Temporal variability in the demography of the palaemonid prawn *Macrobrachium intermedium* in two seagrasses

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**ABSTRACT:** Spatial and temporal variations in the demography of the palaemonid prawn *Macrobrachium intermedium* were investigated in Port Hacking, New South Wales, Australia. Populations in 2 adjacent seagrass meadows, *Zostera capricorni* and *Posidonia australis*, were sampled monthly over 3 yr (1976 to 1978) using a small beam trawl. For most population variables there were no consistent differences between meadows and both meadows showed similarly variable temporal changes. Neither meadow consistently supported larger populations nor recruited more juveniles. In 1976 abundance was greater in *Zostera* than *Posidonia*, the reverse occurred in 1977, whilst there was no difference in 1978. Seasonal and annual changes in abundances were basically similar in both populations and repeated in all 3 yr. Abundances peaked between spring and autumn and were smallest in winter. In both meadows, abundances were greater in 1976 and 1978 than in 1977. Breeding and recruitment of juveniles occurred throughout the year, although ovigerous females were most abundant in summer-autumn and juveniles recruited predominantly in late summer/autumn and in spring. At least 2 cohorts of juveniles were produced annually, the spring cohort being the largest. In 1976 and 1978 more juveniles recruited to the *Zostera* meadow whilst in 1977 more recruited to the *Posidonia* meadow. There were no consistent differences in the size structures of the 2 populations. During spring, juveniles predominated until summer-autumn when populations consisted of adults and only a few juveniles, after which the numbers of adults declined to virtually disappear by winter. Females grew faster and attained a larger size than males. Most individuals survived at least 15 mo, but longevity was estimated to be up to 2 yr. For most population variables, year-to-year variations within each meadow were as great as differences between the 2 meadows within each year. These variations were most likely due to factors extrinsic to the seagrasses themselves. This study stresses the need for long-term studies to verify the consistency of spatial differences between sites.

**INTRODUCTION**


The palaemonid prawn *Macrobrachium intermedium* Stimpson (hereafter *Macrobrachium*) is one of the most abundant prawns inhabiting estuarine areas and in particular, seagrass meadows, in southeastern Australia (Young 1981, Howard 1984). Its life history has been documented for an estuary in southeast Tasmania (Walker 1979) and in Western Port, Victoria (Howard 1981, 1984, Howard & Lowe 1984). Here I report spatial and temporal variations in the abundances, recruitment, reproduction, growth and size structures of populations of *Macrobrachium* in 2 adjacent meadows of different species of seagrass in Port Hacking (New South Wales, Australia) among different seasons over 3 yr. Previously, Young (1981) documented temporal variability in an assemblage of macrofauna in these meadows and concluded that much variability was unexplained. Much of the variability may have been masked, however, in his multispecies analysis. In this study I provide a detailed analysis of the demography of the most abundant species (*Macrobrachium*) in Young’s study, which may give greater insight into factors influencing the distribution and abundance of organisms in these seagrasses. I compare my findings to those reported previously for *Macrobrachium* by Walker (1979), Howard (1981, 1984) and Howard & Lowe (1984) and discuss the demography of *Macrobrachium* in relation to other prawns in seagrasses and other estuarine and nearshore environments.

**MATERIALS AND METHODS**

**Study area.** Port Hacking (34°04.6' S, 151°06.6' E), New South Wales, Australia (Fig. 1), is a drowned river valley, with marine conditions except during periods of heavy rainfall. The study area was located on an intertidal sandbank near Costens Point, with adjacent *Zostera capricorni* Aschers. and *Posidonia australis* Hook. f. meadows. These meadows cover an area of ca 0.69 km² and are covered by about 1.3 m of water at high tide. Although the sandbank is intertidal, its basin shape retained a layer of water 10 to 15 cm deep at low tide.

The *Posidonia* meadow was 10 cm deeper than the *Zostera* meadow, but this difference was much smaller than seasonal and annual variations in depth of water at each site (Fig. 2). Temperatures and salinities of water were similar in both meadows throughout the study (Fig. 2). Maximum temperatures occurred...
between December and March whilst minimum temperatures occurred in July or August of each year (Fig. 2). Salinity was fairly consistent throughout the study and showed no annual patterns, although lower salinities were recorded in October 1976 and March 1978 (Fig. 2).

Sampling. Sampling was done as outlined by Young (1981). Sampling was conducted monthly, over a 3 yr period (1976 to 1978), at night on the full moon and within 0.5 h of high tide. Using a beam trawl, 1 m wide and 0.5 m high with 2 mm mesh in the body and 1 mm mesh in the cod end of the net, 3 replicate trawls were taken in each meadow on each sampling occasion. Trawls were over a distance of 50 m on adjacent but non-overlapping strips of seagrass. The beam trawl did not damage the seagrasses, nor did 3 trawls reduce the population sizes of Macrobrachium (Wadley 1980). Prior to trawling, the depth, temperature and salinity of water were recorded at each site. Samples were retained and the number of Macrobrachium in each trawl were recorded.

When possible, 300 Macrobrachium were randomly chosen from each meadow on each sampling occasion and examined in the laboratory. Carapace length (CL; distance from the posterior orbital margin of the eye to the posterior dorsal mid lateral margin of the carapace) was recorded for each prawn. Measurements were made to the nearest 0.1 mm using a binocular microscope with an ocular micrometer. The sex of each individual was recorded and the number of ovigerous females noted. Sex could not be accurately determined for specimens < 3.1 mm CL and so individuals below this size were considered as 'juvenile'.

**RESULTS**

**Variations in abundances**

Relative abundances of Macrobrachium differed significantly between sites and this differed among seasons (significant interaction in ANOVA; Table 1). Neither site consistently had greater or lesser abundances in any season. In all seasons except winter, abundances were greater in Zostera than in Posidonia in 1976, the opposite occurred in 1977, and there was no significant difference in 1978 (Fig. 3). Despite the significant site × season interaction, abundances at both sites experienced similar temporal changes throughout the study. In all 3 yr, smallest abundances occurred in winter (July), but there was no consistent seasonal pattern at either site with respect to greatest abundances (SNK tests based on data in Fig. 3). Periods of greatest abundances usually occurred from summer to autumn (November to March). Months also differed within seasons, although the non-significant site × months interaction indicated that such effects were similar at both sites. Abundances at each site differed among similar seasons in different years (SNK tests based on data in Fig. 3), although annual variations were similar at both sites. At both sites abundances were greater in 1976 and 1978 than in 1977. Annual variations in abundances at each site were

<table>
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<th>Source of variation</th>
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<th>Total abundance a</th>
<th>No. of ovigerous females b</th>
<th>Percentage of ovigerous females b</th>
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Recruitment of juveniles

Some recruitment of juveniles occurred at both sites throughout each year, although the number of juveniles caught varied between sites and among seasons (Fig. 3). No statistical analysis on this data was done due to heteroscedasticity of the variances. Nonetheless, there appeared to be no consistent pattern across years as to which site recruited most juveniles. In 1976 and 1978 juveniles were generally more abundant in the Zostera meadow, whereas in 1977 they were more abundant in the Posidonia meadow (Fig. 3). Temporal changes in the number of juveniles caught were generally similar at both sites and repeated in all 3 yr. In each year, abundances of juveniles peaked in autumn (February to June), then decreased until late winter/spring (August to September), when a second (usually smaller) peak occurred. This was followed by decreases in abundances until autumn (Fig. 3). The timing of peak periods of recruitment were generally similar at both sites in each year, but varied among years. Abundances of juveniles during each peak period varied between sites within each year and at each site among years (Fig. 3). In each year, except in the Zostera meadow in 1976, the autumn peak in recruitment appeared the larger (Fig. 3).

Despite some recruitment in all months, analyses of size frequency data (see ‘Growth’ below) showed that 2 distinct juvenile cohorts occurred each year (Fig. 4). In all 3 yr the first cohort appeared in late summer/autumn (February/March) and the second in late autumn to spring (April/May to October). In 1976, the first juvenile cohort was clearly evident in the Zostera meadow in February and in the Posidonia meadow in March (Fig. 4). The second cohort first appeared in the Zostera meadow in May and in the Posidonia meadow in June (Fig. 4). In 1978 a third cohort appeared in spring (September) in the Zostera meadow.

Breeding

The smallest sized ovigerous female Macrobrachium caught was 5.1 mm CL. The size and time that females first became ovigerous was the same in both meadows and in all 3 yr. Some females from the first cohort recruited each year (summer/autumn) became ovigerous in late spring, whereas some from the second cohort (autumn/spring) were ovigerous in early summer. This occurred at a size of 5.0 to 5.4 mm CL. The majority of females, however, were not ovigerous until 5.8 to 6.0 mm CL in late summer/autumn (see Fig. 4 for an example of 1976).

Both the abundances of ovigerous females and the percentage of all females that were ovigerous were analysed to determine patterns of breeding. The timing and intensity of peaks in abundances of ovigerous females varied significantly between sites in each year and among years (ANOVA; Table 1; Fig. 5). Ovigerous females were caught in all months of the study except May 1977 (Fig. 5), although they were generally more abundant in summer (November to March) in all years (SNK tests based on data in Fig. 5). The patterns of temporal change in abundances of ovigerous females were similar to those for abundances of the total populations. Neither meadow consistently had the greatest number of ovigerous females in autumn or winter, although in spring and summer in all years they were greater than variations in abundances between sites within each year.
Fig. 4. *Macrobrachium intermedium*. Size structures of populations in each meadow throughout 1976. Date of sampling is in top right hand corner of each graph. Diagonally shaded bars: juveniles; stippled bars: males; open bars: non-ovigerous females; black bars: ovigerous females.
more abundant in the Posidonia meadow (SNK tests based on data in Fig. 5). The percentage of all females that were ovigerous also varied between sites and this differed among seasons (significant interaction in ANOVA; Table 1), but trends were different and more variable than changes in abundances of ovigerous females (Fig. 5). There was no pattern among years, for either site, as to the season in which the greatest or least percentages occurred. Periods of peak percentages of ovigerous females usually occurred, however, in late summer/autumn, while troughs occurred in winter/spring of most years. As for abundances of ovigerous females, the percentage of ovigerous females was greater in Posidonia in spring and summer whilst in autumn and winter there was no difference between meadows.

In both populations there was a progressive change in the size of ovigerous females throughout each year. In spring, ovigerous females were mainly large (Fig. 4) and came from the overwintering population. Over late spring/summer the mean size of ovigerous females decreased as females from that year's recruitment spawned for the first time, and the numbers of overwintering prawns declined. Throughout late summer/autumn the mean size of ovigerous females increased as the first-time spawners grew (Fig. 4). This pattern was generally repeated in all 3 years.

Size structures of populations

There were no consistent differences in the size structures of the 2 populations, despite the number of cohorts present and their relative predominance varying. There was an annual pattern of change in size structures similar to both populations and generally repeated in all 3 yr. When the populations were first sampled in February 1976 they were bimodal, representing separate male and female size groups (Fig. 4). From this time until June 1976 the large male and female size classes gradually disappeared, whilst 2 juvenile size groups appeared and subsequently increased in size. The first juvenile cohort appeared in February/March (late summer) and the second in April/May (autumn) (Fig. 4). During this time, size distributions became polymodal. By August 1976 the populations consisted mainly of juveniles and a few individuals of most of the other size groups. Throughout September to November (spring), size distributions remained polymodal, due to the presence of at least 2 male and 2 female size groups and a juvenile size group at each site. The populations remained this way until January/February 1977, when the smaller and larger size groups merged to form a single male size group and 2 female size groups (Fig. 4). From February to April 1977 the larger male and female size classes gradually disappeared and a new juvenile size class appeared, as in the same period in 1976. Due to low densities there was no clear pattern until September/October 1977. Populations at this time were polymodal and similar to those at the same time in 1976. Changes in the size structures of the populations until the end of 1978 were similar to those described for 1976/77 (Gray 1985).

Growth

Growth of Macrobrachium was estimated from the monthly size frequency data. Individual cohorts of different mean sizes were extracted for each month using probability paper (Cassie 1954) and plotted against time. Due to the long recruitment periods and merging of size groups, it was difficult to obtain discrete size cohorts from the data. Some size groups were bimodal, although they could not be separated reliably by the analysis.

Although variable, changes in the mean sizes of cohorts were similar in both populations in all 3 yr. Females grew faster and attained a larger size than males (Fig. 6). Growth in the cohorts of juveniles was usually quite rapid, about 0.5 mm CL mo$^{-1}$. Sometimes in winter/spring, however, little growth occurred (e.g. Zostera 1976), presumably due to continual recruitment keeping mean sizes low. Male and female cohorts increased at about 0.5 mm CL mo$^{-1}$ and
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0.7 mm mo⁻¹, respectively, but these rates decreased as cohorts reached their mean maximum sizes (Fig. 6). Mean maximum sizes of cohorts were similar in both meadows in all 3 yr; males about 4.8 mm CL; females about 6.0 mm CL. The largest individuals caught were 6.6 mm CL (males) and 9.2 mm CL (females). Differences in the rate of growth in different seasons were not determined because these were masked by prawns being different sizes in each season, low sample sizes during winter and continual recruitment throughout spring.

Longevity for Macrobrachium in Port Hacking was estimated to be up to 2 yr for females and 1.5 yr for males, but most individuals did not appear to live past 15 mo.

DISCUSSION

Spatial and temporal variations in abundances

The data from this study suggests that species of seagrass had no effect on the abundances, or on any other demographic variable, of Macrobrachium. Neither meadow consistently supported the largest population, nor recruited greater numbers of juveniles. Previous studies have attributed differences in the abundances of organisms in different seagrasses to quantitative and qualitative differences in the seagrasses (Kikuchi & Peres 1977, Stoner 1980, 1983a, b, Martin & Cooper 1981, Lewis 1984, Middleton et al. 1984, Bell & Westoby 1986). Variations in the abundances of Macrobrachium between the Zostera and Posidonia meadows described in this study were probably not attributable, however, to morphological differences between the seagrasses. Gray 1991 (companion paper) found that there were no consistent differences in the abundances of Macrobrachium in Zostera and Posidonia meadows at several other localities in 1983 and 1984. It was also unlikely that differences in abundances between sites were caused by differing environmental factors, as these meadows were adjacent and influenced by similar water temperatures and salinities. Likewise, the difference in the depth of water between the 2 sites was also unlikely to have caused the variations in abundances of Macrobrachium between the 2 meadows. The difference in depth was the same across all 3 yr, whereas differences in abundances between the 2 meadows changed among years. Nonetheless, depth of water has been shown to affect the distribution and abundance of other prawns in seagrasses (Young & Carpenter 1977, Baden & Pihl 1984, Emmerson 1986; see Gray 1991). It was most likely that the spatial variability in the abundances of Macrobrachium between the 2 meadows was due to factors extrinsic to the 2 sites themselves, namely variable recruitment, as proposed for the whole vagile assemblage by Young (1981).

The general seasonal pattern of abundance of Macrobrachium in Port Hacking differed slightly from those found by Walker (1979) and Howard (1981, 1984) for populations in higher latitudes in southeastern Australia, where minimum abundances usually occurred during spring. The period of greatest abundance, however, was similar in all studies. Gray (1991), on the other hand, showed that the general seasonal pattern of abundance of Macrobrachium at several localities in other estuaries in the Sydney region was the same as that found in this study. Although the mechanism(s) causing the autumn/winter decreases in abundances of Macrobrachium in Port Hacking (and in other nearby estuaries; see Gray 1991) are not known, I hypothesise that Macrobrachium temporarily move away from the seagrasses into deeper water in winter. Other methods used to catch seagrass fauna (e.g. poisoning and coring) also caught fewer Macrobrachium in winter than at other times (Gray unpubl.), and Macrobrachium has been caught down to depths of 35 m (Walker 1979). During late winter/spring some individuals re-colonize the seagrasses; only a few of the largest sized prawns return, the majority being recruiting juveniles. Similar seasonal depth migrations and overwintering in deeper waters have been reported for other estuarine/nearshore palaemonid prawns (Hogland 1943, Forster 1951, Nixon & Oviatt 1973, Baden & Pihl 1984, Emmerson 1986). There have been, however, only a few reported seasonal movements of seagrass-associated caeande prawns (Kikuchi 1974, Howard 1984, Emmerson 1986), presumably as most are reported resident species. Many of the species that are reported to be permanent...
residents may, in fact, move among habitats. Further research is needed to assess this. In contrast, there have been numerous reports of seasonal movements of several species of penaeid prawns which inhabit seagrasses only as juveniles (Young 1978, Bauer 1985b, Staples et al. 1985).

Year-to-year variations in the seasonal abundances of Macrobrachium in each meadow were generally greater than variations between the 2 meadows within each year. This emphasises the need to consider the consistency of spatial variations between sites over periods greater than 1 yr. Annual variations in abundances were, however, similar at both sites, which may reflect the closeness of sites and similar recruitment events. Low abundance and little recruitment for many species of macrofauna occurred in these meadows in 1977, but not for all species of carids (Young 1981).

Demographic patterns

Some breeding and recruitment took place year round at both sites, which differed from the results obtained by Walker (1979) and Howard (1981). They found that ovigerous females and juveniles were only present between spring and autumn, when they were most abundant in this study. Latitudinal differences in the length of periods of breeding have been recorded for many marine organisms, including palaemonid prawns (Alon & Stancyk 1982, Berglund 1984), and have usually been attributed to differing temperatures of water. Generally, periods of breeding and recruitment are reduced in higher latitudes. Year-round breeding and recruitment has been observed, however, in other temperate and tropical seagrass-associated carids (Heck 1977, Dugan 1983, Emmerson 1986, Bauer 1989). Female Macrobrachium are capable of breeding at least 2 or 3 times in one breeding season (Walker 1979, Gray unpubl.), and may be capable of continuous breeding thereafter, similar to other palaemonid prawns (Bauer 1989).

In spring and summer in all 3 yr, ovigerous female Macrobrachium were more abundant in the Posidonia meadow, which may have been due to this meadow occurring on the outer edge of the sand bank. Gray (1991), however, found that this did not always occur in these same meadows in 1983/1984, nor did it occur at other places in nearby estuaries. Nevertheless, the abundance of ovigerous females in spring primarily depends on the number of overwintering females, and hence females immigrating from deeper water would come across the Posidonia meadow before the Zostera meadow. Other ovigerous female palaemonids migrate into deeper water, usually leaving estuaries, to spawn (Baden & Pihl 1984, Emmerson 1986), but there are no reports of females moving back into shallower water. The gradual seasonal changes in the sizes of ovigerous females throughout each year were similar to those found in other prawn populations which are characterised by 2 reproductive and recruitment periods a year (Hoglund 1943, Alon & Stancyk 1982, Baden & Pihl 1984, Evans & Tallmark 1984).

There was no consistent pattern as to which meadow received more juvenile recruits. Variations in the magnitude of recruitment between the Zostera and Posidonia meadow in each year were as great as the year-to-year variations in recruitment in each meadow. These variations most likely reflect differences in the numbers of recruits at settlement or variations in post-settlement mortality. Gray (1991) showed that there was no effect of species of seagrass on the number of juvenile Macrobrachium caught in other seagrass meadows in nearby estuaries. Despite the variations in the timing and magnitude of recruitment between sites and among years, the number of juvenile cohorts produced each year was similar to both meadows and was generally repeated in all 3 yr. At least 2 distinct size/age cohorts were produced each year: the first (summer/autumn recruits) probably originated from the overwintering prawns that spawned in late spring/summer the previous year and the second (autumn/spring recruits) from the summer/autumn spawners. This pattern of recruitment and production of cohorts differed to that found by Walker (1979) and Howard (1981), but is similar to many other species (carids and penaeids) of prawns (Hoglund 1943, Young 1978, Kennedy & Berber 1981, Alon & Stancyk 1982, Baden & Pihl 1984, Evans & Tallmark 1984, Rothlisberg et al. 1985, Emmerson 1986). Walker (1979), Howard (1981) and Howard & Lowe (1984) found that juveniles were only present between spring and autumn with only one peak, usually in mid-summer, producing a single cohort. Howard (1981) also reported that larvae of Macrobrachium were only present during those periods. Similar intra-specific latitudinal differences in the patterns of reproduction and recruitment have been reported among populations of other prawns (Beck & Cowell 1976, Alon & Stancyk 1982, Berglund 1984, Rothlisberg et al. 1985).

Female Macrobrachium in Port Hacking grew faster and reached a greater mean and maximum CL (and overall length) than males, as found by Walker (1979) and Howard (1981), and also found for other palaemonid prawns (Hoglund 1943, Forster 1951, Beck & Cowell 1976, Truesdale & Mermilliod 1979, Berglund 1981, Alon & Stancyk 1982, Emmerson 1986). Only in some freshwater species of Macrobrachium have males been found to attain a larger size than females (Ling 1969, Koshy 1971, Guest 1979).
Estimates of longevity for *Macrobrachium* vary between 1.5 yr (Walker 1979) and 2 yr (Howard 1981, this study). Estimates of longevity of other estuarine/marine palaemonid prawns also vary between 1 to 1.5 yr (*Palaemonetes pugio*; Alon & Stancyk 1982), and 2 to 3 yr (*Palaemon squilla, P. elegans, P. adspersus, P. pacificus*; Holglund, Forster 1951, Baden & Pihl 1984, Emmerson 1986).

This study shows that the differences in the demography of *Macrobrachium* between the 2 sites sampled varied from year to year. These differences between the 2 populations were unique to each year. If this study had been done over 1 yr, the results and conclusions would have totally differed. This emphasises the need to consider the consistency among years of variations in demography between populations. The variability in demography both within and between the 2 populations of *Macrobrachium* in Port Hacking was as great as those found for other palaemonid prawns over larger spatial scales (between sites in different estuaries) in other studies (Alon & Stancyk 1982, Emmerson 1986). Clearly, there is a need for future research to investigate spatial variations in demography of these prawns over various scales.

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