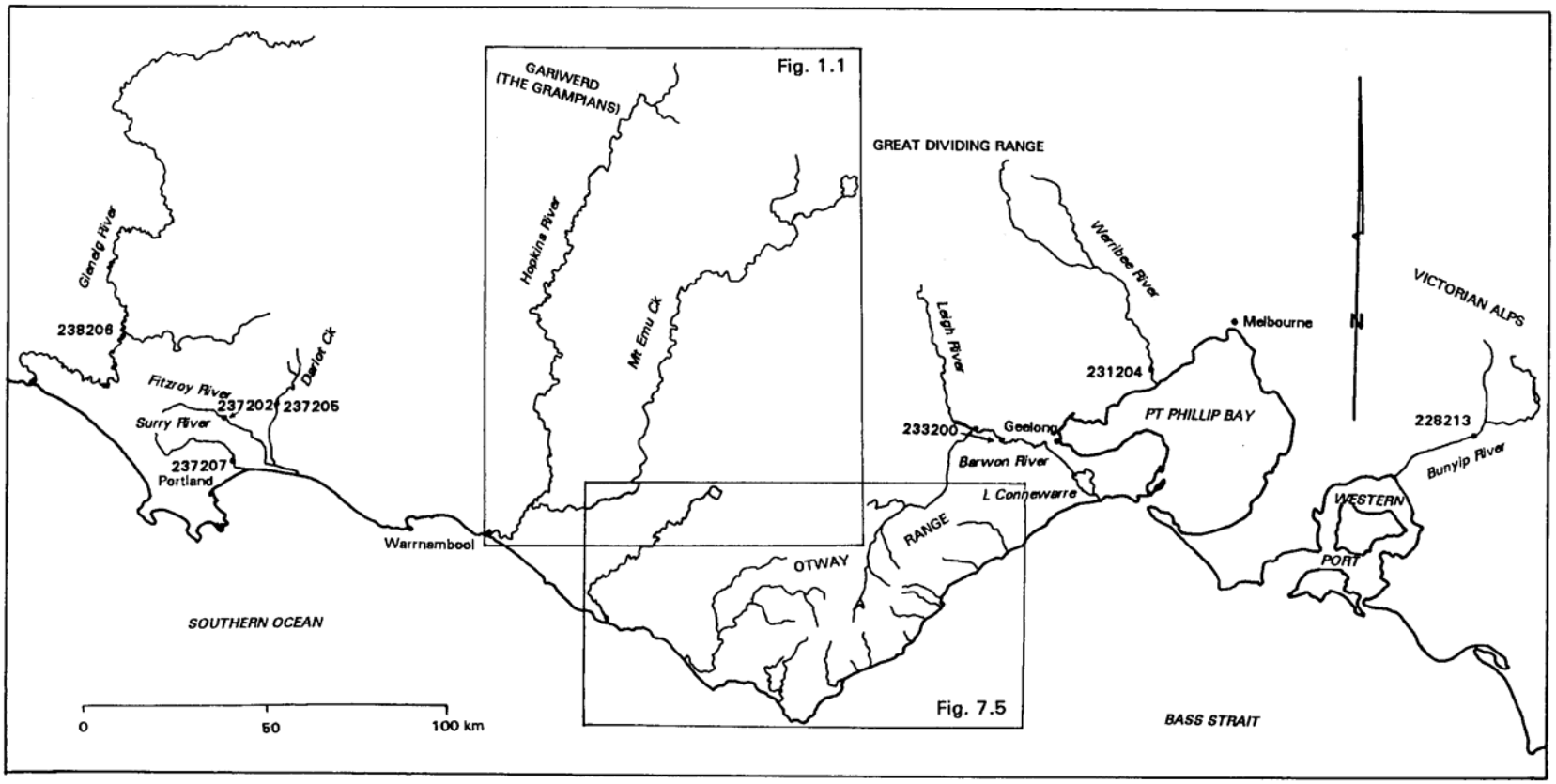


Fig. 7.4. Location of southern Australian rivers (from the Glenelg River to the Bunyip River), the estuaries of which were sampled for *Paratya australiensis* (six-digit numbers refer to gauging stations used in Fig. 7.2.)

Barwon River (Fig 7.4): The Barwon River drains the northern slopes of the Otways range in a north easterly direction. Its tributary, the Leigh River flows south from the Great Dividing Range near Ballarat to join the Barwon at Inverleigh. It then flows west across the western basalt plain through Geelong. Its estuary has three components:
(i) a 9.8 km river channel from the mouth to Lake Connewarre;
(ii) Lake Connewarre;
(iii) a 1.9 km river channel upstream from Lake Connewarre to a barrage that prevents further tidal influence. Samples were taken approximately 400 m upstream of the lake in this U-shaped channel, fringed by *Phragmites australis*. Stratification between river water and the slightly more saline lake water was evident at this site (Fig 7.3u).

Werribee River (Fig 7.4): The Werribee River rises in the Great Dividing Range west of Melbourne and flows south-easterly into Port Phillip Bay. Its estuary extends at least 10 km upstream of the deep, navigable mouth. Upstream, the estuary has an average depth of 1.5 m with occasional holes up to 3 m deep, and several very shallow sections. Stratification was evident on 9 December 1990 (Fig 7.3v). Samples were taken at various locations along the estuary as far as 9.5 km upstream of the mouth.

Bunyip River (Fig 7.4): The Bunyip River rises in the forested highlands in the southern ranges of the Victorian alps, and flows south-westerly and then westerly into Western Port. Its estuary through the drained Koo Wee Rup swamp is an engineered channel allowing a dynamic exchange of sea water with each tide. Some unstable stratification was evident at a site 2 km upstream of the mouth (Fig 7.3w).

7.3. METHODS

7.3.1. SURVEY OF *P. AUSTRALIENSIS* IN SOUTHERN AUSTRALIAN ESTUARIES

The survey of estuaries from the Onkaparinga River south of Adelaide to the Bunyip River east of Melbourne was conducted from 2 to 9 December 1990. This period was selected because it was within the period of peak larval density and juvenile recruitment in the Hopkins River estuary (see Chapters 3 and 6).

Qualitative net samples for adults and juveniles were taken by sweeping a long-handled, square-mouthed dipnet (30 cm×30 cm) with a 1 mm mesh through vegetation using a standard effort of 2 min sweeping through each stand of vegetation. Quantitative plankton samples were taken for larvae using a Clarke-Bumpus plankton net with a mesh size of 120 μm. For each sample, the net was towed through 0.4-0.7 m^3 of water at one depth, except at three

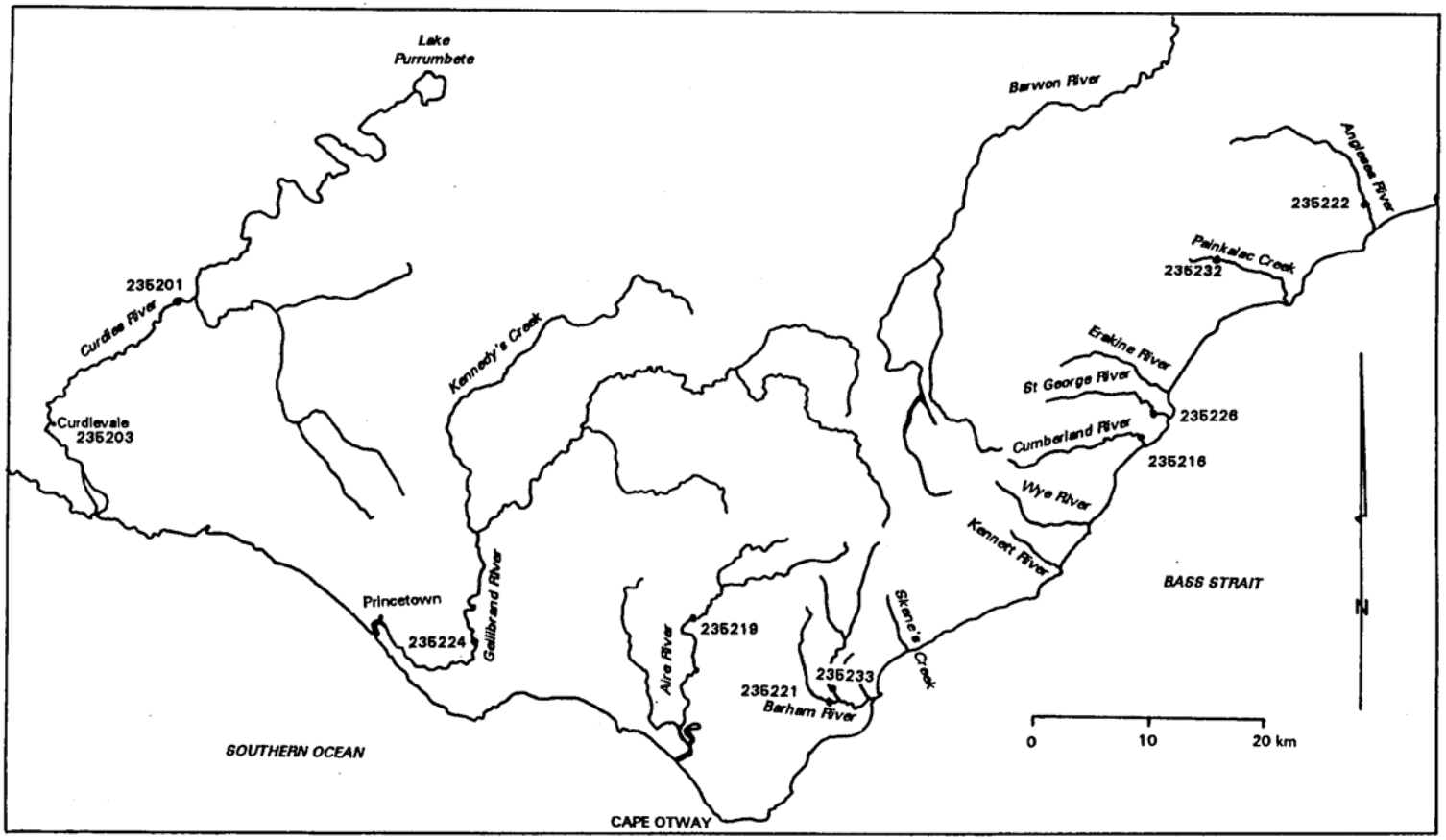


Fig. 7.5. Location of rivers of the Otway Range and the Curdies River, the estuaries of which were sampled for *Paratya australiensis* (six-digit numbers refer to gauging stations used in Fig. 7.2.)

locations where difficulty of access meant the net was towed by hand through a smaller volume. At seven other locations, where the Clarke-Bumpus net could not be used at all, a long-handled dipnet—as described above but with a mesh of 80 μm—was used to take qualitative plankton samples.

At each river, a preliminary survey of salinity and temperature was conducted along the estuary using a 'Yeo-Kal' salinometer (Model 602 Mk III). If the estuary was stratified, a site was chosen where the halocline was 1-2 m below the surface. A dipnet was run through any submerged vegetation present, and a plankton sample was taken just below the halocline—midstream if possible, but if access was difficult, sampling was done as close to midstream as possible. If no *P. australiensis* were found at this site, a site at the head of the estuary was sampled, if possible. If the estuary was not or only weakly stratified then samples were taken as near as possible to marine influence.

All shrimp collected were preserved in 2% formaldehyde, and identified in the laboratory. Larvae were assigned to stages according to Walsh (1993) (see Chapter 5).

7.3.2. COMPARISONS OF DEMOGRAPHIC PATTERNS IN *P. AUSTRALIENSIS* WITHIN AND BETWEEN CATCHMENTS

Sampling scheme

To investigate the upstream extent of *P. australiensis* distribution in the Hopkins River, a single qualitative survey of thirteen sites extending 250 km upstream of the mouth was conducted on 21 August 1991 (Fig. 1.1, Table 7.1). Other qualitative collections were made on 8 August 1990, 16 September 1990, 28 October 1990, 12 December 1990, and 9 February 1991 at five sites extending 140 km upstream of the mouth.

Variation in population structure, egg size and fecundity between estuarine and riverine populations, within and between catchments was investigated from August 1991 to April 1992 in the Hopkins, Curdies and Gellibrand rivers. Qualitative net samples were collected, when possible, from an estuarine site and at least one site upstream of the estuary in each river approximately monthly (see Appendix 1 for sampling dates).

In the Hopkins River, estuarine samples were collected at JP through *Phragmites australis* in September and October 1991, but few *P. australiensis* were present subsequently, due to the lack of *Zostera*. Thus 'estuarine' samples were taken from macrophytes in the lower reach of TS, just above the estuary from November 1991 to April 1992, with extra specimens being collected from *Ruppia* near LG in December and January (see section 2.2 for description of sites). Riverine samples were collected at Panmure from August 1991 to April 1992, at Warrumyea bridge from August to November 1991 and at MH from November 1991 to April 1992 (see Table 7.1).

Table 7.1. Riverine sites of the Hopkins River at which qualitative net collections were made.
x = distance upstream of mouth; h = elevation above sea level;
Map references are Australian 1:100 000 universal map grid references.

Sampling site	x (km)	h (m)	Map reference	Vegetation	Description of section sampled
Tooram Stones (TS)	10	1	7421 Mortlake 381483	a variety of habitats (see Section 2.2)	in channels (at low flow) or fringing grasses (in floods) at downstream end
Below Hopkins Falls	25	10	7421 Mortlake 414557	*Triglochin*	run ≈1-1.5m deep 100m below falls
Confluence (MH)	31	30	7421 Mortlake 431565	*Triglochin*	run ≈1.5m deep between 2 deep pools just below the confluence
Warrumyea Bridge	33	35	7421 Mortlake 436577	inundated grasses in flood; *Triglochin* at low flow	100 m upstream of bridge-backwater riffle in floods; at edge of run at low flow
Panmure (Mt Emu Ck)	46	59	7421 Mortlake 508553	*Potamogeton crispus*, *Triglochin*	at edge of deep pool at Princes Hwy bridge
Kent's Ford	64	87	7421 Mortlake 485714	fringing grasses, *Phragmites*, *Triglochin*	run ≈2-4m deep upstream of bridge
Hexham	107	121	7421 Willaura 483932	fringing grasses in flood; *Vallisneria* at low flow	at lower end of run upstream of bridge
Chatsworth	137	148	7422 Willaura 452086	*Triglochin* and *Phragmites*	small runs and riffles either side of bridge
Wickliffe	177	202	7422 Willaura 516270	inundated grasses	backwaters opposite hotel
Mjr Mitchell Rd	187	221	7422 Willaura 516321	*Triglochin*	run fringed with Phragmites
Delacombe Way	206	231	7422 Willaura 589430	*Triglochin*	run fringed with Phragmites
School Centenary Bridge	220	238	7423 Ararat 626506	*Triglochin*	wide meandering run through flat pasture
Logan Rd (Jackson's Ck)	253	310	7523 Beaufort 778625	*Triglochin* and filamentous algae	small stream in open wooded hills

Sites sampled in the Curdies and Gellibrand Rivers were described in section 7.2. Lake Purrumbete, at the head of the Curdies, was sampled from August to April. The Curdies River estuary was sampled at Dances Lane in August and September and at Curdievale from October to April (but not December). The Gellibrand River was sampled upstream at River Road in October, November and January, and at Kennedy's Creek from January to April.
The Gellibrand River estuary was sampled at Princetown in October, November, January,

March and April. Before each sample was collected, temperature and salinity of water in the weedbed were measured using a Yellow Springs Instrument salinity and conductivity meter (model 33).

Samples were collected qualitatively using a long-handled dipnet with 1 mm mesh. At each location a net was swept through the submerged macrophytes until as many ovigerous females as possible (up to 30) were collected. If few shrimps were present at one site, a second site was sought. Such an occurrence resulted in changes in site locations in the Hopkins and Gellibrand rivers during the sampling period. Shrimps were preserved in 2% formaldehyde. In the laboratory, all adult shrimps were identified and sexed and OCL was measured using a dissecting microscope (×8-×40) and ocular grid. Ovigerous females were stored individually, and eggs were removed and counted. Lengths and widths of five eggs from each female were measured using a dissecting microscope and ocular grid.

Egg size, brood size and reproductive output

Sufficient ovigerous females were collected for comparisons of egg and brood size at TS and MH in the Hopkins River, from Curdievale and Lake Purrumbete in the Curdies River, and from Princetown in the Gellibrand River on 19 November 1991 and 16 January 1992, and from Kennedy's Creek on 16 January 1992. In addition, eggs were analysed from females collected at Lake Purrumbete on 20-21 August and 27 September 1991. The number of broods examined and the number of broods used for each analysis is presented in Table 7.2.

Comparisons of egg size were made using egg volume, calculated assuming each egg was ellipsoid. Thus

$$\text{Volume} = \pi LW^2/6, \text{ where L=egg length and W=egg width.}$$

Mean volume for the five eggs from each brood, transformed by cube-root to equalise variances, was used in analyses. Mashiko (1982) found that, although egg volume of *Palaemon paucidens* could increase in volume by 60% between spawning and hatching, the increase in volume prior to the appearance of eye pigmentation was less than 20%. Smith and Williams (1980) reported only a 26% increase in mean volume of eggs of *P. australiensis* from earliest to final stage. The population in that study bore much larger eggs than found in any population of the current study, and it is possible smaller eggs show a greater percentage increase in size during development. Thus, to minimise variation due to developmental stage of *P. australiensis* eggs, only early stage eggs in which eye pigmentation was yet to appear were used in analyses of egg volume. Some broods from estuarine sites contained two distinct size classes of eggs, and were not used. No relationship was evident between size of the adult shrimp and egg size. Brood size was positively correlated to OCL, and so OCL was treated as a covariate in all analyses of brood size. When brood size was transformed by cube-root, which produced a uniform distribution of residuals, the slopes of the relationship were not significantly different ($P>0.10$) between any samples. Three small broods from Lake

Table 7.2. *Paratya australiensis*. Number of ovigerous females collected for analysis of egg and brood size, and the nature of the broods, from estuarine and upstream sites on the Hopkins, Curdies and Gellibrand rivers on four occasions. Early stage eggs possessed no eye pigmentation and were only used in egg volume and reproductive effort comparisons. Abnormal broods contained two distinct size groups of egg, and were omitted from egg size comparisons. Very small broods were extreme outliers in brood size analysis and were also omitted. Sample sizes for comparisons of brood sizes are shown.

Section	Brood	RIVER							
		Hopkins		Curdies				Gellibrand	
		Nov	Jan	Aug	Sep	Nov	Jan	Nov	Jan
Estuary	Early stage	17	7			14	12	22	13
	Eyed eggs	7	8			10	7	4	6
	Abnormal brood	3	1			2	1	2	1
	Very small brood	0	0			0	0	0	0
	N for brood size	27	16			26	20	28	20
Upstream	Early stage	19	10	11	18	15	13		4
	Eyed eggs	5	5	0	2	4	4		6
	Abnormal brood	0	0	0	0	0	0		0
	Very small brood	0	0	0	0	0	3		0
	N for brood size	24	15	11	20	20	20		10

Purrumbete in January were extremely low outliers and were excluded from the analyses to achieve the assumption of normality. The exclusion of these outliers will be considered in treatment of the results. As an estimate of total reproductive output per brood, the mean egg volume was multiplied by the brood size to give an estimate of total brood volume. The use of egg volume rather than egg mass in the calculation of an estimate of reproductive output is considered justified in light of Clarke's (1993a) demonstration of a linear relationship between egg volume and energy content.

These three parameters (egg volume, brood size, and total brood volume) were subject to the same set of analyses in making comparisons within and between catchments and sampling occasions, except that brood size and total brood volume were analysed using OCL as a covariate. The lack of ovigerous females in the riverine section of the Gellibrand in November meant a fully factorial comparison of estuarine and upstream sites in three rivers on two occasions was not possible. Three-way factorial ANOVAs for the Curdies and the Hopkins with two levels of river, two levels of section (upstream and estuary), and two levels of month (November and January) produced a significant three-way interaction for brood size and total brood volume ($P<0.001$ in both cases), and significant two-way interactions between river and section, and section and month for egg volume ($P=0.031$ and 0.001, respectively). To investigate the nature of these interactions, and to include data from the

Gellibrand, two further sets of two-way ANOVAs were conducted: one with three levels of river and two levels of section for January data only, and the other with three levels of river and two levels of month for estuarine data only. For each parameter, from the three ANOVAs, a total of twenty planned pair-wise comparisons were made, three more than the total degrees of freedom in the three analyses. Thus using the Dunn-Sidák adjustment (Sokal and Rohlf, 1981), significance was accepted at α=0.017 level. The comparisons were planned to test: (1) the effect of section—five comparisons within rivers on each occasion between estuary and upstream; (2) the effect of month—five comparisons between November and January at each site; (3) the effect of river—ten comparisons between the three rivers , for each section on each occasion. Finally, one-way ANOVAs were conducted for the effect of sampling occasion for the four months of samples from Lake Purrumbete. If a significant effect of occasion was found, three pair-wise comparisons were made to compare August, September and November. Although within the degrees of freedom of this analysis, because it was not independent of the previous analyses, significance was accepted at α=0.017 level.

Larval size

Variation in larval size between estuarine and riverine populations in the Hopkins River was also investigated. Estuarine larvae were collected from JP on 24 November, and 15 December 1989, at 1 m depth just below the halocline in salinity of ≈30 using a Clarke-Bumpus net (see section 6.2.1). Riverine larvae were collected from the deep pool on the Mt. Emu Creek at Panmure on 20 December 1989 and 14 January 1990 in salinity of 2, using an oblique tow of a conical plankton net with 120 μm mesh. OCL, rostrum length, total length, and telson length and width (see section 4.2 for definitions) were measured as for egg size, for twelve individuals of each stage from each environment.

The relationship between total length and larval stage was compared in larvae from the two locations by a two-way ANOVA with two levels of location and eight levels of stage. Heterogeneity of variances were corrected with a logarithmic transformation. Interaction between the two factors was partitioned by orthogonal polynomials (Sokal and Rohlf, 1981). The relationship between telson shape and larval stage was also compared in larvae from the two locations by a similar analysis performed on the ratio of telson length:width, with two levels of location and six levels of stage (stages III to VIII only, because in stages I and II the telson is fused to the sixth abdominal segment). Difficulties of analysis can arise when using observations derived from ratios of measurements. However, in this case, heterogeneity of variances was corrected by a logarithmic transformation of the ratio values. To compensate for missing values, a data point was randomly removed from some treatment cells so that N=11 in all cases.

Table 7.3. *Paratya australiensis*. Number of adults collected for electrophoretic analysis from estuarine and upstream sites on the Hopkins, Curdies and Gellibrand rivers on three occasions. Falls = pool below Hopkins Falls (see Fig 1.1).

Month	Section	RIVER					
		Hopkins		Curdies		Gellibrand	
		Site	N	Site	N	Site	N
September	Upstream			L Purrumbete	61		
November	Estuary	TS	66	Curdievale	77	Princetown	60
	Upstream	Panmure	62			River Rd	43
February	Estuary	TS	49			Princetown	61
	Upstream	MH	61			River Rd	66
		Falls	60			Kennedy's Ck	49
		Panmure	45				

7.3.3. ALLOZYME VARIATION IN *P. AUSTRALIENSIS* WITHIN AND BETWEEN CATCHMENTS

Allozyme electrophoresis was carried out on the *P. australiensis* populations studied in the previous section in order to assess variation in the genetic structure within and between catchments and between occasions spanning the breeding season. Adult *P. australiensis* specimens were collected from estuarine and upstream sites of the Hopkins and Gellibrand rivers on 18-19 November 1991 and 12-13 February 1992, and from the Curdies River estuary on 18 November 1991 and from Lake Purrumbete (Curdies, upstream) on 27 September 1991. The number of specimens analysed from each location on each occasion is shown in Table 7.3.

Specimens were taken to the laboratory alive and frozen at -18°C. A piece of tissue comprising a portion of the cephalothorax, including the hepatopancreas, was ground in three volumes of sucrose solution (10 g/100 mL), mercaptoethanol (0.1 g/100 mL) and bromphenol blue (0.1 mg/100 mL) prior to electrophoresis on horizontal starch gels of 12% (mass per volume) 'Starch-Art' hydrolysed potato starch (Smithville: Texas) at 120 mA per gel for 11-13 h. Three enzymes, which were chosen because they were encoded by polymorphic loci among the populations under study, were assayed according to the methods described by Richardson et al. (1986): phosphoglucomutase (*Pgm*), glucosephosphate isomerase (*Pgi*), and mannose-phosphate isomerase (*Mpi*). Each was examined in Tris-maleate buffer. Alleles at each of these loci were labelled alphabetically, in order of decreasing electrophoretic mobility.

Significance of departure from Hardy-Weinberg proportions in each sample was tested using χ^2 analysis of observed and expected homozygote and heterozygote numbers. To avoid statistical difficulties, heterozygous and homozygous pools were pooled, with one degree of freedom for

the χ^2, when expected values in some genotypic classes were small. The significance of allele frequency differences between samples was tested using χ^2 analysis. Temporal variation at each location was tested first by comparing allele frequencies in November 1991 and February 1992 at each of the four sites at which samples were taken on both occasions. If no significant temporal variation was detected, the two samples were pooled and comparisons were made between sites within each catchment and between estuarine sites in each catchment.

Roger's genetic distance was calculated between all pairs of sample populations (Rogers, 1972). A dendrogram based on genetic distance was constructed using the unweighted pair group method of analysis (UPGMA) (Sneath and Sokal, 1973).

7.3.4. MIGRATION OF POST-LARVAL *P. AUSTRALIENSIS* IN THE HOPKINS RIVER

A six-day trial designed to detect nett movement up or downstream in the Hopkins River estuary was held in the narrow strip of *Zostera* immediately downstream (west) of RF (Fig. 2.5) from 3 to 9 January 1990. Two identical traps were fixed to the substrate back-to-back, one facing upstream and one facing downstream. The traps were designed as modified fyke nets, with flared wings of constructed of 355 μm mesh forming an entrance with a gape >1.5 m, which spanned the width of the *Zostera* band. The entrance led to a perspex box 250 × 250 × 350 mm with a 5 mm slit opening approached by a slope covered with nylon fly-wire as substrate (Fig. 7.6a). The box, attached to the entrance wings by 'Velcro' tape, so that it could be removed from the water for emptying, had a latched door on the upper surface with a window of 355 μm mesh, for removal of trapped animals. The two traps were deployed on the 4 January and were cleared every 24 h. Several days of rough weather after 9 December caused damage to the traps, and the untimely end of the trial.

A second trial was conducted with re-designed traps from 19 December 1991 to 11 January 1992. Traps were deployed at the upstream limit of TS, in order to detect net movement towards or away from the estuary. They were similar to the previous design, being a box with a 1 cm slit opening approached by sloping walls, but were made entirely from nylon fly-wire with a 1 mm mesh around a steel frame 50 × 30 × 15 cm (Fig. 7.6b). The traps were emptied through the open end of the fly-wire shell, which was held in place at the rear by pegs. Three pairs of back-to-back nets were deployed in runs approximately 15 cm deep, amongst the network of basalt outcrops and vegetation that characterises TS (see section 2.2). In each pair, one net faced into the current and one faced downstream. Vandalism was a recurring problem, and only one pair of nets was collected successfully almost every day over the trial period.

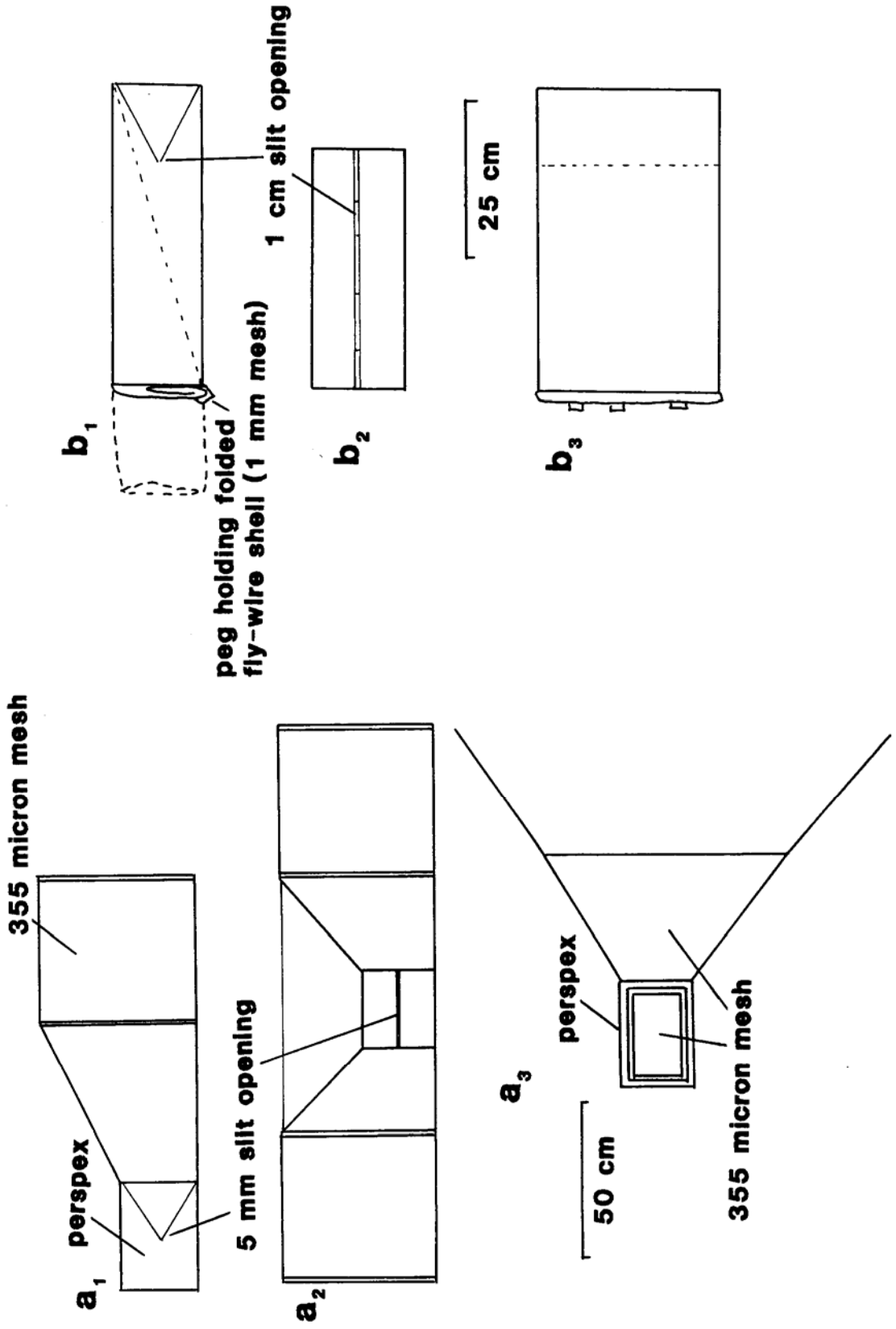


Fig 7.6. Design of traps used to detect movement of caridean shrimps in the Hopkins River estuary. In each case two traps were placed back-to-back, one upstream and one downstream. (a) trap used in first trial at RF, (a_1) side view (a_2) front view (a_3) plan view; (b) trap used in second trial in TS, (b_1) side view (b_2) front view (b_3) plan view

During the first trial, surface and bottom salinity was measured in the *Zostera* meadow each time the traps were cleared using a 'Yeokal' salinometer (model 602 Mk II). During the second trial, each time the traps were cleared, salinity and temperature were measured at the upper limit of TS, and at the surface and bottom of the small *Ruppia* bed at LG using a Yellow Springs Instruments salinity and conductivity meter (model 33). For some periods during the second trial, the tidal level of the estuary was continually measured using a tide gauge fixed to the jetty at Deakin University (Fig.2.1).

In both trials, traps were cleared daily, between 1100 and 1500 h. All animals, including any possible predators were removed and preserved in 2% formaldehyde. In the laboratory, all shrimps were identified, sexed and measured, and the gut contents of any possible predators were inspected and any shrimps identified and counted. The number of shrimp collected in a 24 h period (N) was calculated thus:
if the period between clearings (t_1) was >24 h, then $N = n_1 \times 24/t_1$;
if t_1 was <24 h, then $N = n_1 + (24-t_1) \times n_2/t_2$,
where n_i = number of shrimps in trap on day i, and
t_i = time between clearing traps on day i-1 and day i.

The number of animals caught in a pair of identical, unbaited traps facing opposite directions should indicate differences in nett movement of the animals in the two directions, if there is no current, as was the case in the first trial in the meadow at RF. In the presence of a current, such as in the second trial at TS, the upstream trap will present different flow conditions to the downstream trap, and any differences in numbers caught may be due to behaviour other than simple movement up or downstream. For instance the downstream net may provide shelter from the current and may be a preferred position. However, given a constant flow, any heterogeneity in the differences between traps over time will reflect differences in nett movement up or downstream.

The null hypothesis that the direction of the trap (upstream or downstream) had no effect on the number of *P. australiensis* captured was tested by log-likelihood ratio tests (the G-test of Sokal and Rohlf, 1981) on numbers of juveniles, males, non-ovigerous females and ovigerous females captured in a 24 h period. Due to small numbers of females, numbers from consecutive days were pooled until total number of individuals in both traps was >6 for both ovigerous and non-ovigerous females. The pooled, total and heterogeneity G values between days were calculated for each group.

7.4. RESULTS

7.4.1. THE OCCURRENCE OF *P. AUSTRALIENSIS* IN SOUTHERN AUSTRALIAN ESTUARIES

The occurrence of *P. australiensis* larvae in the deep saline water of estuaries sampled 2-9 December 1990 is shown in Table 7.4. No larvae were found in any rivers west of the Glenelg. None were found in the salt wedges of the Onkaparinga, Bungala, Inman or Hindmarsh estuaries, nor in isolated upstream pools of the Onkaparinga, nor at the mouths of the drains of south-eastern South Australia. And none were found in the Glenelg River itself, which showed stratification similar to its eastern neighbours (Fig. 7.3h) in which larvae were found.

Larvae were collected in all estuaries with stable salt wedges east of the Glenelg River. High densities ($>10^2$ m^{-3}) were collected from all rivers from the Fitzroy to the Aire—all of which have well developed estuaries. The age structure of larvae in these samples showed a trend towards increasing age moving west from Cape Otway. In the Aire and the Cumberland rivers, stage I dominated; in the Curdies, stage II; the Hopkins and the Fitzroy, stage III.

The two rivers either side of this group of estuaries—the Surry and the Barham—were not sampled at ideal sites (collections were made from the shore close to the mouth, rather than at a midstream site near the head of the salt wedge), and yet larvae were collected at these sites. Thus it is expected that these estuaries also support high densities of *P. australiensis* larvae.

Of the small rivers of the Otway range sampled for larvae, only the stratified Kennett River estuary supported *P. australiensis* larvae. None were collected from the surf zone at the mouth of the Cumberland which does not have a well developed estuary, nor from the Anglesea River estuary which had very little freshwater input (Fig. 7.3t). The well-developed estuaries of the Barwon and Werribee rivers supported *P. australiensis* larvae but not at densities as high as the rivers west of Cape Otway. Larvae were also collected from the less stratified estuary of the Bunyip River.

Table 7.5 shows the occurrence of adults and juveniles in the estuaries sampled in the survey. In the all estuaries sampled west of the Glenelg, in which no larvae were found, no adults or juveniles were collected either. However, a single adult was found in *Phragmites* in the Glenelg River estuary, from which no larvae were collected. Further east, juveniles were found in the fringing vegetation of all estuaries from which larvae were collected, except the Bunyip and the Gellibrand. Juveniles were also found in Skenes Creek, and the Erskine and Painkalac rivers in which no larval sampling was conducted. A juvenile was collected from the Anglesea River, in which no larvae were found.

Table 7.4. Abundance and percentage composition of *Paratya australiensis* larval stages in southern Australian estuaries, 2-9 December 1990. Symbols used for qualitative samples (qual.) indicate the number of individuals collected by a standard effort (-, 0; +, 1-10; ++, 10-100; +++, 100-1000). Salinity of the water from which larvae were collected and the longitudinal position in the estuary is indicated.. The dominant larval stage is in bold type in large samples. x = distance from mouth

RIVER	Estuary length (km)	x (km)	Salinity	Volume sampled (m^3)	Larval density (m^{-3})	Percentage of each larval stage							
						I	II	III	IV	V	VI	VII	VIII
Onkaparinga	9+	15	1.5-2	0.13	0								
Bungala	1.5	1.5	21	0.3	0								
Inman	2+	2	29	0.4	0								
Hindmarsh	2+	2	23	0.6	0								
Blackford Dn.	0	not collected											
Drain L	0.5	not collected											
L. Frome Dn.	0.3	0.2	14.8-22.2	0.1	0								
Glenelg	75+	45	20.6	1.3	0								
Surrey	3	1.5	27	0.15	10	0	0	0	100	0	0	0	0
Fitzroy	4.5+	1.5	21.5	0.5	10^3	11	30	**35**	15	7	2	1	0
Hopkins	9.5	7	27.6	0.5	10^3	8	12	**32**	28	14	5	1	0
Curdies	15+	12.5	12.2	0.6	10^3	17	**35**	31	10	5	3	0	0
Gellibrand	10.7	4	27.9-28.9	0.5	10^4	**64**	34	2	0	0	0	0	0
Aire	6.5	6	19	0.5	10^3	**40**	31	10	5	5	6	3	1
Barham	>1	0.5	27.3-33.6	qual.	++	0	0	0	8	5	8	30	**49**
Skenes	0	not collected											
Kennett	0.5+	0.5	30.6	qual.	++	17	**33**	17	17	17	0	0	0
Wye	0.5+	not collected											
Cumberland	0	0	surf zone	qual.	-								
St. George	0.5+	not collected											
Erskine	0.6	not collected											
Painkalac	3	not collected											
Anglesea	3	3	32-33.8	qual.	-								
Barwon	15.5	14	6.7	0.9	10^2	11	**53**	20	9	1	2	1	3
Werribee	10+	8	28.8	0.7	1	0	100	0	0	0	0	0	0
		9.5	11	qual.	-								
Bunyip	3+	1	16.4-26.8	qual.	-								
		3	4-6.5	qual.	++	**48**	30	3	12	3	3	0	0

Table 7.5. Abundance of juvenile (Juvs) and adult *Paratya australiensis* in southern Australian estuaries sampled from 2-9 December 1990. Symbols used to indicate abundance are as in Table 7.4. For each sampling site, vegetation type, salinity, and longitudinal position in the estuary is indicated.

* Adults were only collected from the St. George River estuary on 20 February 1993.

RIVER	Estuary length (km)	Dist. from mouth (km)	Vegetation	Salinity	Adults	Juvs
Onkaparinga	5+		*Zostera*	31	-	-
Bungala	1.5	1.5	*Phragmites*	4.5-24	-	-
Inman	2+	0.05	*Ulva, Enteromorpha*	30.1-32.6	-	-
		2	*Phragmites*	3.3-28.3	-	-
Hindmarsh	2+	0.05	Inundated grasses	17.3	-	-
		2	*Phragmites*	17.6-22.6	-	-
Blackford Drain	0	0	Drift marine algae	14.4	-	-
Drain L	0.5	0.5	*Ulva,* drift algae	10.3	-	-
L. Frome drain	0.3	0.2	none	14.4	not collected	
Glenelg	75+	45	*Phragmites*	1.8	+	-
Surrey	3	1.5	*Zostera*	17.3-28.3	+++	+++
Fitzroy	4.5+	2	*Zostera*	1.1-1.5	+++	+++
Hopkins	9.5	8	*Zostera*	1.6	+++	+++
Curdies	15+	12.5	*Potamogeton crispus*	1.3	+++	+++
Gellibrand	10.7	4	*Phragmites, Triglochin*	3.4	+++	-
Aire	6.5	0.5	inundated *Craspedia*	1.5	-	+++
		6	*Juncus,* grasses	0.1	+++	+++
Barham	>1	0.5	*Phragmites*	8.8-27.3	-	+++
Skenes	0	0.5	*Phragmites*	0.1	++	++
Kennett	0.5+	0.5	*Phragmites*	3.2-27.7	-	+
Wye	0.5+	0.5	*Phragmites*	0.5-22.9	-	-
Cumberland	0	0.5	*Phragmites*	0.1	++	-
St. George	0.5+	0.5	*Juncus, Rubus, Zostera*	20.9	++*	-
Erskine	0.6	0.2	*Phragmites*	16.5-31.1	-	++
Painkalac	3	1	*Zostera, Ruppia*	31.3	-	++
Anglesea	3	0.5	*Zostera*	33.8	-	-
		3	*Phragmites*	31.7-33.8	-	+
Barwon	15.5	14	*Phragmites*	1.4-1.8	++	++
Werribee	10+		not collected			
Bunyip	3+	1	*Phragmites*	7.9	-	-
		3	*Phragmites*	0.1	-	-

Adults were most common in estuaries with submerged macrophytes such as *Zostera*, *Potamogeton crispus*, *Triglochin procera* and inundated terrestrial grasses. They were less common in estuaries where the only macrophyte was *Phragmites australis*, such as the Glenelg and several smaller rivers of the eastern Otways. Adults were less likely to occur in seagrass beds if there was a strong marine influence, as there was in Painkalac Creek and the Anglesea River, but the occurrence of large numbers of adults in the Surry River *Zostera* meadows in salinity 17-28 was an exception.

Juveniles occurred more commonly than adults in higher salinities: e.g. the Erskine River, Painkalac Creek, and the Anglesea River. They also occurred in very high numbers in all estuaries in which adults were abundant. The exception of the Gellibrand may be explained by the younger age structure of the larval population in this estuary (Table 7.4), which suggests later recruitment.

In summary, high densities of larvae were present in all stable, open, well-developed, salt-wedge estuaries in which adults were abundant. The only stable estuary with high larval densities, but no adults was the Barham, which was only sampled in the lower reaches. It is likely that adults would have been present further upstream as was the case in the Aire River (Table 7.5). Adults were most abundant in low salinities among submerged, leafy macrophytes. However, at least some *P. australiensis* larvae, juveniles or adults were present in almost all Victorian estuaries sampled, even if the estuary was stratified less stably or supported little submerged vegetation.

7.4.2. THE DISTRIBUTION OF *P. AUSTRALIENSIS* WITHIN THE HOPKINS RIVER CATCHMENT

Fig. 7.7 shows the occurrence of post-larval *P. australiensis* in the Hopkins River on 21 August 1991. No *P. australiensis* were collected beyond Chatsworth. Collections on 8 August 1990, 16 September 1990, 28 October 1990, 13 December 1990, and 9 February 1991, all produced *P. australiensis* at Hexham and all sites downstream. At Chatsworth, small numbers of *P. australiensis* were collected only on 16 September 1990 and 13 December 1990. Thus within the Hopkins River, *P. australiensis* was most common in lower reaches (<100 m elevation), and have not been found more than 150 km upstream of the mouth (≈200 m elevation).

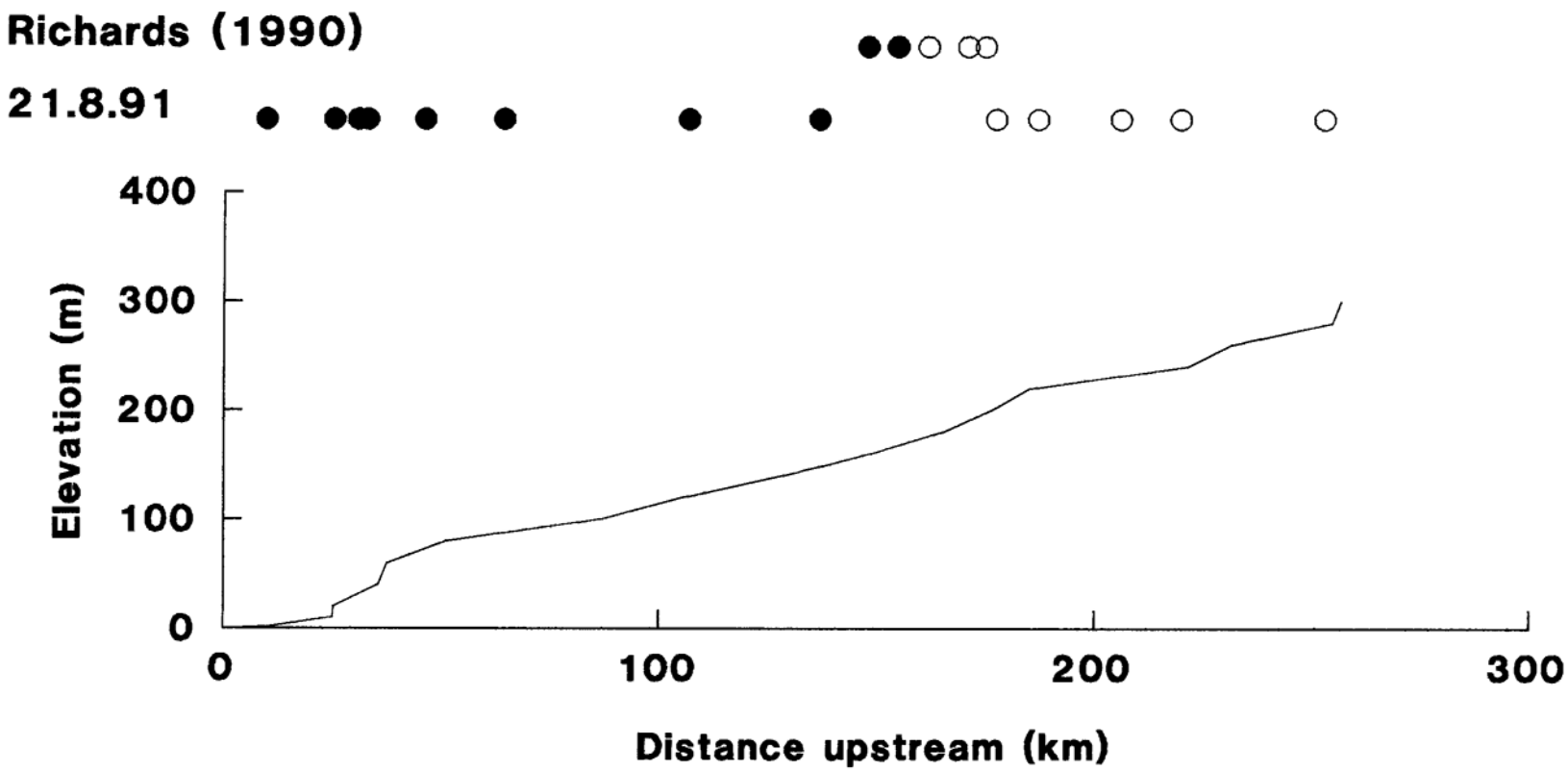


Fig. 7.7. Elevation profile of the Hopkins River from the mouth at Warrnambool to the Great Dividing Range near Ararat, with the occurrence of *Paratya australiensis* at thirteen sites on 20 August 1991, and at seven sites in two tributaries of the Hopkins as reported by Richards (1990). Closed circles indicate the presence of *Paratya australiensis* and open circles indicate its absence.

7.4.3. VARIATION IN LIFE-HISTORY TRAITS WITHIN AND BETWEEN CATCHMENTS

7.4.3.1. PHYSICO-CHEMICAL DATA

Temperature and salinity of water from which *P. australiensis* was collected from August 1991 to March 1992 are presented in Fig. 7.8. In both the Hopkins and the Curdies rivers temperature was relatively constant around 17-21°C from October to March at all sites sampled. These summer temperatures are in contrast to temperatures of 10-15 °C in August and September. A similar trend was observed in the Gellibrand estuary weedbeds, but upstream sites in the Gellibrand remained cooler at 15-17°C over summer. There was usually little difference in salinity between upstream and estuarine sites in the Hopkins River on each sampling occasion. In most of spring and summer, Hopkins River water was more saline than the other two rivers at around 2, but during the August and September flood, salinity was less than 1. In the Curdies and the Gellibrand, salinity in the weedbeds of the estuaries was similar to upstream salinities until December when salinity increased.

7.4.3.2. POPULATION DYNAMICS

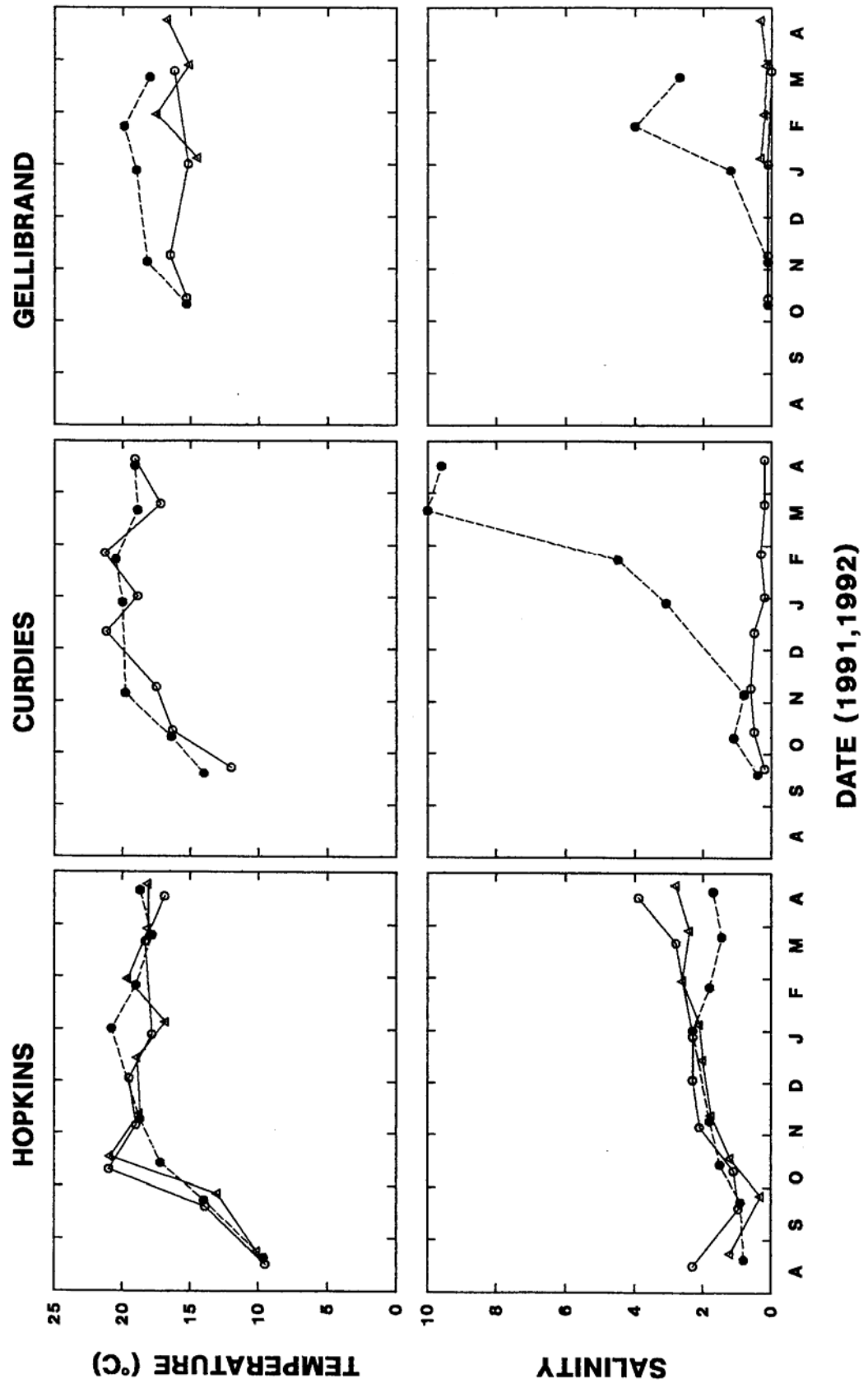
Ovigerous females were collected from Lake Purrumbete and the Hopkins River estuary as early as August 1991, and until as late as February or March 1992 at all sites sampled (Fig. 7.9). It is possible that ovigerous females were also present as early as August in the estuaries of the Curdies and the Gellibrand, because flooding during August and September prevented access to suitable submerged weedbeds at these sites.

Hopkins River

The proportion of mature females that were ovigerous at upstream sites of the Hopkins River until December was very low compared to the proportion at the estuarine sites, TS and JP (Fig. 7.9). Prior to December most females that were ovigerous were large (>6 mm OCL) at all sites (Fig. 7.10). There was a greater proportion of females ovigerous near the estuary than further upstream partly because smaller mature females, which tended not to become ovigerous until later in the season, were more common at upstream sites (Fig. 7.10).

→

Fig. 7.8. Temperature and salinity of water from which qualitative net samples were taken in the Hopkins, Curdies and Gellibrand rivers between August 1991 and April 1992. Closed circles, dashed lines- estuarine sites; open symbols, solid lines- upstream sites (triangles- MH in the Hopkins and Kennedy's Creek in the Gellibrand; circles- Panmure in the Hopkins and River Rd in the Gellibrand)


HOPKINS
CURDIES
GELLIBRAND
TEMPERATURE (°C)
SALINITY
DATE (1991,1992)
A S O N D J F M A A S O N D J F M A A S O N D J F M A

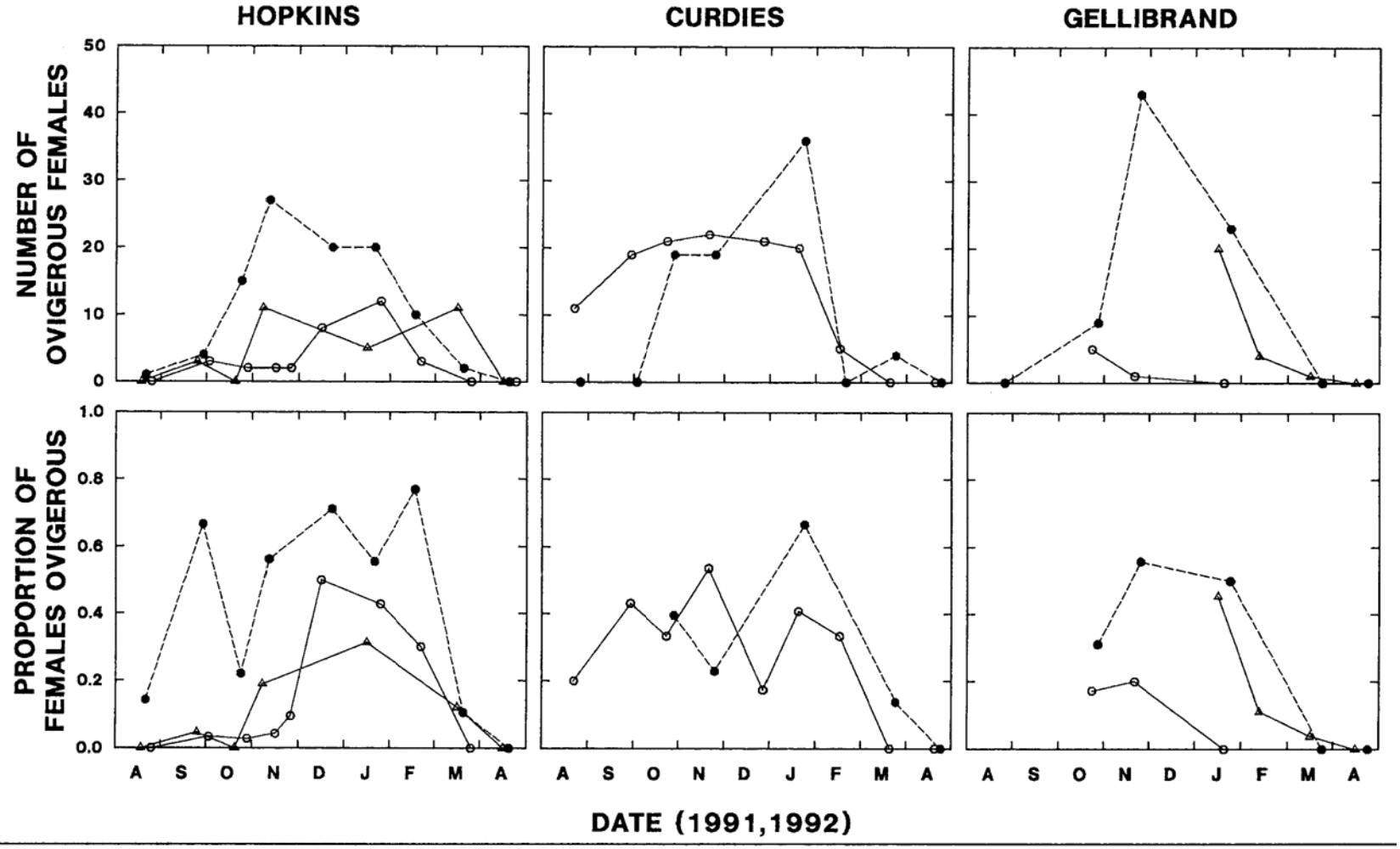


Fig. 7.9. *Paratya australiensis*. Proportion of females that were ovigerous and the abundance of ovigerous females per standard effort in the Hopkins, Curdies and Gellibrand rivers from August 1991 to April 1992. Symbols as in Fig 7.8

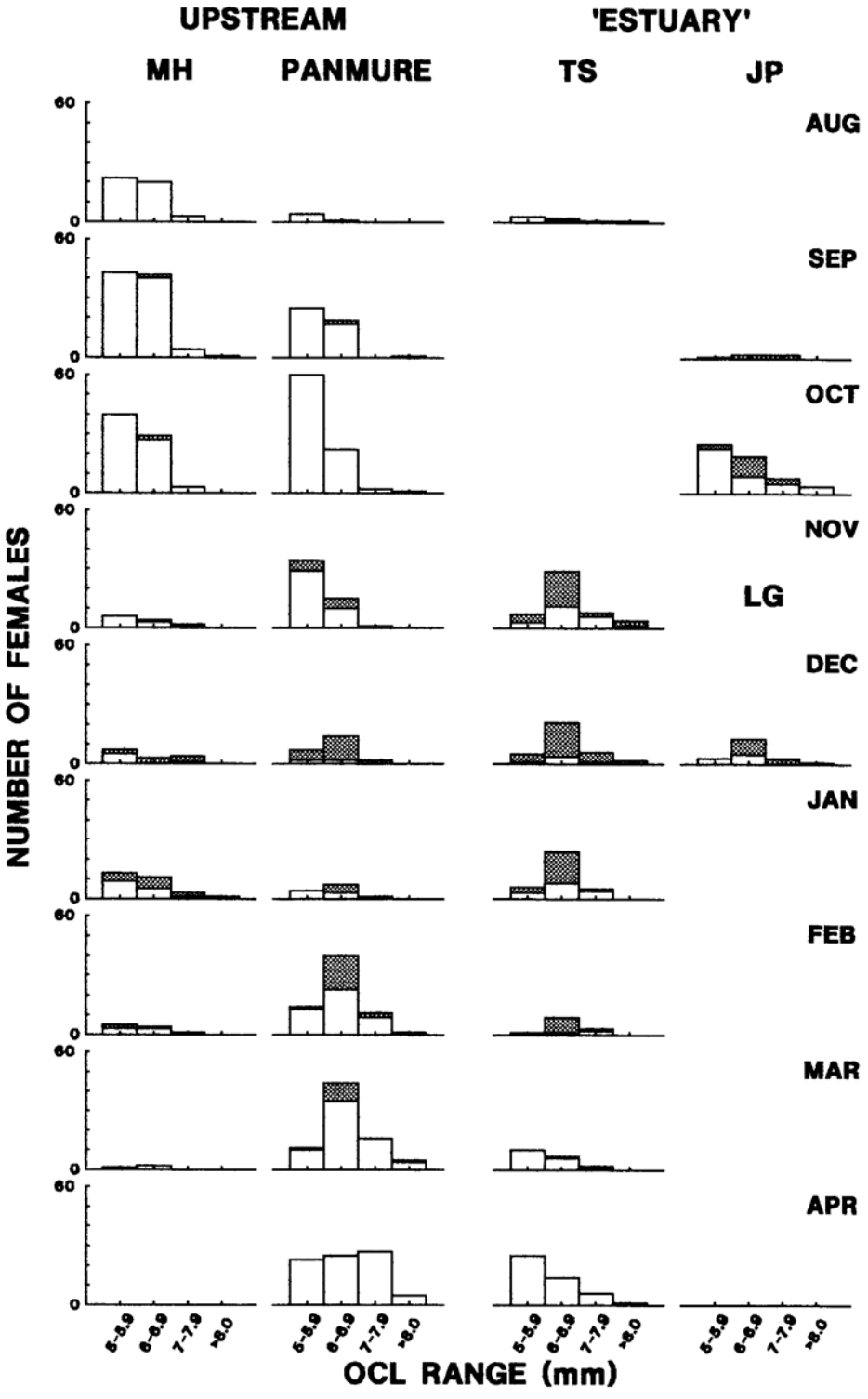


Fig. 7.10. Trends in abundance (number per unit effort) of mature *Paratya australiensis* females and their reproductive status in the Hopkins River at two riverine, upstream sites —MH and Panmure—, and at TS, just above the estuary, and JP and LG in the estuary. Stippled, ovigerous females; unshaded, non-ovigerous females

Curdies River

Lake Purrumbete supported a consistently high number of ovigerous females from August until January (Fig. 7.10). In the Curdies River estuary the proportion of females that were ovigerous peaked in January at a level higher than occurred at any time in Lake Purrumbete, but similar proportions were recorded in other months in which successful sampling was possible. Females at Lake Purrumbete showed quite a different pattern of reproduction from the upstream sites of the Hopkins River, with an earlier and more consistent period of high reproductive activity: from August to January rather than from November to February. Patterns of reproductive activity in the Curdies and Hopkins estuaries were similar from October to April, and it is possible they were similar in August and September also. Large females were more common in the estuary than in Lake Purrumbete, although the modal size frequency was the same (6-6.9 mm OCL) in October and November 1991 (Fig. 7.11), which contributed to the proportions of females that were ovigerous being similar at both sites on those occasions (Fig. 7.10).

Gellibrand River

The Gellibrand was the least intensively sampled river but, as found in the other two, the estuary supported a higher proportion of large females than upstream at River Rd, which resulted in a higher proportion of females that were ovigerous in the estuary (Fig. 7.9, 7.10). However the population further upstream at Kennedy's Creek (which was only sampled from January 1992) was remarkably different from any other. Very large females dominated at this site and most were ovigerous in January. No females <6 mm OCL were found to be ovigerous at this site (Fig.7.11).

7.4.3.3. BROOD SIZE, EGG SIZE AND REPRODUCTIVE OUTPUT

Brood size

Brood size increased with female size (Fig. 7.12), although no such relationship was found for egg size. In the two analyses of brood size that included a section (i.e. estuarine or upstream) effect, the effect of section explained a much larger proportion of the variation in brood size than any other effect, except the covariate OCL (Table 7.6a, c). Broods from estuarine sites were larger than broods from females of the same size upstream (within river, within month), except in the Hopkins River in January (Fig. 7.12, Table 7.6d). Within each location, no difference in brood size was evident between November and January except in the Hopkins estuary (Table 7.6d). In that case, mean brood size at TS (Hopkins, estuarine) decreased between November 1991 and January 1992. This decrease explains the finding of no significant difference between estuarine and upstream broods in the Hopkins River in January.

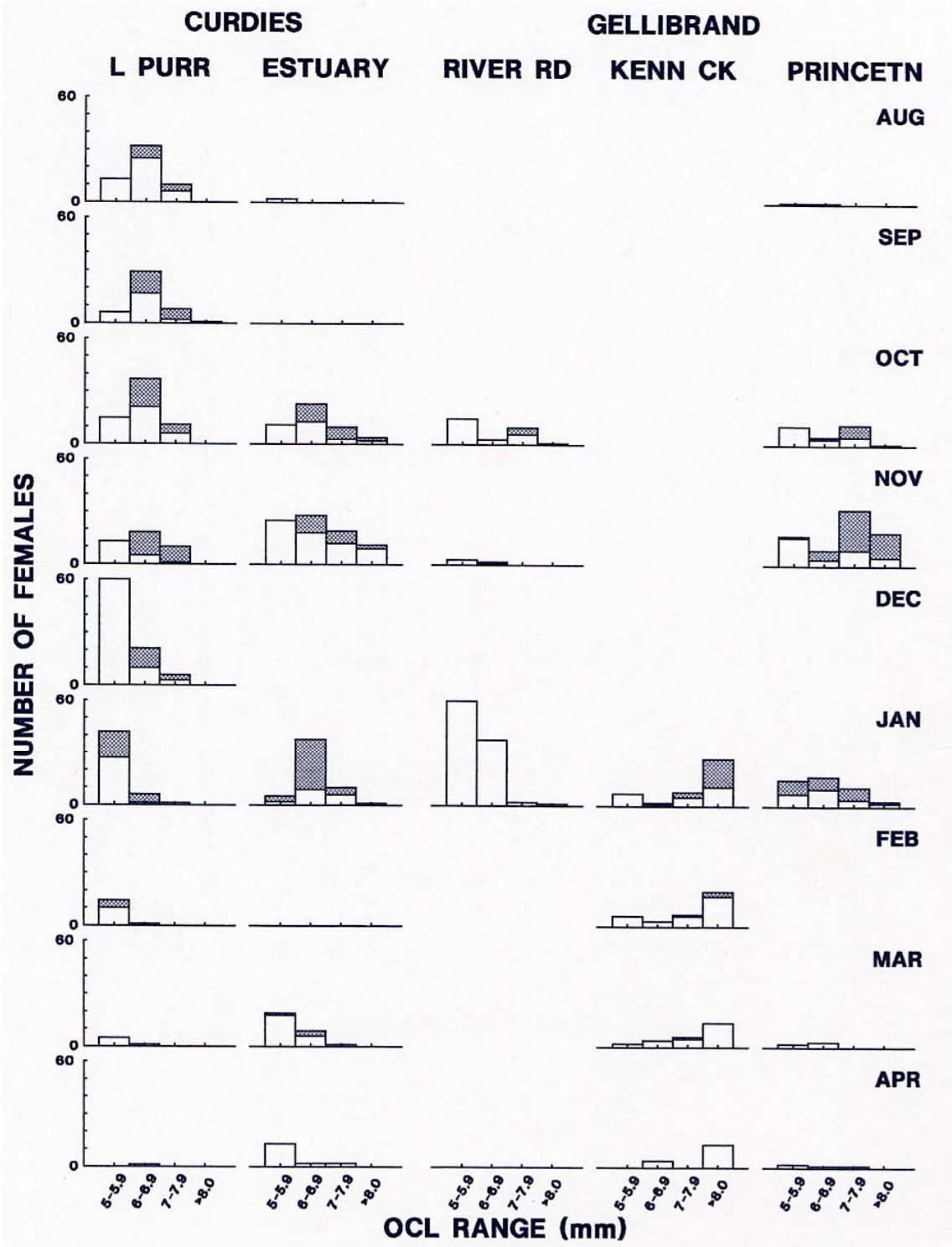


Fig. 7.11. *Paratya australiensis*. As in Fig. 7.9, but for the Curdies River at an upstream lacustrine site (Lake Purrumbete) and an estuarine site (Dances Lane in August and September only and Curdievale) and for the Gellibrand River at two upstream, riverine sites (River Rd and Kennedy's Creek) and an estuarine site at Princetown

Table 7.6. *Paratya australiensis*. Analyses of covariance of cube-root-transformed brood size, with OCL as covariate, with (a) river (Hopkins and Curdies only), section (estuary or upstream), and month (November 1991 and January 1992); (b) all three rivers and month for estuaries only; (c) all three rivers and section for January only; (d) results (P-values) of planned pair-wise comparisons. Significance for planned comparisons (marked by asterisks) was accepted at P<0.017. % variation: percentage of the total variation in brood size explained by each effect

	Source of variation	df	SS	F-ratio	P	% variation
(a)	River	1	0.023	0.07	0.79	<0.1
	Section	1	15.117	46.37	<0.001	12.2
	Month	1	1.283	3.94	0.049	1.0
	River × section	1	0.619	1.90	0.17	0.5
	River × month	1	2.322	7.12	0.008	1.9
	Section × month	1	0.096	0.29	0.589	0.1
	River × section × month	1	3.619	11.10	0.001	2.9
	OCL	1	50.181	153.91	<0.001	40.6
	Error	154	50.210			
(b)	River	2	1.428	1.26	0.39	1.3
	Month	1	1.372	4.83	0.083	1.2
	River × month	2	12.716	11.22	<0.001	11.2
	OCL	1	61.119	215.75	<0.001	53.8
	Error	131	37.073			
(c)	River	2	1.884	2.66	0.075	2.4
	Section	1	18.334	51.69	<0.001	24.3
	River × section	2	5.018	7.07	0.001	8.8
	OCL	1	18.884	53.25	<0.001	36.2
	Error	94	33.338			

(d)

		RIVER		
COMPARISON	MONTH	Hopkins	Curdies	Gellibrand
Estuary v. Upstream	Nov	<0.001*	0.007*	-
	Jan	0.577	<0.001*	<0.001*
COMPARISON	SECTION			
Nov v Jan	Upstream	0.699	0.303	-
	Estuary	<0.001*	0.053	0.280

		COMPARISON		
SECTION	MONTH	Hopkins v Curdies	Curdies v Gellibrand	Hopkins v Gellibrand
Estuary	Nov	0.009*	0.571	0.034
	Jan	<0.001*	0.016*	0.099
Upstream	Nov	0.864	-	-
	Jan	0.159	0.135	0.005*

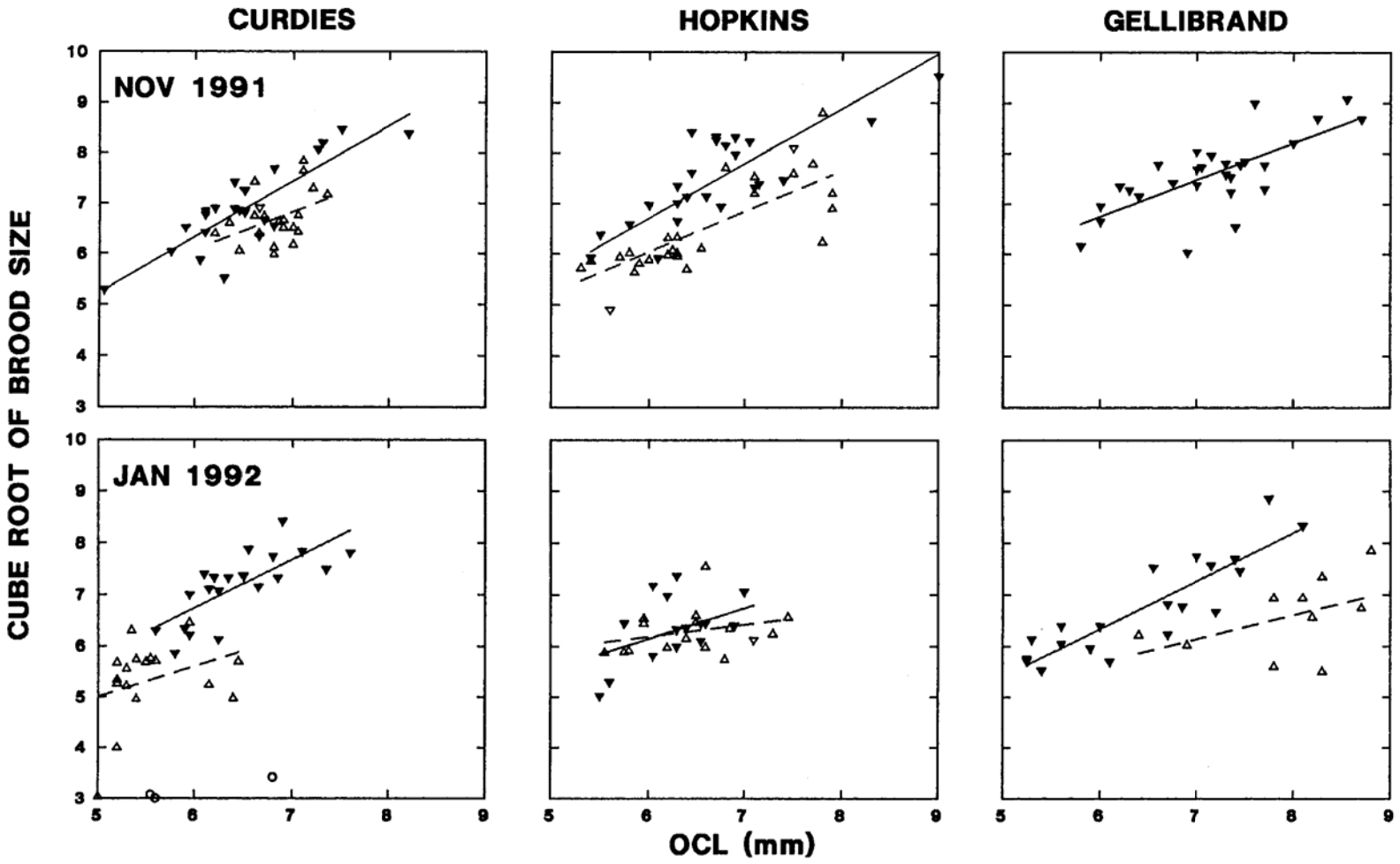


Fig. 7.12. Regression lines for cube root of brood size as a function of female size (OCL) for *Paratya australiensis* from estuarine (closed, inverted triangles, solid line) and upstream sites (open triangles, dashed line) in the Hopkins, Curdies and Gellibrand rivers in November 1991 and January 1992.

Between-rivers comparisons (within section, within month) showed four significant pair-wise differences (Table 7.6d), but no simple trend was apparent. Broods were smaller in the Curdies estuary than in the Hopkins in November but, in January, broods in the Curdies were larger than either the Hopkins or the Gellibrand. In January, broods in Kennedy's Creek (Gellibrand, upstream) were significantly smaller than in upstream sites in the Hopkins but not the Curdies.

The decrease in brood size between November and January at TS, which was not observed at other sites, may have been due to the choice of TS, situated at the upper limit of the Hopkins estuary, as an 'estuarine' sample. This was necessary because of the lack of seagrass in the Hopkins estuary in the summer of 1991/1992. In January 1992, three ovigerous females were also collected from the small *Ruppia* meadow at LG, within the estuary, in water of salinity 16-23 at 22°C. The eggs of these three females were all eyed, and thus were not used in analyses of variance of egg size. To keep the analyses of this section consistent, these three broods were not used in the analyses of brood size either. A one-way ANCOVA of brood size between the 16 broods from TS in January and the 3 from LG, with OCL as covariate (non-heterogeneous slopes: P=0.326), showed brood size to be larger at LG than at TS (P=0.033). Thus the trend for larger broods in estuarine sites than in upstream sites was detected in all rivers on both occasions.

The distribution of brood sizes at Lake Purrumbete (Curdies, upstream) in January 1992 was characterised by several individuals carrying very few eggs (Fig. 7.12). However, even excluding these statistical outliers, the Lake Purrumbete brood sizes were smaller than in the Curdies estuary. The January Lake Purrumbete sample was the only one in which extremely small brood sizes were found. With these outliers excluded, no difference was detected in brood size in Lake Purrumbete in the four months sampled from August 1991 to January 1992 (P=0.108). Comparisons between the January sample and earlier samples from Lake Purrumbete should be interpreted with caution, because the covariate range of the January 1992 sample has very little overlap with previous samples. However, the extremely low outliers suggest a tendency for part of the population to produce smaller broods in January, towards the end of the breeding season.

Egg size

The effect of section accounted for most of the variation in egg volume (Table 7.7a, c), although month and river accounted for larger proportions of variation than was the case for brood size. In the Hopkins and Curdies rivers, egg sizes were larger at upstream sites than in the estuaries in November, but were not significantly different between sections in January (Fig. 7.13, Table 7.7d). This change in trend between months was due to a decrease in egg size from November to January at upstream sites (Fig. 7.13, Table 7.7d), which was not observed in estuaries. At Lake Purrumbete, (Curdies, upstream) there was no significant

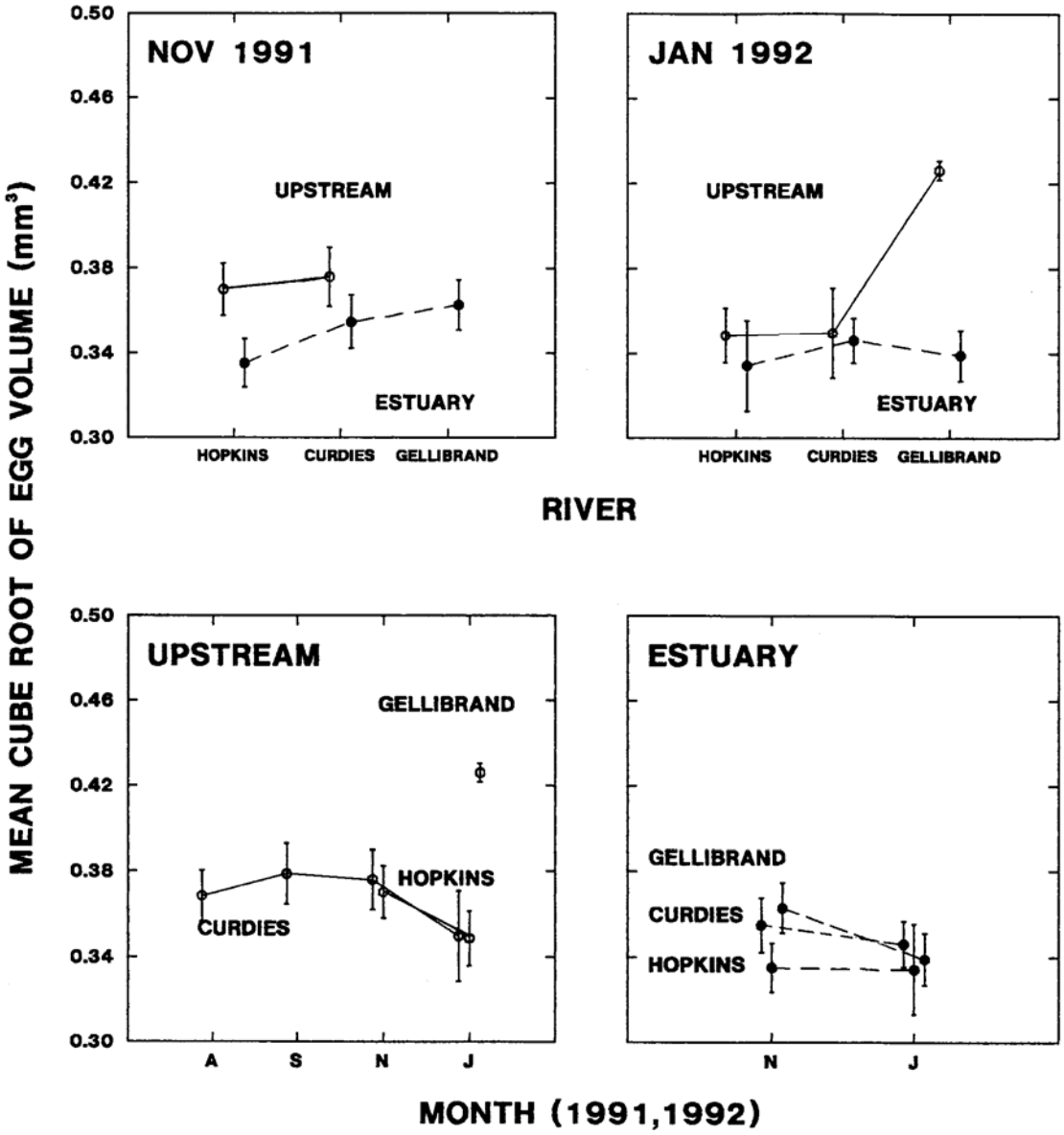


Fig. 7.13. *Paratya australiensis*. Interaction plots for mean (±sd) egg volume showing the effect of river (Hopkins, Curdies and Gellibrand) and section (upstream, open circles; estuary, closed circles) in November 1991 and January 1992, and the effect of month (August, September, November 1991, and January 1992) and river for each section

Table 7.7 *Paratya australiensis*. Analyses of variance of cube-root-transformed volume of eggs with effects and comparisons as in Table 7.6

	Source of variation	df	SS	F-ratio	P	% variation
(a)	River	1	0.002	11.46	0.001	5.8
	Section	1	0.009	42.14	<0.001	21.4
	Month	1	0.005	25.41	<0.001	12.9
	River × section	1	0.001	4.77	0.031	2.4
	River × month	1	<0.001	1.22	0.272	0.6
	Section × month	1	0.002	11.26	0.001	5.7
	River × section × month	1	<0.001	0.08	0.784	<0.1
	Error	101	0.020			
(b)	River	2	0.004	11.86	<0.001	18.4
	Month	1	0.002	14.45	<0.001	11.2
	River × month	2	0.002	5.54	0.006	8.6
	Error	80	0.013			
(c)	River	2	0.014	27.71	<0.001	23.7
	Section	1	0.015	62.02	<0.001	26.6
	River × section	2	0.015	31.07	<0.001	26.6
	Error	54	0.013			

(d)

		RIVER		
COMPARISON	MONTH	Hopkins	Curdies	Gellibrand
Estuary v. Upstream	Nov	<0.001*	<0.001*	-
	Jan	0.068	0.572	<0.001*
COMPARISON	SECTION			
Nov v Jan	Upstream	<0.001*	<0.001*	-
	Estuary	0.892	0.116	<0.001*

		COMPARISON		
SECTION	MONTH	Hopkins v Curdies	Curdies v Gellibrand	Hopkins v Gellibrand
Estuary	Nov	<0.001*	0.065	<0.001*
	Jan	0.053	0.170	0.419
Upstream	Nov	0.241	-	-
	Jan	0.871	<0.001*	<0.001*

difference between the months sampled prior to January (P=0.093 August to September; P=0.234 August to November; P=0.615 September to November). Thus, at Lake Purrumbete, egg size did not change significantly from August to November, but had decreased significantly by January.

Table 7.8. Mean (±sd) egg length and width in mm of *Paratya australiensis* collected from estuarine and upstream sections of the Hopkins, Curdies and Gellibrand rivers in November 1991 and January 1992

Month	Section	Hopkins		Curdies		Gelllibrand	
		Length	Width	Length	Width	Width	Length
November	Upstream	0.63±0.03	0.39±0.01	0.66±0.02	0.39±0.02	-	-
	Estuary	0.58±0.04	0.35±0.01	0.62±0.03	0.37±0.01	0.64±0.02	0.38±0.02
January	Upstream	0.61±0.02	0.37±0.02	0.61±0.04	0.37±0.03	0.73±0.01	0.45±0.01
	Estuary	0.57±0.03	0.35±0.02	0.60±0.03	0.36±0.02	0.61±0.03	0.35±0.01

The eggs of *P. australiensis* from Kennedy's Creek (Gellibrand, upstream) were much larger than at any other site (Fig. 7.13, Tables 7.7d, 7.8). Other than the unusually large eggs of Kennedy's Creek, differences between rivers (within section, within month) were generally not significant, although eggs at TS were smaller than in the other estuaries in November 1991. Mean lengths and widths of eggs from each site in November 1991 and January 1992 are shown in Table 7.8.

Abnormal broods were found only in estuarine sites. Five to ten percent of estuarine broods examined in all rivers in both months were abnormal (Table 7.2). In most cases, the eggs seemed normal in structure, but a minority of the brood (3-45%) were distinctly larger than the dominant size range. A typical example was a brood of 285 eggs from a female of 5.8 mm OCL from TS in November 1992: 247 eggs were 0.55-0.60 mm long and 0.34-0.345 mm wide, while 38 eggs were 0.70-0.75 mm long and 0.40-0.415 mm wide. In one case, 5% of a brood were smaller (range, 0.28-0.32 × 0.28-0.30 mm) than the majority (range, 0.52-0.60 × 0.35-0.37 mm). In the Curdies estuary in November, there were no broods with bimodal size distributions, but two broods were characterised by many malformed eggs. No abnormal broods were encountered in any upstream samples.

Reproductive output

The effect of section was less dominant in the variation of total brood volume than it was for brood and egg size (Table 7.9a, c). The only significant difference in brood volume between sections was in the Curdies River in January (Table 7.9d). Brood volume decreased significantly from November to January in all sites except upstream in the Curdies estuary and upstream in the Hopkins where there was no significant difference (Fig. 7.14, Table 7.9d). At Lake Purrumbete there was no significant difference in brood size in the months sampled prior to the decrease in January ($P>0.19$ in all comparisons). The only significant difference between rivers in corresponding sections in each month was that, in January, brood size was higher in the Curdies estuary than in Gellibrand estuary which was in turn just higher than the Hopkins.

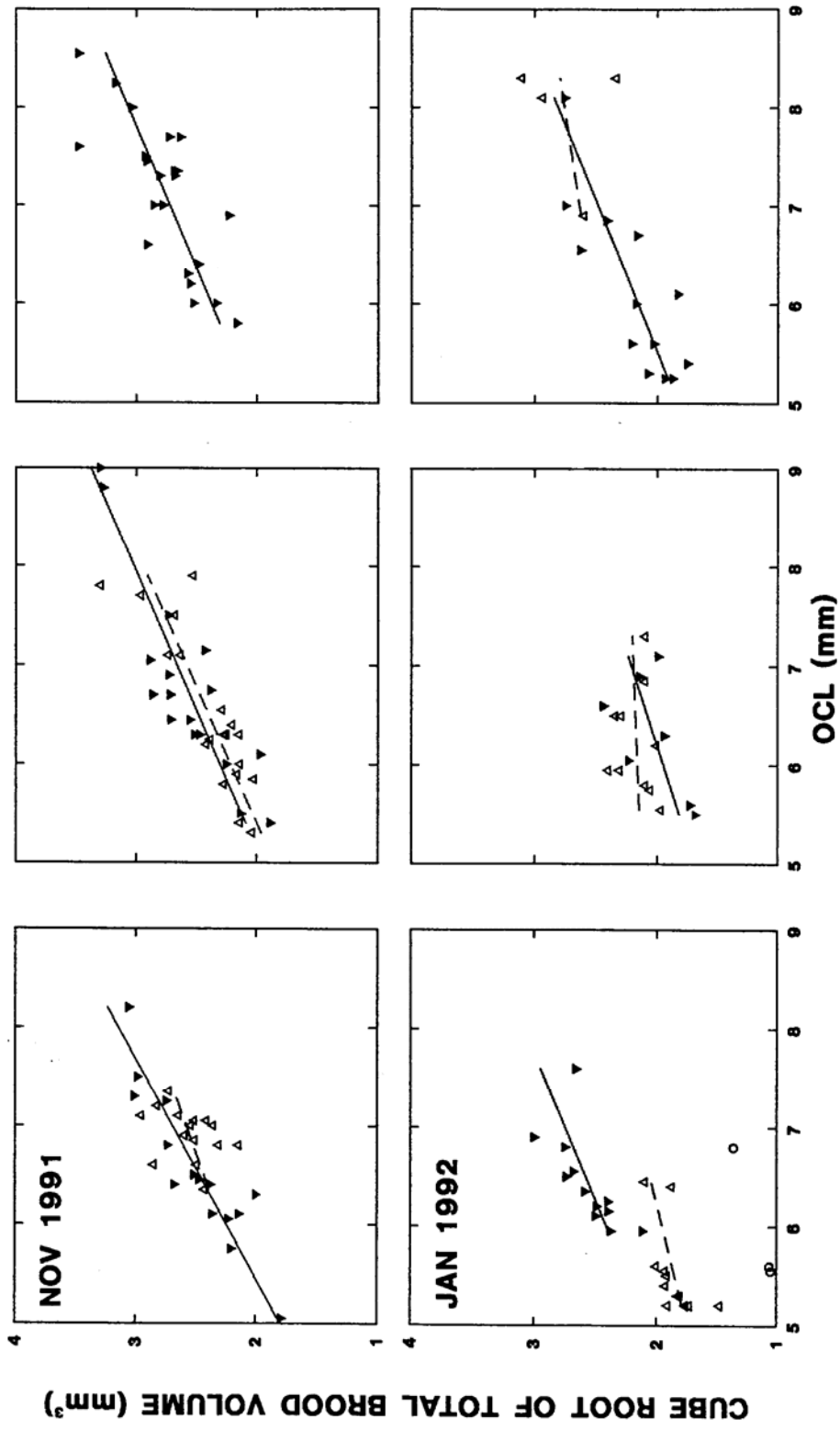


Fig. 7.14. *Paratya australiensis*. As in Fig. 7.12, but for cube-root of total brood volume

Table 7.9. *Paratya australiensis*. Analyses of covariance of total brood volume with OCL as covariate and effects and comparisons as in Table 7.6

	Source of variation	df	SS	F-ratio	P	% variation
(a)	River	1	0.256	7.31	0.008	2.4
	Section	1	0.212	6.04	0.016	2.0
	Month	1	0.534	15.24	<0.001	4.9
	River × section	1	0.422	12.03	0.001	3.9
	River × month	1	0.248	7.065	0.009	2.3
	Section × month	1	0.008	0.22	0.641	0.1
	River × section × month	1	0.480	13.69	<0.001	4.4
	OCL	1	5.269	150.32	<0.001	48.5
	Error	101	3.435			
(b)	River	2	0.629	8.18	0.001	5.6
	Month	1	0.442	11.50	0.001	4.0
	River × month	2	0.714	9.29	<0.001	6.4
	OCL	1	6.310	164.07	<0.001	56.7
	Error	80	3.038			
(c)	River	2	0.371	4.80	0.012	8.0
	Section	1	0.059	1.53	0.221	1.3
	River × section	2	0.930	12.02	<0.001	20.2
	OCL	1	1.276	32.98	<0.001	27.7
	Error	54	1.973			

(d)

		RIVER		
COMPARISON	MONTH	Hopkins	Curdies	Gellibrand
Estuary v. Upstream	Nov	0.156	0.370	-
	Jan	0.107	<0.001*	0.480
COMPARISON	SECTION			
Nov v Jan	Upstream	0.071	0.008*	-
	Estuary	<0.001*	0.151	0.006*

		COMPARISON		
SECTION	MONTH	Hopkins v Curdies	Curdies v Gellibrand	Hopkins v Gellibrand
Estuary	Nov	0.897	0.355	0.313
	Jan	<0.001*	0.003*	0.013*
Upstream	Nov	0.822	-	-
	Jan	0.138	0.066	0.267

These results indicate that, in November, size-specific reproductive output was not significantly different across all sites sampled. The fact that egg and brood sizes differed significantly within rivers between estuarine and upstream sites in November while reproductive output remained constant indicates differing allocation of a constant proportion of available resources between number of offspring and investment per offspring in different

Table 7.10. Morphometric measurements of the larval stages of *Paratya australiensis* collected from an estuarine site, JP, and from a riverine site in the Mt. Emu Ck, Panmure

	Estuary			River		
STAGE	mean±SD	range	N	mean±SD	range	N
a) Total length (mm)						
I	1.73±0.06	(1.62-1.84)	12	1.83±0.09	(1.65-2.00)	12
II	2.09±0.06	(1.98-2.15)	12	2.16±0.10	(1.99-2.35)	12
III	2.51±0.07	(2.41-2.63)	12	2.54±0.08	(2.35-2.63)	12
IV	2.88±0.13	(2.67-3.13)	12	2.86±0.14	(2.67-3.10)	12
V	3.20±0.11	(3.03-3.37)	12	3.26±0.16	(3.00-3.50)	12
VI	3.85±0.23	(3.55-4.21)	12	3.71±0.18	(3.53-4.05)	12
VII	4.34±0.24	(3.95-4.69)	12	4.00±0.13	(3.80-4.20)	12
VIII	5.06±0.24	(4.74-5.41)	12	4.39±0.15	(4.15-4.70)	12
b) Orbit-carapace length (mm)						
I	0.43±0.02	(0.38-0.46)	12	0.47±0.03	(0.41-0.52)	12
II	0.52±0.03	(0.48-0.56)	12	0.55±0.04	(0.48-0.61)	12
III	0.61±0.03	(0.57-0.66)	12	0.65±0.02	(0.61-0.68)	12
IV	0.71±0.03	(0.68-0.76)	12	0.74±0.04	(0.71-0.81)	12
V	0.79±0.04	(0.73-0.87)	12	0.87±0.06	(0.79-0.99)	12
VI	0.94±0.05	(0.87-1.00)	12	0.99±0.07	(0.91-1.11)	12
VII	1.07±0.08	(0.91-1.20)	12	1.11±0.04	(1.04-1.17)	12
VIII	1.25±0.06	(1.14-1.36)	12	1.21±0.05	(1.14-1.32)	12
c) Rostrum Length (mm)						
I	0.28±0.02	(0.25-0.32)	12	0.29±0.03	(0.25-0.35)	12
II	0.32±0.02	(0.29-0.35)	12	0.33±0.02	(0.29-0.35)	12
III	0.35±0.03	(0.30-0.41)	11	0.33±0.04	(0.28-0.41)	12
IV	0.39±0.02	(0.34-0.42)	12	0.35±0.03	(0.30-0.38)	11
V	0.40±0.03	(0.33-0.43)	12	0.39±0.04	(0.30-0.43)	12
VI	0.43±0.04	(0.38-0.49)	12	0.44±0.03	(0.41-0.51)	12
VII	0.48±0.04	(0.41-0.56)	12	0.50±0.05	(0.41-0.57)	12
VIII	0.61±0.04	(0.56-0.69)	12	0.55±0.05	(0.48-0.63)	11
d) Ratio of telson length:width (telson and abdominal segment fused in stages I and II)						
III	1.06±0.09	(0.93-1.17)	12	0.84±0.08	(0.71-1.00)	12
IV	1.45±0.06	(1.29-1.50)	11	1.48±0.21	(1.21-1.90)	12
V	1.89±0.28	(1.54-2.35)	11	2.18±0.40	(1.63-2.88)	12
VI	2.36±0.22	(2.15-2.78)	12	2.76±0.26	(2.20-3.13)	11
VII	2.59±0.27	(2.24-3.21)	12	2.90±0.24	(2.63-3.50)	12
VIII	3.16±0.14	(2.96-3.39)	12	2.98±0.23	(2.73-3.41)	12

groups of *P. australiensis* within the same catchment. The differences were constant across catchments with larger broods of smaller eggs being produced in estuaries. Size-specific reproductive output decreased at most sites from November to January. At upstream sites in the Curdies and the Hopkins, and in the Gellibrand estuary, which had the largest estuarine eggs in November, the drop in reproductive output from November to January resulted from a decrease in egg size. In both the Curdies and the Hopkins estuaries, egg size, which was small in November, did not change in January. At the Curdies estuary there was no drop in reproductive output. The drop in reproductive output at TS was a result of a drop in brood

Table 7.11. Variation in *Paratya australiensis*. (a) Analysis of variance of total length between eight larval stages from two locations (estuarine and riverine). (b) Analysis of variance of the ratio of telson length:width between six larval stages (III-VIII) from the two locations

	SOURCE OF VARIATION	df	SS	F-ratio	P
(a)	STAGE	7	19.093	1517.01	<0.001
	- (Linear regression)	1	18.967	10,549.15	<0.001
	- (Quadratic regression)	1	0.101	56.23	<0.001
	- (Cubic regression)	1	0.007	3.95	0.049
	LOCATION	1	0.016	8.78	0.003
	STAGE (S) × LOCATION (L)	7	0.180	14.30	<0.001
	- $S_{(Linear)} \times L$	1	0.154	85.75	<0.001
	- $S_{(Quadratic)} \times L$	1	0.014	7.80	0.006
	- $S_{(Cubic)} \times L$	1	0.008	4.45	0.036
	ERROR	176	0.316		
(b)	STAGE	5	21.917	392.78	<0.001
	- (Linear regression)	1	20.133	1,804.00	<0.001
	- (Quadratic regression)	1	1.719	154.05	<0.001
	- (Cubic regression)	1	0.046	4.14	0.044
	LOCATION	1	0.026	2.29	0.133
	STAGE (S) × LOCATION (L)	5	0.607	10.88	<0.001
	- $S_{(Linear)} \times L$	1	0.089	7.98	0.006
	- $S_{(Quadratic)} \times L$	1	0.517	46.33	<0.001
	- $S_{(Cubic)} \times L$	1	0.001	0.09	0.765
	ERROR	120	1.339		

size alone, and it should be noted no such drop in brood size was apparent in the Hopkins estuary proper at LG.

7.4.3.4. LARVAL SIZE

Morphometric measurements of larvae from estuarine and riverine environments are presented in Table 7.10. Total length of larvae varied significantly with both stage and location (Table 7.11a), but a significant interaction effect necessitated further partitioning of variation. The linear trends of total length against larval stage differed significantly between locations in both slope ($S_{Linear} \times$ E term) and shape ($S_{Quadratic} \times$ E term). Fig. 7.15a shows the increase in mean total length with larval stage in each location. Stages I and II larvae from the riverine environment were larger than those from the estuary, stages III-VI were of similar sizes in the two locations, and stages VII and VIII were larger in the estuary. Mean OCL measurements of stage I-VI estuarine larvae were smaller than those from corresponding stages in the riverine environment, while Stages VII and VII exhibited similar OCL ranges in both locations (Table 7.10b). These patterns indicate different relationships between OCL and total length in the two environments.

Table 7.12. Allelic frequencies at three loci in thirteen samples of *Paratya australiensis* from estuarine and upstream sites in the Hopkins, Curdies and Gellibrand rivers. N=number of shrimps sampled.

River	Section	Site	Date	*Pgm*				*Pgi*					*Mpi*						N
				A	B	C	D	A	B	C	D	E	A	B	C	D	E	F	
Hopkins	Estuary	TS	Nov	0.00	0.42	0.58	0.00	0.14	0.00	0.86	0.00	0.00	0.00	0.00	0.02	0.99	0.00	0.00	66
			Feb	0.00	0.51	0.49	0.00	0.13	0.00	0.86	0.00	0.01	0.00	0.01	0.06	0.92	0.01	0.00	49
	Upstream	Falls	Feb	0.00	0.39	0.61	0.00	0.18	0.01	0.82	0.00	0.00	0.00	0.01	0.09	0.89	0.01	0.00	60
		MH	Feb	0.00	0.34	0.66	0.01	0.16	0.01	0.83	0.00	0.00	0.00	0.01	0.09	0.89	0.02	0.00	61
		Panmure	Nov	0.01	0.36	0.62	0.01	0.15	0.00	0.85	0.00	0.00	0.00	0.00	0.08	0.92	0.00	0.00	62
			Feb	0.00	0.36	0.64	0.00	0.14	0.00	0.86	0.00	0.00	0.00	0.01	0.04	0.94	0.00	0.00	45
Curdies	Estuary	Curdievale	Nov	0.00	0.31	0.70	0.00	0.42	0.01	0.57	0.00	0.00	0.00	0.00	0.15	0.81	0.04	0.00	77
	Upstream	L. P'bete	Sep	0.00	0.10	0.90	0.00	0.16	0.00	0.84	0.00	0.00	0.01	0.01	0.02	0.97	0.00	0.00	61
Gellibrand	Estuary	Princetown	Nov	0.00	0.38	0.63	0.00	0.25	0.00	0.74	0.01	0.00	0.00	0.03	0.05	0.89	0.02	0.01	60
			Feb	0.00	0.43	0.57	0.01	0.28	0.00	0.72	0.00	0.00	0.00	0.03	0.05	0.89	0.03	0.00	61
	Upstream	River Rd	Nov	0.00	0.31	0.69	0.00	0.28	0.00	0.72	0.00	0.00	0.00	0.06	0.04	0.90	0.00	0.01	43
			Feb	0.00	0.43	0.57	0.00	0.27	0.01	0.71	0.01	0.00	0.00	0.03	0.05	0.92	0.01	0.00	66
		Kenn Ck	Feb	0.00	0.08	0.91	0.01	0.93	0.01	0.06	0.00	0.00	0.00	0.02	0.12	0.74	0.12	0.00	49

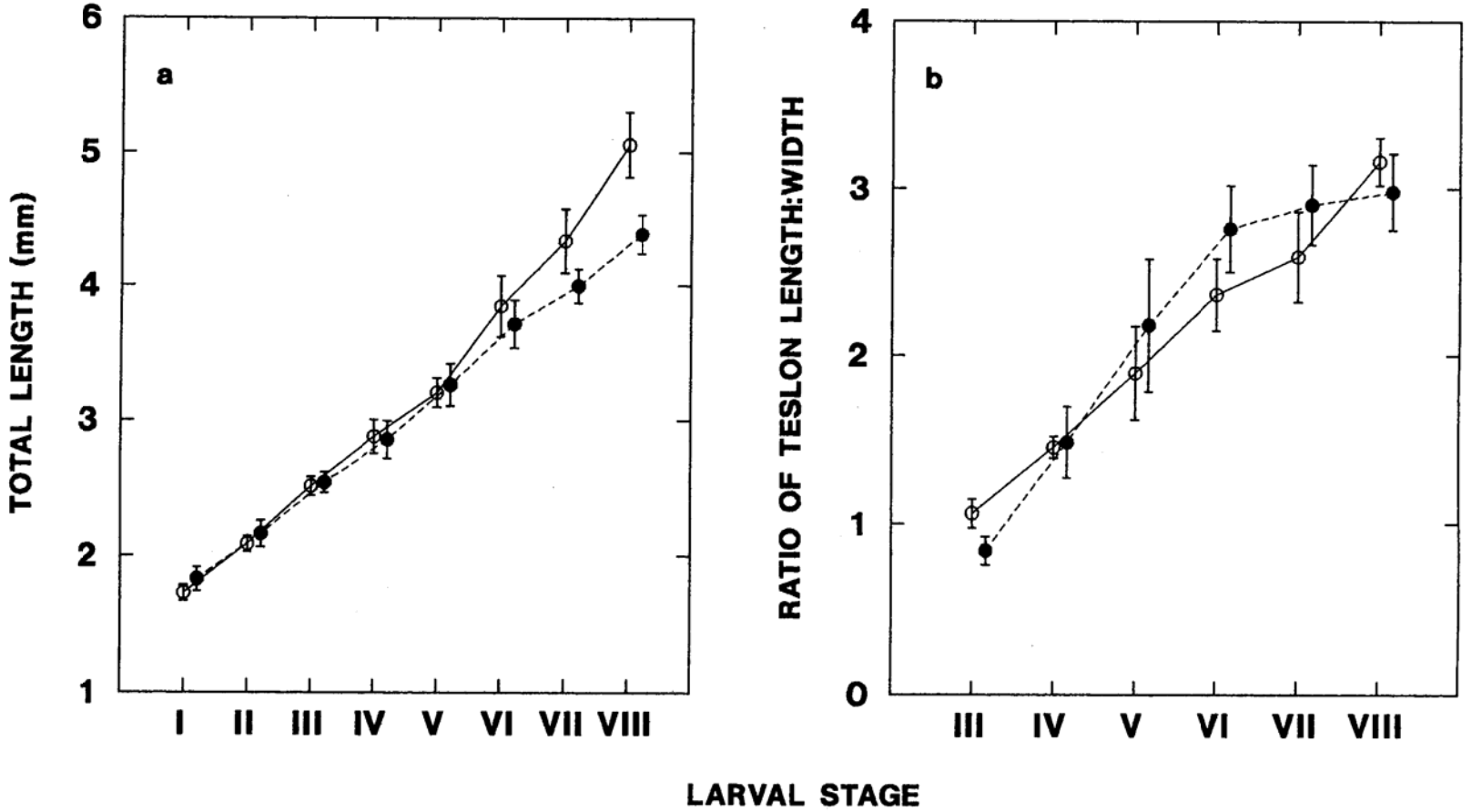


Fig. 7.15. Relationship between (a) mean (±sd) total length and (b) mean (±sd) ratio of telson length:width, and stage in larvae of *Paratya australiensis* from the Hopkins River estuary (open circles) and the Mt. Emu Creek, Panmure (closed circles)

Table 7.13. Summary of χ^2 tests for departure from Hardy-Weinberg expected proportions for each locus within 13 samples of *Paratya australiensis* as in Table 7.13.

Degrees of freedom = 1 in all cases.. - No test possible

River	Section	Site	Date	*Pgm*		*Pgi*		*Mpi*	
				χ^2	P	χ^2	P	χ^2	P
Hopkins	Estuary	TS	Nov	0.319	0.572	0.527	0.468	-	-
			Feb	0.506	0.477	1.361	0.243	0.387	0.534
	Upstream	Falls	Feb	0.426	0.514	0.768	0.381	0.156	0.693
		MH	Feb	0.486	0.486	0.526	0.468	0.061	0.804
		Panmure	Nov	0.348	0.555	0.806	0.369	1.307	0.253
			Feb	2.260	0.133	0.001	0.972	0.156	0.693
Curdies	Estuary	Curdievale	Nov	0.965	0.326	0.004	0.947	0.040	0.841
	Upstream	L. Purrumbete	Sep	0.162	0.687	0.085	0.771	0.070	0.791
Gellibrand	Estuary	Princetown	Nov	0.058	0.810	0.458	0.499	2.999	0.083
			Feb	0.621	0.431	0.028	0.867	1.025	0.311
	Upstream	River Rd	Nov	0.593	0.441	0.583	0.445	0.471	0.443
			Feb	3.433	0.064	0.101	0.750	0.733	0.392
		Kennedy's Ck	Feb	0.767	0.381	2.269	0.132	0.108	0.742

The shape of the telson also differed between locations (Fig. 7.15b, Table 7.10d). Most of the variation in the ratio of telson length: width between locations arises from the differing shape of the regression lines ($S_{Quadratic}$ × E term in Table 7.11b). In larvae collected from the estuary, this ratio closely resembled that of laboratory-reared larvae, with a near linear increase in the ratio with each larval stage. In larvae from the riverine environment, telsons were generally narrower in stages V-VII than those from the corresponding stages collected from the estuary. Stage V larvae collected from the riverine environment exhibited greater variation in this ratio. Some specimens exhibited a form of telson similar to the adult, while still exhibiting the pereiopodal and pleopodal characteristics of stage V larvae.

7.4.4. GENETIC VARIATION WITHIN AND BETWEEN CATCHMENTS

The allelic frequencies for each locus in the thirteen samples of *P. australiensis* are shown in Table 7.12. There were no significant departures from expectations under Hardy-Weinberg equilibrium conditions (Table 7.13). The genotypic distributions at TS and Panmure in the Hopkins River, and at Princetown and River Rd in the Gellibrand River did not differ significantly between November 1991 and February 1992 (Table 7.14a). With November and February samples pooled, there were no significant differences in allelic frequencies between any sites within the Hopkins River, or between the River Rd and Princetown samples in the Gellibrand River (Table 7.14b). These results suggest that, within each of these catchments,

Table 7.14. Summary of heterogeneity χ^2 tests of allelic frequencies of *Paratya australiensis* (a) between samples collected at the same location on two occasions (November 1991 and February 1992) and (b) within and between catchments. Significant differences are indicated by asterisk.

\- No test possible

			Pgm			*Pgi*			*Mpi*		
			χ^2	df	P	χ^2	df	P	χ^2	df	P
(a) Tests for temporal variation: November 1991 v February 1992											
River	Section	Site									
Hopkins	Estuary	TS	1.98	1	0.159	0.02	1	0.889	-		-
	Upstream	Panmure	0.51	1	0.474	0.03	1	0.859	0.53	1	0.465
Gellibrand	Estuary	Princetown	0.69	1	0.408	0.13	1	0.721	0.05	2	0.976
	Upstream	River Rd	3.28	1	0.070	0.02	1	0.889	0.11	1	0.737
(b) Tests for geographic variation: comparisons within and between catchments											
Comparison											
Between all Hopkins sites			5.21	3	0.157	1.74	3	0.627	7.10	3	0.069
Between Curdies sites			16.46	1	<0.001 *	22.82	1	<0.001 *	15.47	1	<0.001 *
Between all Gellibrand sites			34.10	2	<0.001 *	148.92	2	<0.001 *	18.11	4	0.001 *
Between Princetown and River Rd			0.23	1	0.634	0.14	1	0.705	0.32	2	0.854
Between the three estuaries			9.75	2	0.008 *	41.29	2	<0.001 *	29.55	4	0.001 *

P. australiensis does not separate into genetically discrete populations between these locations. However in the Gellibrand River catchment, the genotypic distribution of Kennedy's Creek population was significantly different from the other two sites further downstream (significant results in the comparisons between all Gellibrand sites in Table 7.14b). The uniqueness of the *P. australiensis* population at this site is apparent from the cluster analysis (Fig. 7.16), which shows the Kennedy's Creek sample to be the most genetically distinct of all sampled. In the Curdies River catchment, the genotypic distribution of the Lake Purrumbete population was significantly different from the Curdies estuary sample (Table 7.14b). No population large enough for sampling was found in the Curdies River between these two sites.

The small number of loci examined in this study means that any conclusions from this data must be treated as speculative and should only be used in association with the parallel life-history data for these populations. Of the three catchments studied, *P. australiensis* appears to be least reproductively separated into distinct populations in the Hopkins River, at least in the lower 50 km that were sampled. In the Gellibrand River there is no evidence of reproductive isolation between the estuary and the river at River Rd, 15 km upstream of the head of the estuary. However, the *P. australiensis* population of Kennedy's Creek, 8 km further upstream is surprisingly discrete. There appears to be no physical barrier separating this tributary from the Gellibrand River. Lake Purrumbete is connected to the Curdies River in most seasons, allowing

the potential for migration between the two. However the genetic data presented here suggests that the *P. australiensis* population in the Lake is distinct from the estuarine population.

7.4.5. POST-LARVAL MIGRATION IN THE HOPKINS RIVER

Salinity over the meadow at RF increased over the period of the first trial, from 18.0 (surface)-22.7 (bottom) on 3 January 1990, to 16.4 (surface)-24.2 (bottom) on 7 January, to 27.6 (surface to bottom) on 10 January, when the trial was aborted. No flow was detected at this site during ebb tides, and due to its peripheral position it is assumed that flow would only be detectable over this meadow under high discharge conditions. Over the six days of the first trial, 94.7% of all *P. australiensis* juveniles caught were in the trap facing downstream (Fig. 7.17). The difference in numbers between traps was greatest on the first day with 120 juveniles caught moving upstream, and only four moving downstream. The number caught moving upstream decreased markedly over the subsequent five days, while the number caught in the net facing upstream remained reasonably constant.

The second trial, from 19 December 1991 to 11 January 1992 at TS, spanned two spring tides, from just before a full moon to a week after a new moon (Fig. 7.18a). Variation in daily discharge during this period was not large: from a maximum of 92 ML on the 19 and 20 December to a minimum of 69 ML on the 30 December (Fig. 7.18b). Surface salinity over the *Ruppia* meadow at LG was ≤5 for most of this period, except between 27 December and 2 January, when it rose to a maximum of 18. Salinity at the deepest part of the meadow was more variable (Fig. 7.18d).

Over the period of the second trial, 8861 *P. australiensis* juveniles were caught, of which 88.3% were in the trap facing downstream (Fig.7.19). The numbers of juveniles caught were significantly different between the two traps every day, and the highly significant heterogeneity G-value (Table 7.15a) reflects the wide variation of numbers caught in the trap facing downstream in comparison to the smaller variation in numbers caught in its counterpart facing upstream. There was a distinct rise in the number of juveniles caught moving upstream from 23 December to 1 January, followed by a decline (Fig. 7.19). Two distinct peaks in juvenile numbers moving upstream on 28 December and 1 January coincided with rises in surface salinity over the *Ruppia* meadow at LG (Fig. 7.18c, d).

Six hundred and thirty seven *P. australiensis* with OCL >3.5 mm were collected during the second trial. Of these 77% were male in the trap facing upstream and 95% in the trap facing downstream. It should not be concluded from this data that males were more active or catchable than females, as these proportions are similar to the proportions of males in the population overall at TS from November 1988 to January 1989 (Fig. 4.7).

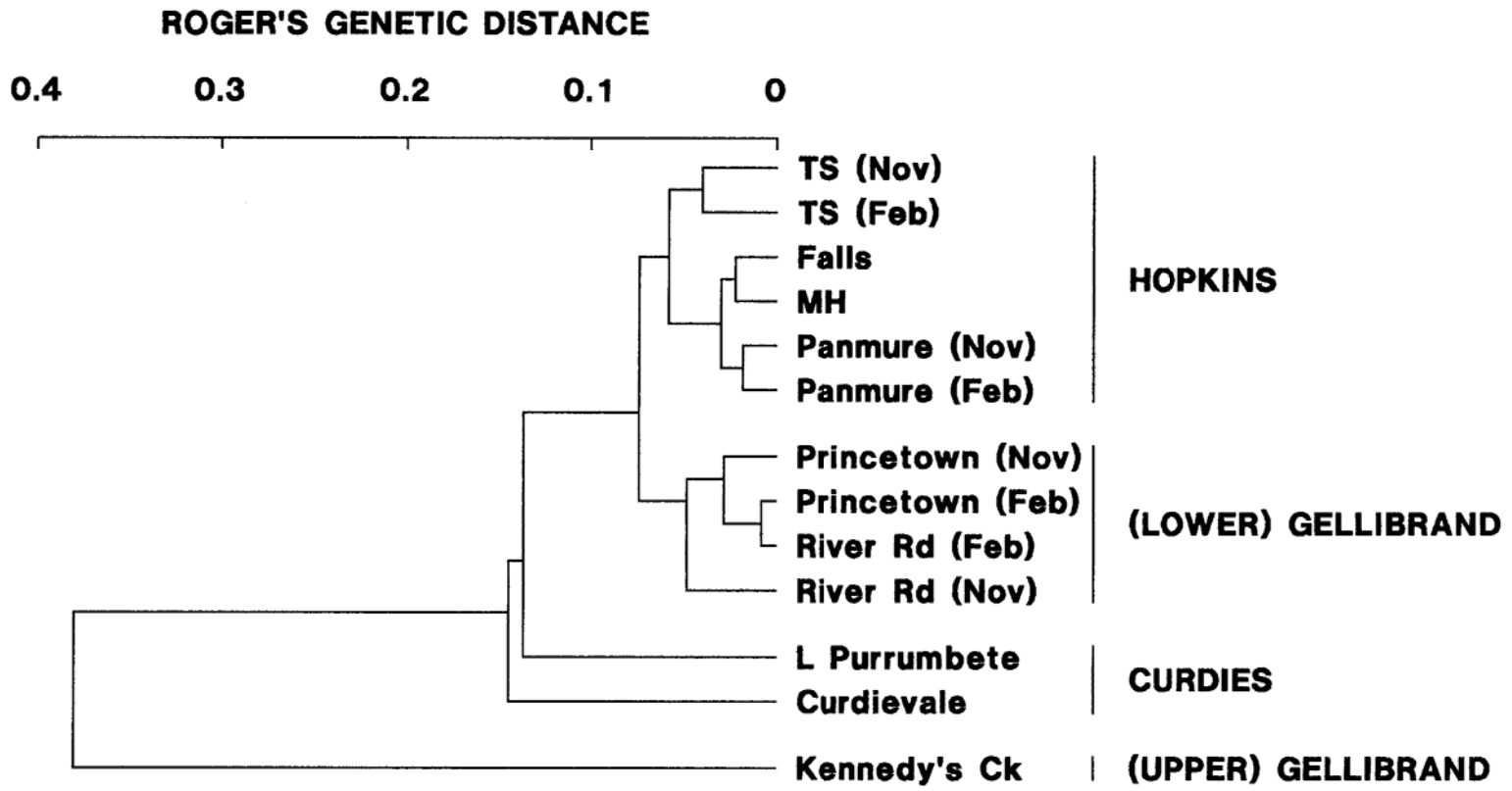


Fig. 7.16. UPGMA dendrogram illustrating genetic relatedness of thirteen samples of *Paratya australiensis* from three catchments

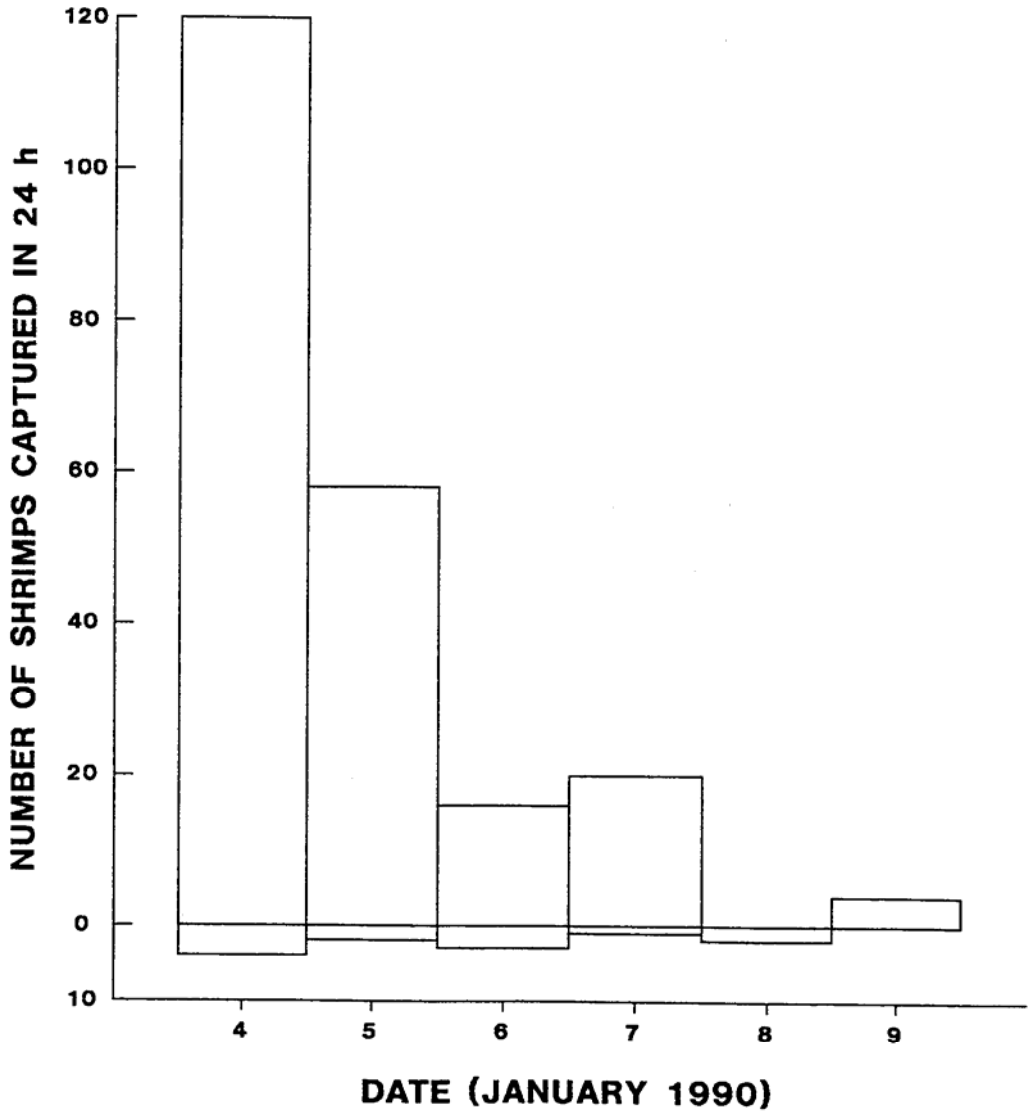


Fig. 7.17. Number of *Paratya australiensis* juveniles caught in each 24 h period in a pair of identical traps in a band of *Zostera* near RF, 3-9 January 1990. Bars above zero, trap facing downstream; bars below zero, trap facing upstream

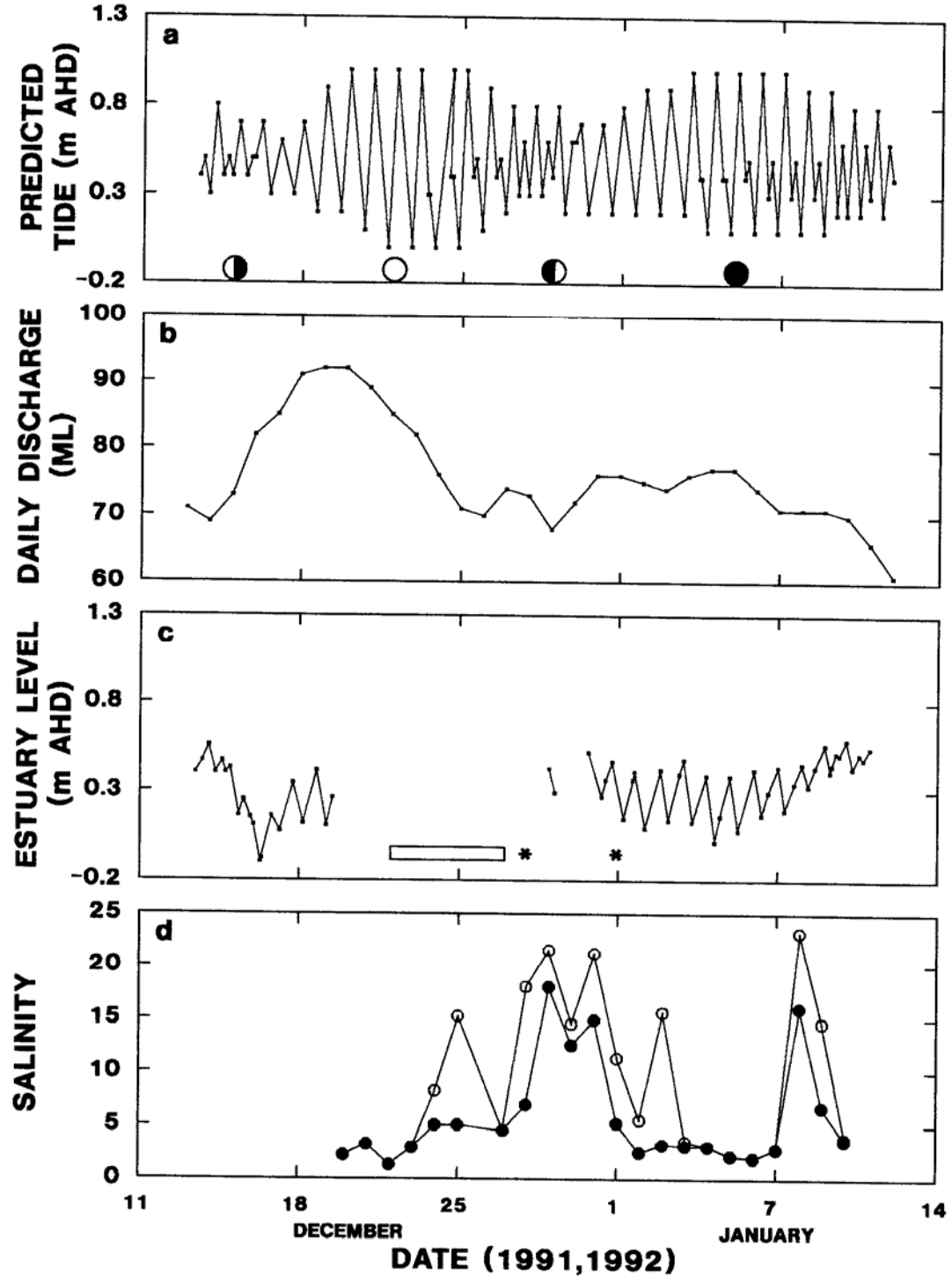


Fig. 7.18. Physico-chemical data for the Hopkins River from 12 December 1991 to 14 January 1992. (a) Predicted tides for Portland and phases of the moon (Department of Defence, Australia, 1991, 1992) (b) Daily discharge in ML at Hopkins Falls gauging station (Fig. 1.1); data from Rural Water Corporation, Victoria (c) Height of the Hopkins River estuary AHD at Deakin University. Bar indicates period of major nett downstream movement of ovigerous *Paratya australiensis* at TS, and asterisks indicate peaks in nett upstream movement of juveniles. (d) Surface (closed circles) and bottom salinity (open circles) in the *Ruppia* meadow at LG

Males were significantly more common in the trap facing downstream in all but five days, and variation in the relative numbers in each trap over the trial period resulted in a highly significant heterogeneity G-value (Table 7.15b). Peaks in numbers caught moving upstream were not as pronounced as for juveniles, but sustained large numbers of males were collected 24-27 December (Fig. 7.19).

Non-ovigerous females were significantly more numerous in the trap facing downstream from 20-23 December, but not at any other time during the sampling period. The pooled and total G-values were not significant (Table 7.15c). Thus there appeared to be no consistent behavioural preference or nett uni-directional movement by non-ovigerous females over the trial period. The significant heterogeneity G-value shows that the relative numbers caught in the two nets were variable (Fig. 7.19).

The small numbers of ovigerous females caught in the traps resulted in low power for any tests of differences between nets. However, the pooled numbers of ovigerous females collected in the trap facing upstream was significantly greater than that in the net facing downstream (Table 7.15d). This downstream movement was opposite in direction to that displayed by all the other groups of *P. australiensis* in this trial. Most movement downstream by ovigerous females was detected 23-27 December (Fig. 7.19), which coincided with the spring tides following the full moon (Fig. 7.18a, c).

Two species of fish with *P. australiensis* juveniles in their guts were collected in the traps. *P. australiensis* juveniles were found in the guts of three out of twenty-one tupongs (*Pseudaphritis urvillii*) >35 mm total length, but not in any smaller than 35 mm. Of twenty-eight big-headed gudgeons (*Philypnodon grandiceps*) >40 mm total length, 16 contained *P. australiensis* juveniles. In both species of fish, amphipods occurred more frequently than *P. australiensis*. A water rat (*Hydromys chrysogaster*) forced its way into one trap on 25 December 1991, and drowned. Its stomach contents were dominated by *P. australiensis*.

→

Fig. 7.19. Number of *Paratya australiensis* juveniles, males, non-ovigerous females (=females), and ovigerous females (=ovigerous) caught in each 24 h period in a pair of identical traps in a run at the upstream limit of TS from 19 December 1991 to 11 January 1992. Note differing scales. Bars above zero, trap facing downstream; bars below zero, trap facing upstream

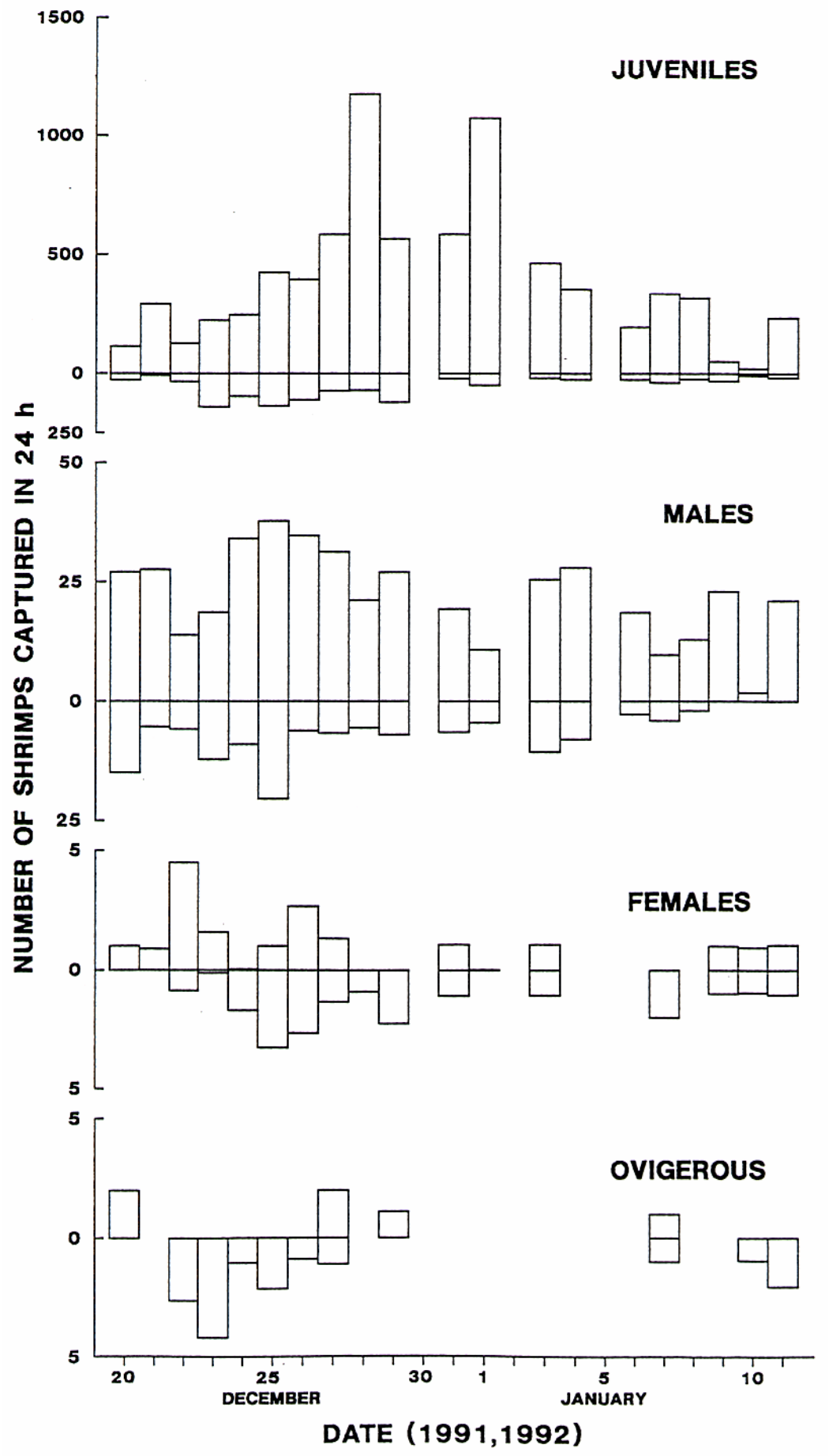

JUVENILES
MALES
FEMALES
OVIGEROUS
NUMBER OF SHRIMPS CAPTURED IN 24 h
1500
1000
500
0
250
50
25
0
25
5
0
5
5
0
5
20
25
30
1
5
10
DECEMBER
JANUARY
DATE (1991,1992)

Table 7.15. Numbers of *Paratya australiensis* juveniles, males, and ovigerous and non-ovigerous females caught daily in a pair of traps at TS, one facing upstream (up) and one facing downstream (down), from 20 December 1991 to 11 January 1992. Tests for differences in numbers between the two traps and for heterogeneity between days (or groups of days if pooling was necessary) are presented.

Date	Up	Down	df	G		Date	Up	Down	df	G	
(a) Juveniles						(b) Males					
20 Dec	27	114	1	57.75	*	20 Dec	15	27	1	3.48	
21 Dec	7	292	1	348.02	*	21 Dec	5	28	1	16.44	*
22 Dec	33	128	1	59.80	*	22 Dec	6	14	1	3.34	
23 Dec	139	225	1	20.41	*	23 Dec	12	19	1	1.37	
24 Dec	96	248	1	69.53	*	24 Dec	9	34	1	15.42	*
25 Dec	136	425	1	157.20	*	25 Dec	20	38	1	5.21	*
26 Dec	110	396	1	170.83	*	26 Dec	6	35	1	21.81	*
27 Dec	71	584	1	459.69	*	27 Dec	7	31	1	17.15	*
28 Dec	70	1177	1	1188.74	*	28 Dec	6	21	1	9.82	*
29 Dec	120	566	1	315.54	*	29 Dec	7	27	1	12.49	*
31 Dec	22	585	1	654.08	*	31 Dec	6	19	1	6.77	*
1 Jan	48	1077	1	1161.80	*	1 Jan	5	11	1	2.70	
3 Jan	18	465	1	515.23	*	3 Jan	11	26	1	6.34	*
4 Jan	24	356	1	347.76	*	4 Jan	8	28	1	11.77	*
6 Jan	25	196	1	151.19	*	6 Jan	3	19	1	13.50	*
7 Jan	38	337	1	273.96	*	7 Jan	4	10	1	2.38	
8 Jan	22	317	1	307.08	*	8-11 Jan	2	59	1	66.96	*
9 Jan	31	51	1	4.93	*						
10 Jan	9	22	1	6.02	*						
11 Jan	17	236	1	224.49	*						
	Pooled		1	5783.59	*				1	38.04	*
	Heterogeneity		19	710.45	*				16	178.90	*
	Total		20	6494.05	*				17	216.94	*
(c) Non-ovigerous females						(d) Ovigerous females					
20-23 Dec	1	8	1	6.15	*	20-23 Dec	7	2	1	2.78	
24-26 Dec	8	4	1	1.40		24-26 Dec	5	2	1	1.46	
27 Dec-3 Jan	7	3	1	1.02		27 Dec-11Jan	4	2	1	0.61	
4-11 Jan	5	3	1	0.51							
	Pooled		1	0.12					1	4.61	*
	Heterogeneity		3	8.95	*				2	0.24	
	Total		4	9.07					3	4.85	

7.5. DISCUSSION

7.5.1. *P. AUSTRALIENSIS* IN SOUTHERN AUSTRALIAN ESTUARIES

Two attributes of the estuaries sampled were important in determining the abundance of *P. australiensis*: their hydrodynamics for larval retention, and the presence of submerged leafy macrophytes as adult habitat.

Hydrodynamics

Larvae were most abundant in open estuaries with stable salt wedges, and least abundant in estuaries with little tidal exchange or little freshwater input and stratification. The three South Australian streams with stable estuaries (Bungala, Inman, and Hindmarsh), but which did not support any *P. australiensis*, all had extensive sandbars blocking their mouths in December 1990. They were all weakly stratified and predominantly highly saline. With such little fresh inflow, any *P. australiensis* in these systems would have been able to recruit to freshwater pools upstream, without danger of being washed downstream. The Anglesea River, a similar estuary in Victoria with little fresh inflow, also contained no larvae, although a small number of juveniles were collected.

In contrast, all but one of the estuaries sampled with a stable, well-developed salt wedge supported *P. australiensis* larvae. The one exception was the Glenelg, the largest estuary sampled. This long, steep-sided estuary was sampled at a site 45 km upstream of the mouth, where the halocline was 1.5 m deep in a total depth of 5 m. It is likely the head of the wedge was a further 25 km upstream, and it is possible that larvae would have been found nearer this site. The other unusual characteristic of this estuary was its littoral vegetation, which is considered below.

The differences in age structure in larvae from different estuaries (Table 7.4) suggest differing times of larval retention in the salt wedge. The Hopkins and the Fitzroy supported the oldest larval populations suggesting larvae were retained earlier there than in the Gellibrand and the Aire, which were dominated by stage I larvae. In this latter pair of rivers, the high densities of stage I larvae suggest that large numbers of larvae had only recently been retained at the site sampled.

Variation in larval age structure along the Hopkins River estuary was shown in Chapter 6, with older larvae occurring closer to the estuary mouth. This pattern of age structure was associated with the gradual intrusion of the salt wedge. Because an attempt was made in this survey to sample all estuaries from a similar part of the salt wedge (where the halocline was 1-2 m below the surface), it is likely that differences observed between estuaries are due to differences in recruitment patterns between estuaries rather than differences in the portion of the estuary sampled. Thus the tendency to find older larvae in estuaries further west of Cape Otway is

likely to be due to a trend of earlier intrusion of salt wedges in the west. Such a possibility is supported by the trend to more annually variable discharge distributions in the west (Fig. 7.2). The annual decline from peak discharge in August and September to low flows from December onwards becomes less pronounced when moving from the Fitzroy and the Hopkins to the streams of the Otway Ranges.

All estuaries in which larvae were found abundantly, except the Gellibrand, supported large numbers of juveniles in fringing vegetation (Table 7.5). The lack of later stage larvae in the Gellibrand, suggesting a later recruitment, may explain the lack of juveniles in the fringing vegetation of this estuary. Even rivers with small or less stable estuaries (e.g. Skenes Ck, Kennett, Erskine and Anglesea rivers) showed evidence of some recruitment of juveniles to their estuaries, although abundances of juveniles were generally lower than in the better developed estuaries.

The presence of macrophytes

The presence of fringing, grassy macrophytes was an attribute common to all estuaries that supported large numbers of adult and/or juvenile *P. australiensis*. Adults and juveniles were most common in *Zostera*, *Potamogeton crispus*, *Triglochin procera* and inundated terrestrial grasses. They occurred less commonly and less abundantly in *Phragmites australis*, which tended to present less submerged surface area.

Adults were most common in low salinities. None were present in *Phragmites* in salinities higher than 2, and while not present in *Zostera* at salinities around 30 in the Painkalac and Anglesea estuaries, adults were abundant among *Zostera* in the Surrey estuary in salinity of 17-28. Juveniles were more commonly present in *Phragmites* and in higher salinities than adults. The presence of juveniles in higher salinities is consistent with results from the Hopkins River surveys, in which *P. australiensis* juveniles persisted through rises in salinity at JP after all adults had gone from the estuary.

No juveniles were collected in the Glenelg River estuary. Because of the steep-sided nature of this estuary, there are very few stands of seagrass, and very little fringing vegetation apt to be inundated, other than *Phragmites*. A single adult *P. australiensis* was collected from one of the common stands of *Phragmites*. It is possible that the large size of the estuary, in concert with the very limited growth of fringing vegetation results in very low densities.

While no vegetation type was identified as the preferred juvenile or adult habitat, estuaries supporting large stands of vegetation supported greater numbers of adults and juveniles. Williams (1977) reported that *P. australiensis* was found in vegetation more frequently than elsewhere. Walker (1972) found *P. australiensis* commonly in a variety of submerged and emergent macrophytes, but less commonly on rocky substrates and amongst leaf litter. Of the macrophytes, he found it to occur less commonly in *Triglochin procera*, and not at all amongst

Phragmites australis or *Spirogyra*. In the current study *P. australiensis* was found in both *T. procera* and *Phragmites*, and amongst mats of filamentous green algae at Tooram Stones. Morris (1991) also found *P. australiensis* to occur in a wide range of microhabitats in the river Murray, including macrophytes (most commonly *Phragmites*), riparian tree roots, snags, and even bare river banks. It was most common in the main river channel and in anabranch channels, while less common (relative to *Caridina mccullochi*) in floodplains and the lentic environments of weir pools. In all these studies in southern Australia, *P. australiensis* exhibited a marked preference for vegetated rather than unvegetated sites, with very few individuals being caught from bare rocks (Morris, 1991), and none in high gradient rocky streams (Walker, 1972). However it occurs commonly in the high gradient streams of southern Queensland, in rocky substrates with no vegetation other than filamentous algae (M. Hancock, Griffith University, personal communication).

Walker (1972) found the foliose *Myriophyllum elatinoides* to be the preferred juvenile habitat in running waters, but not in a lentic environment, where juveniles occurred in all available vegetation types. He suggested the preference for *M. elatinoides* in running water permitted avoidance of current. In this study, greatest juvenile densities collected from any site were from the *Ruppia* and *Zostera* meadows of estuaries.

Thus, in southern Australia at least, *P. australiensis* shows a preference for vegetated cover, but no clear preference for a particular vegetation type is evident across the range of rivers, lakes and estuaries in which it occurs. Within the Hopkins River estuary, *P. australiensis* occurred most commonly in the seagrass meadows, although it could also be found among *Phragmites* and *Juncus* sp.. Both adults and juveniles, on most occasions when they were abundant in 1988, showed positive correlations with seagrass biomass at JP (Chapter 3). However the importance of the amount and structure of seagrass in determining the abundance of *P. australiensis* in the Hopkins River estuary was diminished by the dominance of physical factors in the estuarine environment.

* * *

Within the estuaries sampled, salt wedge hydrodynamics was identified as an important determinant of larval abundance, as was the presence of littoral vegetation to juvenile and adult abundance. The occurrence of adults, juveniles and larvae in an estuary are closely linked, but the absence of adults from an estuary may not negate the presence of larvae or juveniles possibly as a result of a small level of recruitment from upstream of the estuary. Although this mode of recruitment to estuaries was shown in Chapter 6 to be less important than autochthonous recruitment, it is possible a small number of juveniles may be recruited by transport form upstream locations. The estuaries supporting only a small number of adults, juveniles or larvae were morphologically and hydrologically diverse. For instance no larvae, but a single adult, were collected from the large, stably stratified Glenelg, while the small,

tidally dynamic Bunyip contained a moderate number of larvae, but no adults. Neither estuary supported much littoral vegetation. It is therefore tenuous to attribute characteristics to estuaries in which only a small number of individuals were collected. However, estuaries with large numbers of adults, juveniles and larvae had certain unique attributes. All consisted of a deep channel with a stable salt wedge. All were fed by rivers with sufficient discharge to keep the mouth open for several months after peak discharge. And all were bordered by fringing, grassy weeds growing in a layer of low-salinity water. It is probable, given the expansive coastal distribution of *P. australiensis* (Fig. 1.2), that many Australian estuaries support large numbers of *P. australiensis* during at least part of the year.

It is surprising, in light of the widespread estuarine occurrence of *P. australiensis* reported here, that no significant penetration into estuaries has been reported previously. This work has shown the period in which *P. australiensis* are abundant in an estuary may be limited to two to three months after peak river discharge. However, a lower level of occurrence may occur all year round, as has been observed in the estuaries of the Hopkins River (this study) and the Barwon River (Sherwood et al., 1988). *P. australiensis* actively uses estuarine environments for recruitment, and each female may increase her fecundity by producing an early estuarine brood each year. It is understandable that Walker (1972), without this knowledge, interpreted the few individuals he found in estuarine locations as having been inadvertently washed downstream.

There is no evidence of *P. australiensis* using estuaries in south-eastern Queensland (Williams, 1977), and it may be that *P. australiensis* varies with latitude in its tendency to use estuaries. Such a latitudinal trend has been reported for fishes. Within fish species, there is often a tendency towards greater diadromy at high latitudes (McDowall, 1987).

7.5.2. DISTRIBUTION OF *P. AUSTRALIENSIS* WITHIN A RIVER SYSTEM, AND THE IMPORTANCE OF MIGRATION

P. australiensis occurred commonly in the Hopkins River as far upstream as Hexham (elevation 121 m), and was less commonly caught at Chatsworth (elevation 142 m). Richards (1990) reported consistent collection of *P. australiensis* at two sites upstream of Chatsworth (elevation ≈180 m and ≈200 m) in Bushy Creek, a tributary of the Hopkins, but no further upstream (Fig. 7.7). Mitchell and Richards (1991) suggested that decreases in macroinvertebrate species diversity in higher sites may be due to increased salinity levels.

The mean salinity of the main branch of Hopkins River is maximal in this area (salinity 6-7) and decreases further upstream (Mitchell and Richards, 1991). Recourse to salinity tolerance as an explanation of distributional limits of *P. australiensis* in waters of salinity <10 is suspect given the high reported salinity tolerance of this species (Walker, 1972; Williams, 1984; Morris, 1991; this study—Chapter 3) and its common occurrence in saline conditions in estuaries. Thus it

would appear unlikely that limits to salinity tolerance could explain the absence of *P. australiensis* upstream of the Chatsworth area in the main branch of the Hopkins River.

Other species of *Paratya* have been reported as lowland river dwellers (Carpenter, 1982; Shokita, 1979), and the distribution of *P. australiensis* in the Hopkins River fits such a description. However, its occurrence in the highland lakes of Tasmania (Walker, 1972) and the upland streams of southern Queensland (M. Hancock, Griffith University, personal communication) are at odds with this description. Walker (1972) proposed that *P. australiensis* may be limited in its upstream distribution by low temperatures and low ionic content of the highland streams of Tasmania, an unlikely explanation for the Hopkins River.

Rather than being due to physiological tolerances of the adult, the absence of *P. australiensis* from the upper reaches of the Hopkins River may be due to factors affecting the viability of the larval phase. In summer the upper Hopkins often dries to a series of pools with little flow between. The pools of the upper catchment may exhibit physical or chemical attributes unsuitable for larval development during periods of low flow, or predation may be a more important factor. The proportion of predators has been shown to increase in intermittent stream communities during periods of low flow (Closs and Lake, 1994). Such an increase in predation pressure could make the pools of the upper Hopkins River unsuitable larval habitat, even if adults could survive in these sections of the river during higher flow periods.

This study, which has concentrated primarily on the estuary, has revealed several lines of evidence suggesting at least limited migration between seagrass meadows of the estuary, and between the estuary and the lower river. The sudden appearance of large, ovigerous females in their second year, at JP in September 1988 (Fig. 4.3) and 1991 (Fig. 7.11) suggests migration from upstream locations, presumably to breed. Analysis of the sex ratios of the *P. australiensis* populations at TS and JP pointed to migration of females over a greater distance than the 2 km between TS and JP (see Section 4.3). The capture, near the upstream limit of TS, of more ovigerous females moving downstream than upstream supports the proposition of downstream migration to the estuary from above TS. The migration deduced from the traps was associated with spring tides in late December, two months after peak recruitment to the estuary. (Placement of traps in September, when most migration is assumed to occur was impracticable due to high flows.) However, low densities of early stage larvae were present in the estuary as late as April in 1989 (Fig. 6.5). Therefore migration of small numbers of ovigerous females on spring tides may be associated with this late low level of larval recruitment. Breeding migrations in association with spring tides is the only evidence gathered in this study of tidally timed peaks in larval release as reported for other carideans (Paula, 1989).

While ovigerous females were found to be the only category of *P. australiensis* with a tendency to migrate downstream during the trapping period, non-ovigerous females showed no overall

nett movement, although they did show significant nett upstream movement on a few days. These observations are consistent with behavioural studies on *Macrobrachium acanthurus*, a freshwater caridean requiring estuaries for larval development. Hughes and Richard (1973) found non-ovigerous females swam against a current in the laboratory, while ovigerous females swam almost exclusively in a downstream direction. Hughes and Richard (1973) pointed to the importance of downstream migration to allow release of larvae directly into the estuarine larval habitat. *P. australiensis* larvae were only present in the Hopkins River estuary in very small numbers in 1991, when lack of seagrass resulted in a lack of adult shrimps in the estuary (Chapter 6). This supports the proposition of the importance of larval release in the estuary for estuarine recruitment, rather than release upstream and subsequent wash downstream of larvae.

The hypothesis of migration of juveniles out of the estuary was also supported by trap results. Maximum migration tended to be associated with increases in salinity over the seagrass meadows of the upper estuary, rather than lunar cycles. Migration in response to changes in salinity is consistent with analyses of distributions within the estuary, which pointed to the importance of physical conditions in determining shrimp distributions. There is no evidence of mass migrations in *P. australiensis*, as has been observed in other carideans (e.g. Lee and Fielder, 1979), but rather a steady migration from the estuary over a period of at least a few weeks. These results, while indicating the importance of migration in determining shrimp distributions in the lower Hopkins River, do not provide an estimate of distances migrated.

Small scale migration of *P. australiensis* within upland streams of south-eastern Queensland, including up small waterfalls, has been observed (M. Hancock, Griffith University, personal communication), but populations of neighbouring small catchments tend to be genetically distinct (Kingston, 1993). In the Hopkins River, although preliminary electrophoretic analysis did not detect significant genetic divergence between sites, the similarity of November and February samples from each site (Fig. 7.16) suggests there was little mixing of shrimps between sites over the sampling period. The scale of migration in one breeding season may therefore be significantly less than the 36 km between Panmure and TS. Such temporal stability within sites is consistent with the results of Kingston (1993). Kingston's (1993) results of electrophoretic analyses pointed to the dominance of downstream gene flow in the upland streams of south-eastern Queensland. Clues to the relative importance of upstream and downstream gene flow within a catchment may be gleaned from consideration of the catchments in which populations have been identified as genetically distinct by electrophoretic analysis: the Curdies and Gellibrand rivers.

The Curdies River estuary population of *P. australiensis* was genetically divergent from the Lake Purrumbete population. Reproductive patterns in the Lake Purrumbete population were distinctive from other upstream populations. In Lake Purrumbete, there was a consistently high proportion of ovigerous females from August. Only estuarine populations bred in such high

proportions so early (Fig. 7.9). In this lentic environment, there was a much reduced danger of larvae being washed downstream during the August-September flood. The apparent reproductive isolation of the Lake Purrumbete population was despite the potential for migration from the lake into and from the Curdies River. This suggests that the vector by which population homogeneity was maintained within the Hopkins River catchment and the lower Gellibrand may have been larval transport downstream, rather than post-larval migration upstream. Such a conclusion is consistent with the work of Kingston (1993), which presented several lines of evidence pointing to the influence of downstream gene flow on the genetic structure of *P. australiensis* populations.

The population at Kennedy's Creek was distinctive. It was the most genetically distant population of all studied, despite being only 8 km upstream of the River Road population, which was not significantly different from the Gellibrand River estuary population. This population was not sampled until January, so the extent of its breeding season is unknown. It was dominated by large individuals, both males (up to 7.5 mm OCL) and females. Unlike all other populations sampled, in which ovigerous females as small as 5 mm OCL were found, no female <6 mm OCL was found to be ovigerous in Kennedy's Creek. While reproductive output was not significantly different from shrimps in the Gellibrand estuary, eggs in Kennedy's Creek were by far the largest found at any site (Fig. 7.13). Assuming a positive correlation between egg size and larval size (as has been shown in *Palaemon paucidens*: Mashiko, 198), the larger eggs of the Kennedy's Creek population suggest larvae of this populations were large and more competent to avoid downstream displacement, which may account for their apparent reproductive isolation. If their reproductive activity were restricted to the low flow period, from January to March, reproductive isolation would be more easily explained. This population has proved an oddity among the sites sampled. Further study of its population dynamics, larval ecology and morphology is required.

7.5.3. VARIATION IN REPRODUCTIVE TRAITS BETWEEN UPSTREAM AND ESTUARINE ENVIRONMENTS

Genetic control vs phenotypic plasticity

Electrophoretic analysis of *P. australiensis* populations in the upstream and estuarine sections of three catchments has revealed greater genetic divergence between catchments than within (with the exception of the Kennedy's Creek population). This pattern of genetic divergence is in contrast to the consistent phenotypic divergence between populations in upstream, freshwater environments and those in estuaries of the same river system. The effect of section (upstream or estuary) accounted for more variation in both egg size and brood size than the effect of river system. With exceptions to be discussed below, shrimps from estuarine locations carried larger broods of smaller eggs than shrimps of the same size from upstream sites in the same catchment, although the total egg mass in each brood was not significantly different. This consistent phenotypic variation between two environments within three genetically divergent populations suggests a phenotypically based reproductive trade-off between egg size and fecundity in response to environmental factors. However the genetic differentiation evident within the Gellibrand and Curdies catchments suggest there may be a genetic component to the observed phenotypic variation. Within each catchment, larger eggs and smaller broods may have been selected in upstream environments.

A similar pattern of complementary variation in egg size and brood size has been reported in the oriental river prawn *Macrobrachium nipponense*, which primarily inhabits coastal brackish waters of Japan (Mashiko, 1983a; 1990). Mashiko (1992) found variation in egg and brood size between populations within catchments to be largely due to genetic variation, noting that genetic control of egg size was stronger than of brood size.

However, two factors point to *P. australiensis* differing from *M. nipponense*, with phenotypic plasticity being a more important factor determining these reproductive traits than genetic variation. Firstly *M. nipponense*, unlike *P. australiensis*, is not found in lotic environments, and is restricted to lakes and estuaries (Kamita, 1970, cited in Mashiko, 1990). The potential for downstream displacement of larvae from upstream locations is therefore limited, increasing the probability of reproductive isolation of populations. The greater genetic divergence observed in *P. australiensis* between the upstream, lentic environment and the estuary of the Curdies River than between the upstream, lotic environment and the estuary of the Hopkins River supports this proposition. Secondly, within most locations, although no variation in the genetics of each population was observed over the breeding season from November to January, either brood size or egg size did vary significantly over this period. This suggests individual females are able to vary egg size and number in successive broods over a breeding season. Such seasonal variation in egg size over a breeding season has been observed in other multivoltine invertebrates, including terrestrial isopods (Brody and Lawlor, 1984) and marine amphipods (Skadsheim,

1984), while similar variation in egg size was observed between early and late breeding univoltine, intertidal isopods (Willows, 1987).

It is hypothesised that the genetic variation between catchments has arrived from genetic drift, while genetic differentiation between upstream and estuarine components of river systems is due to selection. Further, the differences observed in reproductive traits between the two components of each river is partly due to genetic differentiation, particularly in the Curdies and the Gellibrand, but also, each female exhibits considerable plasticity in the size and number of eggs, and mass of total egg matter in each brood. Breeding experiments as conducted by Mashiko (1992) are required to test these hypotheses.

Egg size and reproductive output

Clarke (1993b) pointed to the independent nature of variation in egg size and variation in overall reproductive investment. Overall investment is set by conditions experienced by the female during egg production, while egg size is most likely related to the conditions awaiting the newly hatched larva. Skadsheim (1984) found reproductive output of amphipods varied over a breeding season, with greater overall investment later in the season when food for adults was more available. Over the same period egg size decreased as food for larvae became more plentiful. Food availability for offspring was also concluded as the determinant of egg size in isopods (Brody and Lawlor, 1984; Willows, 1987)

The importance of egg size to the fitness of offspring has not been well studied in carideans. Mashiko (1985) showed larger eggs of *Palaemon paucidens* hatched into larger larvae, which were able to survive longer and develop further under starvation conditions. In this study, although the development of different sized eggs was not studied directly in the laboratory, early stage *P. australiensis* larvae collected from an upstream site of the Hopkins River, where eggs were larger, were shown to be larger than larvae collected from the estuary, where eggs tended to be smaller. Development of larvae at the two sites differed both in rate and morphological patterns (Fig. 7.15). The more rapid development of the adult telson form in upstream larvae may be in response to flow conditions, as this form of telson development was not observed in laboratory reared larvae from Lake Purrumbete (Chapter 5). The larger size of early stage larvae is likely to be in response to a lesser availability of food in the riverine environment than in the estuarine environment. Final stage larvae in the estuary were larger than their upstream counterparts. This may be due to faster growth or it may be due to a larger number of ecdyses until metamorphosis in the estuary. In either case, the evidence of larval growth to a larger size at metamorphosis is suggestive that the estuarine environment is superior for larval development. The tendency to smaller egg size in *P. australiensis* found in estuaries is therefore consistent with previously reported trends of smaller egg size in response to more favourable conditions for larval development.

Table 7.16. Summary of observed trends in egg size (volume), brood size (egg number), and reproductive output (RO = total brood volume) of *P. australiensis* from estuarine and upstream sections of three rivers (Curdies, Hopkins, and Gellibrand) in two months (November and January). Comparisons are based on analyses shown in Tables 7.6, 7.7, and 7.9. >, <, = indicate significantly greater than, significantly less than, and not significantly different, respectively.

COMPARISON			RIVER		
			Hopkins	Curdies	Gellibrand
	MONTH				
Estuary vs upstream	November	egg size	<	<	
		brood size	>	>	
		RO	=	=	
	January	egg size	=	=	<
		brood size	=	>	>
		RO	=	>	=
	SECTION				
November vs January	Upstream	egg size	>	>	
		brood size	=	=	
		RO	=	>	
	Estuary	egg size	=	=	>
		brood size	>	=	=
		RO	>	=	>

The decrease in reproductive output in three sites from November to January (Table 7.16) suggests a decline in habitat conditions for adults later in the breeding season, although there may be other explanations, as is discussed below for the Lake Purrumbete population. A decline in food availability or habitat conditions in or near estuarine environments is consistent with observations of the population biology of *P. australiensis* in the Hopkins River estuary (Chapters 2-4). A decrease in reproductive output could be a result of increased energy requirements for osmoregulation in increased salinity, or habitat loss due to competitive interactions.

The decrease in egg size in the Gellibrand River estuary suggests food availability for larvae was better later in the breeding season. Egg size did not decrease significantly in the Hopkins and Curdies estuaries between the two sampling occasions, which may indicate no change in habitat quality for larvae at these sites, but such a conclusion would suggest patterns of food availability in the Gellibrand estuary were different from these estuaries. An alternative explanation for the maintenance of egg size in the Curdies and Hopkins estuaries could be that eggs in these estuaries were near the minimum size possible for development in this species, allowing little latitude for decrease in size. Williams and Smith (1979) reported the smallest egg length from a wide collection of *P. australiensis* as 0.50 mm, while Walker (1972) found a

near-coastal population with eggs as small as 0.40 mm. In the Hopkins River estuary, the smallest egg found in a normal brood was 0.50 mm long (although an abnormal brood contained eggs as small as 0.42 mm long). So the eggs found in the Hopkins River estuary were close to the smallest found in any population, supporting the contention that these eggs were the minimum viable size, and hence females would be unable to further decrease investment per offspring at these estuarine sites, even if larval conditions did improve.

However, study of larval abundances in the Hopkins River estuary (Chapter 6) suggested the estuarine environment became less optimal for larval development as river discharge declined. If this were the case, *P. australiensis* might be expected to produce larger eggs in estuarine sites later in the breeding season. However, the decline in habitat quality may be less related to food availability than to predation or competition in the diverse zooplankton community.

Egg size and reproductive output were both constant at Lake Purrumbete from August until November, but were both significantly lower in January. Although this suggests poorer conditions for adults but improved conditions for larvae, it may be related to the small sizes of the females collected in January. A positive relationship between egg size and female size has been recorded in other carideans (Clarke, 1993b). No relationship between female OCL and egg size was detected in any preliminary analyses of egg size variation in the three rivers. However the size range of females in Lake Purrumbete in January was the smallest of all samples. All but three of the females in this sample had OCL less than 5.5 mm. These females were probably in their first year, breeding for the first time. It is possible there is some selective advantage in producing a smaller than maximal brood in the first year rather than waiting a further six months to breed in the next season. Lake Purrumbete was the only upstream site at which this early 0+ cohort was numerous, probably because this was the only upstream site at which a high proportion of females was breeding as early as August.

Trade-off between brood size and egg size

The preceding discussion presented evidence of female *P. australiensis* having the ability to vary egg size and total reproductive investment over a breeding season, and between environments. The complementary reduction in brood size and increase in egg size accompanied by no change in total brood volume between estuaries and upstream in November (Table 7.16) was suggestive of a trade-off between egg size and brood size. However, to prove a trade-off, a direct comparison of the two parameters is necessary. Willows (1987) used partial regression to remove the confounding effect of female size in each of two samples of two populations of the isopod *Ligia oceanica* and found a significant negative correlation between egg size and brood size in three out of four cases. Clarke (1993b) produced a similar result in single samples of three species of polar carideans. The samples used in the current study (Table 7.2) were small compared to the samples of Clarke (1993b) and Willows (1987), and the power of separate partial regressions for each sample was very low.

To achieve an analysis of adequate power, the ANOVAs for brood size (Table 7.6) were repeated using only broods with non-eyed eggs, to make a direct comparison with the ANOVAs for egg volume (Table 7.7) possible. The residuals from these analyses show variation in each parameter once the effects of OCL (in the case of brood size only), river, section, and month have been removed. The relationships between residuals from each brood-size analysis and those from the corresponding egg-size analysis were determined. A negative correlation between residual variation in egg size and that of brood size should indicate a trade-off.

The residuals of the first analysis (three-way ANOVA with two levels of river, two levels of section, and two levels of month: Tables 7.6a, 7.7a) were negatively correlated ($P<0.001$, $P=0.016$ with one outlier removed). This was not the case for the other two analyses ($P=0.043$, but $P=0.573$ with one outlier removed, for the analysis comparing estuaries of all three rivers in both months: Tables 7.6b, 7.7b. $P=0.488$ for the analysis of both sections of all three rivers in January only: Tables 7.6c, 7.7c).

Egg size was generally smaller in estuaries than upstream and smaller in January than November. A discussed earlier, egg size observed in estuaries is probably near the minimum viable size, allowing little latitude for variation in egg size in relation to brood size changes. This would explain why a significant trade-off was observed only amongst populations dominated by individuals with eggs larger than the minimum size. Such a result is consistent with the observations of Lawlor (1976), Willows (1987) and Clarke (1992, 1993b), and is further evidence of a widespread tendency to reproductive trade-offs amongst at least some groups of crustaceans.

* * *

Willows (1987) found variation in reproductive output of *Ligia oceanica* was consistently expressed as variation in egg number, with no effect on egg size. The current study has shown variation in reproductive output in *P. australiensis* may be due to variation in egg size, but in populations in which egg size is already small, variation in egg number may account for variation in reproductive output.

This study has found independent variation of investment per offspring (egg size) and reproductive output (total egg volume) in *P. australiensis*. This is consistent with a number of studies of reproductive allocation in Crustacea, which have attributed variation in investment per offspring to conditions awaiting the offspring and variation in reproductive output to conditions experienced by the adult during vitellogenesis.(Skadsheim ,1984; Willows, 1987; Clarke, 1993b). The observed variation in reproductive traits between locations and over the breeding period can be explained by a variation of the graphical model of the effect of changes in fecundity and mortality on egg size in amphipods developed by Skadsheim (1984) (Fig. 7.20). In the altered model, reproductive output and survival vary both seasonally and spatially.

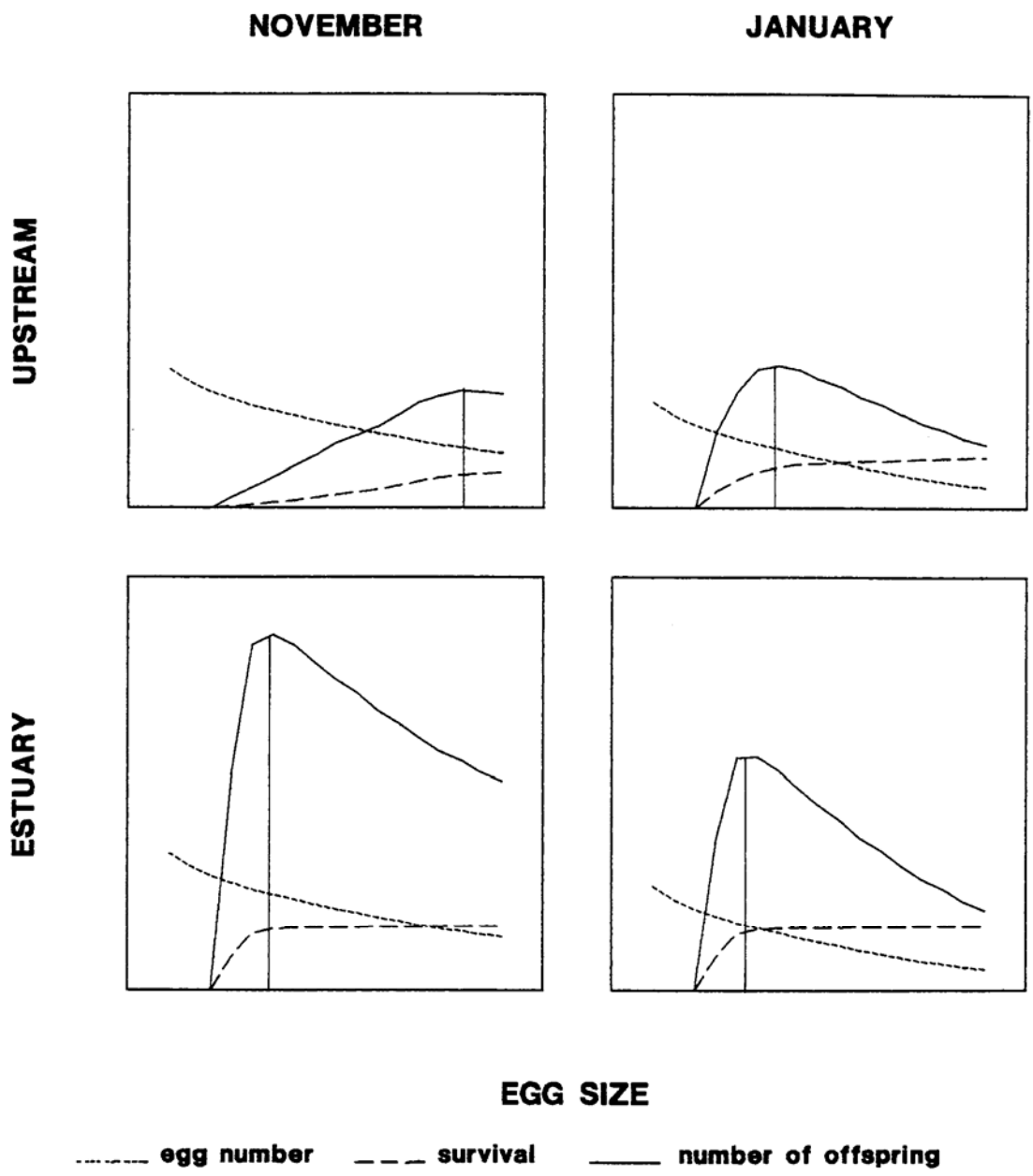


Fig. 7.20. A graphical model of the effect of changes in egg number and larval mortality on egg size (after Skadsheim, 1984). The Y-axis is an arbitrary indication of egg number and larval survival respectively. The number of offspring is derived by multiplying egg number by survival. The vertical line in each graph represents the evolutionary stable egg size, at which the number of surviving offspring is maximised.

As egg size increases, the model assumes the resulting larger offspring will be fitter, more able to develop with limited food availability, and more able to avoid downstream displacement. Such effects are likely to be less important in the estuarine environment, so larval survival will be greater and less dependent on size. Similarly it is assumed, because of reduced flows and increased productivity (resulting in more food for larvae) at upstream sites later in the season, larval survival will be greater and less dependent on size. Reproductive output decreases later in the breeding season, which reduces the optimal egg size at upstream location, but the effect on egg size is minimal in the estuary. Further study is required into the trophic ecology of *P. australiensis* to clarify the role of food availability (both larval and adult, in both estuarine and upstream locations) in determining reproductive allocation. Such work will test the validity of the assumptions of the model.

8. GENERAL DISSCUSSION

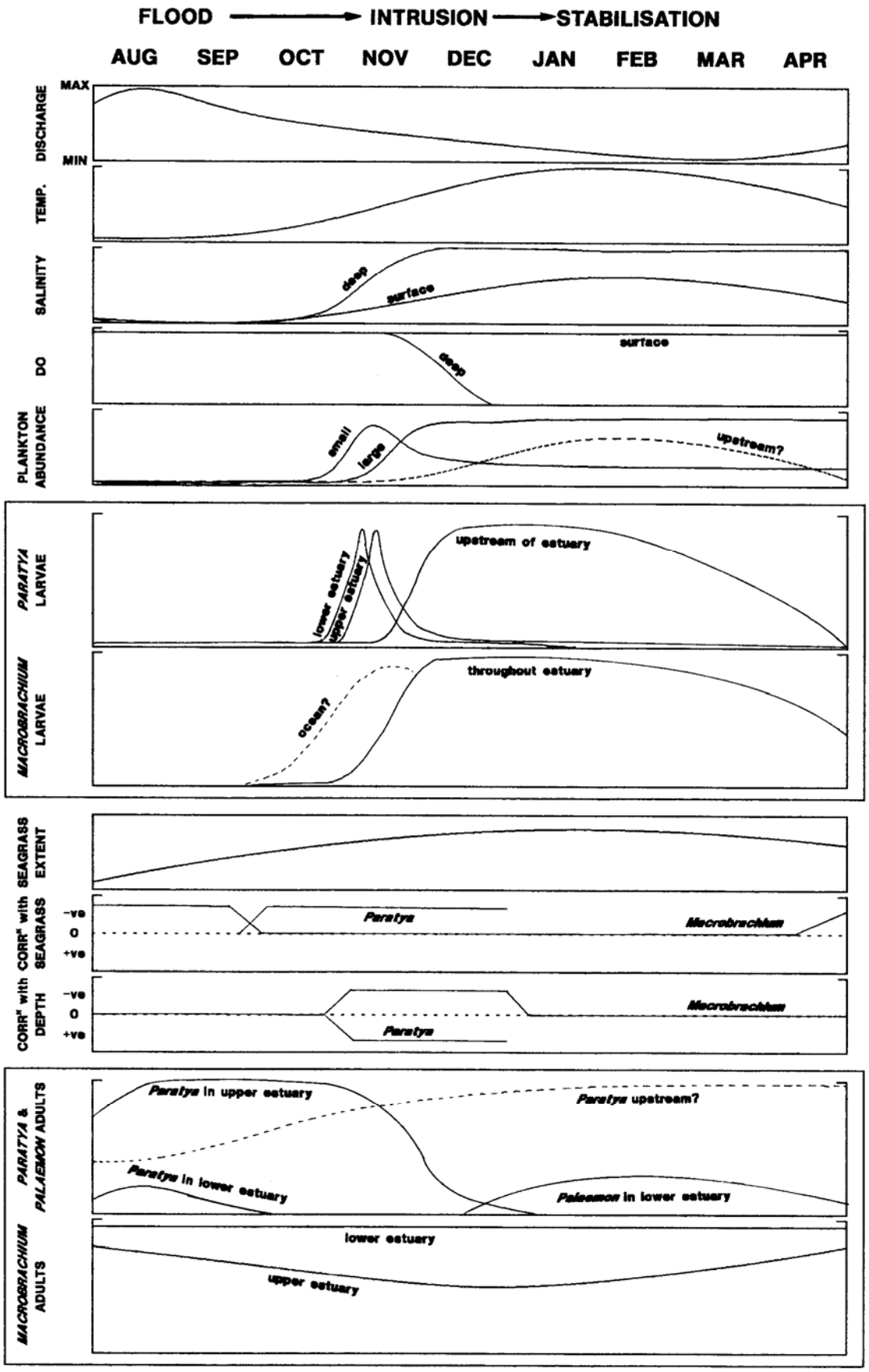
8.1. THE CARIDEAN ASSEMBLAGE OF THE HOPKINS RIVER ESTUARY: IMPLICATIONS FOR COMMUNITY ECOLOGY

This study is the first to investigate the biology of the freshwater atyid *Paratya australiensis* and the marine/estuarine palaemonid *Macrobrachium intermedium* occurring sympatrically in an estuary. *P. australiensis* has only been recorded anecdotally in estuaries prior to this study (Walker, 1972). An estuarine population *M. intermedium* in south-east Tasmania has been studied (Walker, 1979), where it occurred sympatrically with another palaemonid, an undescribed species of *Palaemon*, which showed a greater tendency to estuarine habit than *M. intermedium*. All other studies of *M. intermedium* have been in essentially marine seagrass meadows (Howard, 1981; Gray, 1985). Study of both species in the confined environment of the Hopkins River estuary has revealed aspects of the biology of each species not previously encountered in studies in other environments. *P. australiensis*, previously only studied in freshwater environments (Walker, 1972; Williams, 1977; M. Hancock, Griffith University, personal collection), has been shown to be far more plastic in its life history traits, well adapted to recruit, grow and reproduce in the estuarine environment. *M. intermedium* has been shown to be highly euryhaline, its larvae well adapted for development in the estuarine environment.

The season trends in distribution and abundance of larval and adult caridean shrimps in the Hopkins River estuary are summarised in Fig. 8.1. As has been stressed throughout this work, temporal heterogeneity in physico-chemical parameters, driven by the hydrological cycle, appears to be major determinant of large-scale changes in distributions in the three species. These influences are most obvious in the two least euryhaline species, which apparently migrate into and out of the estuary in association with changes in salinity and temperature. Limits of lower salinity tolerance probably ultimately drive *P. serenus* from the estuary during the food, and limits to upper salinity tolerance may drive *P. australiensis* from the estuary as low flow approaches. The cue for migration into the estuary for *P. australiensis* was likely to be peak discharge being reached. The cue for migration of *P. serenus* into the estuary after the intrusion of the salt wedge is less evident, and requires further investigation. The distribution and abundance of *M. intermedium* in the estuary did not vary widely over the year.

The importance of physico-chemical conditions in determining demographic and large-scale distribution patterns was a common theme of the study—not surprising in any estuary, the dynamics of which is so dominated by riverine input. Physico-chemical factors were less

Fig. 8.1 A systematic summary of seasonal trends in distribution and abundance of epibenthic caridean shrimps in the Hopkins River estuary, and the physical and biotic factors that are proposed as determinants of shrimp distribution and abundance. The period of most change in the dynamics of the estuary is included: from the total flushing of the estuary during the flood to intrusion and subsequent stabilization of the salt wedge. Physico-chemical conditions—discharge (and flow), temperature and salinity—play a dominant role in determining large-scale distributional patterns. Dissolved oxygen concentration (DO) in the salt wedge affects the depth distribution, and ultimately the abundance of larvae. Changes in larval abundance are associated with changes in the structure of the planktonic community: small plankters—copepod nauplii and rotifers—are the early colonizers of the salt wedge (Newton, 1994) associated with the occurrence of *P. australiensis* larvae, while larger plankters dominate later and are associated with the occurrence of *M. intermedium* larvae. Curves representing the abundance of plankton upstream of the estuary, the abundance of *P. australiensis* adults upstream of the estuary, and the abundance of *M. intermedium* larvae in adjacent costal waters are hypothesized. Within-meadow distributions of adult caridean shrimps are determined primarily by biotic interactions. The density of *M. intermedium* is correlated with seagrass biomass at times of minimum meadow extent. As salinities over meadows rise, and *P. australiensis* densities begin to decline, *M. intermedium* and *P. australiensis* show opposite correlations to depth within meadows. Competitive displacement of *P. australiensis* by *M. intermedium* from deeper parts of the meadow, where predation pressure is less intense is proposed.


FLOOD
INTRUSION
STABILISATION
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
DISCHARGE
MAX
MIN
TEMP.
SALINITY
deep
surface
DO
surface
deep
PLANKTON ABUNDANCE
small
large
upstream?
PARATYA LARVAE
lower estuary
upper estuary
upstream of estuary
MACROBRACHIUM LARVAE
throughout estuary
ocean?
SEAGRASS EXTENT
CORR" with SEAGRASS
-ve
0
+ve
Paratya
Macrobrachium
CORR" with DEPTH
-ve
0
+ve
Macrobrachium
Paratya
PARATYA & PALAEMON ADULTS
Paratya in upper estuary
Paratya upstream?
Paratya in lower estuary
Palaemon in lower estuary
MACROBRACHIUM ADULTS
lower estuary
upper estuary

important in determining within-site distributions. Biotic factors such as competition, vegetative complexity, and predation were identified as likely determinants of distributions within meadows, at particular times of the year. *M. intermedium* showed weak correlations with seagrass biomass at times when seagrass was at its least dense and least extensive. It also showed a preference for deeper sites in seagrass meadows in 1-2 months during the stabilization of the salt wedge (Fig. 8.1). It was hypothesized that this preference was a defence against shallow water predators. At the same time, *P. australiensis* was restricted to the shallow parts of the meadows, probably due to competitive exclusion by *M. intermedium* from the deeper parts. During this period of restriction to shallow water, *P. australiensis* showed a positive correlation to seagrass biomass.

Competition between the two species for position within a seagrass meadow was restricted to a month or two. It is possible the importance of the biotic interactions is kept in check by fluctuations in physico-chemical conditions. Such a situation would be consistent with the non-equilibrium, intermediate disturbance hypothesis (Connell, 1978), which aimed to explain observed diversity in a variety of environments. In such a scheme, competitive interactions between *M. intermedium* and *P. australiensis* have the potential to exclude *P. australiensis* from the seagrass meadows of the estuary, but the low salinity conditions during and after the flood increase physiological stress on *M. intermedium*, delaying reproduction in the most upstream meadows. Thus the annual disturbance of the flood permits *P. australiensis* to migrate to and persist in the estuarine seagrass meadows in association with *M. intermedium*.

Both species are evidently generalists in their tolerance to board ranges of physical conditions, and this attribute has a bearing on the diversity of caridean assemblages. The assemblage of three epifaunal caridean species of the Hopkins River estuary has comparable diversity to the two estuarine species studied (Walker, 1979), and the assemblage of four species in Western Port (Howard, 1981). In contrast many more epifaunal caridean species are found in tropical seagrass meadows (e.g. Bauer, 1985; Mellors and Marsh, 1993). A trend to greater diversity from temperate to tropical regions has commonly been reported and, while many theories have been advised to explain this trend, it is often ascribed to a greater variety of niches in tropical environments (e.g. Ricklefs, 1990). A comparison of the caridean assemblage of the Hopkins River estuary with those of south-eastern Tasmanian estuaries (Walker, 1979) and of Western Port (Howard, 1981) can show possible processes that may determine species composition. An animal living in the highly variable estuarine environment must be euryhaline to survive. Ability to survive in a wide range of physical conditions
would be strongly selected. Similarly, the unpredictability of temperature environments probably selects for generalist species able to survive or emigrate during periods of sub-

optimal conditions. In contrast the greater predictability of tropical environments permits greater specialization leading to a greater diversity. Thus *Palaemon serenus* may not be able to survive in estuarine environments as far south as those of Walker's (1979) study, and *P. australiensis* may not be able to utilize estuaries there as successfully, leaving only the more euryhaline *M. intermedium* and *Palaemon* sp. to be common inhabitants of Tasmanian estuaries. The more predictable marine environment of Western Port supports three species, which are presumably less euryhaline, in addition to *M. intermedium*. This conjecture points to the importance of niche breadth (degree of specialization) in varying the number of available niches with predictability of environment (Ricklefs, 1990).

Partly because of the differing optimal conditions for the three caridean species, overlap in reproductive activity, larval occurrences are recruitment was minimized. *P australiensis* larvae occurred in large numbers in the estuary soon after the intrusion of the salt wedge, but their peak had passed before the peak of *M. intermedium*. Patterns of juvenile recruitment were similar. Similarly ovigerous *P. australiensis* disappeared from the estuary as *M. intermedium* reached peak reproductive activity.

Physical factors have not been found to be important in other studies of *M. intermedium* in more marine seagrass meadows (Howard, 1981; Gray 1985). Howard (1981) found predation to be an important modifier of population structure in *M. intermedium* in Western Port, although not a determinant of structure of the Western Port caridean assemblage. Nor did he find competition to strongly influence the organization of the assemblage. The importance of predation in Western Port is of interest because the resource hypothesized as being competed for in the present study is predator-free space in the form of deeper water. Howard (1981) and Howard and Lowe (1984) found predation by water birds to be significant on large shrimps, particularly large females, and the situation is likely to be similar in the Hopkins River estuary, which supports a similar assemblage of water birds. This is in
contrast to the bare sand and mud banks of Chesapeake Bay, USA, once covered in seagrass. In this unvegetated environment, larger fish and crustaceans were identified as the important predators of smaller fish and crustaceans including the carideans *Palaemonetes pugio* and *Crangon septemspinosa*, which tended to use shallow water as refuge from fish predation (Ruiz et al., 1993). Study of the tropic ecology of the seagrass meadows of the Hopkins River estuary would elucidate the importance of predation as a population regulating mechanism in epifaunal carideans, and the relative importance of fish and water birds as predators.

Peak larval densities of *P. australiensis* were recorded in all locations only after a layer of water, in which there was no flow developed at this site. In the estuary, the period of larval retention coincided with the peak occurrence of small plankters such as copepod nauplii and

rotifers (Newton, 1994). The peak in the larval occurrence of *M. intermedium* 1-2 months later was not associated with changes in flow conditions, but was associated with the maximum occurrence of larger plankters (Fig. 8.1). These patterns of larval occurrence may be determined as much by food availability as physical factors. The importance of food availability to larvae and to adults is of concern in consideration of life history patterns, and is considered further in the next section.

Hydrological conditions had a strong influence on larval distributions and therefore recruitment, but physical conditions in the estuary also played a strong part in post-larval migrations. These migrations were also important in determining the structure of the caridean assemblages of the seagrass meadows. Migration is evidently an important determinant of the distribution of all post-larval stages. *P. australiensis*, not only within the estuary, but within catchments. Migrations upstream appear to be in response to rising salinity conditions in the estuary, although no mass migrations, as observed in other caridean species (e.g. Lee and Fielder, 1979), have been detected. Migrations downstream to release larval are probably primarily triggered by changes in the hydrological cycle, although some evidence has been presented of migrations in response to lunar/tidal cycles which may enhance larval retention and minimize predation due to swamping. Migration was less evident in *M. intermedium*, but at least some migration between meadows occurred. The population of *M. intermedium* in the estuary is therefore probably reasonably contained. Larval loss from the estuary is probably minimal due to the timing of larval development to coincide with low flow and possibly a closed estuary. Possible migration into the estuary of juvenile *M. intermedium* that recruited to nearby costal waters was also indicated.

The importance of migration in determining popular structure in these epifaunal caridean shrimps brings into question the model of Bell and Westoby (1986c) constructed to account for variability in abundance of decapods and fish in marine seagrass meadows. Central to their model, which placed large importance on setting patterns of larvae, was the condition that individuals do not leave seagrass meadow once they have settled. This has proved not to be the case for carideans of the Hopkins River estuary, the distributions of which are determined largely by physico-chemical conditions, meditated by high levels of post-larval migration. While adding to Sogard's (1989) evidence of diminished importance of direct recruitment from the larval phase, the present study does not, however, shed light on alternative determinants of epifaunal distributions in meadows such as Bell and Westoby's (1986c), which showed comparatively little seasonal variation in physico-chemical parameters. It is possible that predation pressure may be more intense around the meadows studied by Bell and Westoby (1986c), reducing the chance of migrants surviving forays between meadows. The present study has shown the greatest levels of migration—in *P. australiensis* juveniles—were apparently in response to physico-chemical extremes. It is therefore possible that, in the more marine meadows studied by Bell and Westoby (1986c),

migration between meadows may be less important in the absence of such physico-chemical extremes.

In summary, wide seasonal variation in physico-chemical factors appears to be the dominant determinant of large-scale patterns of distribution and abundance in the three caridean species of the Hopkins River estuary. The influences of physical factors is greater than has been reported for caridean assemblage in other locations. Consequently, migration in response to hydrological changes has been identified as important. Within seagrass meadows, vegetative complexity and interspecific competition appear to play a part in determining the distribution of each species for parts of the year. These biotic determinants of within-meadow distribution suggest the underlying importance of predation as a population regulating mechanism.

8.2. LIFE HISTORY OF *P. AUSTRALENSIS*: BIOGEOGRAPHICAL IMPLICATIONS

The phenotypic plasticity of *P. australiensis* apparent in this study affords the potential for production of an extra brood in years with a 'normal' hydrological pattern, in which the winter/spring flood is sufficient to flush the salt wedge from the estuary, followed by a decline until flow is minimal in upstream pools with no summer spates. In years in which the estuary is not flushed as occurred in 1982 and 1985 (Newton, 1994), and in years in which seagrass growth fails as occurred in 1991/1992, the potential for recruitment to the estuary will be reduced greatly. In summers in which discharge is high enough to flush upstream pools, recruitment to the river will be reduced greatly. The ability of *P. australiensis* to reproduce
in either environment is highly advantageous for an organism inhabiting an unpredictable environment. A similar strategy has been reported in Australian stream insects, in which short and long generation times of cohorts are alternated, allowing them to survive occasional years of drought (Bunn, 1988). Phenotypic plasticity may be more prevalent in stream biota of Australia than elsewhere because Australian rivers, on average, exhibit the most variable flow regimes in the world (McMahon, 1986).

Production of *P. australiensis* larvae during floods was recorded in the present study, with small numbers of first stage of larvae being collected in the estuary from August. In the laboratory, larvae were able to survive for up to eleven days in seawater. On the basis of these two observations it is possible that a very small number of larvae may be able to survive in coastal waters during flood periods long enough to be transported to another estuary. Genetic differences between populations in the three catchments studied in Chapter 7 suggest any gene flow between catchments must be at a low level. However, the lack of differentiation of *P. australiensis* along the entire Australian coastline, and a remarkable

genetic similarity between Victoria and Queensland populations (J. Hughes, Griffith University, personal communication), suggest either very little genetic drift or appreciable gene flow between catchments.

Some evidence of the spread of *P. australiensis* by oceanic means arises from its occurrence in the small coastal streams east of Cape Otway (Fig. 7.5, Tables 7.4, 7.5). In these streams, the only fish species present are those with a marine phase in their life cycles, which could have colonized from the sea (Koehn and O'Connor, 1990). These authors proposed that these streams may not have existed during the last glacial epoch, 18,000 to 15,000 years BP, when the sea bed of what is now Bass Straight formed a land link between Tasmania and mainland Australia (Bowler and Hamada, 1971). Koehn and O'Connor (1990) further proposed that any fish inhabiting these streams prior to 770 BP would have been unlikely to survive the period of reduced rainfall or increased temperature and evaporation around that time (Bowler and Hamada, 1990), when these small coastal streams were likely to be intermittent and susceptible to drought. In contrast, four fish species that spent their entire life-cycle in freshwater inhabit the larger rivers of the Gellibrand, Aire and Barwon, which would not have been affected by the land bridge and less affected by arid conditions (Koehn and O'Connor, 1990). The absence of *P. australiensis* from intermittent streams and temporary waters (Williams, 1977) suggests it, too, would have been unlikely to survive the arid conditions of 770 BP in these small coastal streams. Its occurrence in all of theses streams suggest its dispersal between rivers, like the fish fauna, was by the sea. Williams (quoted in Boulton and Knott, 1984) suggested the spread of *P. australiensis* west of Adelaide has been prevented by the desert barrier of the Nullarbor Plain. The findings of the present study, which suggest dispersal between rivers would only be possible over short distances, support this proposal.

The distribution of the genus *Paratya* forms a disjunct arc along the western rim of the Pacific (Fig. 1.2). In all but one of the regions in which it occurs, it is represented by a single species. The exception is New Caledonia, where four species occur. New Caledonia, New Zealand, and Norfolk, Lord Howe and Chatham islands have been separated from each other and from Australia by large tracts of ocean for the last 82 million years (Cooper and Millener, 1993). It is possible that, before that time, an ancestral *Paratya* inhabited the rivers of the rift region between the Australian portion of Gondwana and the New Zealand region, which connected New Zealand, New Caledonia, and Norfolk and Lord Howe islands.

If the evolution of *Paratya* followed a similar pattern of that inferred for bird and ant faunas on islands (the taxon cycle of Ricklefs and Cox, 1972), the diverse group of more specialized *Paratya* species on New Caledonia (Holthuis, 1970) are likely to be derived from an older invasion event than the species of other locations. The ecology of only three species, *P. australiensis*, *P. curvirostris*, and *P. compressa*, has been studied in detail. Of these, the

Australian *P. australiensis*, and the Japanese *P. compressa* inhabit a wide range of environments, from lowland rivers and estuaries to landlocked fresh waters (Williams, 1977; Shokita, 1979). In the taxon cycle, recently invading species tend to inhabit variable marginal habits, and a wide range of habitats. *P. curvirostris* is found only in lowland rivers of New Zealand and Chatham Island probably recruiting to estuaries, and is rarely fond in streams above 40 m altitude (Carpenter, 1983), and is possibly more specialized than the Japanese and Australian species.

Bishop (1967) identified *Paratya* as the sole oriental element of the Australian decapod fauna, and Williams and Allen (1987) suggested the Australian atyids originated in south-east Asia. However, the latter authors pointed to the Madagascan and African affinities of some Australian cave atyids to suggest that they may be Gondwana relicts. The above observations suggest that *Paratya* may also have a Gondwana origin. It is proposed that ancestral *Paratya* first invaded the New Caledonian portion of the New Zealand region before the formation of the rift from Australia, spreading throughout the rift region around 80 million years BP before the islands became separated by large tracts of ocean. The Asian species of *Paratya* would therefore be the result of more recent dispersal north from Australia to northern Asia, when the Asian and Australian land masses drew closer.

8.3. DIRECTIONS FOR FUTURE RESEARCH

This study has described a previously unreported assemblage of caridean shrimps, and identified the most likely determinants of distribution and abundance of larvae in the plankton, and adults and juveniles in seagrass meadows. It has also shown the life history patterns of *P. australiensis* to be highly variable between estuarine and riverine environments, suggesting adaptive plasticity in reproductive traits. In doing so, this study has raised a number of questions and has pointed to new directions for future research.

The importance of physical factors has dominated this study, but biological interactions were identified as potential influences in shaping the distributions and abundances of the caridean species within seagrass meadows. During the early summer, as salinity and temperature rose, competitive displacement of *P. australiensis* from deeper parts of the upper estuarine seagrass meadows by *M. intermedium* was hypothesized from distributional patterns and from laboratory experiments. Field experiments would more satisfactorily test this hypothesis.

The narrow strip of *Zostera* on the steep bank at JP (meadow 2 in Fig. 2.4) would be a suitable site for exclusion experiments, in which shrimps could be excluded from enclosed sections of the meadow, and individuals of each species could be stocked in an arrangement similar to the laboratory experiments of Chapter 3: one treatment containing both species,

and one or two treatments containing only one species. After a period of equilibration, deep and shallow sections of each enclosed would be sampled. While suffering from the limitations of edge effects of enclosure experiments, such as a design would permit a controlled experiment in more natural conditions than was possible in the laboratory.

Such an experiment would clarify the mechanism of localized habitat partitioning of *P. australiensis* and *M. intermedium*, but would not address the more profound unknown of the aspect of depth that acts as a resource to be competed for. It was postulated in Chapter 3 that deeper sections of the seagrass meadows may provide refuge from predation by water birds, as has been reported by Howard and Lowe (1984). The truth of such a proposition will depend on the importance of predation by fish, which would probably be most significant in deeper parts of the meadow, in relation to predation by water birds, concentrated in the shallower parts. The importance of the trophic ecology of carideans of the estuary has been a common element in many aspects of this study. In addition to the patterns of predation on each species, a study of their diets would help clarify several aspects of this study. It was postulated in Chapter 2 that the epiphytic growth on seagrass may be limited by grazing pressure of *P. australiensis*. The model of reproductive allocation in *P. australiensis* developed in Chapter 7 hinges on availability of food for adults and larvae. Due to the small size of the larvae, any study of feeding preferences would require direct observations and laboratory trials, but once the preferences were determined, a study of temporal and spatial variation in food availability would be straightforward. A study of the diet of adult *P. australiensis* and the seasonal variation in the availability of its food, both in the seagrass meadows of the estuary and in the macrophyte beds of riverine locations, and of the estuarine and riverine planktonic food of the larvae, would provide a stronger basis on which to build further life history models.

Breeding experiments are required to determine the genetic basis of the observed variation in reproductive traits, and the extent of phenotypic plasticity in the traits of egg and brood size. The adaptive advantage of larger offspring in upstream locations also requires further investigation.

The absence of *P. serenus* from previous seagrass studies is surprising. It is most commonly known from intertidal rock pools (Dakin, 1987), and is certainly common in the rock pools along the exposed coast near the mouth of the Hopkins River (personal observation). This study reported *P. serenus* from estuarine seagrass meadows near the mouths of the Hopkins and Moyne river estuaries. The south-west coast of Victoria is distinct from the locations studied by Walker (1979), Howard (1981) and Gray (1985) because of its proximity to a highly energetic coast. This factor may play a part in the importance of estuarine seagrass meadows in the life history of *P. serenus* in this region. The population biology of this species has not been studied prior to this study, and to quantify the importance of estuaries in

its life history will only be possible by further studies of its biology in the marine environment in which it reproduces.

Finally, this study highlighted the uncertain nature of the origin of the *Paratya* species group, which would be clarified by studies of their genetic relationship. The ecology of *P. norfolkensis*, *P. howensis*, and the four New Caledonian species is virtually unknown. A broadly ranging study of their ecology, particularly variation in the degree of specialization in life histories, together with morphological and genetic studies of the *Paratya* group would shed light, not only on the evolution of *Paratya*, but also on the biogeography of the western Pacific rim.

9. APPENDICES

Appendix 1. Dates, locations and nature of sampling trips

Appendix 2. Within-meadow associations of Paratya australiensis and Macrobrachium intermedium with each other, with seagrass biomass and with depth of sampling unit at JP: regressions on which Figs. 2.14 and 2.15c are based.

Appendix 3. Diurnal variation in vertical distribution in Paratya australiensis larvae. Depth distributions of stages I, II. III-IV and V-VIII at two-hourly intervals, from the Hopkins River estuary at KH, 15-16 November 1990, and from the Fitzroy River estuary, 10-12 November 1991.

Appendix 4. Reprint of Walsh (1993). [Not included in electronic version of this thesis.]

Appendix 1. Dates of sampling trips, and nature and location of samples taken.

Abbreviations for locations in the Hopkins River: HB = Hopkins Bridge; MR = Mahoneys Road; RF = Rowan's Flat; JP = Jubilee Park; LG = Lake Gillear exit; TS = Tooram Stones; HF = Hopkins Falls; WB = Warrumyea Bridge; MH = Confluence of Mt Emu Creek and Hopkins River; MP = Panmure (Mt Emu Creek); KF = Kent's Ford; HX = Hexham; CH = Chatsworth

Abbreviations for sample types: CB = Clarke-Bumpus samples, with number of depths sampled in parentheses; CS = core sample, with number of replicates in parentheses; DT =demersal tows at surface and deep midstream, and in fringing meadows; IP = quantitative oblique ichthyoplankton tow; OP = qualitative oblique plankton tow; QN = Qualitative net sample.

* = samples collected by Dr. B. Mitchell; ** = samples collected by G. Newton

		Site												
Date	Code	HB	MR	RF	JP	LG/TS	HF	WB	MH	MP	KF	HX	CH	Other
29 September 1983		QN*			QN*									
19 October 1983		QN*			QN*									
28 November 1983		QN*												
15 December 1983		QN*												
20 January 1984		QN*												
24 January 1984					QN*									
28 February 1984					QN*									
29 February 1984		QN*			IP**	IP**								
21 March 1984		QN*			QN*									
22 March 1984					IP**	IP**								
16 April 1984					IP**	IP**								
17 April 1984		QN*			QN**									
15 May 1984		QN*			QN*									
					IP**	IP**								
13 June 1984		QN*			QN*									
15 June 1984					IP**	IP**								

Appendix 1 (continued)

Date	Code	Site												Other
		HB	MR	RF	JP	LG/TS	HF	WB	MH	MP	KF	HX	CH	
17 July 1984					IP**	IP**								
18 July 1984		QN*			QN*									
15 August 1984					IP**	IP**								
17 August 1984		QN*			QN*									
6 September 1984					IP**	IP**								
28 September 1984		QN*			QN*									
11 October 1984		IP**		IP**	IP**	IP**								
8 November 1984		IP**		IP**	IP**	IP**								
15 December 1984					QN*									
17 December 1984		IP**		IP**	IP**	IP**								
21 January 1985		IP**			IP**	IP**								
22 February 1985					IP**									
30 January 1988			CS (10×3 sizes)											
10 April 1988	2		CS(40)											
12 June 1988	3	CS(12)		CS(12)	CS(12)									
16 July 1988	4	CS(12)		CS(11)	CS(12)									
13 August 1988	5	CS(12)		CS(12)	CS(12)									
10 September 1988	6	CS(12)			CS(11)									
17 September 1988	6A	DT		DT	DT	DT								
23 October 1988	7	CS(11)		CS(10)										
24 October 1988	7A	DT		DT	DT	DT								
19 November 1988	8	CS(9)		CS(10)	CS(11)	CS(5)								
21 November 1988	8A	DT		DT	DT	DT								
15 December 1988	9			CS(12)	CS(12)									
16 December 1988	9	CS(14)				CS(12)								

Appendix 1 (continued)

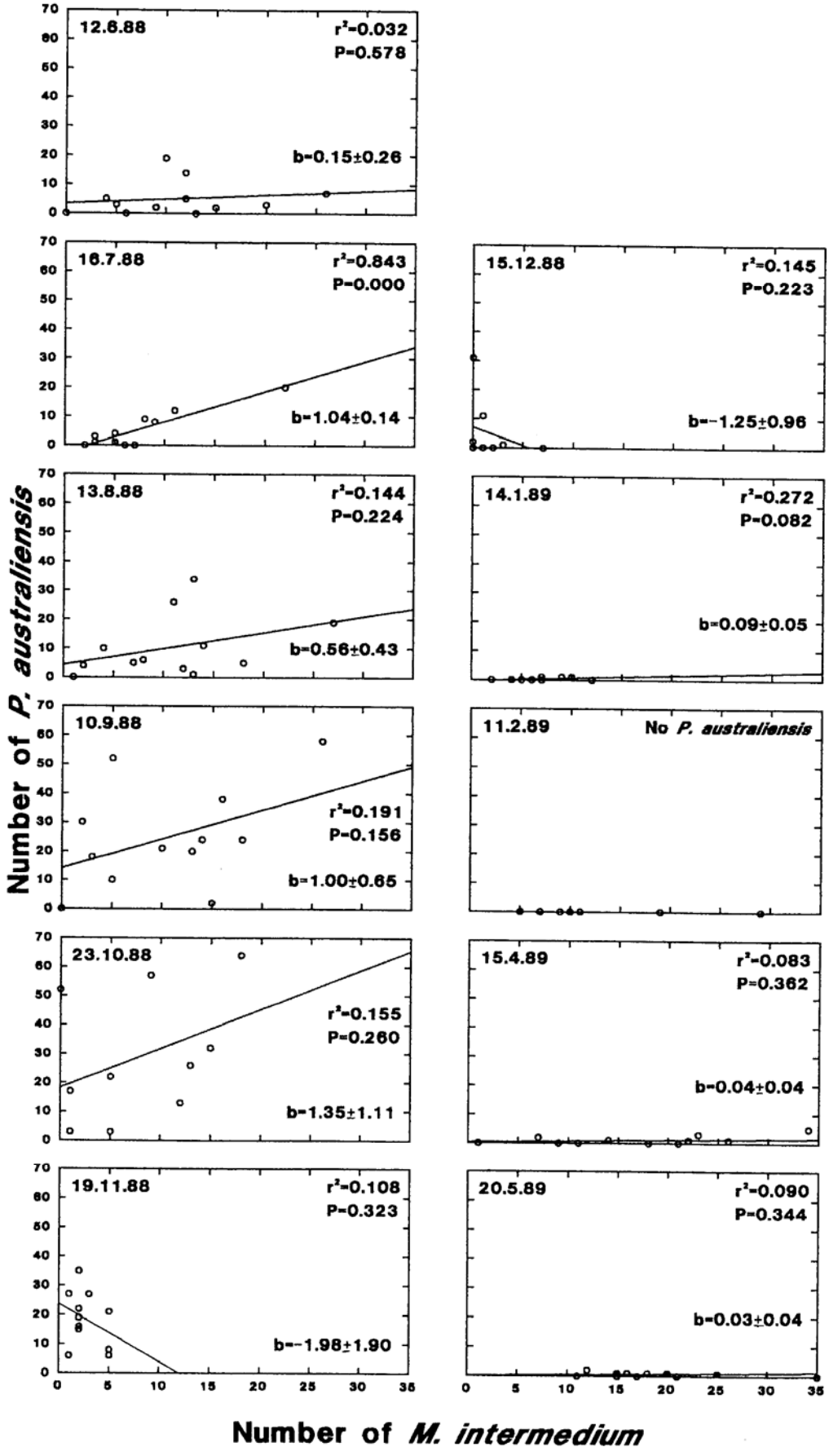
Date	Code	Site												Other
		HB	MR	RF	JP	LG/TS	HF	WB	MH	MP	KF	HX	CH	
17 December 1988	9A	DT		DT	DT	DT								
13 January 1989	10	CS(12)			CS(12)									
14 January 1989	10			CS(12)		CS(12)								
15 January 1989	10A	DT		DT	DT	DT								
11 February 1989	11	CS(11)			CS(11)									
13 February 1989	11A	DT		DT	DT	DT								
31 March 1989	12A	DT		DT	DT	DT								
	12	QN			QN									
15 April 1989	13	CS(12)			CS(12)									
16 April 1989	13A	DT		DT	DT	DT								
20 May 1989	14	CS(11)		CS(12)	CS(12)									
11 July 1989	1				CB(2)									
25 August 1989	2	CB(2)			CB(2)	CB(2)								
8 September 1989	3	CB(2)			CB(4)	CB(4)								
21 September 1989	4	CB(2)			CB(4)	CB(4)								
13 October 1989	5	CB(2)												
23 October 1989	6	CB(2)			CB(4)	CB(4)								
10 November 1989	7	CB(3)			CB(4)	CB(4)								
24 November 1989	8	CB(2)			CB(4)	CB(4)								
15 December 1989	9	CB(2)			CB(4)	CB(4)								
20 December 1989							OP			OP	OP		OP	
12 January 1989	10	CB(2)			CB(4)	CB(4)								
3-11 January 1990				Migration traps										
14 January 1990										OP	OP			
14 February 1990										OP	OP			
8 August 1990					QN		QN	QN			QN	QN		

Appendix 1 (continued)

Date	Code	Site												Other
		HB	MR	RF	JP	LG/TS	HF	WB	MH	MP	KF	HX	CH	
16 September 1990					QN		QN	QN				QN	QN	
2 October 1990														CB in Glenelg
28 October 1990					QN			QN				QN	QN	
15-16 November 1990														24 h survey at KH
2-9 December 1990														South coast survey
13 December 1990					QN			QN				QN	QN	
9 February 1991						QN		QN			QN	QN	QN	
20-21 August 1991						QN		QN	QN				QN	Curdies
27 September 1991					QN			QN		QN				Curdies
22 October 1991					QN	QN		QN		QN				Curdies & Gellibrand
29 October 1991					CB(3)									
9-12 November 1991														50 h survey at Fitzroy
19 November 1991						QN		QN	QN	QN				Curdies & Gellibrand
20 November 1991									CB(3)					
2 December 1991									CB(3)					
4 December 1991						CB(3)								
19 December 1991									CB(3)					Day and night samples
20 December 1991						QN			QN	QN				Curdies
16 January 1992						QN			QN	QN				Curdies & Gellibrand
17 January 1992									CB(3)					
12 February 1992									CB(3)					
13 February 1992						QN			QN	QN				Curdies & Gellibrand
16 March 1992						QN			QN	QN				Curdies & Gellibrand
17 March 1992									CB(3)					
14 April 1992									CB(3)					
15 April 1992						QN			QN	QN				Curdies & Gellibrand

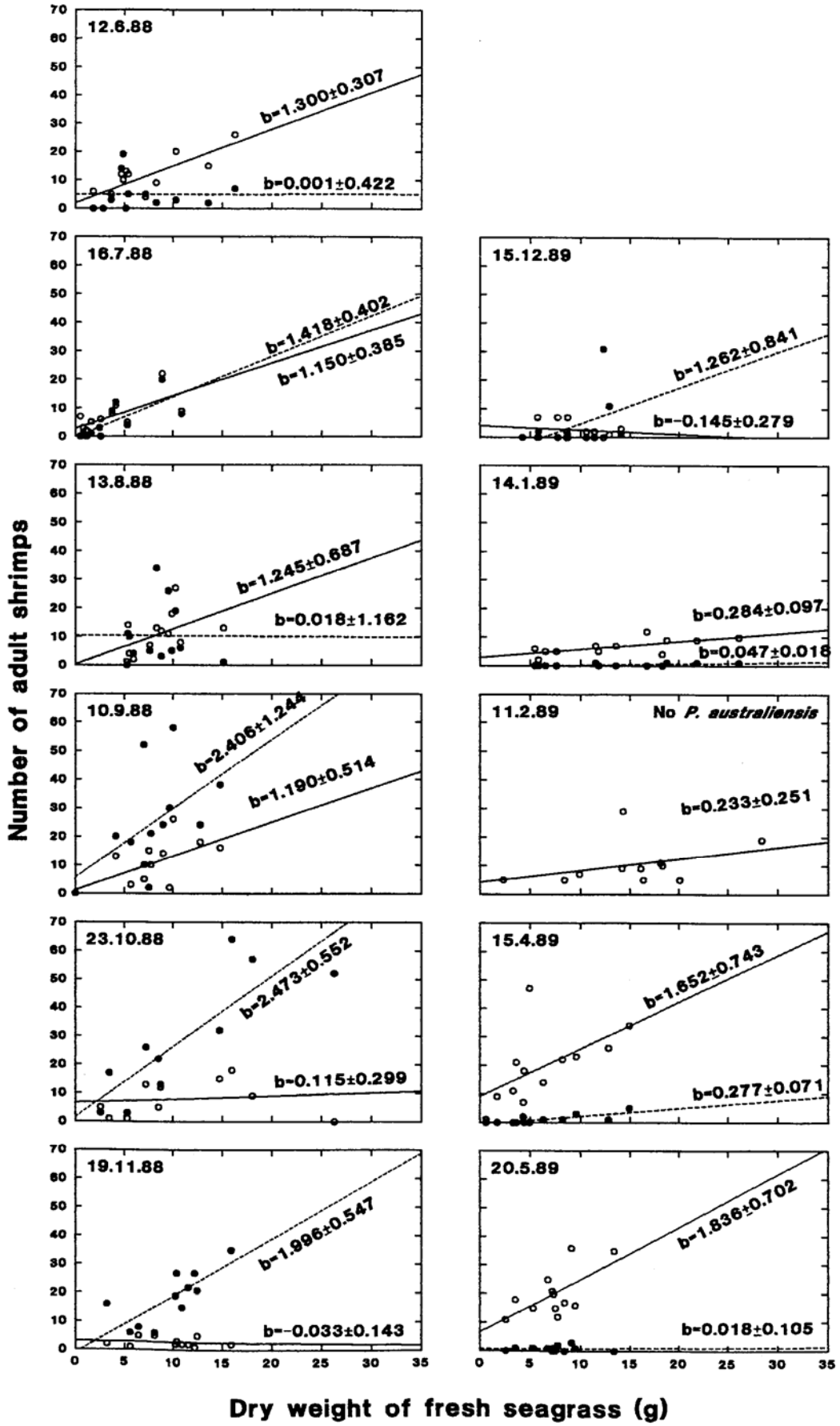
Appendix 2a. Regressions of *Paratya australiensis* numbers per sample unit as a function of *Macrobrachium intermedium* numbers per sample unit, in each sample at JP from 12 June 1998 to 20 May 1989

b = slope of regression (± standard error). Associated probability and r^2 values are indicated.


12.6.88
r²=0.032
P=0.578
b=0.15±0.26
16.7.88
r²=0.843
P=0.000
b=1.04±0.14
15.12.88
r²=0.145
P=0.223
b=-1.25±0.96
13.8.88
r²=0.144
P=0.224
b=0.56±0.43
14.1.89
r²=0.272
P=0.082
b=0.09±0.05
10.9.88
r²=0.191
P=0.156
b=1.00±0.65
11.2.89
No P. australiensis
23.10.88
r²=0.155
P=0.260
b=1.35±1.11
15.4.89
r²=0.083
P=0.362
b=0.04±0.04
19.11.88
r²=0.108
P=0.323
b=-1.98±1.90
20.5.89
r²=0.090
P=0.344
b=0.03±0.04
Number of P. australiensis
Number of M. intermedium

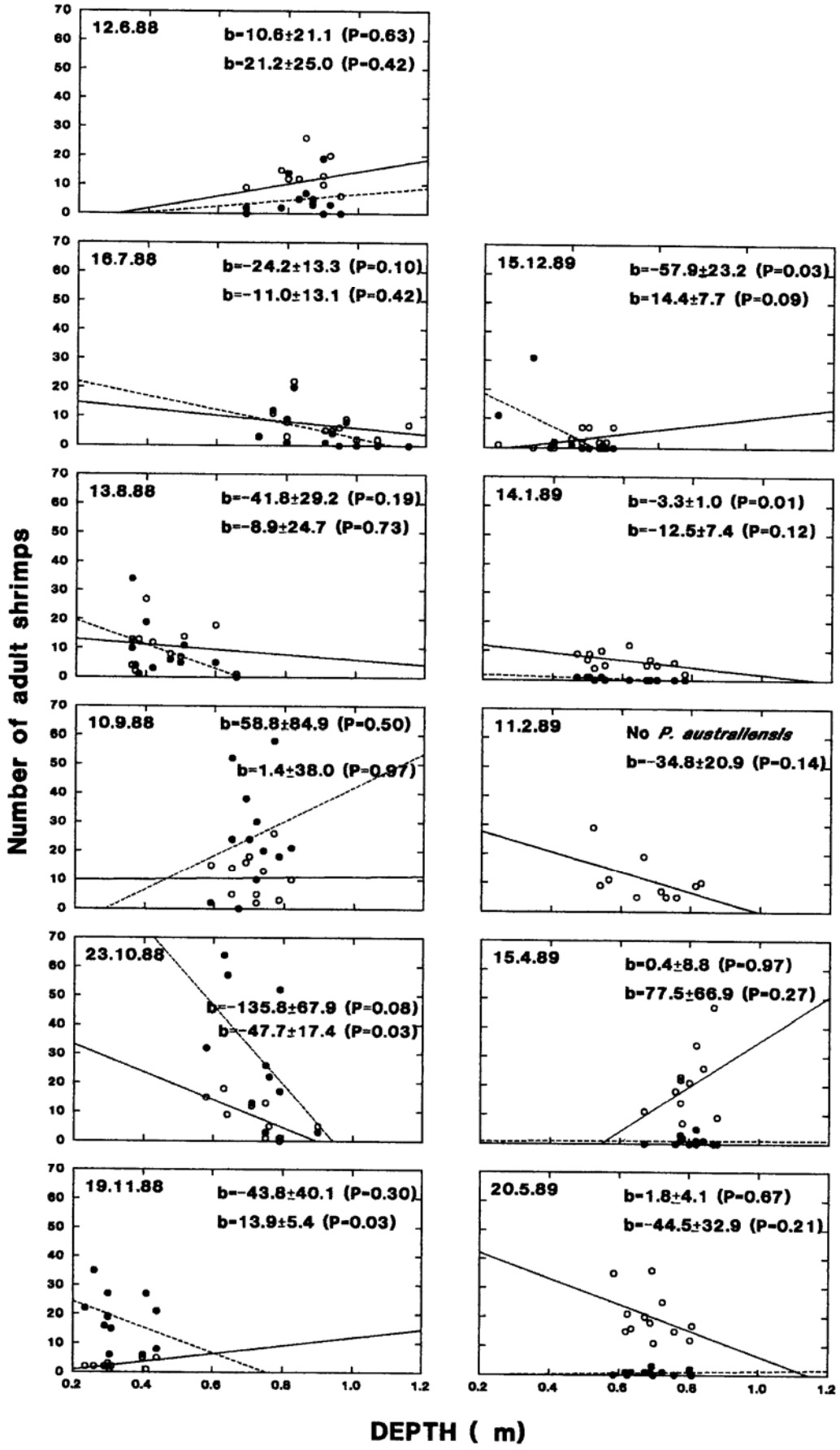
Appendix 2b. Regressions of shrimp numbers per sample unit as a function of biomass of fresh seagrass leaves in each sample unit, in each sample at JP from 12 June 1998 to 20 May 1989

b = slope of regression (± standard error). Closed circles, dashed line, *Paratya australiensis*; open circles, solid line, *Macrobrachium intermedium*

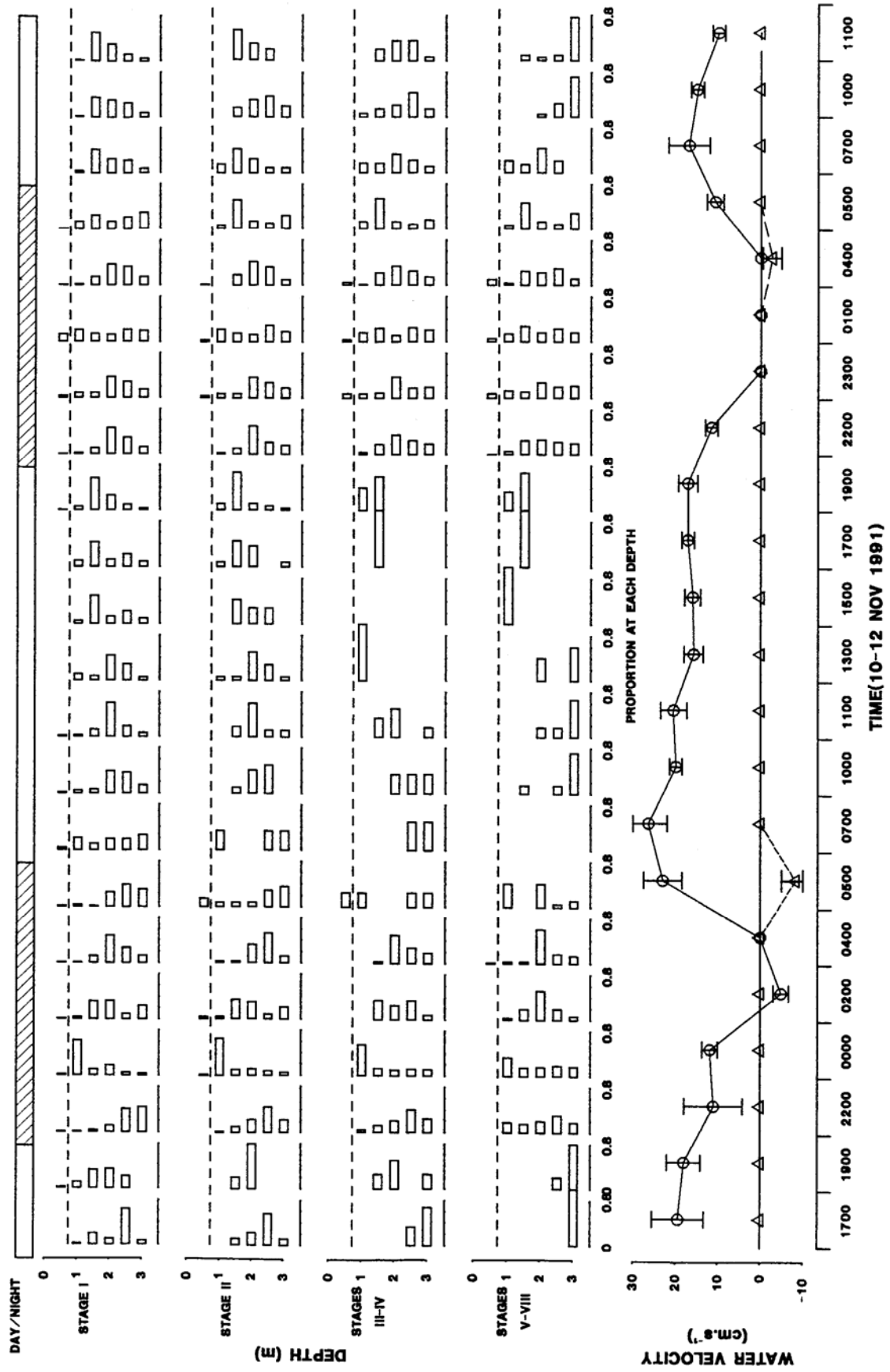

12.6.88
b=1.300±0.307
b=0.001±0.422
16.7.88
b=1.418±0.402
b=1.150±0.385
15.12.89
b=1.262±0.841
b=-0.145±0.279
13.8.88
b=1.245±0.687
b=0.018±1.162
14.1.89
b=0.284±0.097
b=0.047±0.018
10.9.88
b=2.406±1.244
b=1.190±0.514
11.2.89
No P. australiensis
b=0.233±0.251
23.10.88
b=2.473±0.552
b=0.115±0.299
15.4.89
b=1.652±0.743
b=0.277±0.071
19.11.88
b=1.996±0.547
b=-0.033±0.143
20.5.89
b=1.836±0.702
b=0.018±0.105
Number of adult shrimps
Dry weight of fresh seagrass (g)

Appendix 2c. Regressions of shrimp numbers per sample unit as a function of depth of each sample unit for each sample at JP from 12 June 1998 to 20 May 1989

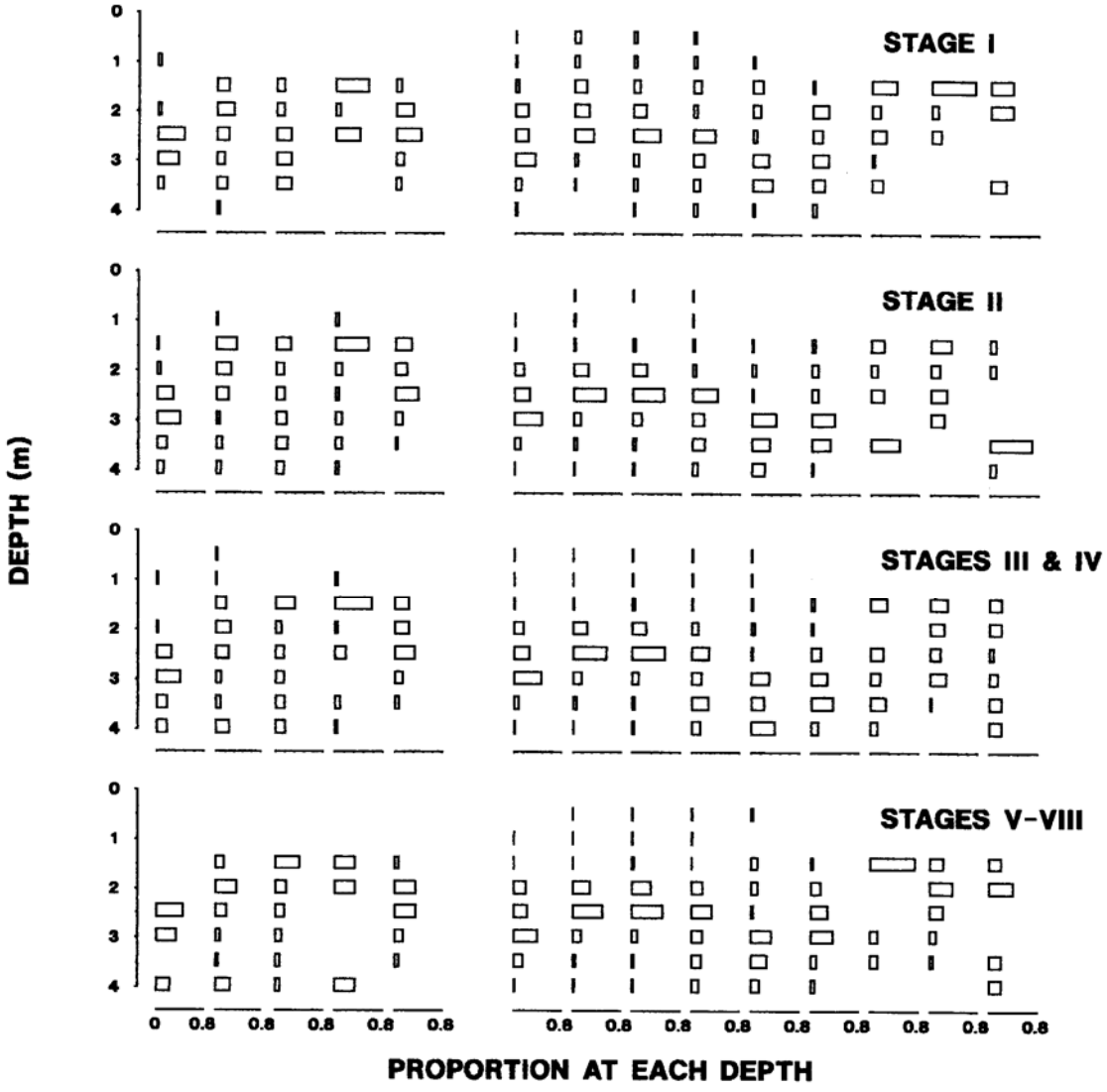
b = slope of regression (± standard error). Closed circles, dashed line, *Paratya australiensis*; open circles, solid line, *Macrobrachium intermedium*

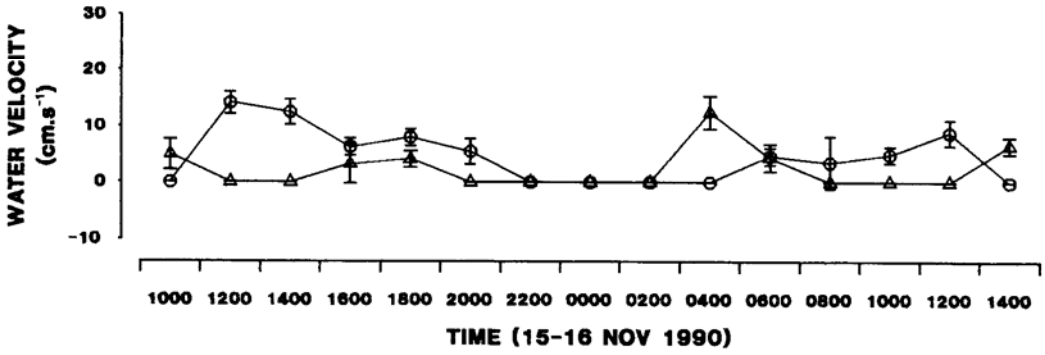

12.6.88
b=10.6±21.1 (P=0.63)
b=21.2±25.0 (P=0.42)
16.7.88
b=-24.2±13.3 (P=0.10)
b=-11.0±13.1 (P=0.42)
15.12.89
b=-57.9±23.2 (P=0.03)
b=14.4±7.7 (P=0.09)
13.8.88
b=-41.8±29.2 (P=0.19)
b=-8.9±24.7 (P=0.73)
14.1.89
b=-3.3±1.0 (P=0.01)
b=-12.5±7.4 (P=0.12)
10.9.88
b=58.8±84.9 (P=0.50)
b=1.4±38.0 (P=0.97)
11.2.89
No P. australiensis
b=-34.8±20.9 (P=0.14)
23.10.88
b=-135.8±67.9 (P=0.08)
b=-47.7±17.4 (P=0.03)
15.4.89
b=0.4±8.8 (P=0.97)
b=77.5±66.9 (P=0.27)
19.11.88
b=-43.8±40.1 (P=0.30)
b=13.9±5.4 (P=0.03)
20.5.89
b=1.8±4.1 (P=0.67)
b=-44.5±32.9 (P=0.21)
Number of adult shrimps
DEPTH (m)

Appendix 3a. Proportion of *Paratya australiensis* larvae in each of six depths in twenty-two samples from the Fitzroy River estuary over 44 h, 10-12 November 1991. Flow rates of water in fresh layer (0.5 m, circles), and in salt wedge (1.5 m, triangles), measured 10-15 min before each sample are also illustrated.


DAY/NIGHT
STAGE I
STAGE II
STAGES III-IV
STAGES V-VIII
DEPTH (m)
PROPORTION AT EACH DEPTH
WATER VELOCITY (cm.s⁻¹)
TIME(10-12 NOV 1991)

Appendix 3b. Proportion of *Paratya australiensis* larvae in each of eight depths in fourteen samples from KH in the Hopkins River estuary over 30 h, 15-16 November 1990. Flow rates of water in fresh layer (0.5 m, triangles, 1 m circles), measured 10-15 min after each sample are also illustrated.


STAGE I
STAGE II
STAGES III & IV
STAGES V-VIII
DEPTH (m)
0
1
2
3
4
0 0.8 0.8 0.8 0.8 0.8
0.8 0.8 0.8 0.8 0.8 0.8 0.8 0.8 0.8
PROPORTION AT EACH DEPTH


WATER VELOCITY (cm.s⁻¹)
30
20
10
0
-10
1000 1200 1400 1600 1800 2000 2200 0000 0200 0400 0600 0800 1000 1200 1400
TIME (15-16 NOV 1990)

10. LITERATURE CITED

Abrunhosa, F. A., and Moura, M. G. (1988). O completo desenvolvimento larval do camarão *Atya scabra* (Leach) (Crustacea: Decapoda: Atyidae), cultivado em laboratório. *Arquivos de Ciências do Mar* **27**, 127-146.

Adams, S. M. (1976). Feeding ecology of eelgrass fish communities. *Transactions of the American Fisheries Society* **105**, 514-519.

Alon, N. C., and Stancyk, S. E. (1982). Variation in life-history patterns of the grass shrimp *Palaemonetes pugio* in two south Carolina estuarine systems. *Marine Biology* **68**, 265-276.

American Society for Testing and Materials (1988). Standard practice for conducting acute toxicity tests with fishes, macroinvertebrates and amphibians. *Annual Book of ASTM Standards* **E-729**, 304-323.

Andrew, N. L., and Mapstone, B. D. (1987). Sampling and description of spatial pattern in marine ecology. *Oceanography and Marine Biology—Annual Review* **25**, 39-90.

Baden, S. P., and Pihl, P. (1984). Abundance, biomass, and production of mobile epibenthic fauna in *Zostera marina* (L.) meadows, western Sweden. *Ophelia* **23**, 65-90.

Bauer, R. T. (1985). Diel and seasonal variation in species composition and abundance of caridean shrimps (Crustacea, Decapoda) from seagrass meadows on the north coast of Puerto Rico. *Bulletin of Marine Science* **36**, 150-162.

Bell, J. D., Steffe, A. S., and Westoby, M. (1988). Location of seagrass beds in estuaries: effects on associated fish and decapods. *Journal of Experimental Marine Biology and Ecology* **122**, 127-146.

Bell, J. D. and Westoby, M. (1986a). Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. *Oecologia* **68**, 205-209.

Bell, J. D. and Westoby, M. (1986b). Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. *Journal of Experimental Marine Biology and Ecology* **104**, 249-274.

Bell, J. D. and Westoby, M. (1986c). Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. *Journal of Experimental Marine Biology and Ecology* **104**, 275-295.

Benzie, J. A. H. (1982). The complete larval development of *Caridina mccullochi* Roux, 1926 (Decapoda, Atyidae) reared in the laboratory. *Journal of Crustacean Biology* **2**, 493-513.

Benzie, J. A. H., and de Silva, P. K. (1983). The abbreviated larval development of *Caridina singhalensis* Ortmann, 1894 (Decapoda, Atyidae). *Journal of Crustacean Biology* **3**, 117-126.

Benzie, J. A. H., and de Silva, P. K. (1988). The distribution and ecology of the freshwater prawn *Caridina singhalensis* Ortmann, 1894, (Decapoda, Atyidae) endemic to Sri Lanka. *Journal of Tropical Ecology* **4**, 347-359.

Berglund, A. (1980). Niche differentiation between two littoral prawns in Gullmar Fjord, Sweden: *Palaemon adspersus* and *P. squilla*. *Holarctic Ecology* **3**, 111-115.

Berglund, A. (1984). Reproductive adaptations in two *Palaemon* prawn species with differing habitat requirements. *Marine Ecology Progress Series* **17**, 77-83.

Berglund, A., and Rosenqvist, G. (1986). Reproductive costs in the prawn *Palaemon adspersus*: effects on growth and predator vulnerability. *Oikos* **46**, 349-354.

Bishop, J. A. (1967). The zoogeography of the Australian freshwater decapod Crustacea. In 'Australian Inland Waters and their Fauna: Eleven Studies'. (Ed A. H. Weatherly) pp 107-122. (ANU Press: Canberra.)

Boulton, A. J., and Knott, B. (1984). Morphological and electrophoretic studies of the Palaemonidae (Crustacea) of the Perth region, Western Australia. *Australian Journal of Marine and Freshwater Research* **35**, 769-783.

Bowler, J. M., and Hamada, T. (1971). Late quaternary stratigraphy and radiocarbon chronology of water levels in Lake Keilambete, Victoria. *Nature* **232**, 330-332.

Brambilla, D. J. (1982). Seasonal variation of egg size and number in a Daphnia pulex population. *Hydrobiologia* **97**, 233-248.

Bray, D. M. (1976). Larval development of two western Australian shrimps, *Palaemonetes australis* Dakin and *Palaemonetes attrinubes* Bray (Decapoda, Palaemonidae), reared in the laboratory. *Records of the Australian Museum* **4**, 145-162.

Broad, A. C. (1957). The relationship between diet and larval development of *Palaemonetes*. *Biological Bulletin* **112**, 162-170.

Brody, M. S., and Lawlor, L. R. (1984). Adaptive variation in offspring size in the terrestrial isopod, *Armadillidium vulgare*. *Oecologia* **61**, 55-59.

Bunn, S. E. (1988). Life histories of some benthic invertebrates from streams of the northern Jarrah forest, Western Australia. *Australian Journal of Marine and Freshwater Research* **39**, 785-804.

Carpenter, A. (1978). Protandry in the freshwater shrimp *Paratya curvirostris* (Heller, 1862), with a review of the phenomenon and its significance in the Decapoda. *Journal of the Royal Society of New Zealand* **8**, 343-358.

Carpenter, A. (1982). Habitat and distribution of the freshwater shrimp *Paratya curvirostris* (Decapoda: Atyidae) in North Canterbury. *Mauri Ora* **10**, 85-98.

Carpenter, A. (1983). Population biology of the freshwater shrimp, *Paratya curvirostris* (Heller, 1862) (Decapoda: Atyidae). *New Zealand Journal of Marine and Freshwater Research* **17**, 147-158.

Cassie, R. M. (1954). Some uses of probability paper in the analysis of polymodal size distributions. *Australian Journal of Marine and Freshwater Research* **5**, 513-522.

Chace, F. A. (1983). The *Atya*-like shrimps of the Indo-Pacific region (Decapoda, Atyidae). *Smithsonian Contributions to Zoology* **384**, 54 pp.

Chace, F. A. (1992). On the classification of the Caridea (Decapoda). *Crustaceana* **63**, 70-80.

Chaloupka, M. Y. (1978). 'An Ecological Study of the Decapod Crustacean Larvae in a Tropical Estuarine Embayment.' B. Sc. (Hons.) Thesis. (School of Biological Sciences, James Cook University of North Queensland: Townsville) 125 pp. plus appendices.

Chinnaya, B. (1974). The embryonic and larval development of *Caridina weberi* de Man in the laboratory (Decapoda, Atyidae). *Brotéria, series trimestral—Ciências Naturais* **43**, 119-134.

Ch'ng, T. K. (1973). 'Aspects of the Biology of the New Zealand Freshwater Shrimp *Paratya curvirostris* (Heller) in the Horokiwi Stream.' B. Sc. (Hons.) Thesis. (Victoria University: Wellington.) 59 pp.

Chong, S. S. C., and Khoo, H. W. (1987). The abbreviated larval development of the freshwater prawn, *Macrobrachium malayanum* (Roux, 1934) (Decapoda, Palaemonidae), reared in the laboratory. *Crustaceana* **53**, 29-42.

Choudhury, P. C. (1971). Responses of larval *Macrobrachium carcinus* (L.) to variations in salinity and diet (Decapoda, Palaemonidae). *Crustaceana* **20**, 113-120.

Chow, S., Fujio, Y., and Nomura, T. (1988). Reproductive isolation and distinct population structure in two types of the freshwater shrimp *Palaemon paucidens*. *Evolution* **42**, 804-813.

Christiansen, F. B., and Fenchel, T. M. (1979). Evolution of marine invertebrate reproductive patterns. *Theoretical Population Biology* **16**, 267-282.

Christy, J. H., and Stancyk, S. E. (1982). Timing of larval production and flux of invertebrate larvae in a well-mixed estuary. In 'Estuarine Comparisons'. (Ed V. S. Kennedy.) pp 489-503. (Academic Press: New York.)

Clarke, A. (1979). On living in cold water: K-strategies in Antarctic benthos. *Marine Biology* **55**, 111-119.

Clarke, A. (1987). Temperature, latitude and reproductive effort. *Marine Ecology Progress Series* **38**, 89-99.

Clarke, A. (1992). Reproduction in the cold: Thorson revisited. *Invertebrate Reproduction and Development* **22**, 175-184.

Clarke, A. (1993a). Egg size and egg composition in polar shrimps (Caridea: Decapoda). *Journal of Experimental Marine Biology and Ecology* **168**, 189-203.

Clarke, A. (1993b). Reproductive trade-offs in caridean shrimps. *Functional Ecology* **7**, 411-419.

Clarke, A., Hopkins, C. C. E., and Nilssen, E. M. (1991). Egg size and reproductive output in deep-water prawn *Pandalus borealis* Krøyer, 1838. *Functional Ecology* **5**, 724-730.

Clarke, G. L., and Bumpus, D. F. (1940). The plankton sampler—an instrument for quantitative plankton investigations. *Limnological Society of America Special Publications* **5**, 1-8.

Closs, G. P., and Lake, P. S. (1994). Spatial and temporal variation in the structure of an intermittent-stream food web. *Ecological Monographs* **64**, 1-21.

Coen, L. D., Heck, K. L., and Abele, L. G. (1981). Experiments on competition and predation among shrimps of seagrass meadows. *Ecology* **62**, 1484-1493.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302-1310.

Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* **122**, 661-696.

Cooper, R. A., and Millener, P. R. (1993). The New Zealand biota: historical background and new research. *Trends in Evolution and Ecology* **8**, 429-433.

Crivelli, A. J. (1982). Biology of three Malacostraca (Decapoda) in a Mediterranean lagoon with particular emphasis on the effect of rapid environmental changes on the activity (catchability) of the species. *Estuarine, Coastal and Shelf Science* **15**, 591-604.

Cronin, T. W. (1982). Estuarine retention of larvae of the crab *Rhithropanopeus harrisii*. *Estuarine, Coastal and Shelf Science* **28**, 207-220.

Cronin, T. W., and Forward, R. B. (1982). Tidally timed behavior: effects on larval distributions in estuaries. In 'Estuarine Comparisons'. (Ed V. S. Kennedy.) pp 505-520. (Academic Press: New York.)

Crowder, L. B., and Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* **63**, 1802-1813.

Dakin, W. J. (1987). 'Australian Seashores. A Guide to the Temperate Shores for the Beach-Lover, the Naturalist, the Shore-Fisherman and the Student.' Edition revised and expanded by I. Bennett. (Angus and Robertson: Sydney.) 411 pp.

Day, R. W., and Quinn, G. P. (1989). Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* **19**, 433-463.

Department of Defence, Australia (1991, 1992). 'Australian National Tide Tables.' Australian Hydrographic Publication 11. (Australian Government Publishing Service: Canberra.)

Department of Water Resources Victoria (1989a). 'Water Victoria: An Environmental Handbook.' (Victorian Government Printing Office: Melbourne.)

Department of Water Resources Victoria (1989b). 'Water Victoria: A Resource Handbook.' (Victorian Government Printing Office: Melbourne.) 311 pp.

de Silva, K. H. G. M. (1988a). Studies on Atyidae (Decapoda, Caridea) of Sri Lanka. III. Aspects of the population ecology of *Caridina simoni* Bouvier, 1904. *Crustaceana* **54**, 85-103.

de Silva, K. H. G. M. (1988b). Studies on Atyidae (Decapoda, Caridea) of Sri Lanka. IV. Some aspects of the population ecology of the endemic freshwater shrimp *Caridina pristis* Roux, 1931. *Crustaceana* **54**, 225-243.

de Silva, K. H. G. M. (1990). *Caridina kumariae*, a new species from Sri Lanka and some aspects of its ecology (Decapoda, Atyidae). *Crustaceana* **59**, 9-24.

de Silva, P. K., and de Silva, K. H. G. M. (1989). Aspects of the population ecology of a tropical freshwater atyid shrimp *Caridina fernandoi* Arud. & Costa, 1962 (Crustacea: Decapoda: Caridea). *Archiv fur Hydrobiologica* **117**, 237-253.

Dew, B. (1963). Animal life in caves. *Australian Natural History* **15**, 158-161.

Dittel, A. I., and Epifanio, C. E. (1990). Seasonal and tidal abundance of crab larvae in a tropical mangrove system, Gulf of Nicoya, Costa Rica. *Marine Ecology Progress Series* **65**, 25-34.

Dudgeon, D. (1985). The population dynamics of some freshwater carideans (Crustacea: Decapoda) in Hong Kong, with special reference to *Neocaridina serrata* (Atyidae). *Hydrobiologia* **120**, 141-149.

Elliott, J. M. (1977). 'Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates.' Scientific Publication No. 25. (Freshwater Biological Association: Cumbria, UK.) 156 pp.

Emmerson, W. D. (1986). The ecology of *Palaemon pacificus* (Stimpson) associated with *Zostera capensis* Setchell. *Transactions of the Royal Society of South Africa* **46**, 79-97.

Epifanio, C. E., and Dittel, A. I. (1982). Comparison of dispersal of crab larvae in Delaware Bay, USA, and the Gulf of Nicoya, Central America. In 'Estuarine Comparisons'. (Ed V. S. Kennedy.) pp 477-487. (Academic Press: New York.)

Epifanio, C. E., Little, K. T., and Rowe, P. M. (1988). Dispersal and recruitment of fiddler crab larvae in the Delaware River estuary. *Marine Ecology Progress Series* **43**, 181-188.

Felgenhauer, B. E., and Abele, L. G. (1983). Ultrastructure and functional morphology of feeding and associated appendages in the tropical fresh-water shrimp *Atya innocous* (Herbst) with notes on its ecology. *Journal of Crustacean Biology* **3**, 336-363.

Fincham, A. A. (1977). Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia). 1. Laboratory methods and a review of *Palaemon (Paleander) elegans* Rathke 1837. *Bulletin of the British Museum of Natural History* (Zoology) **32**, 1-28.

Fincham, A. A., and Figueras, A. J. (1986). Larval keys and diagnoses for the subfamily Palaemoninae (Crustacea: Decapoda: Palaemonidae) in the north-east Atlantic and aspects of functional morphology. *Journal of Natural History* **20**, 302-224.

Fincham, A. A., and Furlong, J. A. (1984). Seasonal swimming rhythms of female palaemonid estuarine prawns and shrimps. *Journal of Natural History* **18**, 425-439.

Finney, D. J. (1978). 'Statistical Method in Biological Assay.' Third edition. (Charles Griffin and Co.: London.) 508 pp.

Forster, G. R. (1951). The biology of the common prawn, *Leander serratus* Pennant. *Journal of the Marine Biological Association of the United Kingdom* **30**, 333-360.

Forward, R. B. (1988). Diel vertical migration: zooplankton photobiology and behaviour. *Oceanography and Marine Biology—Annual Review* **26**, 361-393.

Fryer, G. (1977). Studies on the functional morphology and ecology of the atyid prawns of Dominica. *Philosophical Transactions of the Royal Society of London* **277**, 57-129.

Gemmel, P. (1979a). Feeding habits and structure of the gut of the Australian freshwater prawn *Paratya australiensis* Kemp (Crustacea, Caridea, Atyidae). *Proceedings of the Linnean Society of New South Wales* **103**, 209-216.

Gemmel, P. (1979b). Functional morphology of the feeding appendages of *Paratya australiensis* (Kemp) (Crustacea, Decapoda). *Zoologischer Anzeiger, Jena* **203**, 129-138.

Gill, E. D. (1967). Evolution of the Warrnambool-Port Fairy coast and the Tower Hill eruption, western Victoria. In 'Landform Studies from Australia and New Guinea'. (Eds J. N. Jennings and J. A. Mabbutt.) pp 340-364. (ANU Press: Canberra.)

Gill, E. D. (1984). 'Coastal Processes and the Sanding of Warrnambool Harbour.' (WIAE Press: Warrnambool.) 78 pp.

Gittins, R. (1985). 'Canonical Analysis. A Review with Applications in Ecology.' Biomathematics Vol. 12. (Springer-Verlag: Berlin.) 351 pp.

Glaister, J. P. (1976). Postembryonic growth and development of *Caridina nilotica aurensis* Roux (Decapoda: Atyidae) reared in the laboratory. *Australian Journal of Marine and Freshwater Research* **27**, 263-278.

Gore, R. H. (1985). Molting and growth in decapod larvae. In 'Crustacean Issues'. (Ed F. R. Schram.) Vol. 2. 'Larval Growth.' (Ed A. M. Werner.) pp 1-65. (A. A. Balkema: Rotterdam.)

Gore, R. H., Gallaher, E. E., Scotto, L. E., and Wilson, K. A. (1981). Studies on decapod Crustacea from the Indian River region of Florida. XI. Community composition, structure, biomass and species-areal relationships of seagrass and drift algae-associated macrocrustaceans. *Estuarine, Coastal and Shelf Science* **12**, 485-508.

Gray, C. A. (1985). 'Seasonal Dynamics and Life History of the Palaemonid Shrimp *Macrobrachium intermedium* in Seagrass Meadows in the Sydney Region.' M. Sc. Thesis. (University of Sydney: Sydney.)

Gray, C. A. (1991a). Temporal variability in the demography of the palaemonid prawn *Macrobrachium intermedium* in two seagrasses. *Marine Ecology Progress Series* **75**, 227-237.

Gray, C. A. (1991b). Demographic patterns of the palaemonid prawn *Macrobrachium intermedium* in southeastern Australia: spatial heterogeneity and the effects of species of seagrass. *Marine Ecology Progress Series* **75**, 239-249.

Gray, C. A., and Bell, J. A. (1986). Consequences of two common techniques for sampling vagile macrofauna associated with the seagrass *Zostera capricorni*. *Marine Ecology Progress Series* **28**, 43-48.

Griffiths, F. B., Brown, G. H., Reid, D. D., Parker, R. R. (1984). Estimation of sample zooplankton abundance from Folsom splitter sub-samples. *Journal of Plankton Research* **6**, 721-731.

Grosberg, R. K., and Levitan, D. R. (1992). For adults only? Supply-side ecology and the history of larval biology. *Trends in Evolution and Ecology* **7**, 130-133.

Gurney, R. (1942). 'Larvae of Decapod Crustacea.' (Ray Society: London.) 306 pp.

Hart, R.C. (1981). Population dynamics and production of the tropical freshwater shrimp *Caridina nilotica* in the littoral of Lake Sibaya. *Freshwater Biology*, **11**, 531-547.

Hayashi, K.- I., and Hamano, T. (1984). The complete larval development of *Caridina japonica* De Man (Decapoda, Caridea, Atyidae) reared in the laboratory. *Zoological Science* **1**, 571-589.

Heck, K. L., and Orth, R. J. (1980a). Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—decapod Crustacea. *Estuaries* **3**, 289-295.

Heck, K. L., and Orth, R. J. (1980b). Seagrass habitats: the role of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In 'Estuarine Perspectives'. (Ed V. S. Kennedy.) pp 449-464. (Academic Press: New York.)

Heck, K. L., and Thoman, T. A. (1981). Experiments on predator-prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology* **53**, 125-134.

Hedgepeth, J. W. (1968). The atyid shrimp of the genus *Syncaris* in California. *Internationale Revue der gesamten Hydrobiologie* **53**, 511-524.

Hobbs, H. H., and Hart, C. W. (1982). The shrimp genus *Atya* (Decapoda: Atyidae). *Smithsonian Contributions to Zoology* **364**, 143 pp.

Höglund, H. (1943). On the biology and larval development of *Leander squilla* (L.) forma *typica* de Man. *Svenska Hydrografisk-Biologiska Kommissionens Skrifter*. *Ny Serie. Biologi* **2(6)**, 1-47.

Holmquist, J. G., Powell, G. V. N, and Sogard, S. M. (1989). Decapod and stomatopod communities of seagrass-covered mud banks in Florida Bay: inter- and intra-bank heterogeneity with special reference to isolated subenvironments. *Bulletin of Marine Science* **44**, 251-262.

Holthuis, L. B. (1970). Études hydrobiologiques en Nouvelle-Calédonie (Mission 1965 du Premier Institut de Zoologie de l'Université de Vienne), IX: the freshwater shrimps (Crustacea, Decapoda, Natantia) of New Caledonia. *Cahiers O.R.S.T.O.M., Serie Hydrobiologie* **3**, 87-108.

Holtschmit, K.- H., and Pfeiler, E. (1984). Effect of salinity on survival and development of larvae and postlarvae of *Macrobrachium americanum* Bate (Decapoda, Palaemonidae). *Crustaceana* **46**, 23-28.

Homziak, J., Fonseca, M. S., and Kenworthy, W. J. (1982). Macrobenthic community structure in a transplanted eelgrass (*Zostera marina*) meadow. *Marine Ecology Progress Series* **9**, 211-221.

Hough, A. R., and Naylor, E. (1992). Distribution and position maintenance behaviour of the estuarine mysid *Neomysis integer*. *Journal of the Marine Biological Association U. K.* **72**, 869-876.

Howard, R. K. (1981). 'The Ecology and Trophic Role of Caridean Shrimps in the eelgrass community of Western Port, Victoria.' Ph. D. Thesis. (Zoology Department, University of Melbourne: Melbourne.) 196 pp.

Howard, R. K. (1984). The trophic ecology of caridean shrimps in an eelgrass community. *Aquatic Botany* **18**, 155-174.

Howard, R. K. (1985). Measurements of short-term turnover of epifauna within seagrass beds using an *in situ* staining method. *Marine Ecology Progress Series* **22**, 163-168.

Howard, R. K. (1987). Diel variation in the abundance of epifauna associated with seagrasses of the Indian River, Florida, USA. *Marine Biology* **96**, 137-142.

Howard, R. K., and Lowe, K. W. (1984). Predation by birds as a factor influencing the demography of an intertidal shrimp. *Journal of Experimental Marine Biology and Ecology* **74**, 35-52.

Hubschman, J. H. (1975). Larval development of the freshwater shrimp *Palaemonetes kadiakensis* Rathbun under osmotic stress. *Physiological Ecology* **48**, 97-104.

Hughes, D. A., and Richard, J. D. (1973). Some current directed movements of *Macrobrachium acanthurus* (Wiegmann, 1836) (Decapoda, Palaemonidae) under laboratory conditions. *Ecology* **54**, 927-929.

Hunte, W. (1978). The distribution of freshwater shrimps (Atyidae and Palaemonidae) in Jamaica. *Zoological Journal of the Linnean Society* **64**, 135-150.

Hunte, W. (1979a). The complete larval development of the freshwater shrimp *Micratya poeyi* (Guérin-Méneville) reared in the laboratory (Decapoda, Atyidae). *Crustaceana supplement* **5**, 153-166.

Hunte, W. (1979b). The complete larval development of the freshwater shrimp *Atya innocous* (Herbst) reared in the laboratory (Decapoda, Atyidae). *Crustaceana supplement* **5**, 231-242.

Hutchinson, G. E. (1951). Copepodology for the ornithologist. *Ecology* **32**, 571-577.

Ibrahim, K. H. (1962). Observations on the fishery and biology of the freshwater prawn *Macrobrachium malcolmsonii* Milne Edwards of River Godavari. *Indian Journal of Fisheries* **9**, 433-467.

Jablonski, D., and Lutz, R. A. (1983). Larval ecology of marine benthic invertebrates: palaeobiological implications. *Biological Reviews* **58**, 21-89.

Johnson, D. R., and Hester, B. S (1989). Larval transport and its association with recruitment of blue crabs to Chesapeake Bay. *Estuarine, Coastal and Shelf Science* **28**, 459-472.

Johnson, D. S. (1965). A review of the brackish water prawns of Malaya. *Bulletin of the National Museum of Singapore* **33**, 7-11.

Kamita, T. (1958a). Ecological notes on the shrimps and prawns of Japan VI. On the shrimp, *Paratya compressa* (De Haan). *Zoological Magazine (Tokyo)* **67** 237-241.

Kamita, T. (1958b). Ecological notes on the shrimps and prawns of Japan VII. On the shrimp, *Paratya compressa improvisa* (Kemp). *Zoological Magazine (Tokyo)* **67** 272-276.

Kamita, T. (1967). Some shrimps and prawns from New Caledonia. *Bulletin of the Osaka Museum of Natural History* **20**, 1-10.

Kamita, T. (1970). 'Studies on the Freshwater Shrimps, Prawns and Crayfishes of Japan. Revised Edition.' (Sonoyama-Shoten Press: Matsue.) 213 pp. (cited in Mashiko, 1990.)

Kemp, S. (1917). XVII. Notes on Crustacea Decapoda in the Indian Museum. XI. Atyidae of the genus *Paratya* (=*Xiphocaridina*). *Records of the Indian Museum* **13**, 293-306.

Kikuchi, T. (1974). Japanese contributions on consumer ecology in eelgrass (*Zostera marina* L.) beds, with special reference to trophic relationships and resources in inshore fisheries. *Aquaculture* **4**, 145-160.

Kikuchi, T. (1980). Faunal relationships in temperate seagrass beds. In 'Handbook of Seagrass Biology: an Ecosystem Perspective'. (Eds R. C. Phillips and C. P. McRoy.) pp 153-172. (Garland STPM Press: New York.)

Kingston, M. B. (1993). 'Some Aspects of Gene Flow in Stream and River Systems.' B. Sc. (Hons.) Thesis. (Faculty of Environmental Sciences, Griffith University: Nathan, Queensland.) 102 pp.

Kishi, Y. (1978). Egg size difference between three populations of the goby, *Tridentiger obsculus*. *Japanese Journal of Ichthyology* **24**, 278-280.

Kneib, R. T. (1987). Seasonal abundance, distribution and growth of postlarval and juvenile grass shrimp (*Palaemonetes pugio*) in a Georgia, USA, salt marsh. *Marine Biology* **96**, 215-223.

Knight-Jones, E. W., and Morgan, E. (1966). Responses of marine animals to changes in hydrostatic pressure. *Oceanography and Marine Biology—Annual Review* **4**, 267-299.

Knowlton, R. T. (1974). Larval development processes and controlling factors in decapod Crustacea, with emphasis on Caridea. *Thalassia Jugoslavica* **10**, 139-158.

Koehn, J. D. and O'Connor, W. G. (1990). Distribution of freshwater fish in the Otway region, south-western Victoria. *Proceedings of the Royal Society of Victoria* **102**, 29-39.

Kushlan, J. A. (1981). Sampling characteristics of enclosure fish traps. *Transactions of the American Fisheries Society* **110**, 557-562.

Latz, M. I., and Forward, R. B. (1977). The effect of salinity upon phototaxis and geotaxis in a larval crustacean. *Biological Bulletin* **153**, 163-179.

Lawlor, L. R. (1976). Parental investment and offspring fitness in the terrestrial isopod *Armadillidium vulgare* (Latr.) (Crustacea: Oniscoidea). *Evolution* **30**, 775-785.

Lee, C. L., and Fielder, D. R. (1979). A mass migration of the freshwater prawn, *Macrobrachium australiense* Holthuis, 1950 (Decapoda, Palaemonidae). *Crustaceana* **37**, 219-222.

Lee, C. L., and Fielder, D. R. (1981). The effect of salinity and temperature on the larval development of the freshwater prawn, *Macrobrachium australiense* Holthuis, 1950 from south eastern Queensland, Australia. *Aquaculture* **26**, 167-172.

Lewis, F. G., and Stoner, A. W. (1983). Distribution of macrofauna within seagrass beds: an explanation for patterns of abundance. *Bulletin of Marine Science* **33**, 296-304.

Mashiko, K. (1982). Differences in both the egg size and the clutch size of the freshwater prawn *Palaemon paucidens* de Haan in the Sagami River. *Japanese Journal of Ecology* **32**, 445-451.

Mashiko, K. (1983a). Differences in the egg and clutch sizes of the prawn *Macrobrachium nipponense* (de Haan) between brackish and fresh waters of a river. *Zoological Magazine* **92**, 1-9.

Mashiko, K. (1983b). Evidence of differentiation between the estuarine and upper freshwater population inhabiting the same water system in the long-armed prawn *Macrobrachium nipponense* (de Haan). *Zoological Magazine* **92**, 180-185.

Mashiko, K. (1985). Comparison of survival and development between large and small neonates of a freshwater prawn under starvation conditions. *Zoological Science* **2**, 397-403.

Mashiko, K. (1990). Diversified egg and clutch sizes among local populations of the fresh-water prawn *Macrobrachium nipponense* (De Haan). *Journal of Crustacean Biology* **10**, 306-314.

Mashiko, K. (1992). Genetic egg and clutch size variations in freshwater prawn populations. *Oikos* **63**, 454-458.

Mashiko, K., Kawabata, S., and Okino, T. (1991). Reproductive and population characteristics of a few caridean shrimps collected from Lake Tanganyika, East Africa. *Archiv fur Hydrobiologica* **122**, 69-78.

Mauchline, J. (1988). Egg and brood sizes of oceanic pelagic crustaceans. *Marine Ecology Progress Series* **43**, 251-258.

McConaugha, J. R. (1985). Nutrition and larval growth. In 'Crustacean Issues'. (Ed F. R. Schram.) Vol. 2. 'Larval Growth.' (Ed A. M. Werner.) pp 127-154. (A. A. Balkema: Rotterdam).

McConaugha, J. R. (1988). Export and reinvasion of larvae as regulators of estuarine decapod crustacean populations. *American Fisheries Society Symposium* **3**, 90-103.

McDowall, R. M. (1987). Evolution and importance of diadromy. The occurrence and distribution of diadromy among fishes. *American Fisheries Society Symposium* **1**, 1-13.

McMahon, T. A. (1986). Hydrology and management in Australian streams. In 'Stream Protection: The Management of Rivers for Instream Uses'. (Ed. I. C. Campbell.) pp 23-44. (Water Studies Centre, Chisholm Institute of Technology: Melbourne.)

Mellors, J. E., and Marsh, H. (1993). Relationship between seagrass standing crop and the spatial distribution and abundance of the natantian fauna at Green Island, northern Queensland. *Australian Journal of Marine and Freshwater Research* **44**, 183-191.

Mitchell, B. D., and Richards, K. (1992). Macroinvertebrate communities in two salt affected tributaries of the Hopkins River, Victoria. *International Journal of Salt Lake Research* **1**, 81-102.

Moreira, G. S., McNamara, J. C., and Moreira, P. S. (1986). The effect of salinity on the upper thermal limits of survival and metamorphosis during larval development in *Macrobrachium amazonicum* (Heller) (Decapoda, Palaemonidae). *Crustaceana* **50**, 231-238.

Moreira, G. S., McNamara, J. C., Moreira, P. S., and Weinrich, M. (1980). Temperature and salinity effects on the respiratory metabolism of the first zoeal stage of *Macrobrachium holthuisi* Genofre & Lobão (Decapoda: Palaemonidae). *Journal of Experimental Marine Biology and Ecology* **47**, 141-148.

Morgan, E. (1984). The pressure responses of marine invertebrates: a psycho-physical perspective. *Zoological Journal of the Linnean Society* **80**, 209-230.

Morris, T. (1991). 'A Comparison of the Distribution and Abundance of the Freshwater Shrimp, *Paratya australiensis* and *Caridina mccullochi* (Decapoda: Atyidae), in the Lower River

Murray.' B. Sc. (Hons.) Thesis. (Department of Zoology, University of Adelaide: Adelaide) 60 pp.

Nelson, W. G. (1979). Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *Journal of Experimental Marine Biology and Ecology* **38**, 225-245.

Nelson, W. G. (1981). Experimental studies of decapod and fish predation on seagrass macrobenthos. *Marine Ecology Progress Series* **5**, 141-149.

Newton, G. M. (1994). 'Estuarine Zooplankton Ecology in Relation to Hydrological Cycles of a Salt-wedge Estuary.' Ph. D. Thesis. (School of Aquatic Science and Natural Resources Management, Deakin University: Warrnambool.) 281 pp plus appendices.

Nguyen Ngoc-Ho (1976). The larval development of the prawns *Macrobrachium equidens* and *Macrobrachium* sp. (Decapoda: Palaemonidae), reared in the laboratory. *Journal of Zoology, London* **178**, 15-55.

Nishino, M. (1980). Geographical variations in body size, brood size and egg size of a freshwater shrimp, *Palaemon paucidens* De Haan, with some discussion on brood habit. *Japanese Journal of Limnology* **41**, 185-202.

Nishino, M. (1984). Developmental variation in larval morphology among the freshwater shrimp *Palaemon paucidens* de Haan. *Lake Biwa Monographs* Number 1, 118 pp. (cited in Fincham and Figueras, 1986)

Norcross, B. L., and Shaw, R. F. (1984). Oceanic and estuarine transport of fish eggs and larvae: a review. *Transactions of the American Fisheries Society* **113**, 153-165.

Orth, R. J., Heck, K. L., and van Montrans, J. (1984). Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* **7**, 339-350.

Ortmann, A. E. (1894). A study of the systematic and geographical distribution of the decapod family Atyidae Kingsley. *Proceedings of the Academy of Natural Sciences of Philadelphia* **1894**, 397-416.

Paula, J. (1989). Rhythms of larval release of decapod crustaceans in the Mira Estuary, Portugal. *Marine Biology* **100**, 309-312.

Pearre, S. P. (1979). Problems in the detection and interpretation of vertical migration. *Journal of Plankton Research* **1**, 29-44.

Pihl, L., and Rosenberg, R. (1982). Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, western Sweden. *Journal of Experimental Marine Biology and Ecology* **57**, 273-301.

Raman, K. (1965). Observations on the fishery and biology of the freshwater prawn *Macrobrachium rosenbergii* de Man. *Marine Biological Association of India (Symposium Series)* **2**, 649-669.

Richards, K. (1990). 'The Effects of Increased Salinity on Macroinvertebrates in Two Tributaries of the Hopkins River, Victoria.' B. Sc. (Hons.) Thesis. (Faculty of Applied Science, Deakin University: Warrnambool.) 49 pp.

Richardson, B. J., Baverstock, P. R., and Adams, M. (1986). 'Allozyme Electrophoresis. A Handbook for Animal Systematics and Population Studies.' (Academic Press: San Diego.) 410 pp.

Rickleffs, R. E. (1990). 'Ecology.' Third edition. (W. H. Freeman: New York.)

Rickleffs, R. E., and Cox, G. W. (1972). Taxon cycles in the West Indian avifauna. *The American Naturalist* **106**, 195-219.

Riek, E. F. (1953). The Australian freshwater prawns of the family Atyidae. *Records of the Australian Museum* **15**, 237-254.

Rochanaburanon, T., and Williamson, D. I. (1976). Laboratory survival of larvae of *Palaemon elegans* Rathke and other caridean shrimps in relation to their distribution and ecology. *Estuarine and Coastal Marine Science* **4**, 83-91.

Rogers, J. S. (1972). Measures of genetic similarity and genetic distance. Studies in Genetics VII. University of Texas Publication 7213, pp 145-153.

Roux, J. (1925). Über einige süßwasserdekapoden (Atyidae) des Berliner zoologischen museums. *Zoologischer Anzeiger, Jena* 62, 145-154.

Roux, J. (1926). An account of Australian Atyidae. *Records of the Australian Museum* **15**, 237-254.

Rural Water Commission of Victoria (1990). 'Victorian Surface Water to 1987.' (Government Printer: Melbourne.)

Ruiz, G. M., Hines, A. H., and Posey, M. H. (1993). Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Marine Ecology Progress Series* **99**, 1-16.

Salman, S. D. (1987a). Larval development of *Caridina babaulti basrensis* Al-Adhub and Hamzah (Decapoda, Caridea, Atyidae) reared in the laboratory. *Crustaceana* **52**, 229-244.

Salman, S. D. (1987b). Larval development of *Atyaephyra desmaresti mesopotamica* Al Adhub (Decapoda, Atyidae) reared in the laboratory. *Investigación Pesquera* **51** (supplement 1), 27-42.

Sandifer, P. A. (1973). Effects of temperature and salinity on the larval development of grass shrimp, *Palaemonetes vulgaris* (Decapoda, Caridea). *Fishery Bulletin* **71**, 115-123.

Sandifer, P. A. (1975). The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay. *Estuarine and Coastal Marine Science* **3**, 269-279.

Sastry, A. N. (1983a). Pelagic larval ecology and development. In 'The Biology of Crustacea'. (Ed D. E. Bliss.) Vol 2. 'Behavior and Ecology.' (Eds F. J. Vernberg and W. B. Vernberg.) pp 214-282. (Academic Press: New York and London.)

Sastry, A. N. (1983b). Ecological aspect of reproduction. In 'The Biology of Crustacea'. (Ed D. E. Bliss.) Vol 8. 'Environmental Adaptations.' (Eds F. J. Vernberg and W. B. Vernberg.) pp 179-270. (Academic Press: New York and London.)

Schoener, T. W. (1983). Field experiments on interspecific competition. *The American Naturalist* **122**, 240-285.

Schoener, T. W. (1986). Resource partitioning. In 'Community Ecology: Pattern and Process'. (Eds J. Kikkawa and D. J. Anderson.) pp 91-126. (Blackwell Scientific: Melbourne.)

Sherwood, J. E. (1985). 'Hydrodynamics of South-West Victorian Estuaries.' Research Report 85/1. (Faculty of Applied Science and Technology, Warrnambool Institute of Advanced Education: Warrnambool.) 27 pp.

Sherwood, J. E., and Backhouse, G. N. (1982). 'Hydrodynamics of Salt Wedge Estuaries - Implications for Successful Spawning in Black Bream (*Acanthopagrus butcheri*).' Research Report 82/3. (Faculty of Applied Science and Technology, Warrnambool Institute of Advanced Education: Warrnambool.) 17 pp.

Sherwood, J. E., Mitchell, B. D., Magilton, C. J., Walsh, C. J., and Newton, G. M. (1988). 'A Study of the Barwon Estuary Complex.' Technical Report. (Department of Water Resources: Victoria.) 140 pp.

Shokita, S. (1973). Abbreviated larval development of fresh-water atyid shrimp *Caridina brevirostris* Stimpson from Iriomote Island of the Ryukyus (Decapoda, Atyidae). *Bulletin of the Science and Engineering Division, University of Ryukyus (Mathematics and Natural Sciences)* **16**, 223-231.

Shokita, S. (1976). Early life-history of the land-locked atyid shrimp, *Caridina denticulata ishigakiensis* Fujino et Shokita, from the Ryukyu Islands. *Carcinological Society of Japan, Researches on Crustacea* **7**, 1-10.

Shokita, S. (1979). The distribution and speciation of the inland water shrimps and prawns from the Ryukyu Islands. II. *Bulletin of the College of Science, University of Ryukyus* **28**, 193-278.

Shokita, S. (1981). Life-history of the family Atyidae (Decapoda, Caridea). *Aquabiology* **12,** 15-23.

Siegfried, C. A. (1980). Seasonal abundance and distribution of *Crangon franciscorum* and *Palaemon macrodactylus* (Decapoda, Caridea) in the San Francisco Bay delta. *Biological Bulletin* **159**, 177-192.

Sinclair, M. (1988). 'Marine Populations: An essay on Population Regulation and Speciation.' (University of Washington Press: Seattle and London.) 252 pp.

Skadsheim, A. (1984). Coexistence and reproductive adaptations of amphipods: the role of environmental heterogeneity. *Oikos* **43**, 94-103.

Sloane, R. D. (1984). Distribution, abundance growth and food of freshwater eels (*Anguilla* spp.) in the Douglas River, Tasmania. *Australian Journal of Marine and Freshwater Research* **35**, 325-339.

Smith, M. J., and Williams, W. D. (1980). Infraspecific variation within the Atyidae: A study of morphological variation within a population of *Paratya australiensis* (Crustacea: Decapoda). *Australian Journal of Marine and Freshwater Research* **31**, 397-407.

Smith, M. J., and Williams, W. D. (1982). Taxonomic revision of Australian species of *Atyoida* Randall (Crustacea: Decapoda: Atyidae), with remarks on the taxonomy of the genera *Atyoida* and *Atya* Leach. *Australian Journal of Marine and Freshwater Research* **33**, 343-361.

Smith, R. E. W. (1987). 'The Ecology of *Australatya striolata* (McCulloch and McNeill) (Decapoda: Atyidae).' Ph. D. Thesis. (Zoology Department, James Cook University of North Queensland: Townsville.) 190 pp.

Sneath, P. H. A., and Sokal, R. R. (1973). 'Numerical Taxonomy: the Principles and Practice of Numerical Classification.' (W. H. Freeman and Co.: San Francisco.) 573 pp.

Snedecor, G. W., and Cochran, W. G. (1980). 'Statistical Methods.' Seventh edition. (Iowa State University Press: Ames, Iowa.) 507 pp.

Sogard, S. M. (1989). Colonization of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. *Journal of Experimental Marine Biology and Ecology* **133**, 15-37.

Sokal, R. R., and Rohlf, F. J. (1981). 'Biometry: the Principles and Practice of Statistics in Biological Research.' Second edition. (W. H. Freeman: New York.) 859 pp.

Sorgeloos, P., Lavens, P., Leger, P., Tackaert, W., and Versichele, D. (1986). 'Manual for the culture and use of the brine shrimp, *Artemia* in aquaculture.' (Faculty of Agriculture, State University of Ghent: Belgium.) 319 pp.

Staples, D. J., and Vance, D. J. (1987). Comparative recruitment of the banana prawn, *Penaeus merguiensis*, in five estuaries of the south-eastern Gulf of Carpentaria, Australia. *Australian Journal of Marine and Freshwater Research* **38**, 29-45.

Stearns, S.C. (1992). 'The Evolution of Life Histories.' (Oxford University Press: Oxford.) 249 pp.

Steinberg, D., and Colla, P. (1991). 'LOGIT: A Supplementary module for SYSTAT.' (SYSTAT: Evanston, Illinois.) 225 pp.

Stoner, A. W. (1980). The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bulletin of Marine Science* **30**, 537-551.

Stoner, A. W. (1982). The influence of benthic macrophytes on the foraging behaviour of pinfish *Lagodon rhomboides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* **58**, 271-284.

Strathmann, R. R. (1982). Selection for retention or export of larvae in estuaries. In 'Estuarine Comparisons'. (Ed V. S. Kennedy.) pp 521-536. (Academic Press: New York.)

Strathmann, R. R. (1985). Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annual Review of Ecology and Systematics* **16**, 339-361.

Sulkin, S. D. (1984). Behavioral basis of depth regulation in the larvae of brachyuran crabs. *Marine Ecology Progress Series* **17**, 181-205.

Sulkin, S. D. (1990). Larval orientation mechanisms: the power of controlled experiments. *Ophelia* **32**, 49-62.

Sulkin, S. D., and Van Heukelem, W. (1982). Larval recruitment in the crab *Callinectes sapidus* Rathbun: an amendment to the concept of larval retention in estuaries. In 'Estuarine Comparisons.' (Ed V. S. Kennedy.) pp 505-520. (Academic Press: New York.)

Thorne, M. J., Fielder, D. R., and Greenwood, J. G. (1979). Larval behaviour of *Macrobrachium novaehollandiae* (De Man) (Decapoda, Palaemonidae). *Australian Journal of Marine and Freshwater Research* **30**, 11-23.

Thorp, J. H. (1976). Interference competition as a mechanism of coexistence between two sympatric species of the grass shrimp *Palaemonetes* (Decapoda: Palaemonidae). *Journal of Experimental Marine Biology and Ecology* **25**, 19-35.

Thorson, G. (1936). The larval development, growth and metabolism of Arctic marine bottom invertebrates compared with other seas. *Meddelelser om Grønland* **100**, 1-155.

Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* **25**, 1-45.

Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. *Oceanography and Marine Biology Annual Review* **19**, 513-605.

Underwood, A. J. (1986). The analysis of competition by field experiments. In 'Community Ecology: Pattern and Process'. (Eds J. Kikkawa and D. J. Anderson.) pp 240-268. (Blackwell Scientific: Melbourne.)

Underwood, A. J., and Fairweather, P. G. (1989). Supply-side ecology and benthic marine assemblages. *Trends in Evolution and Ecology* **4**, 16-20.

Vance, R. R. (1973a). On reproductive strategies in marine benthic invertebrates. *The American Naturalist* **107**, 339-352.

Vance, R. R. (1973b). More on reproductive strategies in marine benthic invertebrates. *The American Naturalist* **107**, 353-361.

Virnstein, R. W. (1987). Seagrass-associated invertebrate communities of the southeastern USA: a review. In 'Proceedings of the Symposium on Subtropical-Tropical seagrasses of the southeastern United States'. (Eds M. J. Durako, R. C. Phillips, and R. R. Lewis.) pp 89-116. (Florida Marine Research Publications, No. 42.)

Virnstein, R. W., and Howard, R. K. (1987a). Motile epifauna of marine macrophytes in the Indian River lagoon, Florida. I. Comparisons among three species of seagrasses from adjacent beds. *Bulletin of Marine Science* **41**, 1-12.

Virnstein, R. W., and Howard, R. K. (1987b). Motile epifauna of marine macrophytes in the Indian River lagoon, Florida. II. Comparisons between drift algae and three species of seagrasses. *Bulletin of Marine Science* **41**, 13-26.

Walker, T. M. (1972). 'A Study of the Morphology, Taxonomy, Biology, and Some Aspects of the Ecology of *Paratya australiensis* Kemp from Tasmania.' B. Sc. (Hons.) Thesis. (Zoology Department, University of Tasmania: Hobart) 267 pp.

Walker, T. M. (1979). 'A Study of Sympatry in Two Species of Palaemonidae.' Ph. D. Thesis. (Zoology Department, University of Tasmania: Hobart) 234 pp plus appendices.

Walsh, C. J. (1993). Larval development of *Paratya australiensis* Kemp, 1917 (Decapoda: Caridea: Atyidae) reared in the laboratory, with comparisons of fecundity and egg and larval size between estuarine and riverine environments. *Journal of Crustacean Biology* **13**, 456-480.

Welsh, B. L. (1975). The role of grass shrimp, *Palaemonetes pugio* in a tidal marsh ecosystem. *Ecology* **56**, 513-530.

Wenner, A. M. (1972). Sex ratio as a function of size in marine Crustacea. *The American Naturalist* **106**, 321-350.

Wilbur, H. M. (1984). Complex life cycles and community organization in amphibians. In 'A New Ecology. Novel Approaches to Interactive Systems'. (Eds P. W. Price, C. N. Slobodchikoff, and W. S. Gaud.) pp 195-224. (John Wiley and Sons: New York.)

Wilkinson, L. (1990). 'SYSTAT: The System for Statistics.' (SYSTAT: Evanston, Illinois.) 676 pp.

Williams, W. D. (1964). Subterranean freshwater prawns (Crustacea: Decapoda: Atyidae) in Australia. *Australian Journal of Marine and Freshwater Research* **15**, 93-106.

Williams, W. D. (1977). Some aspects of the ecology of *Paratya australiensis* (Crustacea: Decapoda: Atyidae). *Australian Journal of Marine and Freshwater Research* **28**, 403-415.

Williams, W. D. (1984). 'Salinity as a Water Quality Criterion and Determinant in Australia.' Research project completion report. (Department of Resources and Energy: Australia.) 73 pp.

Williams, W.D., and Allen, G. R. (1987). Origins and adaptations of the fauna of inland waters. In 'Fauna of Australia'. Volume 1A General Articles. (Eds. G. R. Dyne and D. W. Walton.) pp 184-201. (Australian Government Publishing Service: Canberra.)

Williams, W. D., and Smith, M. J. (1979). A taxonomic revision of Australian species of *Paratya* (Crustacea: Atyidae). *Australian Journal of Marine and Freshwater Research* **30**, 815-832.

Williamson, D. I. (1969). Names of the larvae in the Decapoda and Euphasiacea. *Crustaceana* **16**, 210-213.

Williamson, D. I. (1972). Larval development in a marine and a freshwater species of Macrobrachium (Decapoda, Palaemonidae). *Crustaceana* **23**, 282-298.

Williamson, D. I. (1982). Larval morphology and diversity. In 'The Biology of Crustacea'. (Ed D. E. Bliss.) Vol 2. 'Embryology, Morphology and Genetics.' (Ed L. G. Abele.) pp 43-110. (Academic Press: New York and London.)

Willows, R. I. (1987). Intrapopulation variation in the reproductive characteristics of two populations of *Ligia oceanica* (Crustacea: Oniscidea). *Journal of Animal Ecology* **56**, 331-340.

Winkler, D. W., and Wallin, K., (1987). Offspring size and number: a life history model linking effort per offspring and total effort. *The American Naturalist* **129**, 708-720.

Wong, J. T. Y. (1987). Responses to salinity in larvae of a freshwater shrimp, *Macrobrachium nipponense* (de Haan), from Hong Kong. *Aquaculture and Fisheries Management* **18**, 203-207.

Wood, C. E. (1967). Physioecology of the grass shrimp, *Palaemonetes pugio*, in the Galveston Bay estuarine system. *Contributions to Marine Science* **12**, 54-79.

Wooldridge, T., and Erasmus, T. (1980). Utilization of tidal currents by estuarine zooplankton. *Estuarine and Coastal Marine Science* **11**, 107-114.

Xiao, Y., Liu, R., and Cui, Y. (1988). Recruitment of postlarval prawns, *Penaeus orientalis*, to a tidal estuary of Jiaozhou Bay, China. *Chinese Journal of Oceanology and Limnology* **6**, 290-299.

Xiao, Y., and Greenwood, J. G. (1992). Distribution and behaviour of *Acetes sibogae* Hansen (Decapoda, Crustacea) in an estuary in relation to tidal and diel environmental changes. *Journal of Plankton Research* **14**, 393-407.

Yokoya, Y. (1931). On the metamorphosis of two Japanese freshwater shrimps, *Paratya compressa* and *Leander paucidens*, with reference to the development of their appendages. *Journal of the College of Agriculture, Tokyo Imperial University* **11**, 75-170.

Young, D. K., and Young, M. W. (1978). Regulation of species densities of seagrass-associated macrobenthos: evidence from field experiments in the Indian River estuary, Florida. *Journal of Marine Research* **36**, 569-593.

Young, P.C. (1981). Temporal changes in the vagile epibenthic fauna of two seagrass meadows (*Zostera capricorni* and *Posidonia australis*). *Marine Ecology Progress Series* **5**, 91-102.

Yúfera, M., and Rodríguez, A. (1985). Effect of prey density on feeding rates during larval rearing of *Palaemon serratus* Pennant (Crustacea: Palaemonidae). *Aquaculture* **50**, 31-38.