The ecology of *Macrobrachium* species (Decapoda, Palaemonidae) in a coastal stream in north Queensland.

Thesis submitted by

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as partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Department of Zoology at the James Cook University of North Queensland.

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institute of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

I. J. KNEIPP

8 May 1979

ABSTRACT

Five species of *Macrobrachium* occur in the study area, Bluewater Creek, 27 km northwest of Townsville. They are *M. latidactylus* (Thallwitz, 1891), *M. tolmerum* (Riek, 1951), *M. australiense* (Holthuis, 1950), *M. novae-hollandiae* (de Man, 1908) and *M.* species A, probably an undescribed species. A multivariate morphometrics study gave support to the separation of *M.* sp. A and *M. tolmerum* which are morphologically very similar.

Field studies were undertaken in order to infer causal relationships between environmental factors and distribution patterns. These were complemented by laboratory studies of responses to selected environmental factors.

Sampling of adults using baited funnel traps at sixteen sites on thirteen monthly occasions suggested salinity to be a major environmental factor. The downstream limit of distribution of each species appeared to be controlled by salinity, but a range of salinity tolerance was suggested, increasing in the order *M. australiense*, *M. tolmerum*, *M.* sp. A, *M. latidactylus*, *M. novae-hollandiae*. Individuals of *M. novae-hollandiae* and *M. latidactylus* were not found above the zone of tidal influence. Given suitable local conditions, *M. tolmerum* and *M.* sp. A could be found the full length of the study area and *M. australiense* the full length of the freshwater reach. In the freshwater reach, riffle areas were dominated by *M. tolmerum* and large pools by *M. australiense*. Substrate, current and oxygen regime were suggested as being important factors in this pattern.

Larvae in plankton samples were almost exclusively stage I. Those of *M. tolmerum* and *M. latidactylus* could not be distinguished. Larvae of *M. australiense* were rare in plankton samples. Peak production of *M. tolmerum* larvae was in the period January to April, during highest stream flow. Estimated densities reached a maximum of 345 m^{-3} in sites where larvae could be assigned to *M. tolmerum*. In sites further downstream where *M. latidactylus* larvae could also have been present, maximum estimated density was 578 m^{-3}.

Laboratory studies of temperature/salinity tolerance of adult *M. australiense*, *M. tolmerum* and *M. latidactylus* demonstrated increasing salinity tolerance in that order. From response surface analysis, predicted survival time at optimal temperatures and 32°/oo salinity was greater than 20 days for *M. latidactylus*, 20 days for *M. tolmerum* and two days for *M. australiense*.

Optimum salinities for larval development were 10.1°/oo for *M. australiense*, 17.9°/oo for *M. latidactylus* and 25.5°/oo for *M. tolmerum*. *M. australiense* was the only species of these three whose larvae completed development in fresh water. At optimum temperature and salinity, the minimum time for larval development was four days in *M. australiense*, 21 days in *M. latidactylus* and 38 days in *M. tolmerum*.

Salinity requirements of larvae do not appear to limit upstream dispersal of *M. latidactylus* or *M. tolmerum* in the study area, but could do so in longer water courses.

Laboratory studies of substrate preference indicated that both *M. tolmerum* and *M. australiense* preferred a substrate which provided shelter. In a short-term competitive situation, *M. tolmerum* was able to partially displace *M. australiense* from the preferred substrate. Preference for moving water over still water was shown by *M. tolmerum*. The relative substrate and current responses of *M. tolmerum* and *M. australiense* are considered the main determinants of their distribution patterns in the freshwater reaches of the study area. Laboratory studies demonstrated little difference in the tolerance of low levels of dissolved oxygen by *M. tolmerum* and *M. australiense*. However, competition for the more favourable riffle area oxygen regime would tend to produce the observed distribution patterns since *M. tolmerum* was the dominant species.

M. australiense has abbreviated larval development and a small number of large eggs. It is the most freshwater of the species studied, in both larval and adult tolerances. *M. tolmerum* and *M. latidactylus* which have higher salinity tolerance as adults and a requirement for saline water as larvae, have much longer larval development and produce many more, smaller eggs. These three species therefore fall into the established pattern of life cycle changes concomitant with the evolution of the ability of decapod crustaceans to inhabit fresh waters. Examples from the *Macrobrachium* suggest that evolution of large body size of larvae and abbreviation of larval development are important in the colonization of fresh water, the former reducing osmotic stress

and the latter reducing displacement of larvae by flowing water. A paucity of planktonic food in flowing fresh waters may also provide some selective pressure for abbreviation of larval development and for lecithotrophy in the planktonic stages that remain.

It is concluded that distribution patterns of *Macrobrachium* species in the study area are largely determined by temperature, salinity, substrate and current whose effects are interconnected with competition between species and adaptation of the life cycle to fresh water.

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1 INTRODUCTION

The genus *Macrobrachium* Bate, 1868 contains over 100 species of palaemonid prawn which occupy a range of habitats. Although adults of the majority of *Macrobrachium* species are restricted to fresh water, some inhabit either fresh or brackish water, some are restricted to brackish water only and one species is known to complete its life cycle in the sea (Holthuis, 1950; Williamson, 1972). The genus has a world wide tropical and subtropical distribution although no single species occurs over the whole of this range. Some species have wide Indo-West Pacific distributions while others are restricted to the larger land masses. The southern extensions of Africa and South America appear to have presented barriers to dispersal since many species are restricted to either the eastern or western side of one of these continents. Some species have ranges extending to the interior of continents while others are restricted to the peripheries (Holthuis, 1950). Members of the genus are present throughout Australia except in the extreme southwest and the south-east including southern New South Wales, Victoria and Tasmania (Riek, 1951). Because of taxonomic problems and the lack of a comprehensive survey, the number of species of *Macrobrachium* in Australia is uncertain.

Much of the past research on *Macrobrachium* species has been stimulated by their potential for human exploitation. Some species have been traditionally fished in the developing countries and studies of such exploited populations include those by John (1957), Ibrahim (1962), Rao (1965, 1967), George (1969),

Rajyalakshmi and Ranadhir (1969) and Rasalan *et al.* (1969). Interest in artificial culture of *Macrobrachium* species began in the 1960s and the works of Ling (1962, 1969a, 1969b) and Ling and Merican (1962) provided basic biological data and techniques for successful culture of *M. rosenbergii* (de Man). Since then, considerable research effort has been aimed at refining the methods of culturing this species, with particular emphasis on diet (New, 1976). Dobkin (1969) pointed out the advantage of abbreviated larval development in aquaculture and listed several species of *Macrobrachium* in which this was known or suspected to occur. Species other than *M. rosenbergii* which have been investigated with a view to aquaculture include *M. malcolmsonii* (Milne Edwards) (Ramachandra *et al.*, 1972), *M. acanthurus* (Wiegmann) and *M. carcinus* (L) (Dobkin *et al.*, 1974), *M. americanum* Bate (Arana, 1977) and *M. lar* (Fabricius) (Atkinson, 1977).

Several of the above studies have investigated larval development in the context of aquaculture. However, larval development *per se* has also been studied in *M. acanthurus* (Dobkin, 1971; Choudhury, 1970, 1971c), *M. asperulum* (Von Martens) (Shokita, 1977), *M. australiense* Holthuis (Fielder, 1968), *M. carcinus* (Lewis and Ward, 1965; Choudhury, 1971a), *M. equidens* (Dana) (Ngoc-Ho, 1976), *M. formosense* Bate (Shokita, 1970), *M. hendersodayanum* (Tiwari) (Jalihal and Sankolli, 1975), *M. idella* (Hilgendorf) (Pillai and Mohamed, 1973), *M. intermedium* (Stimpson) and *M. niloticum* (Roux) (Williamson, 1972), *M. novae-hollandiae*

(de Man) (Greenwood *et al.*, 1976), *M. olfersii* (Wiegmann) (Dugger and Dobkin, 1975) and *M. shokitai* Fujino et Baba (Shokita, 1973).

Ecological studies on *Macrobrachium* species have been confined largely to observations of distribution patterns and their correlation with environmental factors. Works of this nature include those of Johnson (1965, 1968), Rajyalakshmi (1975), Abele and Blum (1977), Horne and Beisser (1977) and Ohno *et al.* (1977). However, Ville (1971) carried out laboratory studies of temperature and salinity tolerance in order to explain the distribution pattern of *M. vollenhovenii* (Herklots). Consequently, while there exists a large amount of data on some aspects of the biology of a few species, the ecology of natural populations of most species of *Macrobrachium* remains virtually unknown.

Apart from taxonomic works, there have been only four publications concerned specifically with *Macrobrachium* species in Australia. They are Denne, 1968 (osmotic and ionic regulation), Fielder, 1968 and Greenwood *et al.*, 1973 (larval development) and Ruello *et al.*, 1973 (reproductive behaviour).

The present study was therefore designed to contribute to the understanding of the ecology of *Macrobrachium* species in northern Australia. Its immediate aim was to elucidate the major environmental factors determining the distribution and abundance of species present in a north Queensland coastal stream, Bluewater Creek. The strategy was to infer causality by correlation of distribution patterns with environmental factors and to complement this with studies of responses to these factors in the laboratory.

This approach requires selection of the environmental factors to be studied because of the impracticability of monitoring all parameters. Salinity is an obvious factor for consideration because of the range of salinities in which adults of various *Macrobrachium* species have been recorded (Holthuis, 1950). Furthermore, although adults may inhabit fresh water, optimal conditions for larval development of some species may be in saline water (Ling, 1969a; Choudhury, 1971a, 1971c; Pillai and Mohamed, 1973; Dugger and Dobkin, 1975). The ecology of such species must involve a complex interaction of larval and adult salinity requirements.

Other environmental factors which have been implicated as influencing distribution patterns of *Macrobrachium* species are substrate, current, dissolved oxygen, temperature, pH and the concentration of various cations, particularly of calcium (Johnson, 1965, 1968; Rajyalakshmi, 1975; Abele and Blum, 1977; Horne and Beisser, 1977; Ohno *et al.*, 1977). Concentration of cations and pH should not show great variation within the fresh-water reaches of the Bluewater Creek study area. Therefore, provided their values were such as not to exclude *Macrobrachium* species, they should not be important ecological factors. Also, food preferences and the availability of food were considered unlikely to be important in the distribution of *Macrobrachium* species in the present study area. It has been shown that *M. malcolmsonii*, *M. carcinus* and *M. rosenbergii* are omnivorous (Ibrahim, 1962; Lewis *et al.*, 1966; Rao, 1967). In natural conditions, *M. rosenbergii* is an opportunistic feeder (John, 1957) and has been maintained experimentally on a variety of diets (New, 1976).

Similarly, Bray (1978) found that the stomach contents of *M. intermedium* reflected the relative abundance of food sources rather than feeding preferences. For such species, although availability of food may limit population density, the composition of food sources should not be an important determinant of distribution patterns.

The emphasis of this study has been on distribution patterns rather than population density and the environmental factors given most attention were temperature, salinity, substrate, current, dissolved oxygen and interspecific competition. Stream depth was also considered because although *per se* it was unlikely to be of importance, there was a possibility of correlated factors particularly light intensity, being involved. Consideration was given to biotic factors especially modification of the inorganic substrate by allochthonous material and growth of aquatic macrophytes, and predation.

In the following presentation, where possible, relevant discussion is carried out within each section. However, because of the dependance of some conclusions on the results of more than one section, it has been convenient to retain considerable synthesis and discussion until the final section.

2 THE STUDY AREA AND ENVIRONMENTAL PARAMETERS

2.1 GENERAL DESCRIPTION OF THE STUDY AREA

Bluewater Creek enters the Coral Sea at 19° 9' S, 146° 36' E, 27 km northwest of Townsville. It rises in the coastal escarpment (Paluma Range) and takes a relatively direct course across the 20 km wide coastal plain (Fig. 1). The catchment area is approximately 93 km^2 (Queensland Irrigation and Water Supply Commission). Maximum elevation of the stream in its coastal plain section does not exceed 30 m above sea level (Royal Australian Survey Corps, Sheet 8259, 1:100,000 series). Width of the water surface does not exceed 30 m in the freshwater reaches. There is only one major confluence, where Pine Creek joins Bluewater Creek near the escarpment (Fig. 1). In the headwaters beyond the coastal plain there is little permanent water.

Rocks of the escarpment in the vicinity of the headwaters of Bluewater Creek are Upper Carboniferous granite, adamellite and granodiorite (Wyatt *et al.*, 1970). The present course of the stream is through Holocene fluvial deposits (sands and water-worn gravels) derived from the escarpment (Hopley and Murtha, 1975). Because of the nature of these deposits, the stream carries little sediment load except during flooding.

The lower estuary (below site 16 in Fig. 1) consists of a relatively uniform and straight channel gradually increasing in width from 25 m to a maximum of approximately 100 m at the stream mouth. Above the lower estuary, the stream exhibits

three characteristic forms:-

(i) large pools generally 25 to 30 m wide, up to 2 m deep and up to 2 km long;

(ii) riffle zones;

(iii) sand zones, where the stream bed has been filled with coarse sand through which for most of the year the stream proper (up to 10 m wide and 0.5 m deep) meanders.

In its natural state, the vegetation structure of the area is open woodland. *Eucalyptus alba*, the dominant tree species towards the coast, is replaced by *E. drepanophylla* towards the escarpment. Ground cover is dominated by the grasses *Heteropogon contortus* and *Themeda australis*. Extensive cattle grazing practice has modified plant communities in much of the area. Riparian vegetation however, has not been directly interfered with, and is dominated by *Melaleuca leucodendron* and the grasses *Themeda australis* and *Heteropogon contortus*.

The climate of the Townsville region is classified as Aw in the Köppen system (Hopley and Murtha, 1975). It is characterized by high temperatures and markedly seasonal but variable rainfall (Table 1). For the period 1926 to 1965, approximately 71% of rainfall occurred in the months January, February and March. Average annual rainfall for Townsville (1,129 mm) is lower than in areas immediately to the north (Ingham 2,129 mm) and south (Proserpine 1,814 mm). This is due largely to orientation of the coastline which lies parallel to the southeast trade winds in the Townsville region. Consequently,

winter orographic rains which fall in areas to the north and south are rarely received by Townsville. Summer rainfall too, is higher in northerly areas, because of the influence of the inter-tropical convergence zone whose mean maximum southerly extension is in the vicinity of Ingham, 95 km northwest of Townsville (Hopley and Murtha, 1975). Rainfall data for the period January 1975 to August 1976 recorded by the landholder in the upper catchment of Bluewater Creek, are given in Table 2.

Monthly discharge volumes for Bluewater Creek for the period January 1975 to August 1976 (Queensland Irrigation and Water Supply Commission) are also given in Table 2. These indicate a strong seasonality of flow, but that there was some flow throughout the period of study from August 1975 to August 1976.

In order to approximately characterize the fresh water of Bluewater Creek, results of analysis of a sample from the middle reach of the stream (10th January, 1978) are presented in Table 3. Methods were as recommended by the American Public Health Association (1975). Particularly notable is the low level of Ca^{++} (3.6 mgl^{-1}). World average fresh water contains 30 $\mu g\ l^{-1}$ of Ca^{++} (Bayly and Williams, 1973).

The upper limit of tidal influence in Bluewater Creek is approximately 4 km from the stream mouth. Within the tidal reach, salinity at any point in space and time depends on a complex interaction of tidal regime, fresh water flow rate and stream bottom topography. The salinity regime is described in Section 2.3.2.

2.2 THE SAMPLING SITES

Sixteen sampling sites were chosen, extending from within the tidal zone to near the escarpment (Fig. 1). Permanent habitats for *Macrobrachium* species rapidly diminished with progression upstream onto the escarpment. The sampling sites furthest upstream (1, 2 and 3) were located on Pine Creek, a tributary of Bluewater Creek proper. The most seaward sampling site was at a position which was indicated by preliminary sampling to be beyond the downstream limit of *Macrobrachium* for most of the year. Each site consisted of an 18 m transect located in order to be as internally homogeneous as possible. No sites were located in shallow sand bottom areas as these were totally unsuitable for *Macrobrachium* because they provided no shelter. Photographs of typical areas of the stream are presented in Plates 1 to 3. Further characteristics of the sites are given in Table 4.

2.3 SPECIFIC ENVIRONMENTAL PARAMTERS

2.3.1 TEMPERATURE

Bottom temperatures were recorded with a Hamon Model 602 Temperature-Salinity Bridge, at between 1500 and 1700 hours on each sampling day. A reading was taken adjacent to each trap set in the sampling programme (Section 4). Mean values of the five readings taken at each site on each sampling occasion are plotted in Fig. 2. Actual sampling dates are given in Table 13. Sites 9, 10 and 11 were not sampled in August 1976 because there had been considerable human disturbance of the area by swimming and wading.

The minimum mean site temperature (20.5°C) occurred at sites 1, 3, 4, 5 and 6 in September 1975. The maximum (40.0°C) occurred at site 15 in October 1975). This extreme high was due to low fresh water flow coupled with little tidal mixing, resulting in a layer of saline water (17°/oo bottom salinity) being trapped under the surface fresh water. Such conditions prevent normal heat exchange by convection which would result in highest temperatures occurring at or near the surface. There was no shading by riparian vegetation at site 15. At sites not influenced by saline water (1 to 8) the maximum mean site temperature recorded was 33.0°C at sites 7 and 8 in December 1975.

Diel fluctuations in bottom temperature were not monitored on a regular basis, but measurements at various times of the year indicated ranges of up to 6 C° in riffle areas and up to 4 C° in pools of approximately 1 m depth.

The lowest early morning bottom temperature recorded in a riffle area was 19.7°C. Therefore, excluding the abnormally high temperatures occurring in stratified saline water, the overall annual range was approximately from 19.7°C to 33.0°C.

While both diel and annual temperature range in Bluewater Creek were considerably greater than, for example, in the Malayan stream studied by Bishop (1973), temperature conditions in the freshwater reaches could not be described as harsh. The most notable feature of the temperature regime was the extreme temperatures occurring in stratified saline water. Even without the compounding effect of salinity, temperatures of 40°C would be expected to be lethal for *Macrobrachium*.

2.3.2 SALINITY AND CONDUCTIVITY

Bottom salinity was determined with a Hamon Model 602 Temperature-Salinity Bridge, and five readings were taken at each site as for those of temperature (Section 2.3.1). Readings were taken between 1500 and 1700 hours and never when water level at any of the sampling sites was elevated by tidal influence. Mean site values of bottom salinity on each sampling occasion are plotted in Fig. 2.

There is a complex interaction between tidal regime, fresh water flow and stream bottom topography determining salinity levels in the tidal reach of Bluewater Creek. From site 9 to site 16 the stream consists of a series of five pools with differential elevations such that with dry season levels of fresh water flow, they are interconnected by short riffle zones. Consequently, an incoming tide may raise the water level at for example, sites 15 and 16 without influencing the sites in pools further upstream. A diagrammatic representation of the relationship of sites 9 to 16 to stream bottom topography is presented in Fig. 3. Observation of the maximum level of incoming tides and reference to tide height predictions for Townsville (Queensland Department of Harbours and Marine) has allowed the following conclusions regarding tidal influence:-

(i) water level at site 16 is raised almost every day and often twice daily;

(ii) water level at sites 10 and 11 is raised on approximately 20 days per month;

(iii) water level at site 9 is raised on approximately five days per month at spring tides.

Whether or not a rise in water level is accompanied by an increase in salinity, depends upon the salinity profile of the water mass immediately downstream of the point in question. A small rise could involve merely an influx of surface fresh water.

The effect of increased fresh water flow is to restrict the upstream extent of tidal influence by reducing the amount by which a given tide raises the water level and by lowering the salinity regime.

Fig. 2 shows marked seasonality of the salinity pattern concomitant with the fresh water flow regime (Table 2). Irregularity of salinity levels in a downstream progression from site 9 to site 16 in the dry season months was due to stream bottom topography (Fig. 3). Sites 14 and 15 were shallow riffle area sites and thus often exhibited lower salinities than the deeper but more upstream sites 10 to 13.

The maximum upstream extent of tidal influence in Bluewater Creek is approximately 50 m upstream of site 9.

In such a dynamic system, any attempt to describe the salinity regime, short of continuous monitoring, must be only approximate. Nevertheless, the monthly recordings of the present study do indicate seasonal trends. Furthermore, individuals of *Macrobrachium* are relatively mobile and should generally be able to avoid adverse salinity conditions where a choice exists, rather than die. Therefore, examination of instantaneous abundance and salinity levels should provide useful information on salinity preferences.

The salinity meter used for the above determinations was not capable of resolving variations in salinity of the fresh water in the study area. However, subsequent to the main sampling programme it was possible to carry out a series of *in situ* conductivity measurements using a Y.S.I. Model 33 Salinity - Conductivity - Temperature Meter. This instrument was calibrated with standard KCl solutions. No variation of conductivity with depth could be detected in the freshwater sites. The results of five series of bottom measurements corrected to 25°C, are given in Table 5. There was a slight increase in conductivity from upstream to downstream freshwater sites. There was also some seasonal progression at the upstream sites, with highest values immediately prior to, and lowest values during the wet season (February to April 1978).

2.3.3 SUBSTRATE

The inorganic substrate of *Macrobrachium* habitats in the study area falls naturally into two categories, coarse sand and water-worn stones.

Particle size analysis of a sample of typical sand substrate as determined by dry seiving was:-

MESH SIZE (mm)	% AIR DRY WEIGHT RETAINED (MEAN OF 3 x 1,000 g SUBSAMPLES)
4.0	4.66
2.0	39.95
1.0	46.93
0.5	6.96
0.25	0.96
0.063	0.51
<0.063	0.03

This aggregate is classified as very coarse sand on the Wentworth (1922) scale.

The stone substrate pieces are only moderately water-worn and exhibit irregular shapes (Plate 4). The maximum dimension of pieces in a typical sample ranges from 40 mm to 200 mm. It thus falls into the cobble gravel class of the Wentworth scale.

In the study area there appeared to be little variation in the two substrate types. Usually, transition between substrates occurred over a distance of a few metres. Sampling sites 1, 9, 10, 14 and 15 were in stone substrate areas while the remaining sites were on sand.

The physical substrate was subject to modification by the following biotic influences:-

(i) Plant Growth. In freshwater conditions, *Spirogyra* sp. was abundant at certain times of the year in riffle area sites. Its peak growth occurred in August and September when flow rates were low. It decreased in abundance with the onset of summer, possibly because of increasing water temperature. Two species of aquatic macrophytes were abundant in large pools of the freshwater reach. These were *Limnophila indica* and a *Nitella* species. Both were most abundant in the December - January period, but were dislodged by flooding. *Limnophila indica* was concentrated near the stream banks where it formed dense beds, on occasions 1 m deep and 1 m wide. *Nitella* sp. at its peak growth also formed dense

beds along the stream banks, but in addition occurred in small patches (20 cm diameter) throughout the pools, producing up to 50% substrate cover. Dense beds of these macrophytes were not present when the sampling sites were chosen, and by chance, none of the transects included such plant growth during the sampling period. Site 2, however, was for part of its length adjacent to a bed of *Nitella* sp. during December 1975.

(ii) Plant Debris. Large pools throughout the study area were subject to considerable input and accumulation of leaf litter, principally from *Melaleuca leucodendron*. Accumulation of leaf litter reached a maximum immediately prior to the wet season flushing. In areas of sand substrate, this was an important source of shelter for *Macrobrachium* individuals.

2.3.4 DEPTH

Depth measurements were made with a graduated rod. Mean depth at each site on each sampling occasion is plotted in Fig. 4.

Total range of mean depths recorded during the study period was from 14 cm (site 15, July 1976) to 156 cm (site 5, January 1976). The marked decrease in depth at site 3 in January 1976 was due to deposition of sand during flooding in December. This was the only site which exhibited significant instability of substrate during the study period.

2.3.5 CURRENT

Stream surface velocity was measured at each site on each sampling occasion by timing the passage of a float over a measured 10 metres. The plastic float was almost filled with water in order to present as small a profile to the air as possible. Surface velocities are plotted in Fig. 4.

For many months, while the stream was in fact flowing (Table 2), velocities at the sampling sites were too low to be measured. These velocities are plotted as zero values in Fig. 4. The maximum velocity recorded was 1.0 m sec $^{-1}$ but this would have been exceeded during flood peaks. The Irrigation and Water Supply Commission recorded velocities (in the vicinity of sites 7 and 8) of 1.80 m sec $^{-1}$ on 17th February 1974 and 1.44 m sec $^{-1}$ on 4th March 1976.

2.3.6 DISSOLVED OXYGEN

Equipment was not available for *in situ* measurements of dissolved oxygen concentration during the sampling programme. Sampling of water for laboratory determinations was considered inadequate since in many instances, stratification of salinity and hence dissolved oxygen would have made accurate sampling difficult.

The results of several series of *in situ* measurements made subsequent to the sampling programme are given in Table 6. These were bottom measurements taken at between 1500 and 1700 hours with a Y.S.I. Model 57 oxygen meter. Levels were generally close to or above saturation values. Highest percent saturation values

overall were recorded at sites 10 to 16 in saline water and were presumably due to the presence of considerable phytoplankton biomass, since no macrophytes were present on those occasions.

A further series of measurements in the vicinity of sites 4, 5 and 6 and in the riffle area immediately upstream, was taken in order to estimate the extent of diel fluctuation. This was in January 1979, when stream flow rate was low, temperatures high, and growth of aquatic macrophytes at around its annual peak. Five bottom readings at 1 m intervals along a fixed transect were taken at each site on each occasion. Results are presented in Table 7. There was a significant fall in oxygen concentration overnight in both the pool and riffle areas. However, this was more marked at the pool site, presumably because of the presence there of considerable plant biomass and accumulated leaf litter, and the lack of mixing and aeration by turbulence.

2.3.7 BIOTIC FACTORS

2.3.7.1 FOOD SOURCES

The most likely sources of food for *Macrobrachium* species in Bluewater Creek are organic detritus (with its associated bacterial and fungal flora), periphyton and bottom dwelling insect larvae.

For the reasons presented in Section 1, food sources were considered unlikely to be important in the distribution of *Macrobrachium* species in the study area.

2.3.7.2 COMPETITORS

Competition between species of *Macrobrachium* is likely to be of some importance in their ecology and is treated in Sections 4 and 6.

Other species in the study area which are possible competitors of *Macrobrachium* are the freshwater crayfish *Cherax wasselli*, atyid shrimps (*Caridina nilotica* and an unidentified *Caridina* species) and juveniles of the mud crab, *Scylla serrata*.

2.3.7.3 PREDATORS

From specimens occasionally taken in the present sampling programme and from the results of other studies (L. Penridge, pers. comm.) the following fish species are present in the study area and are potential predators of *Macrobrachium*:-

Lates calcarifer (silver barramundi)

Oxyeleotris lineolatus (sleeper)

Therapon unicolor (spangled perch)

Neosilurus hyrtlii (Hyrtl's tandan)

Anguilla reinhardti (freshwater eel)

Two species of cormorant, *Phalacrocorax sulcirostris* and *P. melanoleucos* which are also potential predators of *Macrobrachium* were regularly seen on Bluewater Creek.

3 *MACROBRACHIUM* SPECIES OF BLUEWATER CREEK

3.1 INTRODUCTION

The members of the genus *Macrobrachium* constitute a taxonomically difficult group because of the relatively few morphological characters showing obvious differences between species and because of a high level of intraspecific variation in these characters. Taxonomic characters which have been used are almost all associated with the rostrum and second pair of pereiopods. This is exemplified by the key of Holthuis (1950) for the Indo-West Pacific species of *Macrobrachium*, in which only three of the 69 dichotomies involve other aspects of morphology. Many of the characters used are shapes, relative dimensions of segments, and numbers of teeth or protruberances of the exoskeleton, rather than clear cut presence or absence of features.

The high level of intraspecific variation results from sexual dimorphism, allometric growth and geographic variation. Sexual dimorphism is particularly evident in the second pereiopods and males tend to show greater interspecific differences in these appendages than females. This has resulted in the taxonomy of the genus being based almost entirely on males. Even in males, however, the specific characteristics of the second pereiopods are usually only fully developed in large individuals. Thus the taxonomist must have some knowledge of the size range exhibited by individuals of the population in question.

A further complicating factor in observed individual variation is that of limb loss and regeneration, which, because of allometric growth, can add to variation in form of the second pereiopods for a given body size. Handling of animals during the

present study has shown that these appendages are readily autotomised in some species.

Geographic variation is expected in species for which land and sea present barriers to dispersal. Even without extensive isolation, intraspecific geographic variation is possible, as has been shown in populations of the atyid shrimp *Caridinopsis chevalieri* from West Africa (Rutherford, 1975). Intraspecific geographic variation is important in the taxonomy of the Australian *Macrobrachium* species, as evidenced by the number of subspecies designated by Riek (1951).

The most authoritative taxonomic work to include Australian *Macrobrachium* species is that of Holthuis (1950), but its coverage of the Australian species is incomplete. Riek (1951) revised the Australian freshwater Palaemonidae but that work has some deficiencies because:-

(i) new species were described on the basis of small numbers of individuals from restricted localities with little or no account being taken of intraspecific variation;

(ii) specimens of an undescribed species (*M.* sp. A of the present study) are present in the type material of *M. tolmerum* Riek in the Australian Museum.

Furthermore, one species *(M. latidactylus)* which had not been collected at the time of Riek's revision, is now

known to be present in Australia.

Because of the need for further revision of the Australian *Macrobrachium*, and uncertainty regarding the future status of the taxa of this study, specimens have been lodged in the Australian Museum (registration numbers P28173 - P28177) and descriptions of material from Bluewater Creek are now given. In these descriptions an attempt has been made to quantify as many variables as possible and to take account of intraspecific variation. Even so, they cannot be regarded as descriptions of the species as a whole, since the material is from such a restricted geographical range.

Adults were defined as individuals of 13 mm or greater rostral carapace length and samples were taken at random. Rostral carapace length (RCL) was measured from the tip of the rostrum to the posterior dorsal margin of the carapace; total length was measured from the tip of the rostrum to the tip of the telson with the abdomen extended.

Females are mentioned only in their major differences from males.

3.2 *M. LATIDACTYLUS* (THALLWITZ, 1891)

The distribution of this species was given by Holthuis (1950) as the Malay Peninsula and Malay Archipelago. It was not included in the Australian freshwater *Macrobrachium* by Riek (1951). However, it has been collected from the Mowbray River north of Cairns (Australian Museum P14437) and from the Daintree, Mossman, North Johnstone, South Johnstone and Herbert Rivers (L. Penridge

pers. comm.).

Ten males and 10 females (6 ovigerous) from Bluewater Creek have been lodged in the Australian Museum (P28173).

DESCRIPTION OF MATERIAL FROM BLUEWATER CREEK

ADULT MALES

Size range of 50 individuals examined was 13.8 mm - 29.8 mm rostral carapace length (31.8 mm - 60.9 mm total body length).

Rostrum shape is shown in Fig. 5 and the numbers of dorsal and ventral rostral teeth are given in Table 8; rostrum tip falls short of end of scaphocerite by 0.5 mm to 2.5 mm; dorsal teeth evenly spaced except posterior two which are more widely spaced; 3 or 4 dorsal rostral teeth behind orbit.

Left and right second pereiopods markedly different in size and in nature of the chelae (Fig. 5). Larger second pereiopod, when extended anteriorly, reaches beyond rostrum by a distance equal to total body length in large individuals; relative proportions of segments of large second pereiopod are given in Table 8; palm greatly swollen and dactylus markedly curved towards immovable finger; cutting edges of fingers with teeth along their entire length, teeth decrease in size distally, are irregularly spaced and vary in number from 7 to 15 on dactylus and 6 to 11 on immovable finger; all segments spinose with spines larger and more dense on mesal and lateral surfaces; sparse setation along lateral surface of palm and dactylus. Small second pereiopod half the length of the larger in large individuals; merus, carpus, palm and fingers of approximately

equal length; palm only slightly swollen; fingers with dense array of long non-plumose setae on opposed surfaces and up to 4 small teeth located proximally on cutting edges, usually fewer on immovable finger than on dactylus (Fig. 5); surface of all segments smooth.

Inner pair of lateral spines exceed apex of telson; 4 plumose and 3 to 5 non-plumose setae on either side of apex; ratio of distance between posterior dorsal spines and apex (telson distance 3, Fig. A1) to telson length is given in Table 8.

Carapace smooth, except antero-laterally below hepatic spine where small spines are present.

ADULT FEMALES

Second pereiopods approximately equal; smaller in relation to body size than the smaller second pereiopod of large males; merus, carpus, palm and fingers all approximately equal in length; palm slightly swollen; fingers with only sparse setation, 1 or 2 small teeth proximally on cutting edges; fingers free of spines; merus, carpus and palm spinose, less densely so than large second pereiopod of males.

Eggs small (0.6 mm x 0.4 mm) and range from approximately 500 to 1,600 per egg mass; recently deposited egg masses dark green in colour.

COMMENTS

The *M. latidactylus* material from Bluewater Creek does not show any major morphological differences from the

descriptions of Thallwitz (1891), de Man (1892), Cowles (1914) and Holthuis (1950).

3.3 *M. NOVAE-HOLLANDIAE* (DE MAN, 1908)

Holthuis (1950) gave the distribution of *M. novae-hollandiae* as Queensland, New South Wales and New Caledonia, in fresh water. However, Riek (1951) stated the species had never been collected from fresh water. The present study (Section 4) and the work of Greenwood *et al* (1976) suggest that *M. novae-hollandiae* is a brackish water species.

Nine males from Bluewater Creek have been lodged in the Australian Museum (P28174).

DESCRIPTION OF MATERIAL FROM BLUEWATER CREEK

ADULT MALES

Size range of 20 individuals examined was 17.2 mm - 27.4 mm rostral carapace length (36.4 mm - 60.8 mm total body length).

Rostrum shape is shown in Fig. 6 and the number of dorsal and ventral rostral teeth given in Table 9; rostrum reaches or slightly exceeds (by up to 1 mm) tip of scaphocerite; dorsal teeth evenly spaced except for larger space between two most posterior; 2 or rarely 3 teeth behind orbit.

Second pereiopods similar in size and shape; long and slender compared with other species of Bluewater Creek; relative length increases with body size, in larger individuals when fully extended may exceed rostrum by more than total body

length; proportions of segments of second pereiopods given in Table 9; ratio of length of palm to length of fingers increases markedly with body size; palm straight and of equal width throughout in larger males, tends to be swollen in small males; all segments spinose, density of spines increases with body size; fingers and palm of small individuals with markedly fewer spines; spines of carpus and palm tend to be in longitudinal rows, most noticeably so in larger individuals; fingers of smaller individuals with only a few non-plumose setae, larger individuals with two rows of short plumose setae either side of each cutting edge; fingers with 2 teeth located proximally on cutting edges.

Inner pair of lateral telson spines exceed apex; 4 plumose and 4 non-plumose setae on either side of telson apex; ratio of distance between posterior dorsal telson spines and apex (telson distance 3) to telson length given in Table 9.

Carapace smooth.

ADULT FEMALES

Second pereiopods resemble those of smaller males with palm slightly swollen.

Eggs small and numerous (similar to *M. tolmerum*), light brown in colour when recently deposited.

COMMENTS

There are some differences between the material from Bluewater Creek and the specimen described by de Man (1908), namely the carapace of the present material is devoid of spinules and the second pereiopods are relatively shorter and thicker.

However, these differences are probably a function of size, the specimen described by de Man being 118 mm in total length, while the maximum total length in the present sample was 60.8 mm.

3.4 *M. AUSTRALIENSE* HOLTHUIS, 1950

The distribution of *M. australiense* was given by Holthuis (1950) as Northern Territory, Queensland, New South Wales and South Australia, in fresh water. However, the distributions given for the subspecies described by Riek (1951), *M. australiense australiense*, *M. a. eupharum*, *M. a. cristatum* and *M. a. crassum*, include only Queensland and New South Wales localities.

Ten males and 10 females (7 ovigerous) from Bluewater Creek have been lodged in the Australian Museum (P28175).

DESCRIPTION OF MATERIAL FROM BLUEWATER CREEK

ADULT MALES

Size range of 50 individuals examined was 20.4 mm - 32.5 mm rostral carapace length (40.8 mm - 67.8 mm total body length).

Rostrum shape is shown in Fig. 7 and the number of dorsal and ventral rostral teeth given in Table 10; rostrum shows considerable variation in orientation and relative length, being relatively longer and more elevated in orientation in smaller individuals; rostrum exceeds scaphocerite by 0.5 - 3.5 mm; dorsal teeth evenly spaced along median part of rostrum but increase in spacing towards rostrum tip and behind orbit; 2 or

rarely 3 teeth behind orbit.

Second pereiopods usually slightly unequal in size but otherwise similar; in large individuals when fully extended anteriorly may exceed rostrum tip by almost total body length; proportions of segments of second pereiopods given in Table 10; carpus and merus approximately cylindrical, palm slightly dorso-ventrally compressed and may be laterally swollen particularly in smaller individuals; all segments abundantly spinose; fingers densely clothed in plumose setae (Fig. 7), length and density of setae varies between individuals with fingers of small individuals comparatively bare; each finger has two large teeth located proximally on cutting edge, teeth constant in number but may be bidentate in form.

Inner pair of lateral telson spines exceed apex; 2-3 plumose and 2-3 non-plumose setae either side of apex; ratio of distance between posterior dorsal spines and apex (telson distance 3) to telson length given in Table 10.

Carapace smooth.

ADULT FEMALES

Second pereiopods smaller in relation to body size than those of males; palm slightly swollen; 2 small teeth located proximally on cutting edge of each finger.

Eggs large (1.1 mm x 0.7 mm) and range in number from approximately 30 to 120; recently deposited egg mass light green in colour.

COMMENTS

While this form of *M. australiense* does not correspond exactly to any of the subspecies described by Riek (1951), it is considered to belong to the *australiense* complex because of the proportions of segments of the second pereiopods and the characteristic pattern of teeth and setation on the fingers of these appendages. The form of the rostrum, which is longer and more elevated than in any of Riek's subspecies, is considered not to exclude this species from the *australiense* complex. Examination of material in the Australian Museum has shown that rostral form is highly variable between localities, and that the present material lies at one end of the observed range.

3.5 *M. TOLMERUM* RIEK, 1951.

At the time of the original description of this species it was known only from the type locality, Macrossan, Queensland (Riek, 1951). However, it is present in many streams north of Townsville, and because of the salinity tolerance of larval stages (Section 7) may not be restricted to the Australian mainland.

Fourteen males and 6 females from Bluewater Creek have been lodged in the Australian Museum (P28176).

DESCRIPTION OF MATERIAL FROM BLUEWATER CREEK

ADULT MALES

Size range of 41 individuals examined was 21.4 mm -

38.0 mm rostral carapace length (47.5 mm - 83.3 mm total body length).

Rostrum shape shown in Fig. 8; number of dorsal and ventral rostral teeth given in Table 11; rostrum does not exceed and may fall short of scaphocerite by up to 2 mm; dorsal rostral teeth evenly spaced, 2 or 3 behind orbit.

Second pereiopods rarely equal in size but usually almost so; relative length increases with body size; in larger individuals when fully extended anteriorly, may exceed rostrum tip by total body length; proportions of segments of second pereiopods given in Table 11; ratio of length of palm to length of fingers increases markedly with size; carpus and merus approximately circular in cross section, propus slightly dorso-ventrally compressed; palm tends to be slightly swollen in smaller individuals; all segments of second pereiopods abundantly spinose, rough to the touch; no dense setation on fingers (Fig. 8); large teeth located proximally on cutting edges of both fingers form characteristic pattern in large males but little developed in small males; 3 or 4 (rarely 5) teeth on dactylus, 5 or 6 (rarely 4 or 7) teeth on immovable finger.

Inner pair of lateral telson spines exceed apex of telson; 7 plumose and 5 non-plumose setae on either side of apex; ratio of distance between posterior dorsal telson spines and apex (telson distance 3) to telson length given in Table 11.

Carapace smooth.

ADULT FEMALES

Second pereiopods resemble those of small males but

are shorter in relation to body size; palm slightly swollen; teeth on proximal half of cutting edges of fingers small.

Eggs small (0.6 mm x 0.4 mm) and range in number from approximately 800 to 6,000 per egg mass; recently deposited egg mass dark green in colour.

COMMENTS

The 15 type specimens of *M. tolmerum* Riek in the Australian Museum consist of two species, both of which occur in Bluewater Creek. On examining the *M. tolmerum* type material in December 1976, the specimen labelled as 'male' holotype was found to be a female. It is assumed that this is due to a misplacement of specimens and that a large male included with the paratypes is the true holotype, since that specimen is the size of the holotype given by Riek (1951). The specimen labelled as the female allotype is of another species but the mislabelled 'male holotype' and presumed true male holotype are of the same species. Anticipating that when the Australian *Macrobrachium* are further revised the latter two specimens will become the types of *M. tolmerum*, this name is used here for similar specimens from Bluewater Creek. The other species represented in the type material of *M. tolmerum* is apparently undescribed, and similar specimens from Bluewater Creek are referred to here as *M.* species A.

The description of *M. tolmerum* given by Riek (1951) contains insufficient detail to distinguish between *M. tolmerum* and *M.* species A.

3.6 *M.* SP. A (UNDESCRIBED)

The distribution of this species is unknown.

Twenty males and 2 females from Bluewater Creek have been lodged in the Australian Museum (P28177).

DESCRIPTION OF MATERIAL FROM BLUEWATER CREEK

ADULT MALES

Size range of 41 individuals examined was 15.8 mm - 28.3 mm rostral carapace length (35.0 mm - 59.6 mm total body length).

Rostrum shape shown in Fig. 9; number of dorsal and ventral rostral teeth given in Table 12; rostrum tip falls short of end of scaphocerite by 1.0 mm - 3.5 mm; dorsal rostral teeth evenly spaced except posterior 3 which are slightly more widely spaced; 3 - 5 (usually 4) teeth behind orbit.

Second pereiopods rarely equal in length but usually almost so; relative length increases with body size; in larger animals when fully extended anteriorly may exceed rostrum by total body length; proportions of segments of second pereiopods given in Table 12; ratio of length of palm to length of fingers increases with body size; carpus and merus approximately circular in cross section, palm slightly dorso-ventrally compressed; palm not swollen in smaller individuals; all segments abundantly spinose, rough to the touch; no dense setation on fingers; fingers with large teeth proximally on cutting edges (Fig. 9) in large individuals, not well developed in small individuals; 3 or 4 (rarely 2 or 5) teeth on dactylus, 2-9 (usually 5-7)

on immovable finger.

Inner pair of lateral telson spines exceed apex; usually 7 plumose and 5 non-plumose setae on either side of apex; ratio of distance between posterior dorsal telson spines and apex (telson distance 3) to telson length given in Table 12.

Carapace smooth.

ADULT FEMALES

Second pereiopods smaller in relation to body size than in males; palm not swollen; teeth present on proximal half of cutting edges of fingers but very small and fewer than in males.

Eggs small and numerous (similar to *M. tolmerum*); egg mass light brown in colour when in middle stage of development, recently deposited egg masses not seen.

COMMENTS

Specimens of *M. tolmerum* and *M.* sp. A are morphologically very similar and it was necessary to go to some length in order to determine the status of the two forms. The conclusion is based on the following data:-

(i) Morphological Differences.

(a) Meristic Features. The number of dorsal rostral teeth ranges from 8 to 11 in *M. tolmerum* and 10 to 13 in *M.* sp. A; the number of ventral rostral teeth ranges from 3 to 5 in *M. tolmerum* and 2 to 4 in *M.* sp. A (Tables 11 and 12).

(b) Qualitative Features. The rostrum of

M. tolmerum has a more upturned shape towards the tip than that of *M.* sp. A (Figs. 8 and 9). Body pigmentation, although variable in both species, is darker overall in *M. tolmerum* than *M.* sp. A. The palm of the second pereiopod of small males is often swollen in *M. tolmerum* but never so in *M.* sp. A.

(c) Metric Features. The two forms differ in many of 22 morphometric variables that were studied (Appendix A). Analysis of ratios of variables with carapace length indicated significant difference ($\alpha = 0.05$) between forms in 12 of the variables. When the 22 variables were considered simultaneously, the two forms were found to be discrete. Sixteen of the variables contributed significantly to this separation, but the forms were also discrete in a subset of five selected variables. Thus the populations are discrete and identifiable on a morphometric basis. This result supports visual assessment of the two forms (based on rostrum shape, the number of dorsal rostral teeth, body pigmentation and behaviour) which also suggested complete separation, since at least in mature specimens, there was never any doubt as to the affinity of an individual.

(ii) Behavioural Differences.

Handling of animals subsequent to trapping and observations in aquaria led to subjective impressions of differences in behaviour. Some of these were not readily definable, but three responses were reasonably clear cut. When a group of *M. tolmerum* is placed in a container in bright light with no shelter, they tend to aggregate, forming a cluster which may be several animals in depth. This response was not observed in *M.* sp. A. Secondly, when animals are held, as while making body measurements, individuals of *M.* sp. A tend to react much more vigorously than *M. tolmerum;* the second pereiopods are more agile and the pinching action of the chelae is used more effectively than by *M. tolmerum.* Finally, the second pereiopods were more prone to autotomy in *M.* sp. A than in *M. tolmerum.*

(iii) Distribution Patterns.

The distributions of the two forms in Bluewater Creek were substantially sympatric, although relative numbers varied with time and place (Section 4). The two forms were often taken together in the same trap.

The above observations suggest the *M. tolmerum* and *M.* sp. A of the present study are morphologically discrete and have some behavioural differences. Since they are sympatric, they cannot be designated as subspecies. An alternative to two species being involved is that of polymorphism of a single species. However, this is unlikely since it has not been reported in other *Macrobrachium* species. For the purpose of the present study it was necessary to treat the two forms as species, since if they were not considered as such and future studies deomonstrated two species, many of the conclusions of this study would be invalidated.

In distinguishing between *M. tolmerum* and *M.* sp. A the following morphological characters are the most useful:-

	M. sp. A	*M. tolmerum*
Rostrum	. short, not elevated	. longer, elevated towards tip
	. 10-13 dorsal teeth	. 8-11 dorsal teeth
	. 3-5 dorsal teeth behind orbit	. 2-3 dorsal teeth behind orbit
	. 2-4 ventral teeth	. 3-5 ventral teeth
Second Pereiopods	. palm does not increase in width near articulation of dactylus	. palm increases in width near articulation of dactylus
	. palm never swollen	. palm may be swollen in smaller males and females

Pigmentation . body only lightly pigmented . body darkly pigmented

Alternatively, for adult males, the following discriminant function (see Appendix A) may be used:-

$$SCORE = x_1 + x_2 + x_3 + x_4 + x_5 + 0.888$$

where x_1 = -5.03300 ln (rostrum length)

x_2 = 4.63620 ln (extent of dorsal rostral teeth)

x_3 = -0.73698 ln (telson distance 3)

x_4 = 2.15053 ln (carpus proximal width)

x_5 = -2.63696 ln (propus distal width)

(body dimensions are defined in Fig. A1).

A positive score indicates *M.* sp. A, while a negative score indicates *M. tolmerum*.

4 DISTRIBUTION OF ADULTS

4.1 INTRODUCTION

The factors most likely to be important in determining distribution patterns of *Macrobrachium* species in the study area were temperature, salinity, substrate, current, dissolved oxygen, depth (indirectly), interspecific competition and predation (Section 1). This section is concerned with distribution patterns of adults in relation to these factors. Further analysis of adult catch data is presented in Section 8.

4.2 METHODS

Locations and other details of the sampling sites were given in Section 2.2.

Sampling was by baited funnel traps (Fig. 10), which were wedge shaped enclosures covered with 1.5 mm mesh aluminium gauze supported by a 10 gauge wire frame. Animals entered the trap through a funnel at the wide end of the wedge. The funnel section was hinged and could be removed for access to the trap. Bait was held in a gauze container secured at the rear of the trap by wire staples. Prawns were found to be attracted to a range of baits of animal origin but the most convenient in use was cheese, which was employed throughout the study. The type of cheese and size of baits were standardized. Traps were orientated with the opening facing downstream. They were set between 1600 and 1800 hours and cleared the following morning by 1000 hours. Each transect consisted of 10 points

at 2 m intervals to which five traps were allocated by random numbers. Thus, the shortest distance between any two traps was 2 m. Setting and clearing of traps was carried out either from the stream bank or a small inflatable dinghy. As each trap was cleared, animals were measured (rostral carapace length), examined for reproductive status and returned to the water at the point from which they had been removed. Very small juveniles were returned to the laboratory for identification.

Sampling was carried out at approximate monthly intervals as near as possible to the new moon phase (Table 13). Each series of monthly samples took four nights of trapping to complete, working from site 1 to site 16. Sampling was not possible in early February 1976 because of flooding and the series was continued at the next new moon phase. Sites 9, 10 and 11 could not be sampled in January 1976 because of high flow rate and in August 1976 because there had been considerable human disturbance of the area by swimming and wading. In the text and diagrams that follow, sampling occasions are referred to by the month in which they fell.

Some weaknesses of baited traps as quantitative sampling devices have been discussed by Morrissy (1973) in relation to *Cherax tenuimanus*. Differences in catchability of individuals can be caused by various factors including reproductive status and the moult cycle stage. Furthermore, if results are to be expressed as catch per sampling unit, competition between traps will cause bias (Morrissy, 1975). In the present study

there was assumed to be no competition between traps because:-

(1) Observations at night suggested that animals further than 1 m from a trap were not attracted to the bait, and 2 m was the minimum distance between traps.

(2) Competition between traps on a longitudinal transect would result in smaller catches by upstream traps than by the most downstream trap. There was no significant difference (paired t-test, $\alpha = 0.05$) in catch over the whole sampling programme between the most downstream and second most downstream traps.

The problems of variation in catchability between species, sexes and size classes remain undefined, since it was impracticable to completely clear an area of habitat in order to estimate bias. However, whatever the limitations of the sampling method, no other method was found which could give anything approaching quantitative estimates of relative abundance of *Macrobrachium* species in the types of habitat encountered in this study.

4.3 RESULTS

Catch data are presented as the total catch over the five traps set on each transect, and are tabulated by site, month, species and reproductive category in Appendix B.

4.3.1 *M. LATIDACTYLUS*

M. latidactylus was present only at those sites within the reach of tidal influence (sites 9 to 16). It occurred at high levels of relative abundance at each of these sites at some time during the sampling programme (Fig. 11). Both substrate types (sand and stones) were represented in sites 9 to 16, suggesting that substrate is not an important factor in the distribution of this species within Bluewater Creek.

The relative importance of temperature, salinity, depth (indirectly) and current in the ecology of *M. latidactylus* is difficult to determine because of the inter-relationships between these factors in the tidal zone. Nevertheless, bivariate scatter diagrams of total monthly catch versus these factors (Figs. 12 and 13) indicate the range of conditions experienced and suggest some causal relationships. Measured temperatures associated with catches of *M. latidactylus* ranged from 21.0°C to 36.6°C and salinities from fresh water to 30.8°/oo. Thus considerable tolerance of high temperatures and saline water is indicated. Nevertheless, the pattern was of decreasing catch with increasing temperature (beyond 28°C) and salinity (beyond fresh water) (Fig. 12). However, high temperatures tend to occur under conditions of high salinity in the tidal zone (Section 2.3.1) and the decreasing catches could therefore have been caused by either or both of these factors. In relation to the occurrence of *M. latidactylus* at high temperatures, it should be noted that temperature readings were taken near their maximum

daily values, while traps were set overnight. As temperatures fell during the night, prawns could have moved into areas uninhabitable during the day, thus biasing the apparent temperatures experienced towards higher values. A similar effect is possible in relation to salinity. Notwithstanding possible biases in these results, occurrence of maximum catches in fresh water suggests that even though this species has considerable salinity tolerance, adults of *M. latidactylus* are basically fresh water in their requirements.

The most likely basis for depth preference in *Macrobrachium* species (excluding temperature, salinity and substrate) would be response to light intensity. If this were so, all species in the present study area would prefer deeper water, since they have been observed to avoid high levels of light. However, overall maximum catch of *M. latidactylus* occurred at a depth of 30 cm (Fig. 13) beyond which the maximum catch decreased with increasing depth. It appears therefore that any response to light intensity by *M. latidactylus* in Bluewater Creek does not result in preference of deeper water. Greatest abundance in shallow water is probably due to a preference of fresh water over saline water.

Overall maximum catch occurred at a stream surface velocity of 7 cm sec^{-1}, beyond which the maximum catch decreased (Fig. 13). No individuals of *M. latidactylus* were taken at velocities greater than 60 cm sec^{-1}.

Total catch varied markedly between sites and sampling occasions (Fig. 11), suggesting responses to changing temperature, salinity and current (Figs. 2 and 4). Very few *M. latidactylus* were trapped during August, September, October and November when salinities were high at sites 9 to 16. Then, following the first increase in fresh water flow in November and December (Fig. 4), salinities fell and numbers trapped increased at most of the tidal zone sites. From January to April, all sites were freshwater and overall numbers of *M. latidactylus* increased to a maximum in May. Subsequent increase in salinity during the dry season months was accompanied by decreasing numbers of *M. latidactylus* to levels similar to those of the previous dry season. It is significant that the first sites to show decreasing numbers after the wet season were the sites of highest salinity (sites 12 and 16).

Even though there was a progression of increasing and then decreasing overall numbers of *M. latidactylus* during the sampling period, apparently in response to changing salinity, maximum abundance did not occur at all sites simultaneously. This was probably because of stream velocity differences between the sites. Table 14 compares the mean stream surface velocity (calculated from monthly measurements) for the period February to June 1976 with the sampling occasion on which the highest total catch of sites 9 to 16 occurred. The site with highest mean velocity (site 9) was the last to exhibit maximum abundance, while the lowest velocity sites (sites 13 and 16) were the first.

These observations are consistent with an inverse relationship between abundance of *M. latidactylus* and stream velocity, as was suggested by Fig. 13; that is, it appears that during the high flow rate months, abundance of *M. latidactylus* in otherwise suitable areas is limited by adverse stream velocity. This could be because of dislodgement by current, avoidance of areas of fast current or low catchability because of a tendency to shelter in fast currents.

Stone substrate must provide significant refuge areas during flooding since large numbers of mature individuals were taken in the April 1976 samples, only ten weeks after a flood peak on 8th February 1976 (Queensland Irrigation and Water Supply Commission). Most of these individuals must have survived the flood by sheltering in stone substrate as flooding would undoubtedly dislodge all individuals from sand substrate. Some shelter would also be available amongst tree roots along overhanging stream banks. However, this type of shelter is not extensive in the region of sites 9 to 16, where the stream borders usually consist of sloping banks of sand or waterworn stones.

The large numbers of *M. latidactylus* present in April and May imply significant areas of suitable habitat outside the region from site 9 to site 16, since the increase in numbers was not due solely to recruitment of juveniles (Section 8). Populations of *M. latidactylus* were in fact found (in exploratory sampling) upstream of site 9 (but downstream of site 8). It is therefore suggested that areas upstream of site 9 are progressively colonized as salinities within the tidal zone increase during

the dry season. These areas would then contribute to the large increase in numbers further downstream during and immediately after the wet season. Of these individuals it is possible that some may return to the study area after having been displaced by flooding to the lower estuary or ocean.

Juvenile *Scylla serrata* were occasionally trapped at sites 15 and 16, but were insufficiently abundant to have been a significant competitor of *Macrobrachium* in the study area.

4.3.2 *M. NOVAE-HOLLANDIAE*

M. novae-hollandiae was relatively rare in the study area and with the exception of one individual, was taken only at sites 9 to 16 (Fig. 14). This species occurred on both substrate types, suggesting that substrate was not a major factor in its distribution.

There was no marked reduction in total catch with increasing temperature in the range 20°C to 36°C or increasing salinity in the range 0°/oo to 32°/oo (Fig. 15). These data suggest greater tolerance of high temperature and salinity than shown by *M. latidactylus*. Similar comments as were made in Section 4.3.1 regarding apparent occurrences in high temperatures apply. The individuals recorded as occurring at 40°C (Fig. 15) are assumed to have moved into the area as the temperature fell overnight.

The relationships of total catch to depth and current (Fig. 16) show largest numbers taken at shallow depths and slow currents. Maximum numbers were taken at slightly greater depth (60 cm)

than in the case of *M. latidactylus*, probably because of the higher salinity tolerance/preference of *M. novae-hollandiae*.

Highest total catches occurred in November and December (Fig. 14) in contrast to *M. latidactylus* which was most abundant after the wet season. This is consistent with a preference for saline water by *M. novae-hollandiae*. However, its absence from site 16 for most of the year was unexpected, since in the months May to August 1976, salinity at that site was within the range experienced by this species at other sites. A possible explanation is the lack of shelter at site 16, where the sand substrate was not modified by plant growth or detritus.

4.3.3 *M. TOLMERUM*

In contrast to *M. latidactylus* and *M. novae-hollandiae*, *M. tolmerum* was trapped as far upstream as site 1 and as far downstream as site 16 (Fig. 17). Maximum total catch was lower than that of *M. latidactylus*. Sites 1 and 9 produced higher total catches than other sites on almost all sampling occasions. Catches were usually low or zero at the sand substrate sites (sites 2 to 8 and 12, 13 and 16). Substrate is therefore suggested as an important factor in the distribution of *M. tolmerum* in Bluewater Creek. In areas upstream of tidal influence, site 1 was the only riffle area regularly sampled during the field programme. However, subsequent exploratory sampling confirmed the presence of *M. tolmerum* in several other freshwater riffle areas. There exists therefore, a clear distribution pattern of this species

in the freshwater reach of the study area: it is relatively abundant in riffle areas but almost totally absent from large pools. These two habitats differ in several factors, including substrate, current, and temperature and oxygen regimes. Laboratory studies on responses to these factors are described in Section 6.

The overall maximum total catch of *M. tolmerum* occurred at 30°C and there were no catches at temperatures above 34°C (Fig. 18). *M. tolmerum* was thus not taken in temperatures as high as were *M. latidactylus* and *M. novae-hollandiae*.

There was only one record of *M. tolmerum* at a salinity exceeding 16°/oo (Fig. 18), and most individuals were taken in fresh water. These data suggest that *M. tolmerum* has lower salinity tolerance than *M. latidactylus*. This pattern was not due to preference for stone substrate since stone substrate was available at the higher salinity sites 14 and 15.

Distribution of *M. tolmerum* total catch in relation to depth (Fig. 19) was similar to that of *M. latidactylus*, but *M. tolmerum* was taken at much higher stream volocities than the former. This observation is consistent with a preference for flowing water by *M. tolmerum*, a possible basis for its abundance in riffle areas.

Because of the low relative abundance of *M. tolmerum*, responses of the populations to seasonal variation in salinity are not as obvious as in *M. latidactylus*. However, it is significant that numbers at sites downstream of site 9 were always low and maximum overall numbers at those sites occurred during the wet season when freshwater conditions prevailed (Fig. 17). At site 1,

greatest numbers occurred in February and August 1976, when a large proportion of the population consisted of juveniles (Section 8.5). In the region of sites 9 to 16, there was a peak of recruitment in February and March. The occurrence of small numbers of individuals at the large pool sites (sites 4 to 8) during the wet season (particularly March) may have been due to dislodgement from riffle areas during flooding. Alternatively, they may have been migrating upstream, a possibility further discussed in Section 9. Sites 2 and 3 were pool sites, but in a relatively small pool and close to the riffle area below. The occurrence of small numbers of *M. tolmerum* at these sites (Fig. 17) is therefore not inconsistent with the conclusion that *M. tolmerum* is largely restricted to riffle areas.

Occasional specimens of the freshwater crayfish *Cherax wasselli* were trapped at site 1 but this species was not abundant enough to have been a significant competitor of *Macrobrachium* in Bluewater Creek.

4.3.4 *M. AUSTRALIENSE*

The distribution of *M. australiense* (Fig. 20) was in marked contrast to that of any other *Macrobrachium* species in the study area. It was taken almost exclusively at the upstream sites (sites 1 to 8) above the reach of tidal influence. Salinity is therefore obviously implicated in limiting the downstream dispersal of adults of this species. Within the

freshwater reach of the study area, the distribution of *M. australiense* was complementary to that of *M. tolmerum:* riffle areas were dominated by *M. tolmerum*, large pools by *M. australiense*. Exploratory sampling failed to find significant numbers of *M. australiense* in any riffle area.

There was no trend in total catch of *M. australiense* with increasing depth or temperature within the ranges experienced by this species (Fig. 21). However, faster currents were associated with lower maximum catches (Fig. 22), and this implicates current in the contrasting distribution patterns of *M. tolmerum* and *M. australiense*.

The populations of *M. australiense* were relatively stable (Fig. 20) compared with other species in the study area. Variation in catch at site 3 was due largely to instability of the sand substrate resulting in marked changes to the habitat during flooding in December 1975 (Section 2.3.4). Other fluctuations in abundance were probably the result of dislodgement during flooding and of predation. Dislodgement must be significant in areas of sand substrate where the only shelter available is leaf litter and readily dislodged macrophytes. However, populations persisted through flooding, indicating that a substantial proportion of individuals must be able to find shelter along the stream banks. Predation pressure was probably considerable during June, July and August 1976, when the barramundi, *Lates calcarifer* and the eel, *Anguilla reinhardti*, were observed at night to be

particularly abundant and active.

Atyid shrimps were particularly abundant in the large pools of Bluewater Creek. However, they appeared to be largely restricted to areas along the stream banks where they feed amongst overhanging vegetation, moving usually by swimming. *Macrobrachium* were rarely observed in this situation; they are less active swimmers and prefer more solid substrates. Atyids were rarely trapped during the sampling programme probably because of their distribution and feeding behaviour.

4.3.5 *M.* SP. A

Overall relative abundance of *M.* sp. A was low and so conclusions regarding its ecology are difficult to draw. Its distribution pattern was similar to that of *M. tolmerum*, with occurrences throughout the study area and apparent preference for riffle areas over pools (Fig. 23).

Distribution of total catch in relation to temperature, salinity, depth and current (Figs. 24 and 25) show similar patterns to those of *M. tolmerum*. However, *M.* sp. A occurred only rarely at site 9 (Fig. 23), one of the highest density sites for *M. tolmerum*. Catches of *M.* sp. A were often greater than those of *M. tolmerum* at site 3 (sand substrate), suggesting some difference in substrate preference between the two species.

4.4 DISCUSSION

The relatively stable habitats of the freshwater reach of Bluewater Creek support correspondingly stable populations of *Macrobrachium* species. In contrast, the tidal reach is subject to continuously changing temperature, salinity and current. Consequently, there is considerable spatial and temporal variation in abundance of the species present.

Apparent responses in abundance to adverse conditions could result from mortality, emigration or reduced catchability. In the tidal zone, immediately following the wet season, increasing temperature and salinity should not cause mortality since the mobility of the animals and continuity between pools would allow movement upstream away from unfavourable areas. However, as rising salinity progresses upstream during winter, mortality would be expected to increase because of crowding into the reduced area of suitable habitat, or into areas providing insufficient shelter from predators. The importance of reduced catchability in producing reduced catches under adverse conditions cannot be determined. However, because it is indicative of conditions, which if persistent, must reduce the viability of the species in the area, reduced catchability should not lead to erroneous conclusions. Furthermore, no attempt has been made to draw conclusions from marginal variations in abundance; they have been based only on the more obvious features of distribution patterns.

The distribution patterns observed during the present study suggest that temperature, salinity, substrate and current are important factors in the ecology of the species involved. Salinity appears to differentially limit the downstream distribution of all five species present. *M. novae-hollandiae* appears to have the highest salinity tolerance, showing no marked decrease in abundance with increasing salinity. Holthuis (1950) listed *M. novae-hollandiae* as a freshwater species, but Riek (1951) stated that it had never been collected from fresh water in Australia. Results of the present study are consistent with it being a brackish-water species. The most freshwater species in Bluewater Creek, *M. australiense*, is a widespread Australian species, not restricted to coastal areas. It was shown by Denne (1968) to be physiologically well adapted to fresh water compared with a more brackish-water species, *M. equidens*. No previous ecological data are available for the other species in the study area. *M. latidactylus* was listed by Holthuis (1950) as a freshwater species. *M. tolmerum*, described by Riek (1951) was then known only from the type locality ('Black River, Macrossan, ... from a purely freshwater habitat at least five miles above the tidal zone'). As mentioned in Section 3, the type material of *M. tolmerum* Riek in the Australian Museum contains specimens of the *M.* sp. A of this study, suggesting these two species may have similar distributions in areas outside Bluewater Creek.

Predation may have influenced population density of *M. australiense* on occasions (Section 4.3.4) but it is unlikely to have a significant effect on distribution limits. For those species inhabiting stone substrate areas, predation would be even less significant, since prawns there are more sheltered, and shallow depth would tend to exclude the larger fish predators.

The most abundant potential competitors of *Macrobrachium* in Bluewater Creek were the atyid shrimps, but their distribution pattern (Section 4.3.4) would largely restrict any competition to areas along the stream banks. Even in these areas, *Macrobrachium* adults, being of larger size, would be expected to dominate the atyids in any competition for space. Nevertheless, the atyids could be a significant competitor for food in areas where they are abundant. Such competition could influence the population density of *Macrobrachium* species, but should not have a significant effect on gross distribution patterns.

A summary of the distribution pattern of each *Macrobrachium* species in Bluewater Creek is given in Table 15.

While the observed distribution patterns of *Macrobrachium* species in Bluewater Creek have implied several factors in their determination, some important problems remain. Firstly, although the downstream distribution of *M. latidactylus* is undoubtedly due to salinity levels, factors limiting its upstream dispersal are not apparent. The adults do not require

brackish water since they were most abundant in fresh water. It may be that the lower ionic content of upstream sites (see conductivity values in Table 5) are not tolerated. This is unlikely, however, since *M. latidactylus* was not present at site 8, and conductivity there was only marginally lower than at the more downstream sites during the wet season. A second aspect of the distribution patterns which raises questions is that of the restriction of *M. tolmerum* to riffle areas and *M. australiense* to pools. Since these two habitats differ in substrate, current, depth and oxygen regime, causality is difficult to determine from field observations. This facet of the distribution patterns is investigated further in Section 6. Both the forementioned aspects of distribution patterns could involve competition between *Macrobrachium* species. Unfortunately it was not possible to pursue this possibility with regard to *M. latidactylus*, but competition between *M. tolmerum* and *M. australiense* is considered in Section 6.

5 DISTRIBUTION OF LARVAE

5.1 INTRODUCTION

Consideration of larval stages is particularly crucial in obtaining an understanding of adult distribution patterns within the genus *Macrobrachium*. Most *Macrobrachium* species inhabit fresh water as adults, but the life cycles of many are relatively poorly adapted to the freshwater environment. In some freshwater species, larvae require saline water for successful development (see Section 1). Such a requirement obviously limits the potential for a species to penetrate inland waters. Conversely, it allows more scope for broad geographic dispersal via the sea. Other species which develop in fresh water have planktonic larvae (indicated by the natatory exopods of the larval maxillipeds) (Fielder, 1968; Williamson, 1972). The necessity for retention of planktonic larvae within the freshwater reaches of a stream has important implications in the biology and distribution of the species.

The aim of this study of distribution of larvae was to provide data which, considered in conjunction with hydrological data and laboratory studies on the requirements of larvae, would be relevant to adult distribution patterns.

5.2 METHODS

Plankton samples were taken at five stations (Fig. 1) on the same days as monthly sampling of adults in those areas.

All samples were taken between 2100 and 2300 hours. Sampling gear consisted of a 280 μm mesh net of length 180 cm with a rectangular mouth 38.5 cm by 18 cm tapering to a cod end 6 cm in diameter. Floats were attached to the cod end and mouth frame such that the upper edge of the mouth of the net moved through the water approximately 10 cm below the surface. Surface sampling was necessary because of the shallow depth of some of the stations during much of the year. Even at deeper stations, sampling near the bottom with a plankton net was found to be impracticable because of variations in depth. A flow meter was attached in the mouth of the net in order to obtain an approximate measure of the volume of water filtered for each sample. The flow meter was calibrated by towing through the water on a frame without the plankton net attached. The net was towed approximately 50 m against the current for each sample. The volume of water filtered was thus dependent upon stream velocity. Towing speed was approximately 1 m per second referenced to the water. Approximate constancy of towing speed between samples was ensured since the net was pulled in with a rope by hand, and 1 m per second was the maximum velocity achievable in still water. Samples were preserved in 10% formalin and a total count of larvae in each sample made.

Because of the deposition of sand during the 1975/76 wet season, plankton station I was too shallow to sample after February 1976 and station V was too shallow in August 1976.

5.3 RESULTS

Because only one ovigerous female of *M.* sp. A was trapped during the sampling of adult populations (Table 35), the relative contribution of this species to larvae in the plankton was assumed to be negligible. Larvae of *M. australiense* were readily distinguished from other species by their large size and relatively advanced development in stage I (Section 8.4). However, *M. novae-hollandiae*, *M. tolmerum* and *M. latidactylus* larvae could not be distinguished, despite the fact that the larval stages of the first species have been described in detail (Greenwood *et al.*, 1976), and specimens of the latter two species were available from laboratory rearing experiments carried out during the present study. However, since adults of *M. latidactylus* and *M. novae-hollandiae* did not occur at sites 1 to 8, larvae from plankton stations I, II and III can be assumed to be either *M. tolmerum* or *M. australiense* which are readily distinguished. At stations IV and V, all four species could have been present and conclusions based on data from those stations are limited.

The *Macrobrachium* larvae present in the plankton samples were almost exclusively at stage I of development. In only six samples were larvae at later stages taken and these were all *M. australiense* (Table 16). The estimated numbers of stage I larvae per cubic metre of water filtered at each station on each sampling occasion are presented in Fig. 26.

Maximum numbers of *M. australiense* larvae were present before, and early in the wet season. Numbers in the samples were too low to justify conclusions regarding the reproductive season on these data alone. However, the occurrence of ovigerous females presented a similar pattern (Section 8.2), indicating that breeding activity was reflected by abundance of larvae.

The pattern of abundance of *M. tolmerum* larvae at stations II and III was in marked contrast to that of *M. australiense*, with greatest numbers occurring during the period of maximum stream flow (January to April). Furthermore, *M. tolmerum* larvae were much more abundant than those of *M. australiense*.

Consideration of the numbers of ovigerous females present on different sampling occasions (Table 35) does little to help resolve the *Macrobrachium* larvae at stations IV and V into their component species. However, it indicates that the combined reproductive activity of *M. latidactylus*, *M. novae-hollandiae* and *M. tolmerum* extended over the entire sampling period. Thus the presence of larvae (other than *M. australiense*) in the plankton for a greater part of the year at stations IV and V than at stations I, II and III was probably due to the involvement of three species, rather than to extension of the breeding season of *M. tolmerum* in more downstream areas.

5.4 DISCUSSION

Since *M. tolmerum* egg masses contain many more eggs than those of *M. australiense* (Section 8.1) the occurrence of greater numbers of *M. tolmerum* larvae in the plankton is not surprising. However, in the total data for plankton stations II and III over the sampling period, *M. tolmerum* larvae were approximately 700 times as abundant as those of *M. australiense*. Annual egg production of *M. tolmerum* is estimated as only 16 times that of an equal sized population of *M. australiense* (Section 8.3) and, therefore, the greater than expected relative abundance of *M. tolmerum* larvae must be due to either greater numbers of *M. tolmerum* than *M. australiense* adults or behavioural differences of the larvae leading to bias in the plankton samples. It is unlikely that *M. tolmerum* exceeds *M. australiense* by sufficient numbers to produce the observed effect, and differences in behaviour of the larvae are therefore suggested. A tendency for *M. australiense* larvae to remain nearer the substrate than those of *M. tolmerum* could explain this observation.

Considering the large numbers of *M. tolmerum* stage I larvae present on many occasions, the absence of stage II larvae is surprising. Three possible reasons are:-

(i) High mortality rate in fresh water. Several freshwater species of *Macrobrachium* have been shown to require saline water in the larval phase.

These include *M. rosenbergii* (Ling, 1969a), *M. vollenhovenii* (Ville, 1971), *M. carcinus* (Choudhury, 1971a) and *M. acanthurus* (Choudhury, 1971b). For others, similar requirements have been inferred from distribution patterns and spawning migrations (George, 1969; Panikkar, 1968; Rasalan *et al.*, 1969). During the present study, *M. tolmerum* larvae were also shown to have a requirement for saline water (Section 7). This accounts for the absence of stage II larvae at freshwater stations, but does not explain their absence from stations IV and V during the months when these areas were saline (August to December 1975 and June to August 1976).

(ii) Ontogenetic behavioural changes. There are several possible ontogenetic behavioural changes which could affect the results of plankton samples. Firstly, decreased swimming activity in later stages could lead to their absence from surface layers. Ling (1969a) stated that all larval stages of *M. rosenbergii* were active swimmers and planktonic but such observations, made under artificial conditions, may not be indicative of natural behaviour. Secondly, variation in diel activity patterns between stage I and stage II larvae could lead to spatial separation and bias in plankton samples. However, this is unlikely to be marked enough to produce the

observed total absence of stage II larvae from the samples. Thirdly, ontogenetic changes in salinity preference could lead to spatial separation of larval stages in stratified water, as occurred at plankton stations IV and V during much of the year. Hughes and Richard (1973) demonstrated response to salinity changes by *M. acanthurus* larvae, but variation of this response with larval development was not studied.

(iii) Displacement before reaching stage II. In the temperature range 25° to 30°C, the first larval stage of *M. tolmerum* is of 3 to 5 days duration (Section 8.4). At an average velocity of 1.2 m sec^{-1} a body of water would move from site 1 to the mouth of the stream in approximately 4.5 hours. Therefore, stream velocity during flooding would be sufficient to displace *M. tolmerum* larvae before stage II was reached. Within the tidal zone (plankton stations IV and V) much lower velocities could potentially displace larvae from the study area in three days. Furthermore, as freshwater flow decreases, tidal flushing within the tidal zone increases, and so, regardless of the time of year, water movements are likely to displace *M. tolmerum* larvae hatched in the upper tidal reach to a position downstream

of plankton station V before they moult to stage II.

Thus it appears that inability to survive in fresh water and displacement by water movements are sufficient to explain the absence of stage II *M. tolmerum* larvae from the plankton samples. However, the possibility of the involvement of ontogenetic behavioural changes cannot be discounted.

Larvae of *M. latidactylus* also require brackish water for development (Section 7), but adults are usually located near brackish water (Section 4.3.1). Absence of later stage *M. latidactylus* larvae from plankton samples is therefore attributed to displacement by water movements before stage II is reached. While larvae of this species moult to stage II after only one day at 25° - 30°C (Section 8.4), adults are usually located further downstream than *M. tolmerum*, and thus less time would be required for displacement of larvae downstream beyond plankton station V.

Similarly, the absence of later stage *M. novae-hollandiae* larvae from plankton samples was probably due to displacement by water movements. They moult to stage II after 3 to 4 days (Greenwood *et al.*, 1976), and would be expected to require saline water since this is a brackish-water species.

6 LABORATORY STUDIES WITH ADULTS

There were insufficient numbers of *M. novae-hollandiae* and *M.* sp A in the study area for laboratory studies on those species. This section is therefore concerned with the three dominant *Macrobrachium* species of Bluewater Creek, *M. latidactylus*, *M. tolmerum* and *M. australiense*.

6.1 TEMPERATURE - SALINITY TOLERANCE

6.1.1 INTRODUCTION

Despite the large volume of literature on temperature and salinity effects in the Crustacea (Lockwood, 1962; Dorgelo, 1976), most research in this field concerning the Palaemonidae has been on northern hemisphere species of *Palaemon*, *Palaemonetes* and *Leander* (Panikkar, 1941; Parry, 1954, 1955, 1957; Lofts, 1956; Dobkin and Manning, 1964; Potts and Parry, 1964; Parry and Potts, 1965; Rudy, 1967; Spaargaren, 1972; Reynolds, 1975; Thorp and Hoss, 1975; Turner *et al.*, 1975). Works concerning post-larvae and adults of *Macrobrachium* species include those of Denne (1968), Sandifer *et al.* (1975), Nelson *et al.* (1977) and Silverthorn and Reese (1978).

The distribution patterns of *Macrobrachium* species in Bluewater Creek suggested that salinity was a major environmental factor, differentially controlling the downstream limit of distribution of all five species (Section 4). Temperature was

indicated to be important in the tidal reach, where abnormally high values occur under conditions of salinity stratification. Furthermore, the interrelationship between temperature and salinity effects would be expected to be of some importance, as is usual for aquatic animals (Kinne, 1964; Dorgelo, 1976).

The aim of this study was to estimate the relative temperature-salinity tolerances of *M. latidactylus*, *M. tolmerum* and *M. australiense* to complement the inferences made from distributional data.

6.1.2 METHODS

The approach was one of factorial experiments and response surface analysis.

Experiments were restricted to males because they were usually more abundant in the field and were expected to show less individual variation in temperature-salinity response, which in females could be influenced by reproductive status. Individuals of *M. latidactylus* were obtained from sites 14 and 15; *M. tolmerum* from sites 1 and 2; and *M. australiense* from sites 4, 5 and 6. They were acclimated for 10 days in a recirculating freshwater aquarium system (conductivity, K_{25} = 80 to 120 µS) at 27°C ± 0.5 C° with a 12/12 photoperiod. During acclimation, animals were fed a composition food prepared by mixing equal volumes of commercial fish food pellets and macerated whole

Macrobrachium. Approximate constancy of feeding rate was ensured by providing a slight excess of food every second day. No food was given during experiments or on the day prior to their commencement.

Experimental treatments included temperatures of 15°C to 38°C in combination with salinities ranging from 0°/oo to 32°/oo. Those treatments used which produced data points are indicated in Tables 17, 18 and 19.

Six individuals were tested at each temperature-salinity combination. They were selected by hand and, to reduce the effects of any non-random selection, one individual was assigned to each treatment, then a second to each treatment and so on. Juveniles and unusually large individuals were not used. Rostral carapace length of each test animal was recorded so that size effects could be considered in the analysis.

Test animals were held individually in plastic containers partially submerged in constant temperature water baths (±0.1 C°). Each experimental container held 350 ml of water aerated by fine streams of bubbles. It was not possible to monitor dissolved oxygen concentration during experiments, but trials indicated that equilibrium levels were reached in all temperature-salinity combinations within four hours of the containers being placed in the water baths and aeration commencing. A four hour equilibration period was therefore allowed before introducing the test animals. Introduction of the animals did

not appreciably lower dissolved oxygen concentrations. Test animals were transferred to new equilibrated water each day. Experimental salinities were obtained by mixing filtered sea water (Whatman GF/C glass fibre filter) and fresh water (conductivity, K_{25} = 70 to 80 µS) from Bluewater Creek. Salinities were checked on an Auto Lab Model 601 Mk IIIB inductive salinometer and were always within 0.1°/oo of the nominal value. In the text that follows, fresh water is designated as 0°/oo salinity.

All tests used direct transfer from acclimation conditions to the experimental treatments. Animals were considered dead if they were unable to right themselves after being inverted and survival time was taken from commencement of the experiment to the time when an individual was observed dead. Results are expressed as the mean survival time of the six individuals tested at each temperature-salinity combination. Experiments were terminated after four days duration and treatments which did not produce 100 °/o mortality in that time did not provide data points for the analysis.

Response surfaces were fitted to the data by least squares regression using the SPSS program REGRESSION (Nie *et al.*, 1975) with a forward stepwise procedure and elimination of redundant terms. The regression models fitted were polynomials (of up to third order) in temperature, salinity and rostral carapace length. Inclusion of additional terms was terminated when no further reduction in the standard error of estimate was

possible. Response surfaces were represented graphically as isopleth diagrams drawn by a Houston plotter and plotting program prepared by T. Dixon of the James Cook University Computer Centre. The mean survival time data were analysed as their natural logarithm transforms, since examination of residuals (Draper and Smith, 1966) indicated that this achieved normality and homogeneity of variance of each data set.

6.1.3 RESULTS

Mean rostral carapace length and mean survival time at experimental temperature-salinity combinations are given in Table 17 *(M. latidactylus)*, Table 18 *(M. tolmerum)* and Table 19 *(M. australiense)*. Results of regression analyses of these data are summarized in Table 20 *(M. latidactylus)*, Table 21 *(M. tolmerum)* and Table 22 *(M. australiense)*. Isopleth diagrams of the survival response surfaces for all three species are presented in Fig. 27. The *M. tolmerum* and *M. australiense* response surface equations contained terms in rostral carapace length. The isopleth diagrams for those species represent the response surfaces at the mean value of the mean rostral carapace lengths for the groups of test animals.

In all three species, predicted survival at high temperatures (35^{o} to 38^{o}) was little affected by salinity (Fig. 27), as indicated by the almost straight isopleths lying parallel to the salinity axes. Longest survival times at high temperatures were predicted for *M. latidactylus* followed by

M. tolmerum and then *M. australiense*. Individuals of no species would be expected to survive indefinitely subsequent to transfer from an acclimation temperature of 27°C (in fresh water) to a temperature of 35°C or higher. Predicted low temperature (15° to 20°) survival of *M. latidactylus* was not appreciably affected by salinity; a slight effect was present in *M. tolmerum* and there was a marked effect in *M. australiense*. At low temperatures in fresh water, longest survival times were predicted for *M. australiense* followed by *M. tolmerum* and then *M. latidactylus*. At 32°/oo, longest low temperature survival times were predicted for *M. tolmerum* followed by *M. australiense* and *M. latidactylus* with similar tolerances. At medial temperatures (20° to 30°) the predicted survival time of all three species decreased with increasing salinity. However, this effect was most marked in *M. australiense*, considerable in *M. tolmerum* and almost negligible in *M. latidactylus* within the experimental range.

The most important conclusion to be drawn from these data is that euryhalinity increases in the order *M. australiense* - *M. tolmerum* - *M. latidactylus*.

6.1.4 DISCUSSION

There were some irregularities in the survival response data, probably caused by genetic differences and variation in field acclimation, compounded by the small numbers of individuals able to be tested. However, this does not invalidate the conclusions which are based on only the more obvious differences between species.

Of the *Macrobrachium* species of Bluewater Creek, only *M. australiense* has been subjected to previous investigation of temperature or salinity effects. Denne (1968) found *M. australiense* individuals to hyper-osmoregulate in conditions ranging from fresh water to a salinity of approximately 25°/oo, the upper tolerance limit. The present study did not determine long term lethal limits, but it confirms that *M. australiense* has only limited salinity tolerance. The brackish-water species *M. equidens*, also investigated by Denne (1968), does not tolerate salinities below approximately 2°/oo. This contrasts with *M. latidactylus*, *M. tolmerum* and *M. australiense*, all of which survive in fresh water.

The temperature-salinity tolerance of an animal at a particular point in time can be influenced by many factors, including:-

(1) Temperature and salinity acclimation. Not only do acclimation temperature and salinity directly affect temperature and salinity lethal limits respectively, but acclimation temperature may influence salinity tolerance, and acclimation salinity may affect temperature tolerance (Dorgelo, 1976).

(2) Dissolved oxygen concentration. McLeese (1956) found that lowered levels of dissolved oxygen decreased the upper lethal salinity for *Homarus*

americanus. The temperature-salinity survival response surface of *Crangon septemspinosa* was translated to lower temperatures and higher salinities at reduced dissolved oxygen concentration (Haefner, 1970).

(3) Nutritional status. Rippingale and Hodgkin (1977) found that well fed individuals of the copepod *Sulcanus conflictus* had higher salinity tolerance than unfed individuals, which was attributed to the energy requirement of osmoregulation. However, there appears to be no general conclusion regarding the energy cost of osmoregulation in aquatic animals, as it depends on the mechanism of osmoregulation and the nature of the osmotic stress (Lockwood, 1962). Nelson *et al.*, (1977) in a study of juveniles of *Macrobrachium rosenbergii*, found that increasing temperature in the range of 20°C to 34°C caused an increase in metabolic rate, but increasing salinity in the range 0°/oo to 28°/oo caused a decrease in metabolic rate. However, they concluded that no part of the decrease in metabolic rate could be attributed to approach of the iso-osmotic point (18°/oo) and therefore the energy requirement of osmoregulation was not a significant factor.

(4) Developmental stage. The larvae of *M. latidactylus*, *M. tolmerum* and *M. australiense* exhibit temperature-salinity survival responses (Section 7) in each case different from that of adults. Therefore it is reasonable to expect some progression of response within the post-larval phase, rather than a complete transition in temperature-salinity tolerance upon moulting to the first post-larval instar.

Thus, even if temperature-salinity tolerance were the prime factor in the ecology of a species, because of the complexity of its dependence on the above factors, exact prediction of distribution limits would be difficult. Therefore, relative tolerances are considered here, rather than exact lethal limits for the species concerned. Distribution patterns suggested salinity tolerance increased in the order *M. australiense* - *M. tolmerum* - *M. latidactylus* (Section 4). This was confirmed by the laboratory studies, and it is concluded therefore that salinity is an important distributional factor for these three species, being at least partly involved in differentially limiting their downstream dispersal. Interspecific differences in temperature tolerances were not great and should not differentially limit the distribution patterns. However, it is clear that none of the three dominant species could survive in temperatures near 40^{o}C, as occurred in stratified saline water. Temperatures in the study area (Section 2.3.1) would never reach the lower lethal limits for adults of the *Macrobrachium* species present, except when associated with high salinity.

6.2 SUBSTRATE, CURRENT AND COMPETITIVE DISPLACEMENT

6.2.1 INTRODUCTION

In the freshwater reach of Bluewater Creek, *M. tolmerum* and *M. australiense* have complementary distributions. Large pools are for most of the year occupied only by *M. australiense*, while in riffle areas *M. tolmerum* is present and *M. australiense* absent. It was suggested in Section 4 that substrate, current and competitive displacement were possible factors in determination of these distribution patterns. The following laboratory studies were designed to further investigate these hypotheses. Substrate was not implicated by the field studies as a major ecological factor for *M. latidactylus*, although the involvement of current and competition could not be discounted. Unfortunately, time precluded investigation of all three dominant species in this series of experiments, which were consequently restricted to *M. tolmerum* and *M. australiense*.

6.2.2 METHODS

The experimental rationale was that if groups of *Macrobrachium* individuals could be observed in simulated natural conditions in which a choice of habitats was available, then the mean time spent in respective areas would reflect preferences and/or competitive pressures.

A circular pond 2.5 m in diameter and 30 cm deep was constructed. The bottom was covered with a 3 cm layer of

coarse sand substrate from the study area. In two opposite quadrants a layer of either waterworn stones or leaf litter was placed. A pump was used to induce circular water movement. Its inlet was beneath a perforated protective cover at the centre of the pond and its four outlets were directed tangentially at the perimeter. Mean velocities at the perimeter of the pond of 0.09 m sec^{-1} could thus be generated while velocity at the centre remained close to zero.

Experimental animals were tagged with reflective tape (5 mm x 5 mm) attached by tying around the body with fine copper wire immediately behind the carapace. Tags of different colours were used to distinguish the species. Above the pond an observation platform was erected such that the pool could be photographed at night using electronic flash, in order to record the positions of experimental animals.

Animals were obtained from site 1 *(M. tolmerum)* and sites 4, 5 and 6 *(M. australiense)*. After tagging they were held in aquaria for 24 hours in case of ill effects; no such effects were ever observed. Tagged animals were released at the centre of the pond 24 hours before observations began.

The following seven experiments were carried out with the given numbers of animals in the pond:-

A. Substrate preference (sand/stones choice) with no current.

1. *M. tolmerum* alone (10 males and 10 females)

2. *M. australiense* alone (10 males and 10 females)

3. *M. tolmerum* and *M. australiense* (10 males and 10 females of each species).

B. Substrate preference (sand/leaf litter choice) with no current.

1. *M. tolmerum* alone (10 males and 10 females)

2. *M. australiense* alone (10 males and 10 females)

3. *M. tolmerum* and *M. australiense* (10 males and 10 females of each species).

C. Current preference (fast/slow) and substrate preference (sand/stones).

M. tolmerum and *M. australiense* (10 males and 10 females of each species).

The same sets of individuals were used for experiments within A and B above; different sets of individuals were used for A, B and C.

All experiments were carried out around the new moon phase.

Both species were inactive during daylight, sheltering in whichever protective substrate was available. Photographic records were therefore made only at night. Each experiment consisted of observations made during one night; sixty photographic exposures were made, in three series of 20, one at 1900 hours (approximately ½ to 1 hour after dark), one at 2400 hours and one at 0500 hours (approximately ½ to 1 hour before dawn). Exposures

within each series were made at three minute intervals.

In order to analyse the distribution of experimental animals in relation to current, the photographic transparencies were projected onto a screen on which equal outer (fast current) and inner (slow current) areas of the pond had been marked.

The number of animals on stone or leaf litter substrate could not be determined directly, since even during darkness some individuals were usually sheltering. For this reason it was not possible to conduct experiments offering a choice between stone and leaf litter substrates.

6.2.3 RESULTS

Individuals of the *Macrobrachium* species of this study move away from a light beam at night, and it is possible that the flash lighting used to make experimental observations could bias the results by causing the animals to take shelter. However, there was no significant difference in the proportion of animals sheltering at the commencement and completion of each series of 20 exposures, and it was concluded that the electronic flash had no effect on behaviour.

Frequency distributions of the number of individuals on sand substrate for the pooled 60 records in the substrate preference experiments (without current) are shown in Figs. 28 and 29. From both the sand/stones and sand/leaf litter choice experiments a similar pattern emerged. The two species had similar frequency distributions of the number of individuals on sand substrate in the

single species experiments. In the combined species experiments however, there were fewer individuals of *M. tolmerum* (compared with the respective single species experiments) and more of *M. australiense* on sand substrate. In the single species experiments, the *M. tolmerum* and *M. australiense* distributions were similar to each other and similar for both sand/stones and sand/leaf litter substrate choices. Furthermore, in each of the single species experiments, the mean and mode of the distribution were considerably less than 10, indicating a preference by both species for the sheltering substrate. Therefore, movement of the *M. australiense* distributions towards higher numbers on sand in the combined species experiments indicates a partial displacement of this species from the preferred substrate by *M. tolmerum*. Conversely, there was a movement of the *M. tolmerum* distributions towards lower numbers on sand in the combined species experiments. Thus, even though *M. tolmerum* was the dominant species, a two-way interaction occurred.

Irregularity of the *M. australiense* frequency distributions in combined species experiments (Figs. 28 and 29) suggests polymodality. Examination of the breakdown of frequency distributions into their component series of observations (Tables 23 and 24) does indicate a time effect. In the sand/stones combined species experiment, the frequency distribution mode moved from its series 1 value to a higher value in series 2 and back to a lower value in series 3. A similar, though not so marked effect is evident in the sand/leaf litter results. This effect

is to be expected, since during daylight, all individuals occupy the sheltering substrate.

Comparison of Fig. 30 with Fig. 28 shows a marked effect of current on the frequency distribution of the number of individuals observed on sand substrate (sand/stones choice). The mean values were:-

	CONTROL	CURRENT
M. tolmerum	2.20	4.35
M. australiense	10.50	6.30

with a least significant difference of 0.82 ($\alpha = 0.05$). Thus, while there was a significant difference between the means for the two species in the presence of current, this difference was much smaller than in the absence of current. The effect of current was to increase the numbers of *M. tolmerum* and decrease the numbers of *M. australiense* individuals observed on sand substrate.

Paralleling these results were changes in the mean number of animals sheltering (not recorded and therefore concealed in stone substrate). The mean values were:-

	CONTROL	CURRENT
M. tolmerum	4.00	3.70
M. australiense	2.45	3.73

with a least significant difference of 0.61 ($\alpha = 0.05$). Thus there were significantly more *M. australiense* sheltering in the presence of current than in its absence. Consequently, while there were more *M. tolmerum* than *M. australiense* sheltering in the control

experiment, there were approximately equal numbers sheltering in the presence of current.

Frequency distributions of occurrence in the outer zone of the pond in the presence and absence of current are given in Fig. 31. They are the results of combined species experiments with a choice between sand and stone substrates. Since the number of individuals on stone substrate could not be determined directly, analysis of numbers in outer and inner zones of the pond is based on those individuals visible (not sheltering). Mean values for the percentage of non-sheltering individuals observed in the outer zone were:-

	CONTROL	CURRENT
M. tolmerum	45.4	59.3
M. australiense	31.4	32.4

with a least significant difference of 4.9 ($\alpha = 0.05$). Thus there were significantly more *M. tolmerum* in the outer zone during the presence of current than in the control, but no difference was shown by *M. australiense*. The presence of more *M. tolmerum* than *M. australiense* in the outer zone during the control experiment may have been due to a shelter effect of the pond wall. This would be consistent with the greater tendency of *M. tolmerum* to seek shelter.

6.2.4 DISCUSSION

The results described above show that both *M. tolmerum* and *M. australiense* prefer a substrate which provides shelter, even

during darkness, and that *M. tolmerum* is able to partially displace *M. australiense* from the preferred substrate during nocturnal activity. However, even though *M. tolmerum* was the dominant species, there was a two-way interaction, resulting in some displacement of *M. tolmerum* further towards stone substrate in the presence of *M. australiense*. Since these observations were made for only 24 hour periods and in a restrictive environment, it is probable that under natural conditons, spatial separation of the species as a result of competition, may be even more complete.

No previous laboratory studies of substrate preference by species of *Macrobrachium* have been reported. However, the work of Rees (1975) is relevant, since the isopods concerned *(Gnorimosphaeroma oregonensis oregonensis* and *Exosphaeroma amplicauda)* have a similar sheltering association with the substrate as do *Macrobrachium* species. The two species of isopods have preferences for substrate particle size, but in a competitive situation *G. oregonensis oregonensis* displaces *E. amplicauda*, the degree of displacement being dependent on their relative densities. In the *M. tolmerum/M. australiense* interaction, relative densities could have a similar effect on the experimental result: a higher proportion of *M. tolmerum* would be expected to result in more complete exclusion of *M. australiense* from the preferred substrate.

It was not possible to investigate the mechanism of interaction between *M. tolmerum* and *M. australiense*. However, because of their similar habits, the interaction is probably similar to that between certain species of crayfish. Penn and Fitzpatrick (1963) observed direct interspecific aggression between *Cambarellus shufeldti* and *C. puer* which resulted in dominance by *C. shufeldti* of 82% of the groups of experimental animals observed. Competitive exclusion was thus implicated in an observed range extension of *C. shufeldti* at the expense of *C. puer*.

The work of Bovbjerg (1970) has much in common with the present study. It concerns the crayfish *Orconectes virilis* and *O. immunis* which have similar geographic ranges in North America. Within this range, their distributions are substantially disjunct, *O. virilis* being a stream species and *O. immunis* a pond species. Field data suggested substrate to be an important factor in determining their distributions. Laboratory observations, however, showed that both species preferred rock substrate when given the choice of rock, gravel or soft substrate in the absence of the other species. But when both species were present, *O. virilis* was able to compete more successfully for the preferred substrate. Further observations of the outcomes of tension contacts indicated *O. virilis* to be the dominant species in aggressive behaviour.

The observed disjunct distributions of *M. tolmerum* and *M. australiense* in Bluewater Creek almost certainly involve

substrate preference. However, because it was not possible to make direct comparisons between stone and leaf litter substrate in the preference experiments, the exact role of competitive displacement is uncertain. Possibly, given a choice, *M. australiense* would prefer leaf litter to stone substrate. If so, the observed distribution patterns could arise without interspecific competition. Nevertheless, in the absence of interspecific competition it is unlikely that such complete separation of the two species would occur.

While the present study and others in the literature report examples of substrate preference, its demonstration does not necessarily indicate a biological requirement for the preferred substrate *per se*. In the present instance, there are several factors involved in the difference between *M. tolmerum* and *M. australiense* habitats. The nature of the substrate may act merely as a cue, indicating suitability of the area, while the biological need may be for other factors correlated with substrate such as current and dissolved oxygen regime.

Individuals of *M. tolmerum* showed a preference for moving water over still water, and this preference was exercised despite the presence of *M. australiense*. On the other hand, *M. australiense* showed an increased tendency to shelter in the presence of current; this may have been caused by increased activity of *M. tolmerum*. These observations are consistent with the involvement of current in the restriction of *M. australiense* to large pools and *M. tolmerum* to riffle areas in Bluewater Creek.

The importance of current as an ecological factor in streams has been illustrated by many studies as reviewed by Hynes (1970) and Macan (1974). However, most such studies have been on stream insects and other groups whose requirements and habits are considerably different from those of *Macrobrachium*. Several authors have made field observations on the association of *Macrobrachium* species with particular current regimes (Section 4) but there have been no laboratory studies supporting these inferences. Hughes and Richard (1973) carried out laboratory studies on responses of *M. acanthurus* to current, but that work was aimed at explaining spawning migrations rather than habitat preference. Nevertheless, it demonstrated a capacity for behavioural response to current.

As emphasised by Bishop (1973), the effects of current on the distribution of stream invertebrates are usually indirect, for example through determination of substrate character or enrichment of oxygen in the boundary layer. Since it is extremely difficult to measure the current experienced by a small animal, determination of the direct effects of current on distribution patterns is in turn difficult.

There are three avenues whereby current might influence distribution patterns of *Macrobrachium* species. Each could involve an effect due to mortality or an effect due to preference or a combination of both. These are now discussed in relation to *M. tolmerum* and *M. australiense*.

(i) Ability to maintain position in flowing water. This is obviously important for many groups of freshwater organisms, and various adaptations for existence in flowing water have evolved. The degree of morphological difference between *M. tolmerum* and *M. australiense* should not convey any significant advantage to either species. However, individuals of *M. tolmerum* reach a greater maximum body size than *M. australiense* in the Bluewater Creek study area. The correspondingly smaller surface area to volume ratio of large *M. tolmerum* individuals might be advantageous in areas of fast current. It is significant, however, that individuals of all sizes of *M. tolmerum* occur in riffle areas. One of the periods of maximum recruitment of juvenile *M. tolmerum* was in March and April (Section 8.5) when stream velocity was high. Therefore, body size is probably not an important component affecting the ability of *M. tolmerum* and *M. australiense* to maintain position in flowing water. Behaviour may be important in maintaining position, and in particular, a greater tendency to seek shelter would be advantageous. However, laboratory experiments indicated no significant differences between *M. tolmerum* and *M. australiense* in their tendency to shelter from moving water. Thus there are no obvious differences between *M. tolmerum* and *M. australiense*

that might result in significant difference in ability to maintain position in flowing water.

(ii) Requirements of larvae.

In many species of *Macrobrachium*, adults inhabit fresh water while larvae require brackish water to complete development (Section 1). Survival of larvae of such species is dependent upon their being hatched in saline water or in flowing water which will rapidly transport them to areas of suitable salinity. Several species are known to undergo spawning migrations (Panikkar, 1968; George, 1969; Rasalan *et al.*, 1969). However, the brackish water requirements of larval *M. malcolmsonii* of the Godavary River are satisfied in the absence of a spawning migration by the synchronisation of breeding with monsoon flooding. In continuously fast flowing streams, the larval requirements of such species could be satisfied without either a spawning migration or critical timing of reproduction. In species which evolved under conditions of continuous stream flow, one would expect a degree of current preference. Populations of such species which subsequently colonized streams with a range of current regimes would select flowing water habitats in preference to still water. Similarly, in a stream with intermittent flow, it would be reasonable to expect maximum reproductive activity during times when

conditions were most favourable (during periods of flow). It is shown in Section 7 that the larvae of *M. tolmerum* require brackish water, and in the light of the suggestions made above, this requirement is a possible basis for the current preference shown by adults of the species.

(iii) Dissolved oxygen requirements.

Current obviously has an effect, through several indirect routes, on the oxygen regime of a freshwater habitat. In the present context it is sufficient to note the more direct effects. Firstly, oxygen concentration would probably never reach critically low levels in riffle areas because of the aeration effect of turbulence. Secondly, in addition to any difference in overall oxygen regime between riffle areas and pools, replacement of the medium is brought about by current. Whereas in still conditions an animal must create currents which bring oxygenated water into its vicinity, in flowing water this task is greatly reduced.

The oxygen requirements of *M. tolmerum* and *M. australiense* are considered in relation to the regimes of their respective habitats in Section 6.3.

6.3 DISSOLVED OXYGEN CONCENTRATION

6.3.1 INTRODUCTION

There is a large volume of literature concerning the rate of oxygen consumption in aquatic animals and the influence of various factors on it (Schlieper, 1971; Macan, 1974). However, knowledge of oxygen consumption rate does not give the ecologist a direct measure of critical levels of dissolved oxygen within which an organism can survive, and measurement of tolerances is desirable. Tolerance of dissolved oxygen concentration by marine organisms has been reviewed by Vernberg (1972). Studies on the tolerance of low dissolved oxygen concentration by crustaceans include those of Burbanck *et al.* (1948), McLeese (1956), Sprague (1963), Moore and Burn (1968) and Bovbjerg (1970). Both low and high levels of dissolved oxygen have been shown to have adverse effects on aquatic animals (Macan, 1974). In fresh water, these conditions are likely to occur in still or slowly moving water with high levels of aquatic plant biomass. In swiftly flowing and turbulent waters, oxygen concentrations tend to be maintained close to saturation levels. Thus, in a stream there may be considerable change in the oxygen regime with progression from the headwaters to lowland reaches (Bishop, 1973).

In Bluewater Creek, *Macrobrachium australiense* is generally restricted to large pools, while *M. tolmerum* is generally restricted to riffle areas (Section 4), and the difference in oxygen regime between these two habitats (Section 2.3.6) is a

potential factor in the distribution patterns. Not only is the absolute oxygen regime more favourable in riffle areas, but as has been emphasised by Eriksen (1966), renewal of the respiratory environment by water movement is also a consideration of importance. A requirement of the oxygen regime of riffle areas by *M. tolmerum* may be the basis for its observed preference for moving water over still water (Section 6.2). The following experiments were therefore designed to test for differences between *M. tolmerum* and *M. australiense* in tolerance of low levels of dissolved oxygen.

6.3.2 METHODS

Testing was carried out on males only, in order to avoid variability due to reproductive status of females. Individuals were obtained from the vicinity of site 1 *(M. tolmerum)* and sites 4, 5 and 6 *(M. australiense)*. They were acclimated at 30°C in flowing, aerated fresh water for five days, during which time they were fed a slight excess of a prepared diet (Section 6.1.2) every second day. No food was given during experiments or on the day of commencement of experiments. Test animals were selected for uniform size and healthy condition.

Tolerance testing was carried out with an apparatus designed by R. Pearson and L. Penridge of the James Cook University. A constant flow of fresh water containing the required level of dissolved oxygen was supplied to four glass test chambers of 2 litres capacity each, which were submerged in a constant temperature water bath. Water flow was maintained by variable speed peristaltic

pumps feeding from saturated and deoxygenated water reservoirs. Mixing from these two sources achieved the required level of dissolved oxygen. A third peristaltic pump supplied water from the oxygenated reservoir to two experimental control chambers. Deoxygenation was achieved by passing nitrogen gas through a vertical column of water as it was fed to the reservoir. The pH of the deoxygenated water was maintained between 7.2 and 7.5 by passing carbon dioxide through the deoxygenating column. The temperature of the reservoirs and test chamber water bath was controlled by thermostatic aquarium heaters. Oxygen levels were monitored with a Y.S.I. Model 57 oxygen meter.

Test exposures were made at 30^{o}C over a maximum of 96 hours with a 12/12 photoperiod. Observations were made at 15 minute intervals for the first hour, then at 30 minute intervals for three hours and subsequently every four hours.

The time to 50% mortality within treatments was estimated from the least squares regression of the probit transformation of cumulative percent mortality on the logarithm of exposure time (Finney, 1962).

6.3.3 RESULTS

The number of individuals tested, percent survival to 96 hours, mean survival time and time to 50% mortality (LT50) at three levels of dissolved oxygen concentration are presented in Table 25. There is no great difference between males

of *M. tolmerum* and *M. australiense* in their physiological tolerance of low oxygen concentration. Neither species suffered mortality in 96 hours at 2.0 mg l^{-1} of oxygen, and the mortalities were similar at lower levels. The shorter LT50 at 1.5 mg l^{-1} for *M. tolmerum* suggests that this species may have slightly less tolerance than *M. australiense*, but in order to confirm such small differences, larger numbers of animals would need to be tested.

6.3.4 DISCUSSION

The results presented above show that there is little difference in physiological tolerance of low levels of dissolved oxygen by males of *M. tolmerum* and *M. australiense*. The lowest dissolved oxygen concentration measured in the field was 2.0 mg l^{-1} Table 7). Since this was a minimum overnight value and concentrations as low as this occurred only in restricted areas (near dense growth of macrophytes), neither *M. tolmerum* nor *M. australiense* should suffer significant mortality from low oxygen levels in the field. However, the laboratory results were obtained under constant conditions and the effect of fluctuating levels of dissolved oxygen is not known.

There is a possibility of behavioural preferences which need not be fully reflected in physiological tolerances. The extent to which *Macrobrachium* individuals are able to detect spatial variation in dissolved oxygen concentration is unknown. However, Cook and Boyd (1965) found that the amphipod *Gammarus oceanicus* avoided regions of anoxia in the laboratory and the

behaviour pattern suggested the involvement of a chemosensory mechanism.

Even if *M. tolmerum* and *M. australiense* have identical oxygen requirements and preferences, involvement of oxygen regime in the distribution patterns of these two species cannot be discounted. Since in a competitive situation, *M. tolmerum* is able to displace *M. australiense* from the preferred substrate (Section 6.2), such an interaction is also possible in relation to the preferred oxygen regime. In the presence of such competitive displacement, preference by both species for the riffle area oxygen regime would not be inconsistent with observed distribution patterns.

7 LABORATORY STUDIES WITH LARVAE

7.1 INTRODUCTION

Field studies suggested that adults of four of the five species of *Macrobrachium* in Bluewater Creek preferred fresh water (Section 4) and this was confirmed for the three dominant species, *M. latidactylus*, *M. tolmerum* and *M. australiense*, by laboratory studies of temperature-salinity tolerance (Section 6.1). This section describes laboratory studies of temperature-salinity requirements for larval development in the three dominant species. The aim was to determine the optimum constant conditions for larval development and the range of conditions under which larvae complete development.

7.2 METHODS

The approach was one of factorial experiments and response surface analysis.

Even though females produced fertile eggs under laboratory conditions, these rarely completed incubation. Larvae for temperature-salinity experiments were therefore obtained from ovigerous females trapped in the study area; *M. latidactylus* from sites 14 and 15, *M. tolmerum* from the vicinity of site 1 and *M. australiense* from sites 4, 5 and 6. Ovigerous females were obtained on several collecting occasions in order to provide sufficient larvae of any one species. This introduced a possible source of variation from field acclimation effects on the embryos.

In order to minimise such effects, only females with embryos in early to mid development when captured were used, thus allowing at least five days acclimation of the embryos in the laboratory before hatching. Ovigerous females were held in a recirculating freshwater aquarium system (conductivity, K_{25} = 80 - 120 µS) at a temperature of 27°C ± 0.5 C° under a 12/12 photoperiod. They were held individually in 1.5 l plastic tanks overflowing through windows of nylon mesh which retained the larvae on hatching. Hatching always occurred overnight and experiments were commenced around noon the following day (designated day 0 in the following text).

During experiments, batches of larvae were held in 150 ml of water of the required salinity in plastic culture vessels, the lids of which were perforated to allow ventilation. The water was not aerated, as the mechanical effect of air bubbles was found to reduce the survival of larvae. Experimental salinities were obtained by mixing filtered seawater (Whatman GF/C glass fibre filter) and fresh water (conductivity, K_{25} = 70 - 75 µS) from the study area. Salinities were checked on an Auto Lab Model 601 Mk III B inductive salinometer, and were always within 0.1°/oo of the nominal value. In the text following, fresh water is referred to as 0°/oo. Culture vessels were partially submerged in constant temperature (±0.1 C°) water baths. Larvae were transferred to fresh experimental water every day, and commencing on the third day, recently hatched *Artemia* nauplii were added at the rate of approximately 7 per ml of culture water. *Artemia*

nauplii die within 12 hours of being placed in fresh water. Therefore, in order to avoid fouling of the 0°/oo experimental cultures, *Artemia* were added to all cultures at approximately 1700 hours daily and the *Macrobrachium* larvae were transferred to new experimental water at 0900 hours daily. Larvae were designated dead and removed from the culture when no swimming response was elicited by touching with a pasteur pipette.

The temperature-salinity combinations used are given in Tables 29, 30 and 31. Three replicates were run at each temperature-salinity combination.

For assessment of temperature-salinity tolerance, Dorgelo (1976) recommended direct transfer from acclimation to experimental conditions. However, preliminary experiments with *Macrobrachium* larvae gave highly variable survival times when they were transferred directly to the more extreme temperature treatments. Therefore, larvae were transferred directly from fresh water to all salinities, but were introduced to their ultimate temperature by staging through one hour exposures to the intermediate temperature treatments.

Since the aim of the study was to determine temperature-salinity effects on survival through larval development, the response would ideally have been expressed as the proportion of larvae surviving to the first post-larval instar. However, because of the long period of larval development in *M. tolmerum* and *M. latidactylus*, survival rates to post-larvae were low, even under optimal temperature-salinity conditions. Thus, only a

limited number of temperature-salinity combinations produced post-larvae, and using survival to post-larvae as the response unit would have given only a small number of data points, and no information regarding most of the response surface. A unit of response was therefore sought which would take values over most of the experimental space, and that selected was the survivor days proportion (SDP). This was defined as the number of survivor days of a batch of larvae expressed as a proportion of the maximum possible survivor days to the day of appearance of the first post-larva in any treatment for that species. For example, the first post-larvae of *M. australiense* to appear in any experimental treatment appeared on day 4. Thus, in a batch of 10 larvae the maximum number of survivor days was 40. If 5 of these larvae survived 3 days and the remainder survived beyond 4 days, the SDP would be calculated as $SDP = \frac{(5 \times 3) + (5 \times 4)}{40}$

$= 0.875$

Response surface analysis was carried out as for adult temperature-salinity survival data (Section 6.1.2). Examination of residuals was used to empirically select the most appropriate transformations of the dependent variable. The positions of local maxima of response surfaces were calculated using the IMSL sub-routine ZXMIN (Anon, 1977).

Using the response surfaces of the SDP, it is also possible to estimate the proportion of larvae which would survive to a given time in a given experimental treatment. This is derived as follows. For treatments in which 100% mortality occurs before

the day of first appearance of post-larvae, the survivor days proportion is related to mean survival time (MST) thus; MST (days) = SDP x days to first post-larvae. In this region of the response surface, if the distribution of survival time about the MST at a given temperature-salinity combination can be described, then the proportion of larvae surviving for a given time under that treatment can be predicted. To this end, a pooled estimate of variance of the logarithm of survival time (using all treatments from which MST could be calculated) was made for each species. The logarithm transformation normalised the distributions and stabilized variance. Then, since the standard normal deviate z is given by $z = \frac{x - \mu}{\sigma}$ the proportion of larvae surviving to time x, given the mean value μ and pooled standard deviation σ, can be obtained from the standard normal probability density function. Conversely, it is possible to determine the mean survival time (μ) which will result in a given proportion of larvae surviving to time x.

7.3 RESULTS

The numbers of larvae tested at each temperature-salinity combination are given in Table 29 *(M. latidactylus)*, Table 30 *(M. tolmerum)* and Table 31 *(M. australiense)*. Time to appearance of first post-larvae and % survival to post-larvae at each temperature-salinity combination producing post-larvae are given in Table 26 *(M. latidactylus)*, Table 27 *(M. tolmerum)* and Table 28 *(M. australiense)*. Highest overall survival rate

was shown by *M. australiense* larvae and lowest by *M. tolmerum* larvae. Similarly, *M. australiense* survived to post-larvae in a wider range of temperature-salinity combinations than either of the other species. This was no doubt due mainly to the relative lengths of larval development, *M. australiense* moulting to post-larvae in a minimum of 4 days, *M. latidactylus* in 21 days and *M. tolmerum* in 38 days. There were too few treatments producing post-larvae to allow estimation of optimum conditions from survival to post-larvae data. However, it is noted that maximum survival to post-larvae occurred at 30° - 16°/oo in *M. australiense*, 25° - 20°/oo in *M. latidactylus* and 25° - 32°/oo in *M. tolmerum*. It is also significant that *M. australiense* had high rates of survival in fresh water whereas *M. tolmerum* and *M. latidactylus* did not survive to post-larvae under those conditions. As expected, in all species, the rate of larval development was markedly affected by temperature. There were also salinity effects, but these were much less marked over the experimental range than those of temperature.

The survivor days proportion (SDP) for each replicate at each temperature-salinity combination is presented in Table 29 *(M. latidactylus)*, Table 30 *(M. tolmerum)* and Table 31 *(M. australiense)*. Since the first appearance of post-larvae was on day 4 for *M. australiense*, day 21 for *M. latidactylus* and day 38 for *M. tolmerum*, the respective SDP values have been based on those times. Summaries of the regression of the SDP on temperature and salinity are given in Table 32 *(M. latidactylus)*, Table 33 *(M. tolmerum)* and Table 34 *(M. australiense)*. The response surfaces thus derived

are represented as isopleth diagrams in Fig. 32. Each of the regression models showed significant lack of fit (Tables 32, 33 and 34) but this is not uncommon in analysis of complex response surfaces (e.g. Alderdice and Forrester, 1971a, 1971b). Since the lack of fit was probably due in part to irregularities of response caused by genetic and acclimation differences of the batches of larvae, the fitting of higher order polynomials to reduce the lack of fit was considered unwarranted.

The predicted SDP maxima were at 25.32°C and 17.93°/oo for *M. latidactylus*, 23.40°C and 25.52°/oo for *M. tolmerum* and at 25.81°C and 10.07°/oo for *M. australiense*. For each species, both temperature and salinity within the experimental range had marked effects on the predicted survivor days proportion.

Using pooled estimates of variance of mean survival time and the standard normal probability density function (Section 7.2), the mean survival times which would be expected to be associated with only 1% of larvae surviving for given numbers of days were:-

	DAYS SURVIVED BY 1% OF LARVAE	MST (days)
M. tolmerum	37	13.75
M. latidactylus	20	8.10
M. australiense	4	0.96

These mean survival times are equivalent to the 36.2% isopleth for *M. tolmerum*, the 38.6% isopleth for *M. latidactylus* and the 23.9% isopleth for *australiense* in Fig. 32. Since the minimum

time for larval development was 38 days in *M. tolmerum*, 21 days in *M. latidactylus* and 4 days in *M. australiense*, these isopleths represent the temperature-salinity space outside which there is little chance of larvae completing development. The critical isopleth for *M. tolmerum* includes only a small range of temperature and salinity; that of *M. latidactylus* encloses a much larger area while that of *M. australiense* lies largely outside the experimental space. Only in *M. australiense* does the critical isopleth include fresh water. At optimum temperatures, the upper critical salinities are not defined by the response surfaces, but while a proportion of the larvae of each species would be expected to survive at $32^{o}/_{oo}$ salinity, the upper salinity limit for larval development would be higher for *M. tolmerum* and *M. latidactylus* than *M. australiense*.

7.4 DISCUSSION

The aim of this study was to investigate the effects of temperature and salinity on survival rates of larvae. Thus it is necessary to justify the use of the survivor days proportion as an estimator of survival through larval development. The SDP could be biased by treatment effects on the rate of larval development. For example, at low temperatures, larvae could have a high SDP but only a low rate of survival to post-larvae; at low temperatures, the SDP would therefore overestimate the suitability of the temperature-salinity conditions for larval development. Salinity had only a minor effect on the length of larval develop-

ment and consequently, any bias in the SDP due to treatment effects on the rate of development would be largely in relation to temperature. Therefore, since the most important conclusions of this study concern the relative salinity requirements of the three species, bias of the SDP is not considered a major problem. The rates of survival to post-larvae (Tables, 26, 27 and 28) did in fact correspond well with the optimal regions predicted from the SDP data (Fig. 32).

The following conclusions are drawn regarding the laboratory survival of larvae of *M. tolmerum*, *M. latidactylus* and *M. australiense* from Bluewater Creek:-

(i) larvae of *M. latidactylus*, *M. tolmerum* and *M. australiense* all have highest survival rates in saline water;

(ii) at optimum salinity, the optimum temperature for survival of larvae increases in the order *M. tolmerum* - *M. latidactylus* - *M. australiense*;

(iii) at optimum temperature, the optimum salinity for survival of larvae increases in the order *M. australiense* - *M. latidactylus* - *M. tolmerum*;

(iv) the range of temperatures and salinities in which larval development can be expected to be completed is greatest for *M. australiense*, less for *M. latidactylus* and least for *M. tolmerum*;

(v) at optimum temperatures, a proportion of larvae of all three species can be expected to complete

development at 32°/oo salinity;

(vi) *M. australiense* is the only species whose larvae can be expected to complete development in fresh water.

There have been no published studies on the temperature-salinity requirements of the larvae of *M. latidactylus*, *M. tolmerum* or *M. australiense*. However, Fielder (1968) reared larvae of *M. australiense* from Ross River, Townsville in fresh water.

Similar considerations regarding extrapolation of laboratory physiological tolerances to the field as were mentioned in Section 6.1.4 apply here. Changes in the survival response to temperature and salinity during larval development, as have been shown in the crab *Rhithropanopeus harrisii* (Costlow *et al.*, 1966), are likely, especially since in the *Macrobrachium* species studied, the salinity optima for larvae and adults are different. If a range of salinities were available in the field, and larvae were able to maintain position in optimal salinity regions, it is possible that higher survival rates might be achieved there than in the laboratory under constant conditions. However, given the limited locomotory ability of larvae and the temporal and spatial variation of natural salinity conditions, this would be rare.

A further consideration is that of nutrition. It is unlikely that the experimental diet (*Artemia* nauplii) was optimal for *Macrobrachium* larvae. If a more suitable diet were available in the field, overall survival rates would be higher

than those in the laboratory. This would increase the ranges of temperature and salinity suitable for larval development as compared with those determined by laboratory experiments. In this respect, larvae of *M. australiense* may have had an advantage over the other species in the laboratory by virtue of their comparatively large store of yolk and relative independence from external food sources. Even so, considering the short survival times of *M. tolmerum* and *M. latidactylus* larvae in fresh water, it is unlikely that more suitable diet would allow their survival to post-larvae under such conditions. Furthermore, subjective assessment of plankton samples suggested that the freshwater stations had low abundance and diversity of zooplankton. Thus, the experimental diet may have been superior to that available in the freshwater reach of the study area.

The general implications of larval temperature-salinity requirements are discussed in Section 9.

8 ASPECTS OF GENERAL BIOLOGY

Because of the low numbers of *M.* sp. A. and *M. novae-hollandiae* in the study area, data in this section refer largely to the dominant species, *M. latidactylus*, *M. tolmerum* and *M. australiense*.

The aspects of general biology investigated were those with direct relevance to the aims of the study, and their implications are discussed in Section 9.

8.1 EGGS AND FECUNDITY

To estimate fecundity, total counts of eggs carried by ovigerous females were made. It was not possible to use egg masses all in the same stage of development and therefore, some of the variation in fecundity may be due to progressive loss of eggs during incubation. However, Shokita (1973) found no marked difference in the relationship of the number of eggs to body length at different stages of embryonic development in *M. shokitai*.

M. australiense which has large eggs (1.1 mm x 0.7 mm, when recently deposited) produced the lowest number of eggs per egg mass of the species in the study area. The range was from 38 (rostral carapace length 15.3 mm) to 115 (RCL 19.2 mm). Fielder (1968) reported that *M. australiense* females from Ross River, Townsville carried from 97 to 197 eggs per egg mass. Shakuntala (1977) found that the number of eggs per egg mass of *M. lamarrei* ranged from 20 to 158.

In comparison with *M. australiense*, both *M. tolmerum* and *M. latidactylus* produce small eggs (0.6 mm x 0.4 mm) in greater numbers. The number of eggs per egg mass ranged from 503 (RCL 12.4 mm) to 1,605 (RCL 18.6 mm) in *M. latidactylus* and from 819 (RCL 15.3 mm) to 5,818 (RCL 30.3 mm) in *M. tolmerum*. The size of the eggs of *M. latidactylus* and *M. tolmerum* is similar to that of *M. rosenbergii* (Ling, 1969a), but a sample of 20 females of the last species carried up to 276,003 eggs (Patra, 1976). Individuals of *M. rosenbergii* attain much larger body size than *M. latidactylus* and *M. tolmerum*.

Specimens were not available for determination of egg size and number in *M.* sp. A and *M. novae-hollandiae*, but from occasional observations during the adult sampling programme, they are similar in these features to *M. tolmerum* and *M. latidactylus*.

The number of eggs carried by ovigerous females of *M. australiense*, *M. tolmerum* and *M. latidactylus* is plotted against rostral carapace length in Fig. 33. Least squares regression of the number of eggs on the cube of rostral carapace length gave the following relationships:-

(i) *M. latidactylus*

$Y = 353.20 + 0.1581 X$ ($r^2 = 0.6787$).

(ii) *M. tolmerum*

$Y = 135.42 + 0.1996 X$ ($r^2 = 0.8591$).

For *M. australiense* there was no significant regression of the number of eggs on either rostral carapace length or its cube.

One might expect the number of eggs to be limited by the volume available for ovarian development or by the volume of the maximum egg mass which can be carried by an individual of a given body size. The number of eggs per egg mass would then be expected to be proportional to the cube of linear body dimensions. This was found to be so in *M. lamarrei* (Shakuntala, 1977) but in *M. dayanum* (Koshy and Tiwari, 1975) and *M. shokitai* (Shokita, 1973) the relationship between number of eggs and linear body dimension appears substantially linear. Koshy and Tiwari also fitted a straight line to the egg number/body size relationship in *M. lamarrei* (compare with Shakuntala) but examination of the data suggests a power curve would be more appropriate.

The lack of significant regression of the number of eggs per egg mass on rostral carapace length of *M. australiense* does not necessarily imply any peculiarity in determination of egg numbers in that species. Assuming that the number of eggs is controlled by available space, because of the large size of *M. australiense* eggs, the difference in number carried by females of 16 mm and 20 mm RCL would not be great. For example, if in an individual of 16 mm RCL the space available for the egg mass measures 5 mm x 2 mm x 2 mm (20 mm^3) and this is occupied by 50 eggs, the volume occupied per egg is 0.40 mm^3. If the linear dimensions of the egg mass space increase in proportion to rostral carapace length, the volume available for eggs in an individual of 20 mm RCL is 25.0 mm^3, which can contain approximately 62 eggs.

This order of increase in egg number over the given range of rostral carapace length is compatible with the points plotted for *M. australiense* in Fig. 33.

8.2 SEASONALITY OF REPRODUCTION

The numbers of ovigerous and non-ovigerous females of each species taken on each sampling occasion are given in Table 35. *M. tolmerum* from sites 1 to 8 and sites 9 to 16 are presented separately because of the spatial isolation of the main centres of population sampled and possible differences in environmental conditions experienced.

M. australiense and *M. latidactylus* reproduced over most of the year. Maximum numbers of ovigerous females of *M. australiense* occurred during the dry season months (August to December) and at the beginning of the wet season (January); minimum numbers occurred during and immediately after the wet season (February to June). In contrast, maximum numbers of ovigerous *M. latidactylus* females were taken during and immediately after the wet season (March to July) and minimum numbers during the remaining dry season months. Overall numbers of *M. tolmerum* ovigerous females were low, but the data suggest maximum reproductive activity at both upstream and downstream sites during the wet season months (January to April) and a further peak at the upstream sites during August and September. Only one ovigerous female of *M.* sp. A was taken during the study. Within the area sampled, *M. novae-hollandiae* exhibited maximum reproductive

activity during the high salinity dry season months (August to December). During the months of low abundance (January, February and March) the extent of reproductive activity is not known since this is a brackish-water species (Section 4.3.2) which may have moved downstream outside the sampling area in response to low salinity.

8.3 EGG PRODUCTION

In order to compare the reproductive potential of *M. australiense*, *M. tolmerum* and *M. latidactylus* in the study area, estimates of total egg production by a given stable population over the thirteen months of study have been made.

Egg production in a given time t is given by

$$EP = N.\ fo.\ E.\ \frac{t}{ti}$$

where N is the population number

fo is the proportion of individuals ovigerous

ti is the incubation time

E is the number of eggs per egg mass.

Incubation times for *M. tolmerum* and *M. latidactylus* were derived from females which mated and subsequently hatched larvae in the laboratory. For both these species, the mean incubation time at 27°C was estimated as 15 days. No *M. australiense* females oviposited in the laboratory, but observation of females which had been taken from the field with eggs in very early embryonic development indicated incubation time to be at least 20 days at 27°C.

For the present purpose it was assumed to be 21 days.

To calculate total egg production during the study period, the above equation was evaluated for each of the thirteen months (assumed 30 days long) of the study. A stable population of 1,000 adults was assumed. The proportion of ovigerous individuals was held constant during each month, but varied between months according to data in Appendix B. Incubation time was assumed constant. A constant value of the number of eggs per egg mass was used for each species; for *M. tolmerum* and *M. latidactylus* this was derived by substituting the mean rostral carapace lengths of all ovigerous females taken during the sampling programme into the relationships derived in Section 8.1; for *M. australiense*, the value taken was the mean number of eggs of the sample of egg masses examined in Section 8.1.

Total numbers of eggs produced during the thirteen month period by stable populations of 1000 adults were thus calculated as:-

M. latidactylus	5,247,383
M. tolmerum	3,342,267
M. australiense	210,371

Notwithstanding the assumptions made in arriving at these figures, it is apparent that even though *M. australiense* has an extended breeding season, its total egg production is low compared with that of *M. latidactylus* and *M. tolmerum*.

8.4 LARVAL DEVELOPMENT

In order to take account of adaptations of life cycles to the freshwater environment, the general patterns of larval development in the *Macrobrachium* species of Bluewater Creek are now described.

M. latidactylus

The larval development of *M. latidactylus* has not previously been described.

Gross morphology of laboratory hatched stage I larvae is shown in Fig. 34. Total length (from tip of telson to front of eye capsule) of 20 individuals ranged from 1.70 mm to 1.85 mm with a mean of 1.77 mm. The first two pairs of pereiopods are present as biramous rudiments. The telson bears 7 pairs of plumose setae on its posterior margin and is undifferentiated from the sixth abdominal segment. Pleopods and uropods are absent.

Under optimal conditions of temperature and salinity (Section 7) the duration of the first larval instar was approximately 36 hours. The minimum time for completion of larval development was 21 days at 30°C and 36 days at 25°C. It was not possible to recognise distinct morphological stages beyond stage IV in mass cultures, but since that stage was reached by day 8 at 30°C, at least eight larval instars would be expected before moulting to the first post-larval instar.

At 27.0°C and 10°/oo, 15°/oo, 20°/oo and 25°/oo salinity, starved larvae died before stage III. The addition of

Artemia nauplii to cultures allowed completion of larval development under suitable conditions of temperature and salinity. Larvae from stage II onwards accepted *Artemia* nauplii, but appeared to capture live nauplii only by chance. In contrast, first instar post-larvae actively captured live *Artemia* with the chelae of the first and second pereiopods. Similar observations have been made on the feeding behaviour of *M. rosenbergii* larvae and post-larvae (Moller, 1978).

M. tolmerum

The larval development of *M. tolmerum* has not been described in the literature.

In gross morphology, the stage I larvae of *M. tolmerum* are indistinguishable from those of *M. latidactylus* (Fig. 34), except that their total length is slightly less. Total length of 20 individuals ranged from 1.60 to 1.65 mm with a mean of 1.62 mm.

The duration of stage I was 3 to 5 days in the temperature range 25 to 30°C. The minimum time for completion of larval development was 38 days at 30°C and 49 days at 25°C. Stage IV was reached in 9 to 10 days at 30°C, and if moulting continues at the same rate, there are approximately 12 larval instars.

Observations regarding feeding were as for *M. latidactylus*.

M. australiense

The larval development of *M. australiense* from Ross River, Townsville, has been described by Fielder (1968) and no obvious morphological differences to this were shown by larvae

hatched from Bluewater Creek females.

M. australiense has three zoeal instars before the first post-larval instar. In the first stage, rudiments of all the pereiopods and pleopods are present. Total length of 20 specimens ranged from 3.3 to 3.5 mm with a mean of 3.40 mm.

In the temperature range 20° to 30°C, the duration of the first larval stage was 1 to 2 days. The minimum time for completion of larval development was 4 days at 30°C and 6 days at 25°C.

Under optimal conditions of temperature and salinity, *M. australiense* larvae can complete development to the first post-larval instar without feeding. However, survival was enhanced by the addition of *Artemia* nauplii to the cultures, even though the *Macrobrachium* larvae were not seen to capture *Artemia*, and were observed feeding on detritus only in stage III. However, as with *M. tolmerum* and *M. latidactylus*, first stage post-larvae actively captured and fed on live *Artemia* nauplii.

M. novae-hollandiae

Only one batch of eggs of this species hatched in the laboratory. Stage I larvae exhibited no observable differences in gross morphology from those described by Greenwood *et al.* (1976). Size and degree of development of appendages in stage I were similar to those of *M. tolmerum* and *M. latidactylus*. Total length of 20 individuals ranged from 1.60 to 1.85 mm with a mean of 1.75 mm.

M. sp. A

No larvae of this species were hatched in the laboratory, but its eggs were similar in size to those of *M. tolmerum* and *M. latidactylus* (Section 8.1), suggesting a long larval phase.

The range of patterns of larval development characterised by Sollaud (1923) for the Palaemoninae in general, has now been demonstrated to occur within the genus *Macrobrachium*. Many species are known to have the more typical long larval development involving many larval stages. These include *M. rosenbergii* (Uno and Kwon, 1969), *M. acanthurus* (Choudhury, 1970), *M. carcinus* (Choudhury, 1971a), *M. niloticum* and *M. intermedium* (Williamson, 1972), *M. idella* (Pillai and Mohamed, 1973), *M. olfersii* (Dugger and Dobkin, 1975), *M. equidens* (Ngoc-Ho, 1976) and *M. lar* (Atkinson, 1977). In contrast, *M. shokitai* (Shokita, 1973), *M. hendersodayanum* (Jalihal and Sankolli 1975) and *M. asperulum* (Shokita, 1977) have no planktonic larval stages.

M. australiense lies between the forementioned two groups, having a short larval development, but retention of planktonic stages. *M. latidactylus*, *M. tolmerum*, *M. novae-hollandiae* and probably *M.* sp. A of this study all have the typical long larval development.

General implications of the patterns of development of the *Macrobrachium* species of Bluewater Creek are discussed in Section 9.

8.5 RECRUITMENT OF JUVENILES

Insufficient numbers of *M.* sp. A and *M. novae-hollandiae* were taken to warrant discussion in this section. Size frequency distributions for the remaining three species on each sampling occasion are presented in Figs. 35, 36 and 37. The data for *M. tolmerum* are presented separately for sites 1 to 8 and 9 to 16 because of the distance between the two main centres of population sampled, and the possibility of different environmental conditions being experienced. Juveniles are designated as individuals of less than 13 mm rostral carapace length, the size below which sexual differentiation is not readily apparent.

M. latidactylus (Fig. 35)

There was no obvious peak in recruitment and population size structure was relatively stable throughout the year. This suggests continuous recruitment, which is consistent with the extended period of reproductive activity (Table 35). Since the large increase in total catch in April and May cannot be attributed to recruitment of juveniles, increased catchability or immigration are suggested as possible causes.

M. australiense (Fig. 36)

The population size structure was relatively stable throughout the year, with no marked peaks in recruitment. This is again consistent with the extended period of reproductive activity (Table 35).

M. tolmerum (Fig. 37)

In contrast with the above two species, *M. tolmerum* exhibited marked peaks in recruitment at both upstream and downstream sites. These observations are consistent with the more restricted periods of reproductive activity, suggested by data in Table 35 to be in August-September and January to April.

9 GENERAL DISCUSSION AND CONCLUSION

Laboratory and field studies have indicated that the distribution patterns of *Macrobrachium* species in Bluewater Creek are determined by complex interactions of biotic and abiotic factors.

Salinity limits the downstream distribution of all five species present, but does so differentially because of their relative tolerances. Thus, at any point in time, the limits of distribution are usually progressively further downstream in the order *M. australiense* - *M. tolmerum* - *M.* sp. A - *M. latidactylus* - *M. novae-hollandiae* (Section 4). However, only *M. novae-hollandiae* prefers saline water, the remaining species preferring fresh water. *M. latidactylus* is often present in brackish water and its distribution does not extend far upstream of the tidal zone. Since this limited distribution is not because of a preference for brackish water, interspecific competition may be involved. Laboratory studies (Section 6.2) demonstrated competitive displacement of *M. australiense* by *M. tolmerum*. Such competitive pressures between *M. tolmerum* and *M. latidactylus* in conjunction with their relative fitness in saline water, would tend to produce the observed restriction of *M. latidactylus* to areas within and immediately upstream of the tidal reach. Similarly, the absence of *M. latidactylus* from freshwater areas where *M. tolmerum* is not present (large pools) could be due in part to competition from the dominant species there, *M. australiense*.

Temperature is an important factor, both through its effect on salinity tolerance (Section 6.1) and in its own right. While low temperatures are unlikely to limit the distribution of *Macrobrachium* species in Bluewater Creek, temperatures of up to 40°C which occur in stratified saline water, are lethal.

Substrate was suggested by laboratory and field studies to be an important factor in determining the distributions of *M. tolmerum* and *M. australiense* in the freshwater reach where *M. tolmerum* dominates riffle areas and *M. australiense* dominates large pools. However, the difference between these two habitats involves other factors, including current and oxygen regime. It is possible that in the preference exhibited by *M. tolmerum*, substrate acts merely as a behavioural cue while the biological need is for another correlated factor. Some preference for moving water to still water was shown by *M. tolmerum*, but even so, the requirement may not be for current *per se*. A possible basis for current preference is the associated oxygen regime, but laboratory studies demonstrated little difference between *M. tolmerum* and *M. australiense* in their tolerance of low levels of dissolved oxygen. Nevertheless, given identical tolerance and a preference by both species for the riffle area oxygen regime, *M. tolmerum*, being the dominant species would be expected to displace *M. australiense* from the preferred habitat.

Current *per se* was involved in the distribution patterns through dislodgement of animals during flooding and in

the distribution of *M. latidactylus* which appeared to avoid areas of high stream velocity. Current is also suggested below as being extremely important to the survival of larvae of some species.

There are significant differences between species in the temperature-salinity requirements of *Macrobrachium* larvae from Bluewater Creek. Laboratory studies indicated that of the three most abundant species, only *M. australiense* could complete its larval development in fresh water. Thus in *M. tolmerum* and *M. latidactylus*, while adults prefer fresh water, the larvae must be transported to saline conditions in order to complete development. Since there was no evidence of spawning migrations, the success of larvae of these species is closely dependent on freshwater flow. For *M. latidactylus*, which always occurs close to saline water, larvae released at most times of the year have a high probability of reaching suitable conditions of salinity. This is supported by the relatively continuous recruitment of juveniles indicated by the stable population size structure (Fig. 35). In contrast, ovigerous females and larvae of *M. tolmerum* occur at the most upstream sampling sites. Larvae hatched in such localities obviously have much less chance of survival. Predicted mean survival time for *M. tolmerum* larvae in fresh water at 27°C is approximately three days, and none survived more than five days in fresh water at any temperature (Section 7). The stream flow regime during the study period (Fig. 4) was such that the only months during which larvae of *M. tolmerum* released at,

or upstream of, site 8 could be expected to be transported to saline water, were the wet season months, January to April. During that period it is likely that most larvae would be carried to sea, with little chance of returning to the estuary. However, the presence of small numbers of juveniles of *M. tolmerum* during the months subsequent to the wet season indicates that some larvae survived during the high flow rate months; whether they survived within the estuary or returned as juveniles after having completed larval development at sea, is unknown. Nevertheless, it is suggested that adults of *M. tolmerum* in areas at, or further upstream than site 8, contribute little to future generations and that most of the effective reproduction is by individuals located further downstream, close to or within the tidal reach.

The requirement of saline water by *M. tolmerum* larvae implies that all adults in freshwater localities have arrived there by migration. Size frequency data for the upstream sites (comprised largely of records from sites 1 and 2) in Fig. 37 show marked peaks of recruitment of juveniles in February and August 1976. This suggests that most upstream migration may be carried out by immature individuals. Upstream migration of juveniles has also been reported for *M. malcolmsonii* (Ibrahim, 1962). In contrast, there was no evidence of upstream migration of juvenile *M. latidactylus;* if such had occurred there would have been some records of *M. latidactylus* further upstream than site 9. Thus there appears to be a distinct behavioural difference between *M. tolmerum* and *M. latidactylus*, a factor which may be largely

responsible for the limited upstream dispersal of the latter species.

Species such as *M. tolmerum* and *M. latidactylus* whose larvae require saline water, are obviously limited in their ability to penetrate inland waters. In the present study area, the distribution of *M. tolmerum* was not limited by this constraint but it would be expected to be limited in longer waterways. No data are available regarding the Australian distribution of *M. tolmerum*, but it is significant that in exploratory sampling of headwaters of tributaries of the Burdekin River at Paluma (80 km north-west of Townsville) no *M. tolmerum* were taken. These localities were approximately 300 km from the estuary. *M. australiense*, which can complete larval development in fresh water, was present; it is known to have a wide Australian distribution (Riek, 1951).

Parallelling the respective salinity requirements of the larvae of *M. tolmerum*, *M. latidactylus* and *M. australiense* are the lengths of larval development. The minimum times for completion of larval development under laboratory conditions were 38 days for *M. tolmerum*, 21 days for *M. latidactylus* and 4 days for *M. australiense*. Thus, these species provide an example of the abbreviation of larval development concomitant with adaptation to the freshwater environment. The two species whose larvae require saline water have long periods of larval development while *M. australiense* whose larvae can survive in fresh water, has a short larval development (Section 8.4).

Abbreviation of larval development is widespread in the decapod Crustacea, and is particularly common in freshwater species (Gurney, 1942). It is pertinent to ask therefore, whether the ability of these species to inhabit fresh water is related to the abbreviation of larval development. Within the genus *Macrobrachium* there is a range of patterns of larval development and a range of adaptation to the freshwater environment. Consideration of this group should therefore provide some insight into the above question.

Evolution of freshwater species of *Macrobrachium* from marine ancestors would have taken place largely in streams rather than lakes. Thus, the environment would have been one of flowing water, a feature of considerable importance in evolution of the life cycle. As adults became adapted to fresh water, and penetrated further upstream, larvae would gradually become more tolerant of reduced salinity. However, because of continual downstream displacement of larvae by stream flow to more saline areas, specific larval adaptations to fresh water would progress more slowly than those of adults. Thus, larval stages would always be a limiting factor in penetration of fresh water. So long as larvae continued to require sea water for their development, there would be no selective advantage in abbreviation of larval development. However, once the requirements of larvae began to progress towards brackish water, such forces would come into effect because of the disadvantages of displacement of planktonic larvae. On the basis of this suggested pattern of events, evolution of

fresh water tolerance and abbreviation of larval development are seen as distinct but interrelated processes.

As has been emphasised by Lucas (1972), body size and hence surface area to volume ratio is an important factor in the ability of decapod larvae to survive in dilute media. Thus, in *Macrobrachium* species, larger body size would be expected in those larvae more tolerant of fresh water, given otherwise equal osmoregulatory abilities. The first stage larvae of *M. tolmerum*, *M. latidactylus* and *M. australiense* from Bluewater Creek have increasing body size in that order, which corresponds to their ability to survive in dilute media. The freezing point depression of the bloods of *M. australiense* and *M. equidens* (a brackish-water species) are approximately equal under normal environmental conditions (Denne, 1968). Since *M. tolmerum* and *M. latidactylus* are more freshwater in their requirements than *M. equidens*, they too would be expected to have blood osmotic concentrations similar to that of *M. australiense*. If this is so, the relative sizes of the larvae of *M. tolmerum*, *M. latidactylus* and *M. australiense* would be of considerable importance in their relative ability to tolerate fresh water.

Since larger body size is an advantage to larvae exposed to fresh water, it is understandable that within the *Macrobrachium*, increasing size of larvae is usually concomitant with abbreviation of larval development. However, the example of *M. niloticum* from Lake Chad (Williamson, 1972) supports the above suggestion that

these processes can be independent. In Lake Chad, a freshwater lake (Beadle, 1974), *M. niloticum* completes its whole life cycle. It has a long larval development, but the larvae are of large body size (approximately 3.5 mm total length at stage I) similar to that of *M. australiense* from Bluewater Creek. This example furthermore indicates that abbreviation of larval development is not a prerequisite for success in fresh water *per se*, and lends support to the supposition that occurrence of this phenomenon in freshwater species is an adaptation to flowing water. Several species of *Macrobrachium* are known to have no planktonic larval stages (Section 8.4); they are species which inhabit swiftly flowing freshwater environments. The *M. australiense* from Bluewater Creek has a short larval development, but planktonic stages remain. It is significant that this species inhabits deeper, slow flowing areas.

A further possible advantage of abbreviated larval development in *Macrobrachium* species concerns larval nutrition. Flowing fresh waters generally support low levels of plankton biomass and diversity compared with the estuarine and marine environments (Hynes, 1970). The trophic environment of such habitats may provide some of the selective pressure for abbreviation of the planktonic larval phase and for lecithotrophy (as observed in *M. australiense)* in remaining larval stages.

Thus, consideration of *Macrobrachium* species leads to the following suggestions regarding adaptation of the decapod life cycle to freshwater environments:-

(i) the body size of larvae is an important factor in their ability to tolerate fresh water;

(ii) tolerance of fresh water by larvae and abbreviation of larval development are distinct processes which may be interrelated;

(iii) abbreviation of larval development in freshwater species is an adaptation to flowing water;

(iv) the paucity of planktonic food sources in flowing fresh waters may be a further selective pressure for abbreviation of larval development and for lecithotrophy in planktonic larval stages.

CONCLUSION

Major factors determining gross distribution patterns of *Macrobrachium* species in Bluewater Creek are temperature, salinity, substrate and current whose effects are interconnected with competition between species and adaptations of the life cycle to fresh water. Within the gross distribution of each species, further modification of population density may be caused by predation, availability of food and competition from other crustaceans.

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TABLE 1. Temperature and rainfall data for Townsville for the period 1926 - 65 (Department of National Development Resource Series, Climate Burdekin - Townsville Region).

	TEMPERATURE (°C)		RAINFALL (mm)		
MONTH	MEAN DAILY MAX.	MEAN DAILY MIN.	MEAN	50% PROB.[1]	RAIN DAYS[2]
JANUARY	30.7	24.6	267	208	15.3
FEBRUARY	30.6	24.2	319	290	16.6
MARCH	30.3	23.3	219	170	14.0
APRIL	29.3	21.4	57	36	7.8
MAY	27.3	18.6	25	10	5.8
JUNE	25.2	16.6	30	15	4.6
JULY	24.4	15.4	21	5	3.1
AUGUST	25.3	16.4	9	-	2.8
SEPTEMBER	26.8	18.8	9	-	1.9
OCTOBER	28.4	21.4	26	15	4.7
NOVEMBER	29.6	23.2	47	25	6.3
DECEMBER	30.6	24.2	98	69	9.1
YEAR	27.9	20.7	1129	1039	92.0

[1]Rainfall likely to be equalled or exceeded by 50% of records.

[2]Mean number of days on which 1 point (0.254mm) or more was recorded.

TABLE 2. Monthly rainfall recorded in the upper catchment of Bluewater Creek (the landholder) and total monthly discharge of the stream (Irrigation and Water Supply Commission) for the period January 1975 to August 1976.

MONTH	RAINFALL (mm)	DISCHARGE ($m^3 \times 10^3$)
JAN 1975	216	3311
FEB	136	2654
MAR	465	27917
APR	14	6193
MAY	0	782
JUN	0	286
JUL	35	62
AUG	10	879
SEP	131	1515
OCT	3	2313
NOV	23	1348
DEC	791	40792
JAN 1976	250	14359
FEB	405	41876
MAR	269	14133
APR	10	2783
MAY	0	861
JUN	10	376
JUL	0	143
AUG	0	106

TABLE 3. Results of analysis of a water sample from the middle reach of Bluewater Creek on 10th January. 1978.

PARAMETER	VALUE
pH (Laboratory)	7.35
Suspended solids	2.0
Colour	10
Turbidity	15
Organic N (mg l^{-1})	0.025
Total P (µg l^{-1})	28.8
Ortho P (µg l^{-1})	4.0
Cl^{-} (mg l^{-1})	6.71
$SO_4^{=}$ (mg l^{-1})	0.65
Na^{+} (mg l^{-1})	6.5
Ca^{++} (mg l^{-1})	3.6
Mg^{++} (mg l^{-1})	2.0
K^{++} (mg l^{-1})	0.9

TABLE 4. Location and general characteristics of sites used in the sampling programme for adult *Macrobrachium*.

SITE	DISTANCE FROM MOUTH (km)	STREAM WIDTH (m)	LOCATION OF TRANSECT IN STREAM	HABITAT TYPE	SUBSTRATE	MAXIMUM SALINITY (^{o}/oo)
1	19	2-4	midstream, longitudinal	riffle	stone	fresh
2	19	5	adjacent bank, longitudinal	pool	sand	fresh
3	19	8	midstream, longitudinal	pool	sand	fresh
4	12	25	adjacent bank, longitudinal	pool	sand	fresh
5	12	25	midstream, longitudinal	pool	sand	fresh
6	12	25	adjacent bank, longitudinal	pool	sand	fresh
7	8	20	adjacent bank, longitudinal	pool	sand	fresh
8	8	20	midstream, longitudinal	pool	sand	fresh
9	4	4	adjacent bank, longitudinal	riffle	stone	8.3
10	4	6	adjacent bank, longitudinal	pool	stone	25.6
11	4	6	midstream, longitudinal	pool	sand	25.8
12	3.8	8	adjacent bank, longitudinal	pool	sand	32.6
13	3.8	8	midstream, longitudinal	pool	sand	31.6
14	3.5	19	downstream end of pool, transverse	riffle	stone	12.2
15	3.3	20	downstream end of pool, transverse	riffle	stone	17.2
16	3.2	25	midstream, longitudinal	pool	sand	33.8

TABLE 5. Conductivity (K_{25}, µS) at freshwater sites in Bluewater Creek on five occasions. Missing values indicate the presence of brackish water due to tidal influence.

	SAMPLE DATE				
SITE	10.i.78	16.ii.78	16.iii.78	20.iv.78	2.vi.78
1	60	45	46	43	53
2	60	47	47	44	54
3	61	45	46	43	55
4	63	48	52	41	55
5	64	48	52	41	55
6	65	51	52	41	55
7	66	55	61	44	55
8	66	54	62	44	55
9		60	82	47	
10		60	106	48	
11		60	104	48	60
12		68	111	49	
13		60	107	48	
14		60	109	48	60
15		61	107	48	63
16		85	111		

TABLE 6. Dissolved oxygen concentration expressed as mg l^{-1} (A) and % saturation (B) at Bluewater Creek sampling sites on each of five occasions.

	SAMPLE DATE									
	10.i.78		16.ii.78		16.iii.78		20.iv.78		2.vi.78	
SITE	A	B	A	B	A	B	A	B	A	B
1	7.0	94.6	7.4	98.3	7.4	97.1	7.6	98.2	8.4	100.3
2	3.1	40.3	7.5	98.4	7.4	97.1	7.6	98.4	8.3	99.1
3	5.0	64.2	7.4	97.4	7.4	96.9	7.6	98.4	8.3	98.7
4	7.2	98.9	7.1	91.9	8.1	103.9	8.2	101.5	7.7	91.6
5	7.1	96.7	7.1	91.1	8.0	103.0	8.0	99.4	7.8	92.3
6	7.3	98.5	7.0	89.8	8.0	103.4	8.1	100.3	7.9	93.4
7	7.2	100.5	7.6	100.1	8.1	107.0	8.0	102.6	8.0	96.9
8	7.7	107.6	7.7	101.2	8.0	106.2	8.0	102.8	8.1	98.5
9	6.0	94.3	7.6	101.8	7.8	105.0	7.9	98.7	7.8	95.8
10	7.7	125.5	7.6	101.8	7.9	105.6	7.9	98.2	8.2	100.0
11	8.1	131.1	7.6	100.9	7.8	104.3	8.0	99.4	8.2	99.7
12	8.2	137.6	7.5	100.5	7.8	104.5	7.9	97.8	8.1	99.8
13	10.0	174.4	7.6	102.7	8.2	110.8	8.1	100.7	8.3	101.7
14	8.0	133.7	7.6	102.7	7.8	105.0	8.0	99.4	8.4	101.6
15	7.4	121.8	7.5	101.3	7.8	105.0	8.0	99.4	8.4	101.4
16	10.6	181.0	7.3	99.5	8.2	111.7	7.8	104.9	10.8	152.0

TABLE 7. Overnight levels of dissolved oxygen at a riffle area and a pool site in the vicinity of Bluewater Creek sampling sites 4, 5 and 6 on 9th and 10th January, 1979. Results are expressed as mg l^{-1} (A) and % saturation (B). Five readings were taken along a fixed transect at each site on each occasion.

TIME	POOL SITE		RIFFLE SITE	
	A	B	A	B
1700	10.0	132.8	9.5	130.5
	9.5	128.4	9.4	130.3
	9.8	131.3	9.5	130.5
	10.0	132.8	9.5	131.0
	9.5	126.2	9.4	129.2
2100	7.6	100.9	7.8	103.6
	6.3	83.7	7.7	102.3
	6.3	83.7	7.9	104.9
	6.0	79.7	7.7	102.6
	2.0	28.6	7.8	103.6
0100	7.2	95.6	6.4	83.6
	5.8	76.8	6.3	82.5
	4.0	52.9	6.5	84.9
	5.2	69.1	6.4	83.6
	2.0	26.3	6.5	85.0
0500	6.0	78.3	6.2	80.4
	4.5	58.9	6.4	82.8
	4.8	62.7	6.3	81.7
	4.1	53.7	6.4	83.0
	2.0	26.2	6.1	79.1

TABLE 8. *M. latidactylus*. Mean value and range of selected morphological variables from a sample of 50 adult males. Appendage segments are those of the larger second pereiopod. Measured dimensions are defined in Fig. A1 .

VARIABLE	MEAN	RANGE
Number dorsal rostral teeth	13.66	12 - 15
Number ventral rostral teeth	3.48	2 - 6
Ratio rostrum length/carapace length	0.66	0.58 - 0.74
Ratio dactylus length/palm length	0.73	0.60 - 1.03
Ratio propus length/carpus length	1.95	1.74 - 3.14
Ratio carpus length/merus length	1.42	0.92 - 1.58
Ratio propus proximal width/palm length	0.23	0.18 - 0.29
Ratio propus distal width/palm length	0.35	0.31 - 0.41
Ratio carpus proximal width/carpus length	0.09	0.07 - 0.14
Ratio carpus distal width/carpus length	0.21	0.17 - 0.33
Ratio telson distance 3/telson length	0.26	0.22 - 0.31

TABLE 9. *M. novae-hollandiae*. Mean value and range of selected morphological variables from a sample of 20 adult males. Appendage segments are those of the larger second pereiopod. Measured dimensions are defined in Fig. A1 .

VARIABLE	MEAN	RANGE
Number dorsal rostral teeth	9.65	9 - 10
Number ventral rostral teeth	4.30	3 - 5
Ratio rostrum length/carapace length	0.94	0.79 - 1.10
Ratio dactylus length/palm length	0.61	0.43 - 0.82
Ratio propus length/carpus length	1.22	1.00 - 1.37
Ratio carpus length/merus length	1.60	1.42 - 1.80
Ratio propus proximal width/palm length	0.13	0.09 - 0.16
Ratio propus distal width/palm length	0.13	0.09 - 0.16
Ratio carpus proximal width/carpus length	0.06	0.05 - 0.07
Ratio carpus distal width/carpus length	0.10	0.07 - 0.12
Ratio telson distance 3/telson length	0.28	0.23 - 0.32

TABLE 10. *M. australiense*. Mean value and range of selected morphological variables from a sample of 50 adult males. Appendage segments are those of the larger second pereiopod. Measured dimensions are defined in Fig. A1 .

VARIABLE	MEAN	RANGE
Number dorsal rostral teeth	9.34	7 - 12
Number ventral rostral teeth	6.70	5 - 8
Ratio rostrum length/carapace length	1.03	0.78 - 1.43
Ratio dactylus length/palm length	0.81	0.62 - 0.98
Ratio propus length/carpus length	1.56	1.24 - 1.75
Ratio carpus length/merus length	1.11	1.00 - 1.20
Ratio propus proximal width/palm length	0.18	0.15 - 0.21
Ratio propus distal width/palm length	0.20	0.17 - 0.24
Ratio carpus proximal width/carpus length	0.09	0.07 - 0.12
Ratio carpus distal width/carpus length	0.15	0.07 - 0.17
Ratio telson distance 3/telson length	0.31	0.23 - 0.37

TABLE 11. *M. tolmerum*. Mean value and range of selected morphological variables from a sample of 41 adult males. Appendage segments are those of the larger second pereiopod. Measured dimensions are defined in Fig. A1 .

VARIABLE	MEAN	RANGE
Number dorsal rostral teeth	9.83	8 - 11
Number ventral rostral teeth	3.51	3 - 5
Ratio rostrum length/carapace length	0.67	0.59 - 0.85
Ratio dactylus length/palm length	0.49	0.34 - 1.41
Ratio propus length/carpus length	1.65	0.97 - 1.99
Ratio carpus length/merus length	1.30	1.13 - 2.00
Ratio propus proximal width/palm length	0.14	0.07 - 0.39
Ratio propus distal width/palm length	0.16	0.10 - 0.39
Ratio carpus proximal width/carpus length	0.10	0.06 - 0.14
Ratio carpus distal width/carpus length	0.16	0.12 - 0.23
Ratio telson distance 3/telson length	0.29	0.25 - 0.33

TABLE 12. *M.* sp. A. Mean value and range of selected morphological variables from a sample of 41 adult males. Appendage segments are those of the larger second pereiopod. Measured dimensions are defined in Fig. A1 .

VARIABLE	MEAN	RANGE
Number dorsal rostral teeth	11.95	10 - 13
Number ventral rostral teeth	3.10	2 - 4
Ratio rostrum length/carapace length	0.57	0.49 - 0.65
Ratio dactylus length/palm length	0.46	0.37 - 0.70
Ratio propus length/carpus length	1.61	1.35 - 3.42
Ratio carpus length/merus length	1.48	0.72 - 1.67
Ratio propus proximal width/palm length	0.14	0.10 - 0.18
Ratio propus distal width/palm length	0.13	0.10 - 0.18
Ratio carpus proximal width/carpus length	0.11	0.08 - 0.20
Ratio carpus distal width/carpus length	0.15	0.12 - 0.31
Ratio telson distance 3/telson length	0.25	0.21 - 0.29

TABLE 13. Dates of sampling populations of adults and recording of environmental factors at sampling site 1, and corresponding dates of the nearest new moon.

SAMPLE DATE	NEW MOON DATE
4 August 1975	7 August 1975
9 September	6 September
6 October	5 October
4 November	3 November
3 December	3 December
6 January 1976	2 January 1976
23 February	1 March
22 March	31 March
26 April	29 April
24 May	29 May
28 June	28 June
26 July	27 July
30 August	25 August

TABLE 14. Mean stream surface velocity during the months February to June 1976 and the sampling occasion on which the highest total catch of *M. latidactylus* occurred for sites 9 to 16.

SITE	SAMPLE WITH MAXIMUM CATCH	MEAN SURFACE VELOCITY (cm sec^{-1})
9	July	57
10	May	22
11	May	30
12	May	18
13	April	12
14	May	28
15	May	33
16	March	12

TABLE 15. Summary of the distribution patterns of *Macrobrachium* species in Bluewater Creek.

SPECIES	DISTRIBUTION
M. novae-hollandiae	Brackish water with no apparent substrate preference. Low abundance.
M. latidactylus	Fresh and brackish water within the tidal reach; most abundant in fresh water. No apparent substrate preference. Decreasing abundance with increasing current.
M. tolmerum	Fresh water riffle areas throughout the stream. Rarely in saline water. Greater tolerance of high stream velocity than *M. latidactylus*.
M. australiense	Strictly freshwater and occurring only upstream of the tidal zone. Almost entirely restricted to large pools with sand substrate.
M sp. A.	Similar to *M. tolmerum*; freshwater riffle areas; more abundant on sand substrate than *M. tolmerum*. Low abundance.

TABLE 16. Abundance of *M. australiense* larvae at developmental stages later than Stage I taken in plankton samples.

MONTH	STATION	LARVAE m^{-3}
Sept. 1975	II	0.60
	III	0.34
	V	0.17
Nov. 1975	II	0.46
	III	0.37
Dec. 1975	II	0.86
Mar. 1976	III	0.18

TABLE 17. Mean rostral carapace lengths (RCL) and mean survival times of groups of six adult males of *M. latidactylus* at experimental temperature-salinity combinations.

TEMP (^{o}C)	SALINITY (^{o}/oo)	MEAN RCL (mm)	MEAN SURVIVAL TIME (minutes)
15	0	16.9	10
15	8	17.1	10
15	16	17.5	10
15	24	16.6	10
15	32	17.4	10
17	32	16.8	131
20	32	18.8	1615
35	32	16.4	1009
36	0	17.2	414
36	8	16.8	627
36	16	16.1	589
36	24	16.5	285
36	32	16.8	114
37	0	17.2	54
37	8	16.4	52
37	16	16.2	112
37	24	15.8	41
37	32	16.6	42
38	0	17.4	25
38	8	15.7	17
38	16	16.4	14
38	24	18.0	16
38	32	17.1	18

TABLE 18. Mean rostral carapace lengths (RCL) and mean survival times for groups of six adult males of *M. tolmerum* at experimental temperature-salinity combinations.

TEMP (°C)	SALINITY (°/oo)	MEAN RCL (mm)	MEAN SURVIVAL TIME (minutes)
15	8	22.9	26
15	16	20.7	29
15	24	19.3	25
15	32	18.8	32
17	32	18.6	1181
30	32	18.7	2264
35	24	20.9	1968
35	32	18.9	654
36	0	19.7	1162
36	8	22.5	602
36	16	22.7	429
36	24	21.7	371
36	32	21.5	162
37	0	20.6	225
37	8	20.4	32
37	16	21.0	51
37	24	19.9	45
37	32	19.3	44

TABLE 19. Mean rostral carapace lengths (RCL) and mean survival times for groups of six adult males of *M. australiense* at experimental temperature-salinity combinations.

TEMP (^{o}C)	SALINITY (^{o}/oo)	MEAN RCL (mm)	MEAN SURVIVAL TIME (minutes)
15	24	22.8	25
15	32	24.1	12
17	24	21.6	1115
17	32	23.2	419
25	32	22.7	771
30	32	22.7	544
35	0	24.4	448
35	8	22.2	59
35	16	22.4	724
35	24	22.5	97
35	32	23.5	74
36	0	22.2	31
36	8	23.4	98
36	16	23.3	41
36	24	22.4	42
36	32	24.5	59
37	0	23.0	6
37	8	21.8	5
37	16	23.8	6
37	24	21.9	5
37	32	22.6	5

TABLE 20. Regression analysis of *M. latidactylus* adults mean survival time data.

DEPENDENT VARIABLE: ln (mean survival time)

INDEPENDENT VARIABLE	COEFFICIENT	R^2 CHANGE	PARTIAL F
Temperature	1.8504	0.0858	380.98
Temperature^3	-0.0008161	0.8571	365.97
Salinity^2 x temperature	-0.00001511	0.0130	5.61
Constant	-22.588		

R^2 : 0.9559

NUMBER OF OBSERVATIONS : 23

STANDARD ERROR OF ESTIMATE : 0.3766

ANALYSIS OF VARIANCE:

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	3	58.43093	19.47698	137.29
Residual	19	2.69549	0.14187	

TABLE 21. Regression analysis of *M. tolmerum* adults mean survival time data.

DEPENDENT VARIABLE: ln (mean survival time)

INDEPENDENT VARIABLE	COEFFICIENT	R^2 CHANGE	PARTIAL F
Temperature	5.2925	0.1253	24.26
Temperature^2	-0.1027	0.5795	21.43
Temperature^2 x salinity	0.001715	0.0569	5.77
RCL x salinity	0.01059	0.0173	1.20
Temperature x salinity	-0.07743	0.0253	7.42
Salinity^2	0.03338	0.0298	4.49
Salinity^3	-0.0003758	0.0255	2.82
Salinity^2 x temperature	-0.0003522	0.0231	1.77
Constant	-50.104		

R^2 : 0.8827

NUMBER OF OBSERVATIONS : 18

STANDARD ERROR OF ESTIMATE : 0.7747

ANALYSIS OF VARIANCE:

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	8	40.63668	5.07958	8.46
Residual	9	5.40154	0.60017	

TABLE 22. Regression analysis of *M. australiense* adults mean survival time data.

DEPENDENT VARIABLE : ln (mean survival time)

INDEPENDENT VARIABLE	COEFFICIENT	R^2 CHANGE	PARTIAL F
Salinity	-0.1843	0.0310	1.21
Temperature^3	-0.0005574	0.1678	1.38
Temperature^2	-0.002598	0.5027	0.01
Temperature^2 x salinity	0.0001254	0.0488	0.91
RCL x temperature	0.04692	0.0189	1.81
RCL	-1.2639	0.0184	1.22
Constant	23.523		

R^2 : 0.7876

NUMBER OF OBSERVATIONS : 21

STANDARD ERROR OF ESTIMATE : 1.0128

ANALYSIS OF VARIANCE:

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	6	53.26775	8.87796	8.655
Residual	14	14.36092	1.02578	

TABLE 23. Laboratory substrate preference, sand/stones choice. Frequency distribution of the number of individuals observed on sand substrate in each of three series of 20 observations. Results of three experiments are shown - *M. tolmerum* alone, *M. australiense* alone and the two species together.

No. ON SAND	SPECIES SEPARATE						SPECIES COMBINED					
	M. tolmerum			*M. australiense*			*M. tolmerum*			*M. australiense*		
	1	2	3	1	2	3	1	2	3	1	2	3
0			1				2	1				
1	1		2	1		4	3	8	4	1		
2		3	4	3	1	4	8	9	6			
3	1	2	3	3	6	4	2	2	8			
4	7	4	2	5	4	5	1		1	1		
5	3	3	6	3	5		3		1	3		
6	1	6	1	3	3	2				1		
7	5	1		2	1	1	1			5		1
8	1		1							6		
9		1								1		3
10	1											7
11										2	1	5
12											1	2
13											3	2
14											8	
15											5	
16											2	
17												
18												
19												
20												

TABLE 24. Laboratory substrate preference, sand/leaf litter choice. Frequency distribution of the number of individuals observed on sand substrate in each of the three series of 20 observations. Results of three experiments are shown - *M. tolmerum* alone, *M. australiense* alone and the two species together.

No.	SPECIES SEPARATE						SPECIES COMBINED					
ON	*M. tolmerum*			*M. australiense*			*M. tolmerum*			*M. australiense*		
SAND	1	2	3	1	2	3	1	2	3	1	2	3
0								1	2			
1			1				2	3	1			
2	1		5	1		1	3	3	5			
3		4				2	6	6	5			
4	1	5	3	4	4	1	4	2	6			
5	1	4	3	1	5	5	2	3	1			1
6	3	4	5	4	4	1	1	2		1		
7	1	3	2	1	3	2	2			1		6
8	1		1	3	1	6				2		2
9	9			1	1	1				2	2	5
10				4	2	1				2	2	4
11	3			1						5	4	2
12											4	
13										3	3	
14										3	2	
15										1	2	
16											1	
17												
18												
19												
20												

TABLE 25. Tolerance of low dissolved oxygen concentration by *M. tolmerum* and *M. australiense* males in fresh water at 30°C.

O_2 CONC. (mg l^{-1})	SPECIES	n	% SURVIVAL TO 96 HOURS	MEAN SURVIVAL TIME (hours)	LT 50 (hours)
2.0	*M. tolmerum*	10	100.0	> 96	> 96
2.0	*M. australiense*	10	100.0	> 96	> 96
1.5	*M. tolmerum*	12	66.7	N.E.[1]	> 96
1.5	*M. australiense*	16	62.5	N.E.[1]	> 96
1.0	*M. tolmerum*	12	0.0	1.63	0.69
1.0	*M. australiense*	20	0.0	1.66	1.28

[1] No estimate possible.

TABLE 26. *M. latidactylus* larvae. Time to first post-larva and % survival to post-larvae at experimental temperature - salinity combinations.

TREATMENT		TIME TO FIRST	% SURVIVAL
TEMP (^{o}C)	SALINITY (^{o}/oo)	POST-LARVA (DAYS)	TO POST-LARVAE
25	10	37	27.8
25	20	36	44.4
25	30	41	5.6
30	10	23	11.1
30	20	21	27.8

TABLE 27. *M. tolmerum* larvae. Time to first post-larva and % survival to post-larvae at experimental temperature - salinity combinations.

TREATMENT		TIME TO FIRST	% SURVIVAL
TEMP (^{o}C)	SALINITY (^{o}/oo)	POST-LARVA (DAYS)	TO POST-LARVAE
25	16	49	2.6
25	24	49	3.0
25	32	50	7.7
30	24	38	6.7

TABLE 28. *M. australiense* larvae. Time to first post-larva and % survival to post-larvae at experimental temperature - salinity combinations.

TREATMENT		TIME TO FIRST	% SURVIVAL
TEMP (^{o}C)	SALINITY (^{o}/oo)	POST-LARVA (DAYS)	TO POST-LARVAE
20	8	12	72.7
20	16	12	93.9
20	24	12	50.0
25	0	5	97.1
25	8	6	96.6
25	16	6	84.8
25	24	6	74.2
30	0	4	75.0
30	8	4	90.0
30	16	4	100.0
30	24	4	75.0
30	32	5	3.0
35	8	4	29.0
35	16	4	42.4

TABLE 29. Survivor days proportion (SDP) and the number of *M. latidactylus* larvae tested (n) in each replicate of each temperature - salinity combination.

TREATMENT		REPLICATE 1		2		3	
TEMP (^{o}C)	SALINITY (^{o}/oo)	n	SDP	n	SDP	n	SDP
15	0	6	0.000	6	0.000	6	0.000
15	10	6	0.214	6	0.270	6	0.246
15	20	6	0.230	6	0.262	6	0.286
15	30	6	0.238	6	0.246	6	0.230
15	32	17	0.154	13	0.165	16	0.173
17	32	14	0.153	11	0.182	14	0.191
20	0	6	0.064	6	0.000	6	0.064
20	10	6	0.778	6	0.611	6	0.833
20	20	6	0.960	6	0.857	6	1.000
20	30	6	0.849	6	0.992	6	0.714
20	32	12	0.480	20	0.495	10	0.510
25	0	6	0.079	6	0.056	6	0.071
25	10	6	1.000	6	1.000	6	0.976
25	20	6	1.000	6	1.000	6	1.000
25	30	6	0.889	6	0.849	6	0.889
25	32	12	0.579	13	0.462	23	0.536
30	0	6	0.000	8	0.060	6	0.048
30	10	6	1.000	6	0.706	6	0.476
30	20	6	0.968	6	0.587	6	1.000
30	30	6	0.762	6	0.825	6	0.722
30	32	14	0.326	9	0.254	16	0.311
35	0	6	0.000	6	0.000	6	0.000
35	10	6	0.183	6	0.183	6	0.191
35	20	6	0.206	6	0.175	-	-
35	30	6	0.143	5	0.095	6	0.175
35	32	16	0.161	31	0.149	14	0.163

TABLE 30. Survivor days proportion (SDP) and the number of *M. tolmerum* larvae (n) tested in each replicate of each temperature - salinity combination.

TREATMENT		REPLICATE 1		2		3	
TEMP (°C)	SALINITY (°/oo)	n	SDP	n	SDP	n	SDP
15	0	11	0.026	14	0.026	15	0.026
15	8	11	0.117	13	0.193	11	0.219
15	16	12	0.303	13	0.289	16	0.294
15	24	14	0.263	12	0.250	15	0.233
15	32	10	0.217	12	0.234	13	0.233
20	0	10	0.058	13	0.065	15	0.067
20	8	14	0.147	11	0.187	12	0.199
20	16	11	0.261	12	0.260	17	0.231
20	24	14	0.321	11	0.281	14	0.398
20	32	11	0.290	12	0.416	16	0.252
25	0	12	0.079	12	0.057	13	0.083
25	8	13	0.185	12	0.151	12	0.197
25	16	11	0.374	12	0.399	14	0.654
25	24	10	0.665	12	0.650	11	0.734
25	32	14	0.544	12	0.616	13	0.599
30	0	11	0.050	12	0.066	11	0.067
30	8	12	0.125	12	0.112	15	0.100
30	16	10	0.245	11	0.300	16	0.263
30	24	14	0.513	14	0.450	17	0.466
30	32	14	0.278	12	0.591	15	0.393
35	0	13	0.032	14	0.026	15	0.028
35	8	11	0.084	19	0.082	14	0.077
35	16	14	0.085	13	0.083	16	0.091
35	24	12	0.097	10	0.074	11	0.074
35	32	10	0.079	15	0.072	13	0.081

TABLE 31. Survivor days proportion (SDP) and the number of *M. australiense* larvae (n) tested in each replicate of each temperature - salinity combination.

TREATMENT		REPLICATE 1		2		3	
TEMP (^{o}C)	SALINITY (^{o}/oo)	n	SDP	n	SDP	n	SDP
15	0	10	0.225	10	0.600	13	0.212
15	8	11	0.727	10	1.000	11	0.682
15	16	10	0.825	10	0.925	10	0.750
15	24	10	0.675	11	0.977	10	0.775
15	32	10	0.250	10	0.400	12	0.479
17	0	10	0.275	10	0.375	10	0.200
17	8	10	0.875	8	0.719	10	1.000
17	16	10	0.975	10	0.950	10	1.000
17	24	10	0.700	12	0.917	13	0.750
17	32	10	0.275	11	0.341	12	0.208
20	0	11	1.000	10	1.000	11	0.841
20	8	10	1.000	11	1.000	12	0.938
20	16	10	1.000	12	0.958	11	1.000
20	24	11	1.000	11	1.000	10	0.950
20	32	12	0.229	12	0.188	11	0.205
25	0	15	1.000	10	1.000	10	1.000
25	8	10	1.000	10	1.000	9	1.000
25	16	12	0.917	11	0.955	10	0.950
25	24	10	1.000	11	0.773	10	1.000
25	32	12	0.525	11	0.091	10	0.300
30	0	10	1.000	10	1.000	12	0.938
30	8	11	0.932	9	0.972	10	0.975
30	16	12	1.000	11	1.000	10	1.000
30	24	10	1.000	11	0.977	11	0.705
30	32	11	0.432	12	0.688	10	0.225
35	0	10	0.000	10	0.000	10	0.000
35	8	10	0.800	11	0.636	10	0.975
35	16	11	0.796	11	0.568	11	0.864
35	24	12	0.000	11	0.136	11	0.227
35	32	12	0.000	11	0.000	12	0.000

TABLE 32. Regression analysis of *M. latidactylus* larvae survivor days proportion data.

DEPENDENT VARIABLE : $(SDP)^{\frac{1}{2}}$

INDEPENDENT VARIABLE	COEFFICIENT	R^2 CHANGE	PARTIAL F
Salinity	0.08794	0.1863	89.40
$Salinity^2$	-0.003294	0.3821	17.85
$Temperature^3$	-0.00005849	0.0228	239.16
Temperature	0.1125	0.3057	223.12
$Salinity^3$	0.00003128	0.0051	3.68
Constant	-1.557		

R^2 : 0.9020

NUMBER OF OBSERVATIONS : 77

STANDARD ERROR OF ESTIMATE : 0.1020

ANALYSIS OF VARIANCE:

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	5	6.80499	1.36100	130.69
Residual	71	0.73940	0.01041	
Lack of fit	20	0.53293	0.02665	6.58
Pure error	51	0.20647	0.00405	

TABLE 33. Regression analysis of *M. tolmerum* larvae survivor days proportion data.

DEPENDENT VARIABLE : $\ln (\sin^{-1} (SDP)^{\frac{1}{2}} + 1)$

INDEPENDENT VARIABLE	COEFFICIENT	R^2 CHANGE	PARTIAL F
Temperature	0.1206	0.0588	99.52
Salinity	0.1168	0.4449	105.04
Temperature^3	-0.00006011	0.2438	84.62
Salinity^2	-0.003458	0.1211	35.69
Temperature^2 x salinity	-0.00006076	0.0101	17.13
Salinity^2 x temperature	0.00007788	0.0186	12.36
Constant	0.7522		

R^2 : 0.8974

NUMBER OF OBSERVATIONS : 75

STANDARD ERROR OF ESTIMATE : 0.1564

ANALYSIS OF VARIANCE:

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	6	14.55679	2.42613	99.17
Residual	68	1.66362	0.02446	
Lack of fit	18	1.26346	0.07019	8.77
Pure error	50	0.40016	0.00800	

TABLE 34. Regression analysis of *M. australiense* larvae survivor days proportion data.

DEPENDENT VARIABLE : SDP^2

INDEPENDENT VARIABLE	COEFFICIENT	R^2 CHANGE	PARTIAL F
Salinity	0.2209	0.1300	41.86
$Salinity^2$	-0.00318	0.3379	24.94
$Temperature^3$	-0.0002285	0.0333	84.61
$Temperature^2$	0.009075	0.2061	84.12
Temperature x salinity	-0.01227	0.0094	24.94
$Temperature^2$ x salinity	0.0002054	0.0536	19.85
$Salinity^2$ x temperature	0.00004965	0.0092	3.41
Constant	-1.1438		

R^2 : 0.7794

NUMBER OF OBSERVATIONS : 90

STANDARD ERROR OF ESTIMATE : 0.1942

ANALYSIS OF VARIANCE :

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	7	10.93301	1.56186	41.40
Residual	82	3.09368	0.03773	
Lack of Fit	22	1.64783	0.07490	3.11
Pure Error	60	1.44585	0.02410	

TABLE 35. The numbers of ovigerous and non-ovigerous females of each species taken on each sampling occasion. The *M. tolmerum* catch is divided into upstream (sites 1 to 8) and downstream (sites 9 to 16) sites; for the other species, the catch is over all sites.

MONTH	*M. australiense*		*M. latidactylus*		*M.* sp. A		*M. novae-hollandiae*		*M. tolmerum* SITES 1-8		*M. tolmerum* SITES 9-16	
	Ovig.	Non Ovig.	Ovig.	Non Ovig.	Ovig.	Non Ovig.	Ovig.	Non Ovig.	Ovig.	Non Ovig.	Ovig.	Non Ovig.
AUG	87	34	2	4	0	0	6	4	1	1	0	5
SEP	13	39	1	0	0	0	4	1	3	0	0	2
OCT	30	38	0	0	0	2	2	5	0	0	0	2
NOV	49	21	4	19	0	4	4	12	0	0	0	9
DEC	31	69	5	2	0	0	1	12	0	5	0	0
JAN	36	41	7	8	0	1	0	0	0	1	1	4
FEB	11	24	6	5	1	1	0	1	2	0	13	13
MAR	6	27	12	9	0	0	0	1	0	2	0	13
APR	0	58	11	29	0	1	0	6	0	2	2	11
MAY	0	69	18	66	0	1	0	5	0	5	0	13
JUN	8	48	14	32	0	0	0	5	0	1	0	5
JUL	51	25	11	10	0	1	2	3	0	2	0	9
AUG	22	33	2	1	0	3	0	0	3	2	0	0

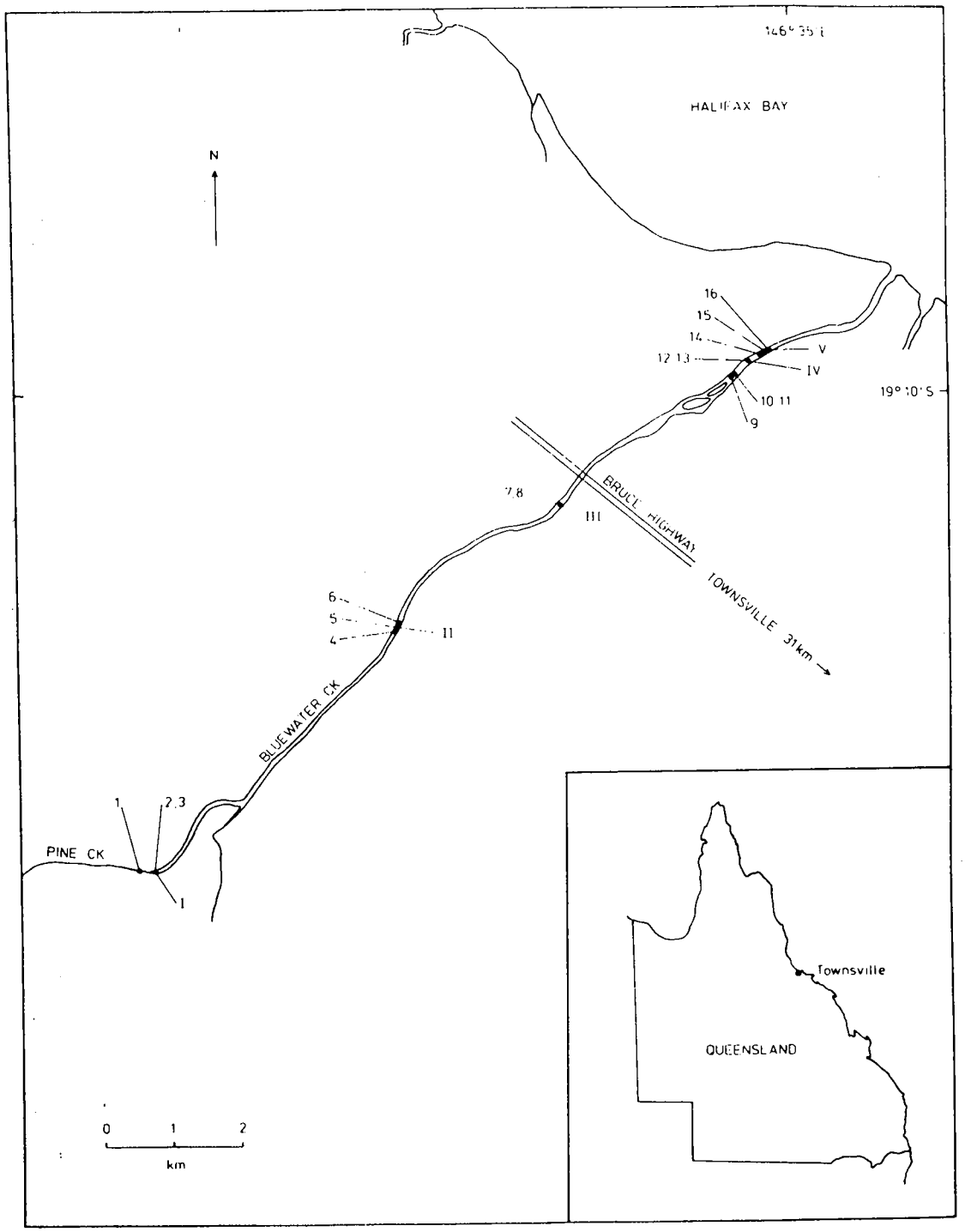
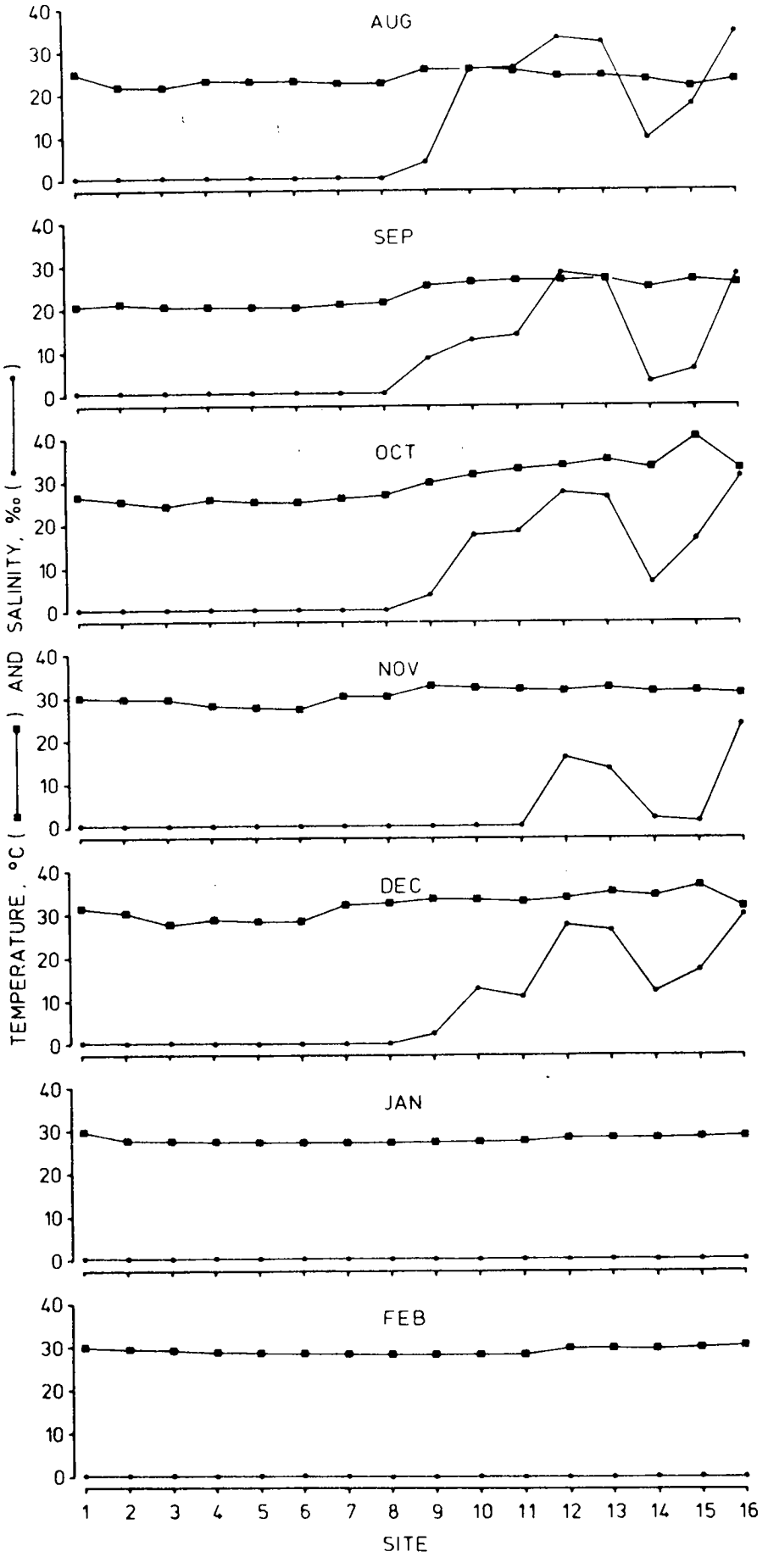


Fig. 1. Map of the study area showing sites of sampling adult *Macrobrachium* (arabic numerals) and plankton sampling stations (roman numerals).


AUG
SEP
OCT
NOV
DEC
JAN
FEB
40
30
20
10
0
TEMPERATURE, °C (■) AND SALINITY, ‰ (●)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
SITE

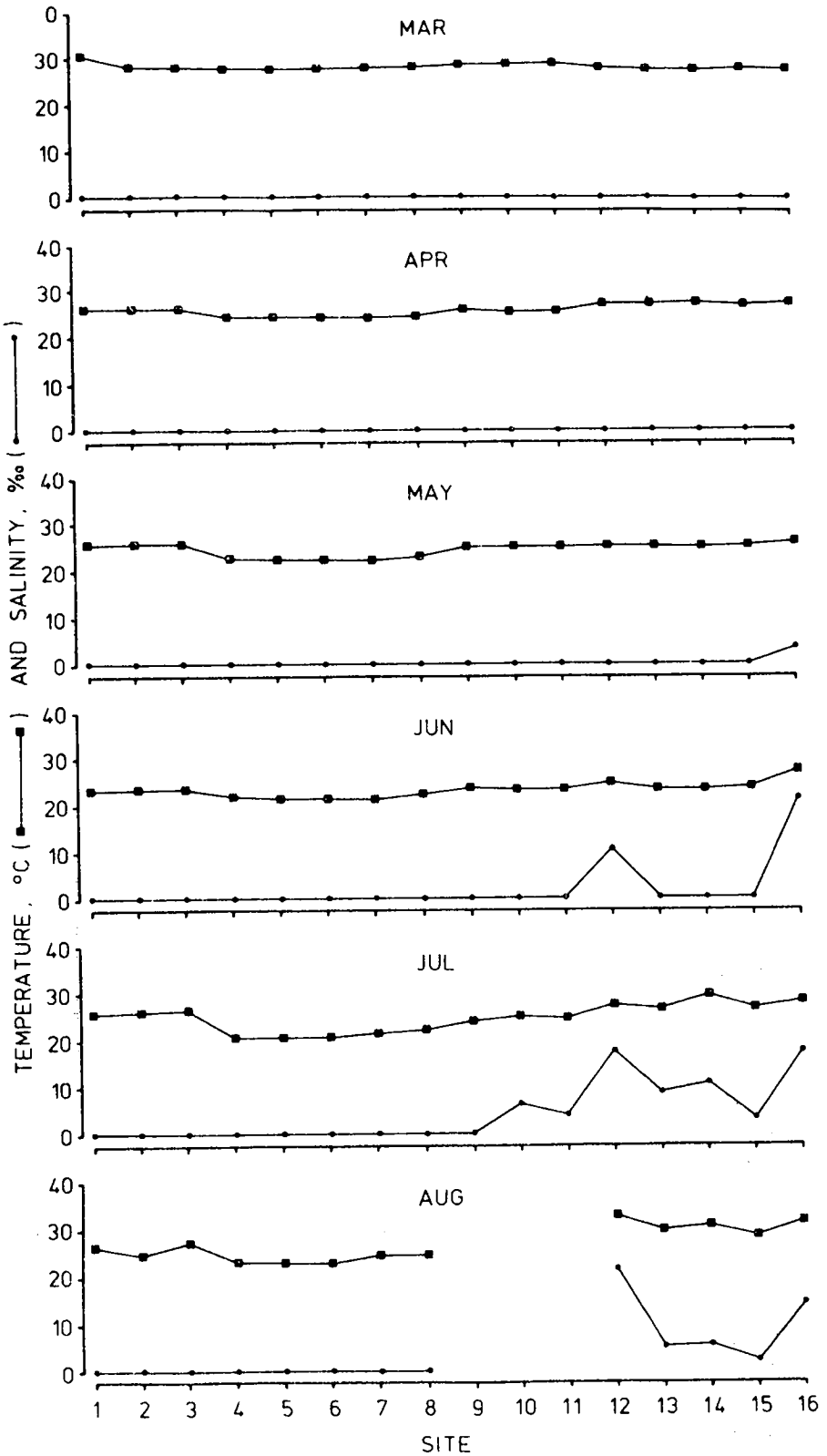


Fig. 2. Mean bottom temperature and salinity (n = 5) at each site on each sampling occasion from August 1975 to August 1976.

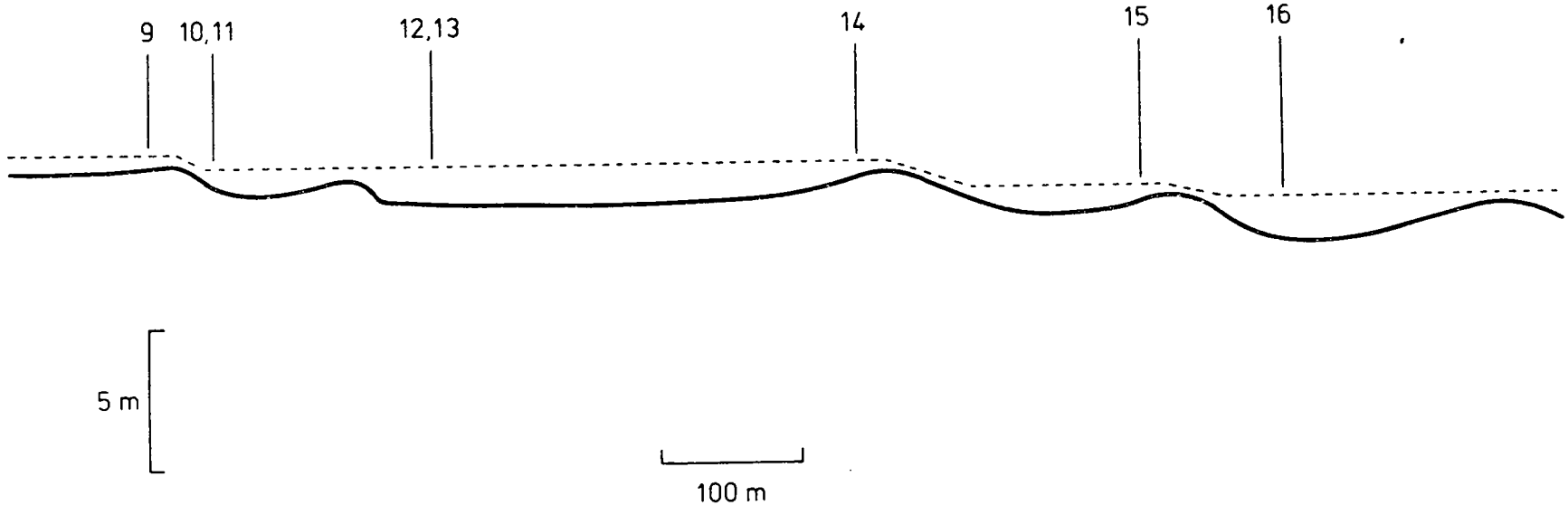
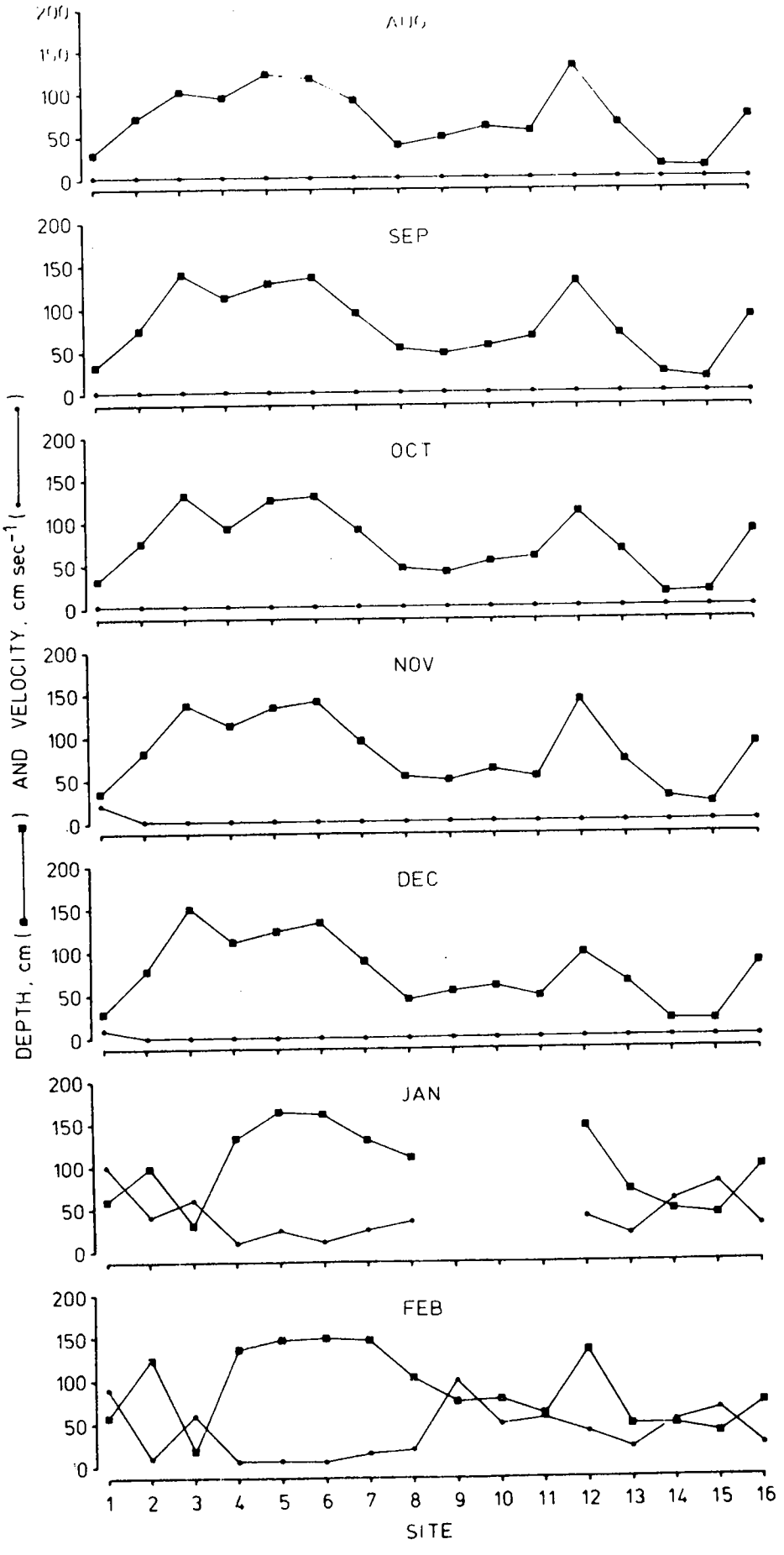


Fig. 3. Diagrammatic representation of the relation of sites 9 to 16 to stream bottom topography. The stream bottom is represented by the solid line and the water surface by the broken line.


AUG
SEP
OCT
NOV
DEC
JAN
FEB
200
150
100
50
0
DEPTH, cm (●——●) AND VELOCITY, cm sec⁻¹ (●——●)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
SITE

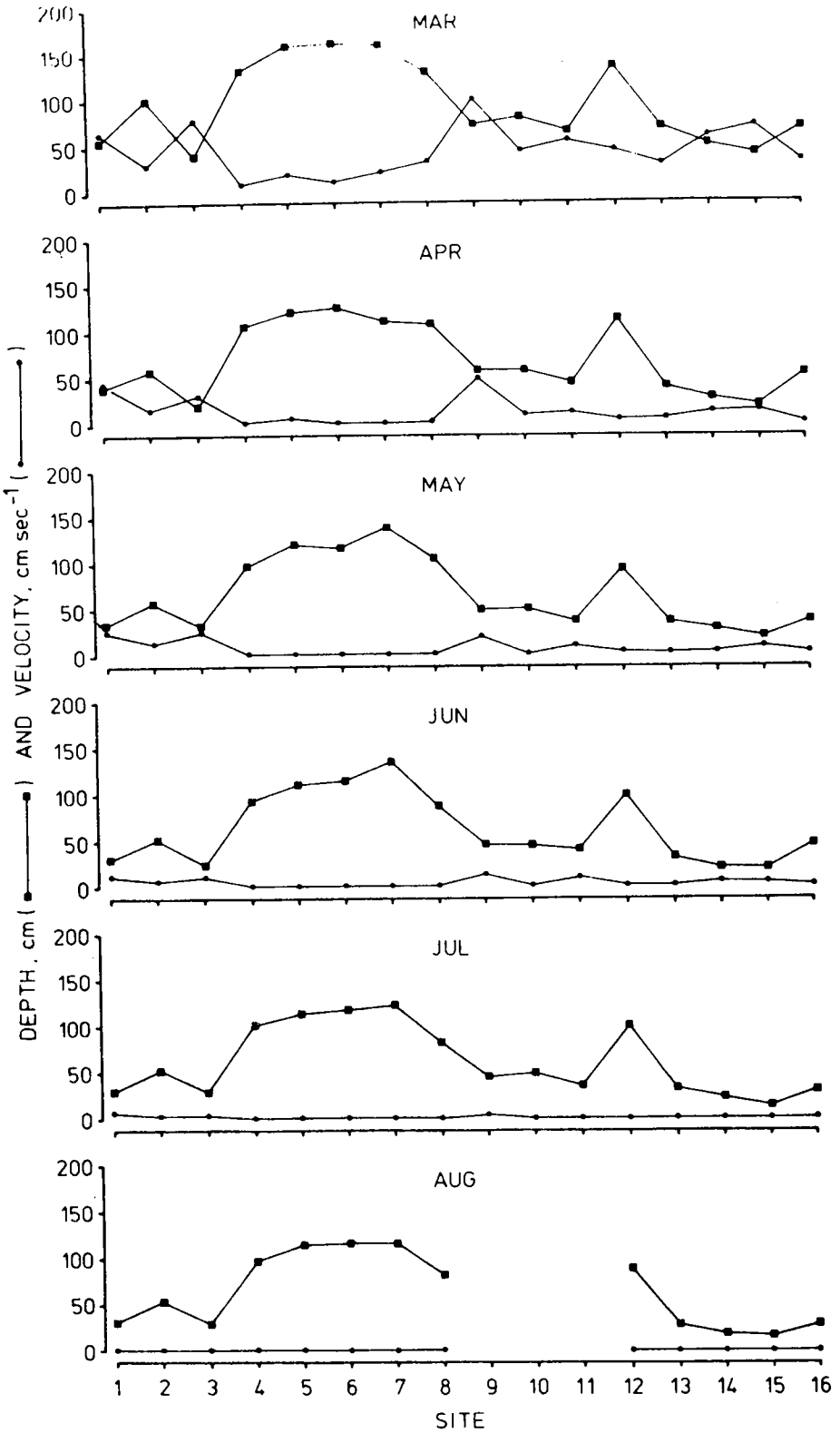


Fig. 4. Mean depth (n = 5) and surface velocity at each site on each sampling occasion from August 1975 to August 1976. Because of high stream velocity, measurements were not possible at sites 9, 10 and 11 in January 1976.

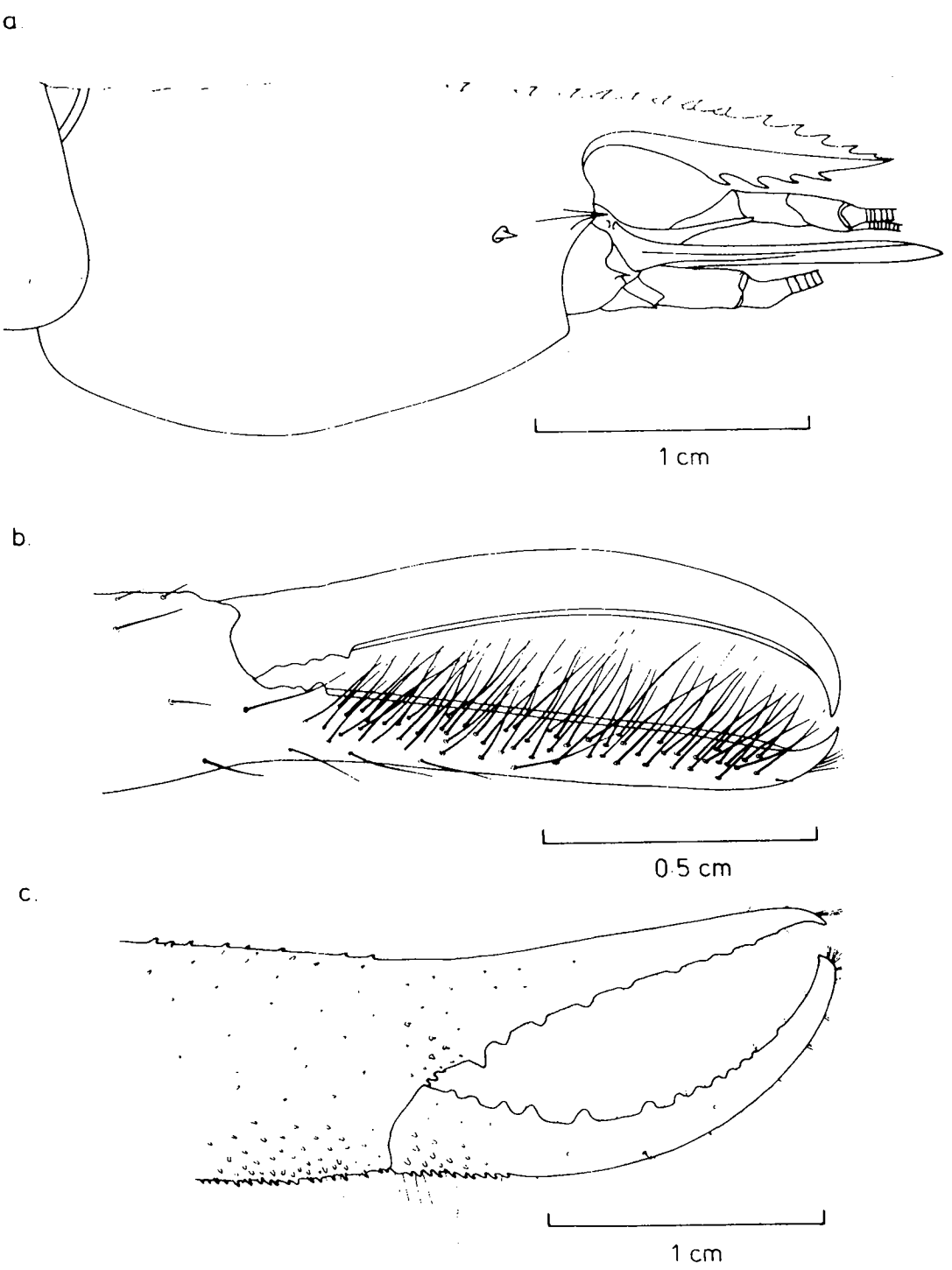


Fig. 5. *M. latidactylus* male.

a. carapace and basal segments of antennule and antenna.

b. dorsal view of chela of left second pereiopod with setae omitted from the dactylus.

c. dorsal view of chela of right second pereiopod.

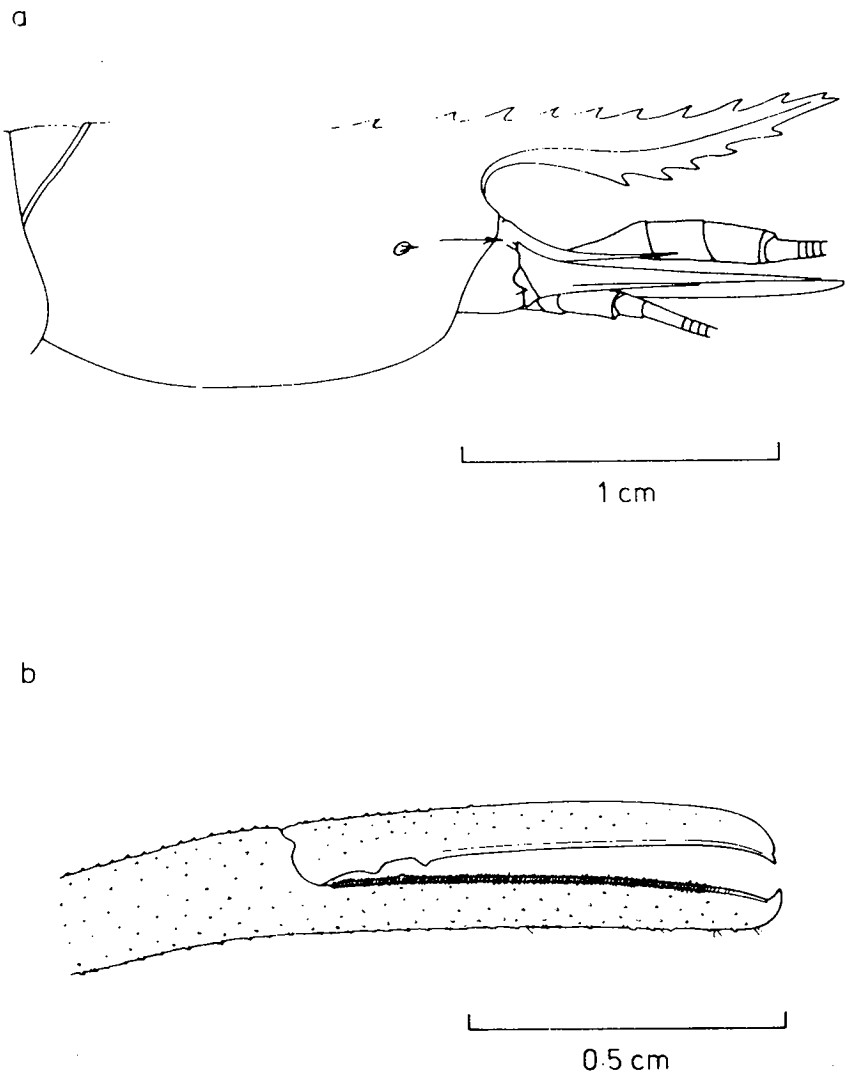


Fig. 6. *M. novae-hollandiae* male.

a. carapace and basal segments of antennule and antenna.

b. dorsal view of chela of left second pereiopod with setae omitted from the dactylus.

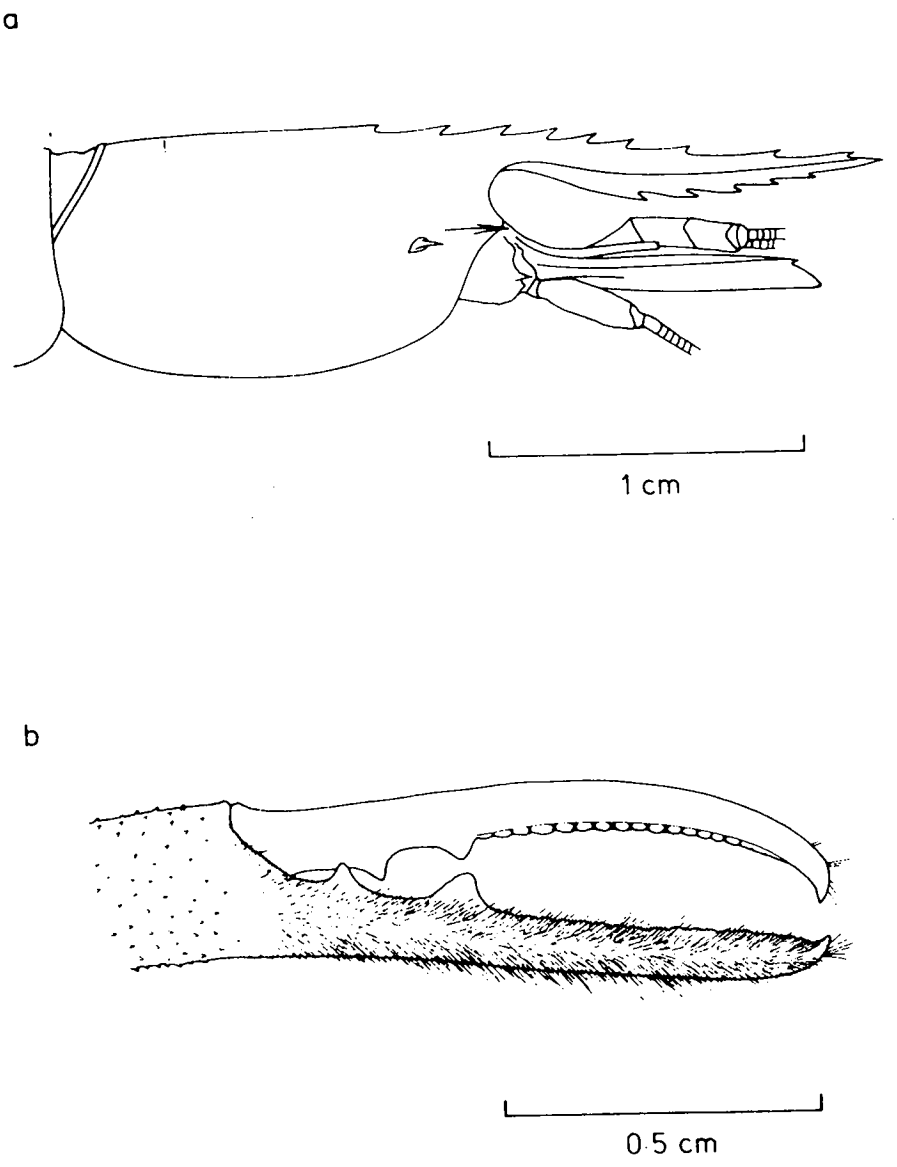
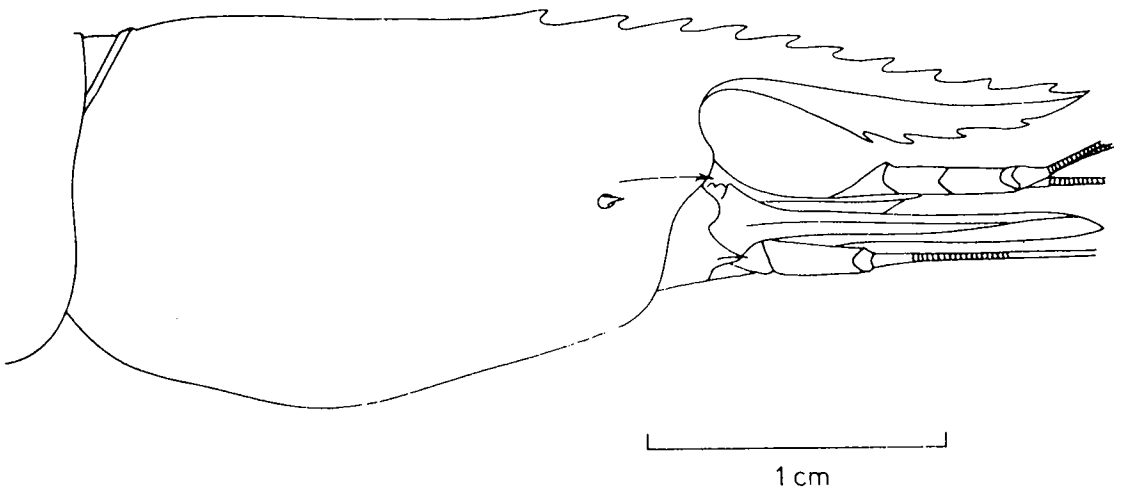


Fig. 7. *M. australiense* male.

a. carapace and basal segments of antennule and antenna.

b. dorsal view of chela of left second pereiopod with setae omitted from dactylus.

a.



b.

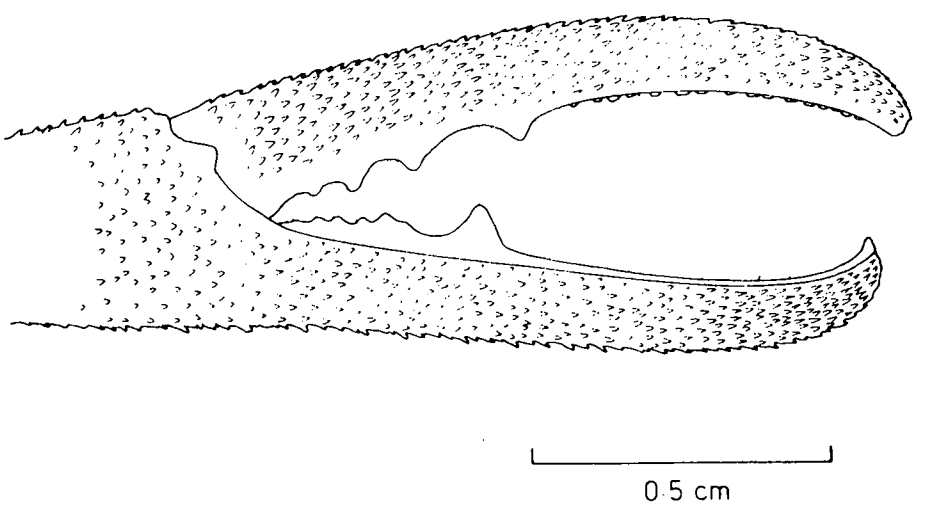
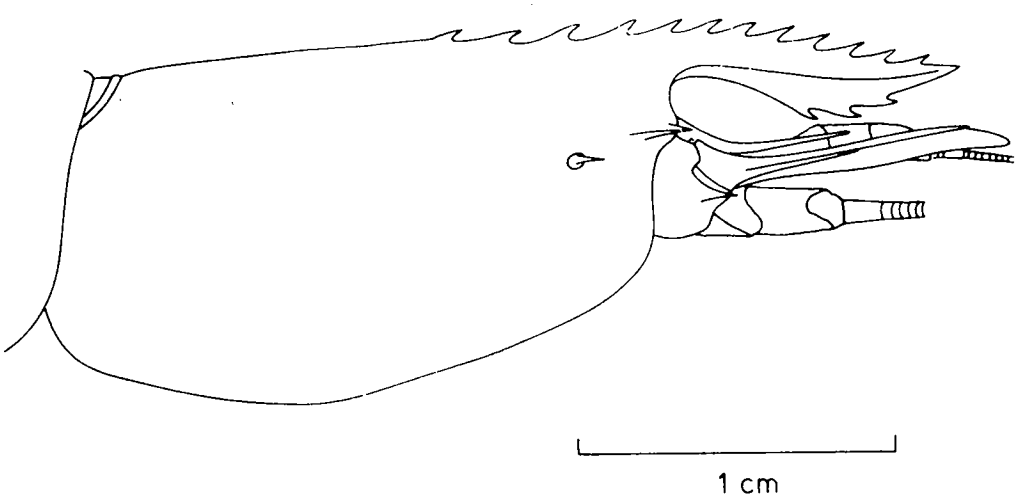


Fig. 8. *M. tolmerum* male.

a. carapace and basal segments of antennule and antenna.

b. dorsal view of chela of left second pereiopod.

a.



b.

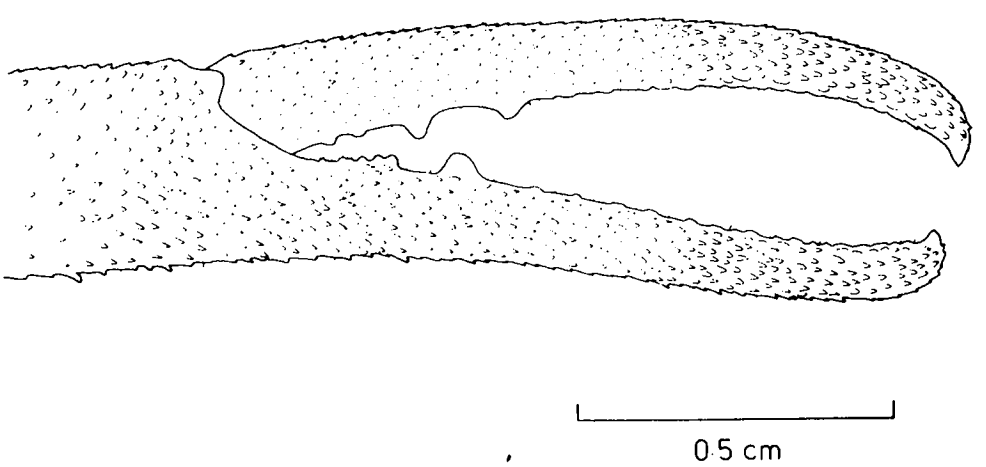


Fig. 9. *M.* sp. A male.

a. carapace and basal segments of antennule and antenna.

b. dorsal view of chela of left second pereiopod.

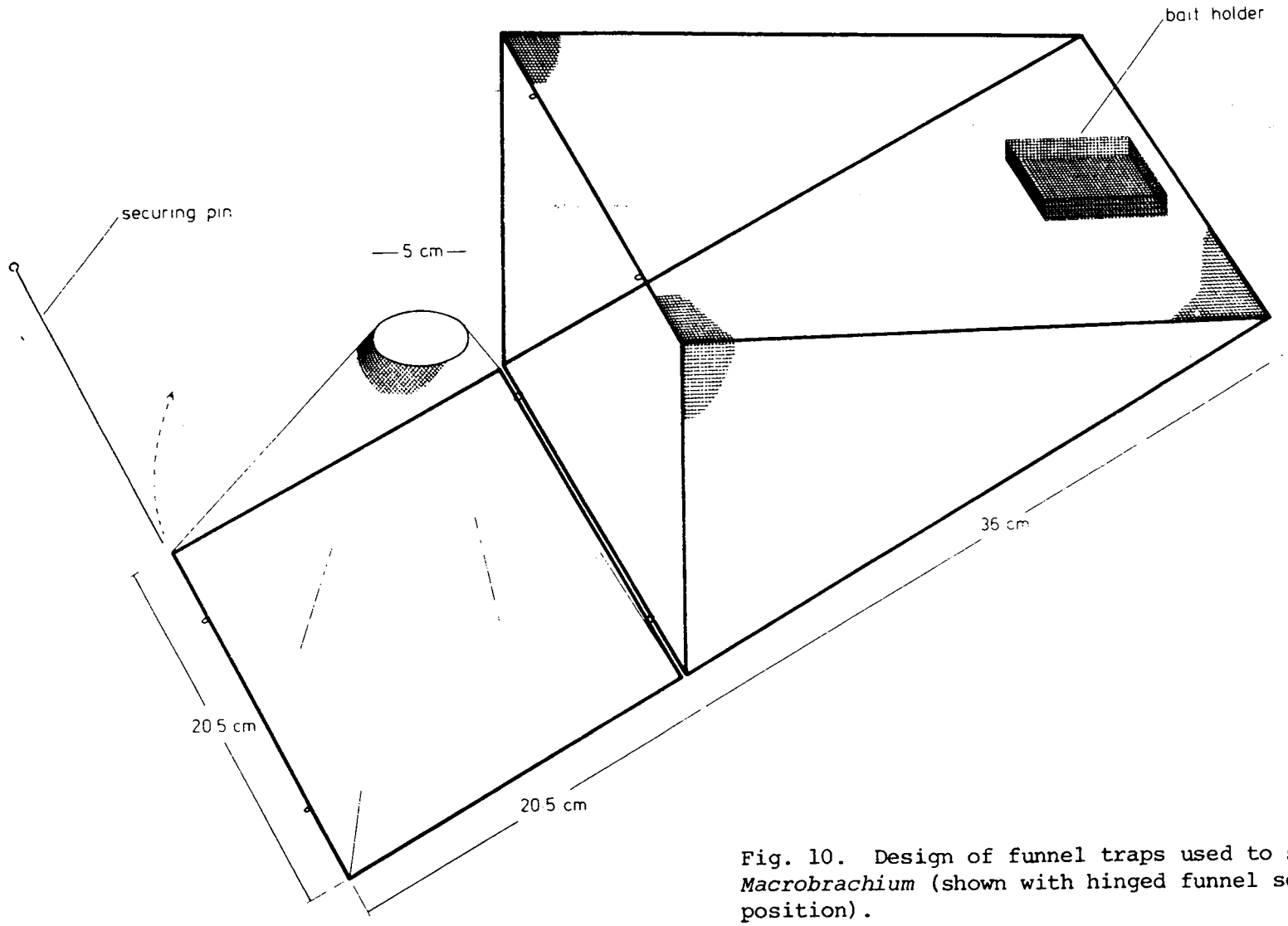
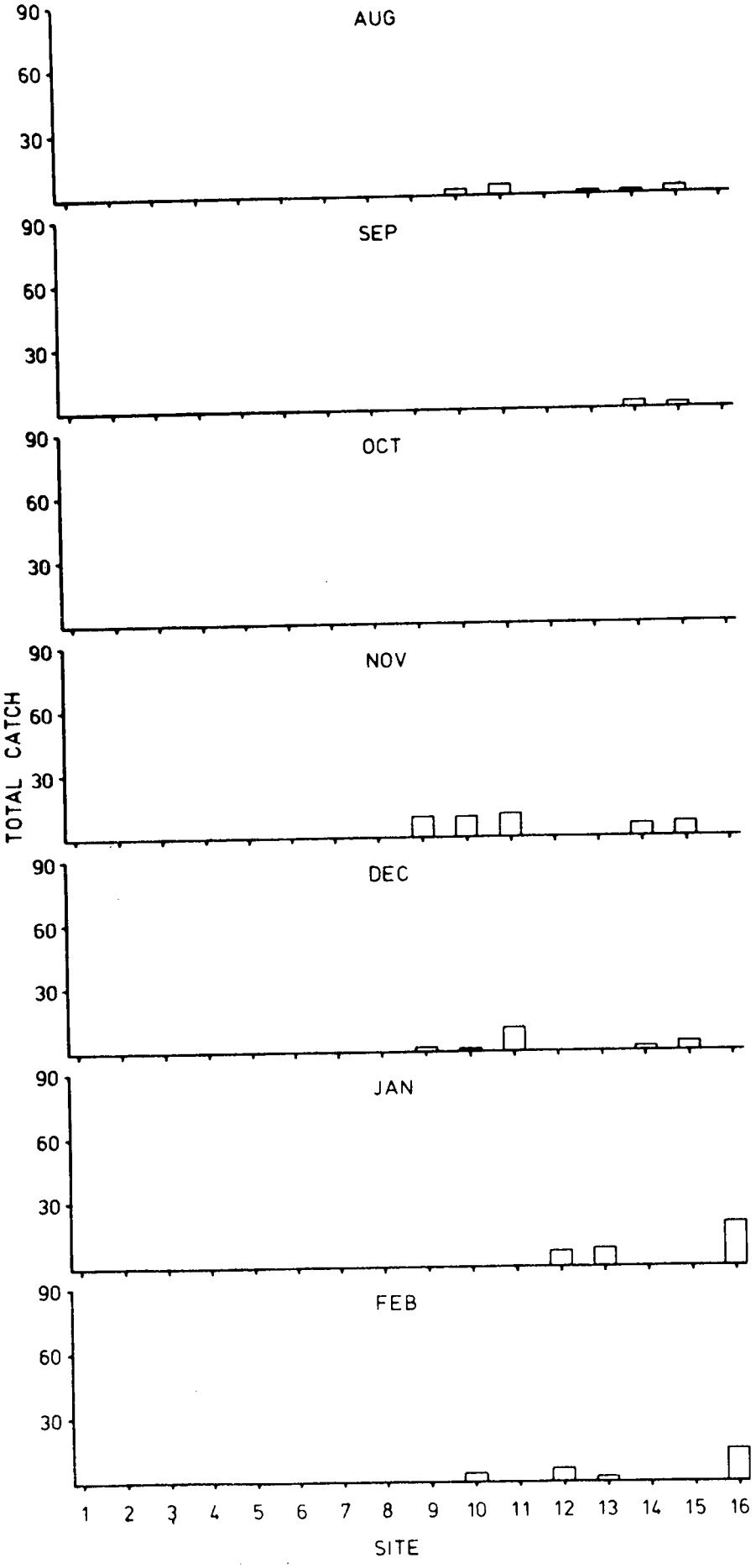


Fig. 10. Design of funnel traps used to sample adult *Macrobrachium* (shown with hinged funnel section in open position).


AUG
SEP
OCT
NOV
DEC
JAN
FEB
90
60
30
TOTAL CATCH
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
SITE

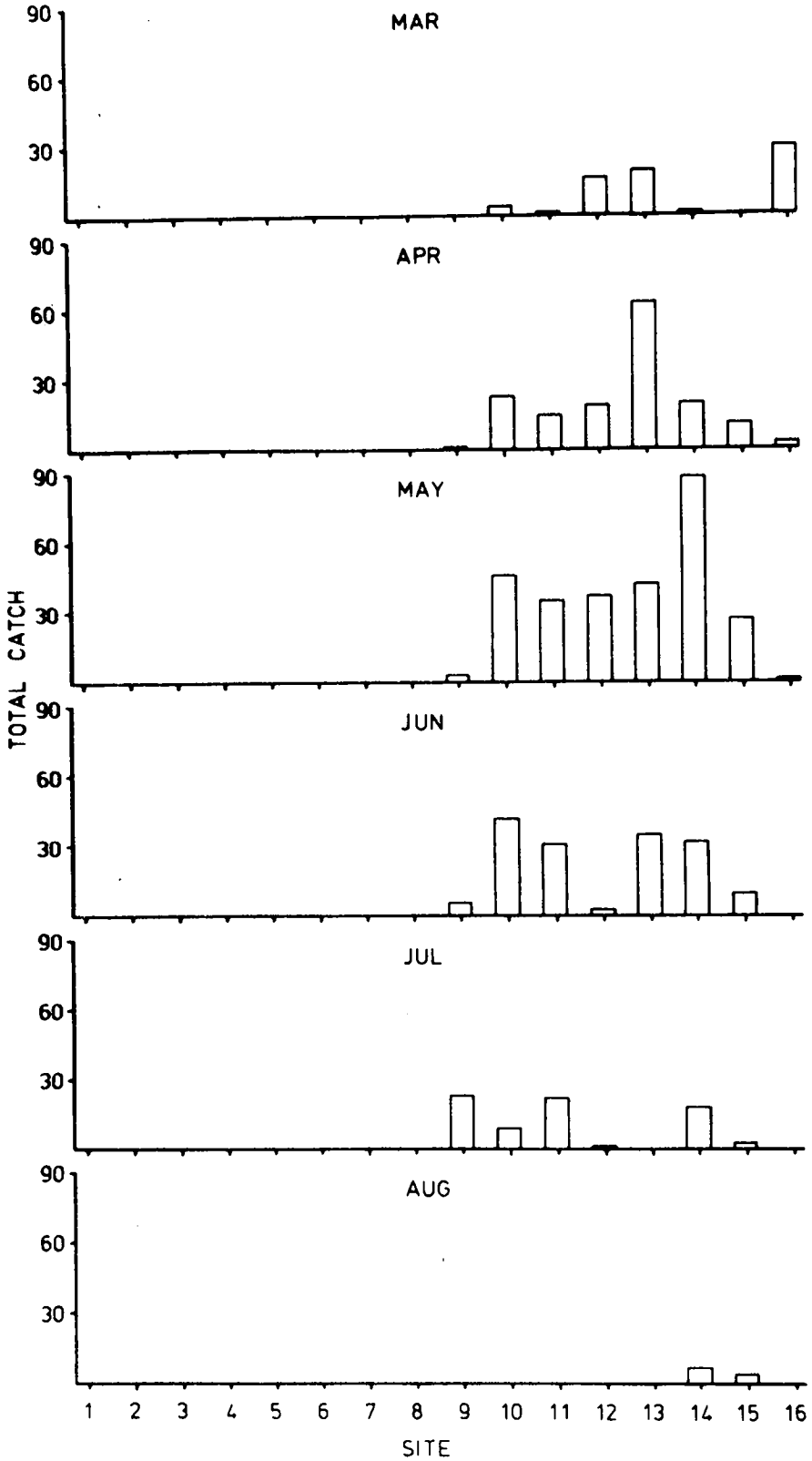


Fig. 11. Total catch of *M. latidactylus* at each site on each sampling occasion from August 1975 to August 1976.

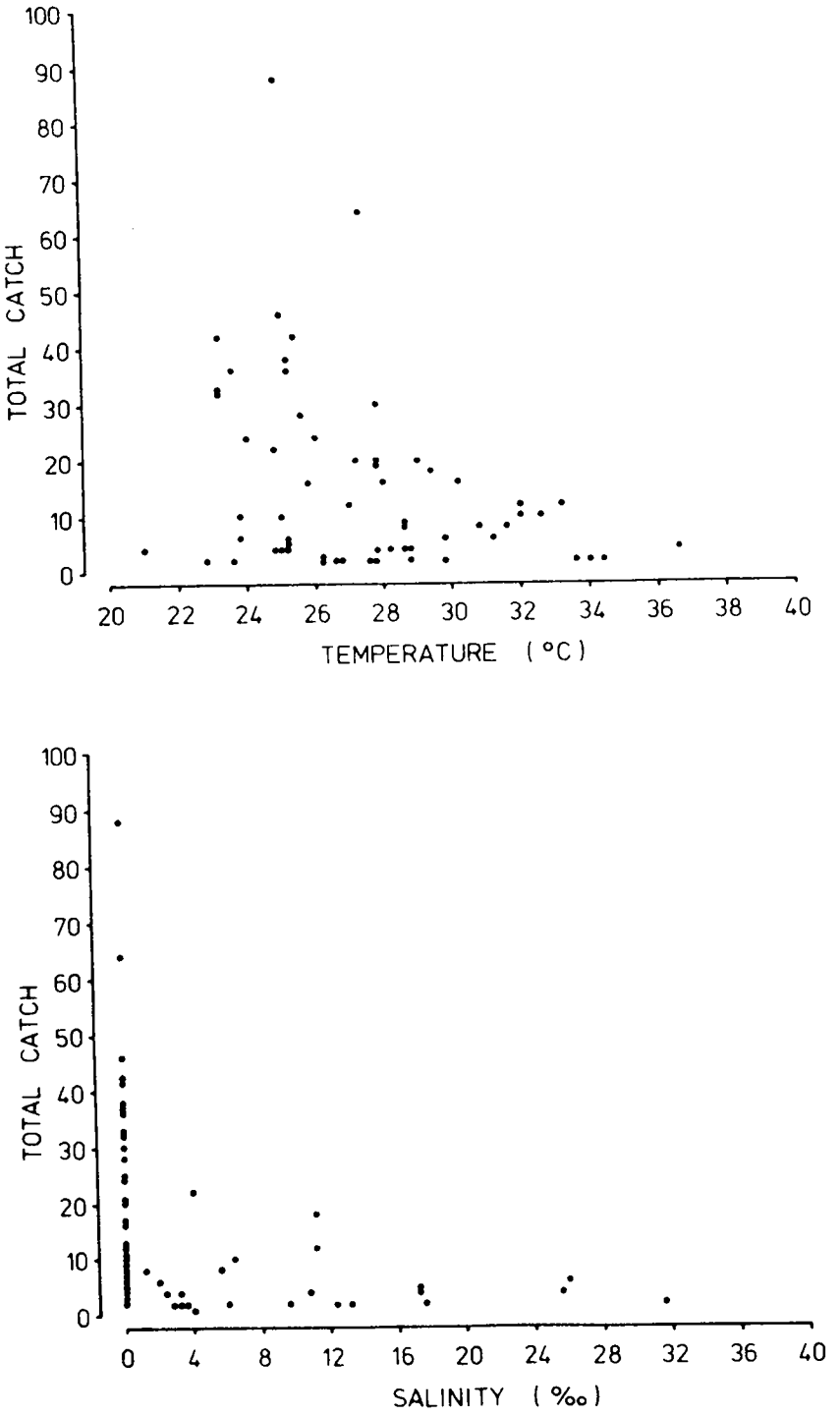


Fig. 12. Total catch of *M. latidactylus* versus temperature and salinity at each site on each sampling occasion. Zero catches have been omitted.

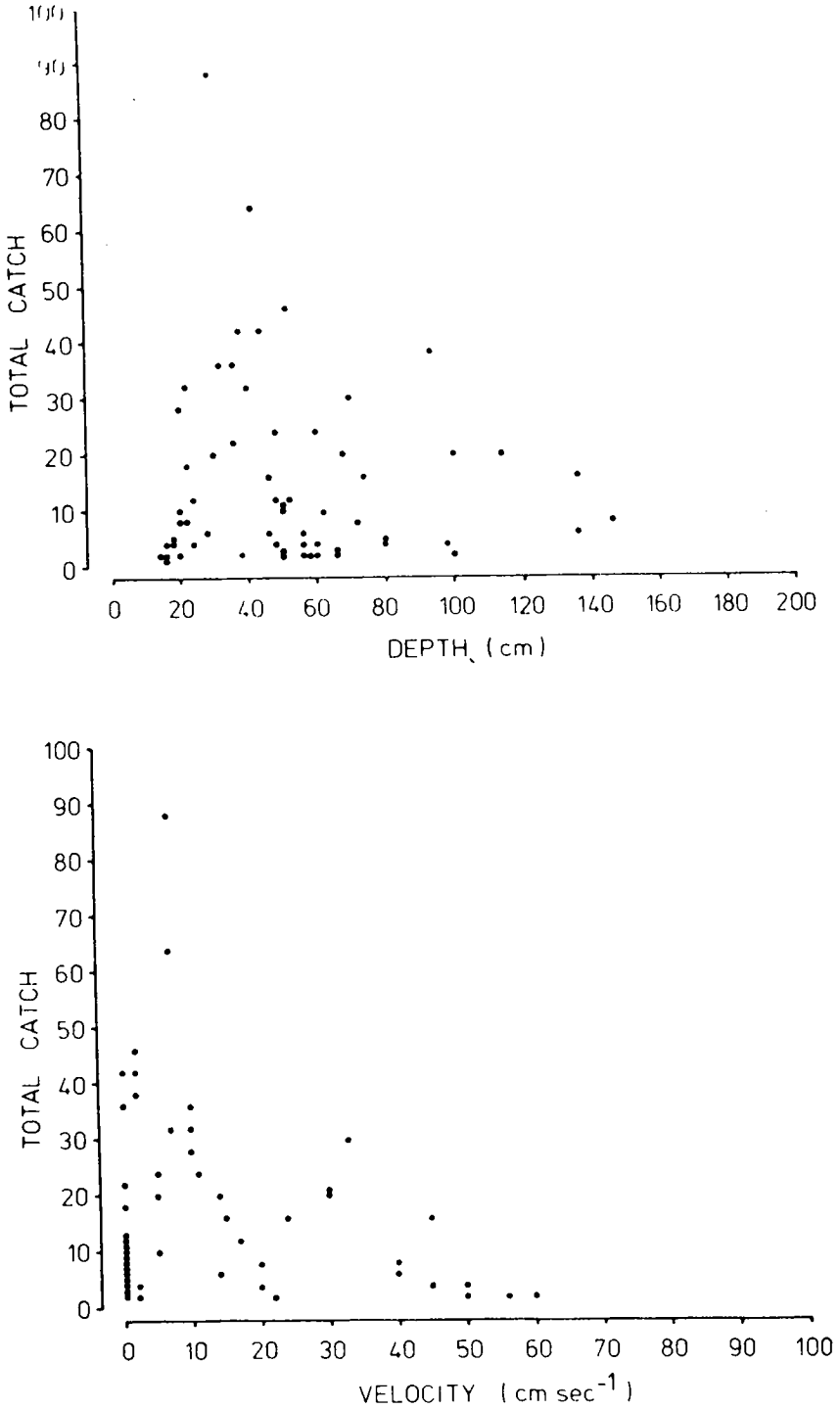
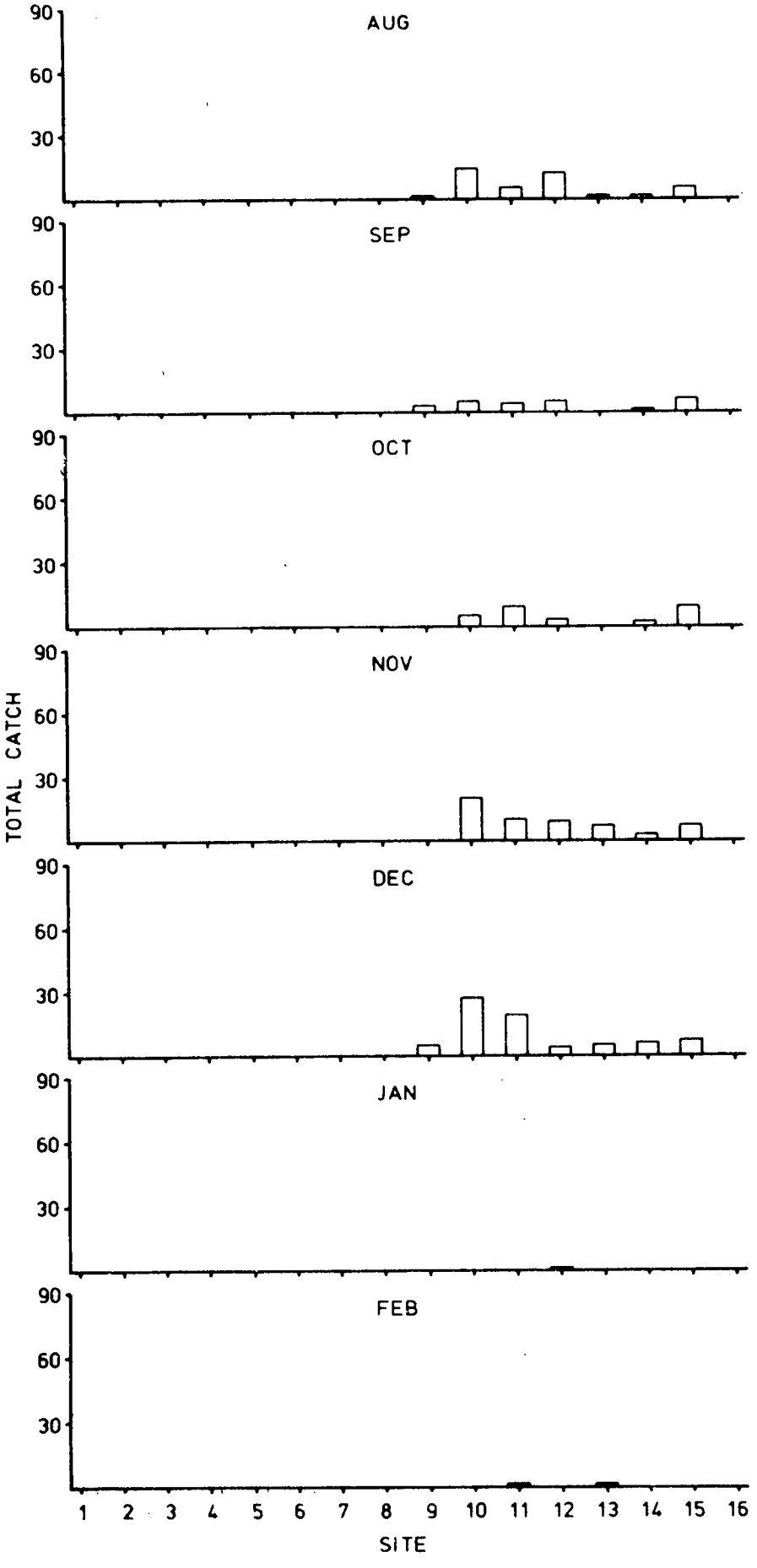


Fig. 13. Total catch of *M. latidactylus* versus depth and surface velocity at each site on each sampling occasion. Zero catches have been omitted.


AUG
SEP
OCT
NOV
DEC
JAN
FEB
90
60
30
TOTAL CATCH
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
SITE

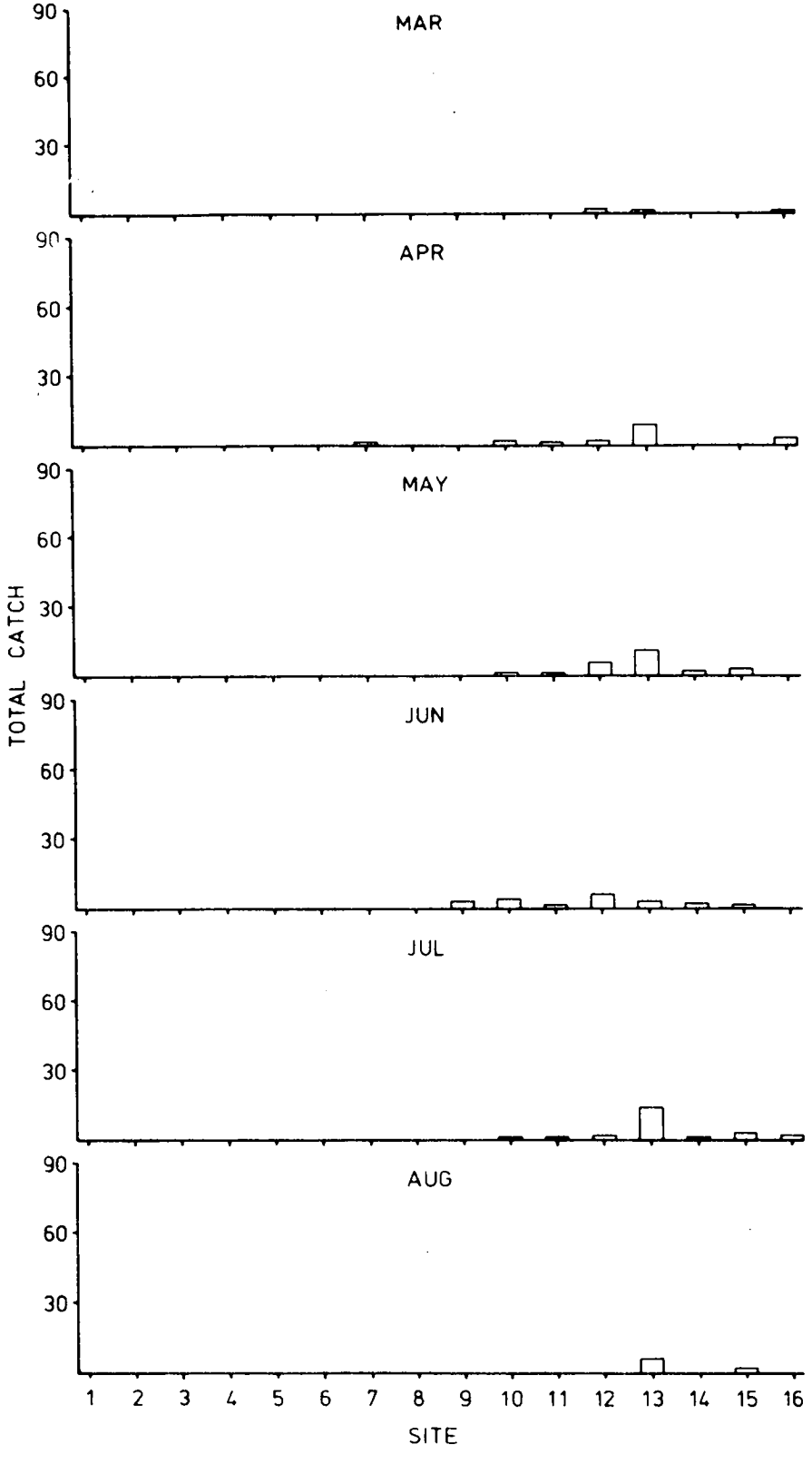


Fig. 14. Total catch of *M. novae-hollandiae* at each site on each sampling occasion from August 1975 to August 1976.

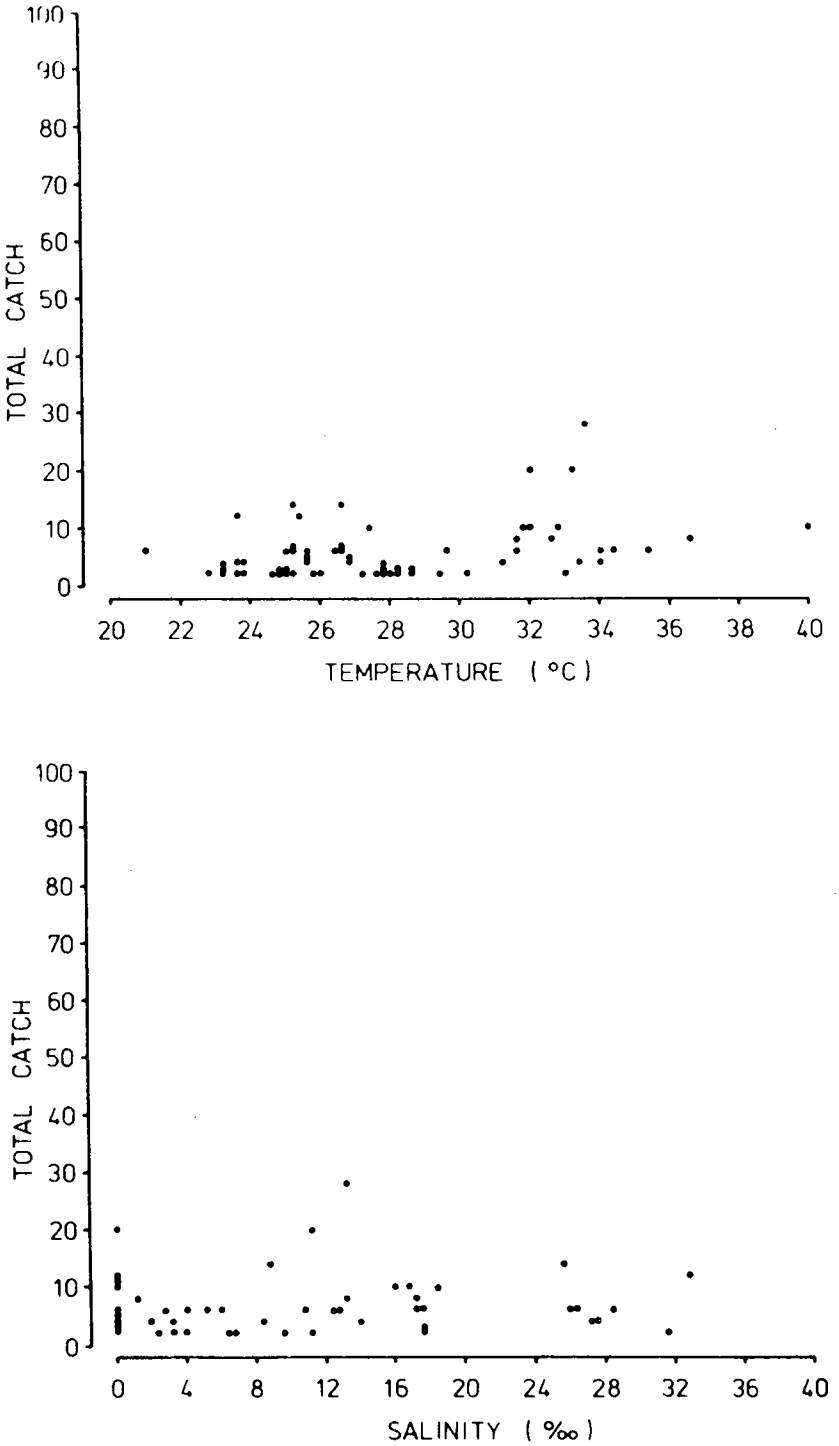


Fig. 15. Total catch of *M. novae-hollandiae* versus temperature and salinity at each site on each sampling occasion. Zero catches have been omitted.

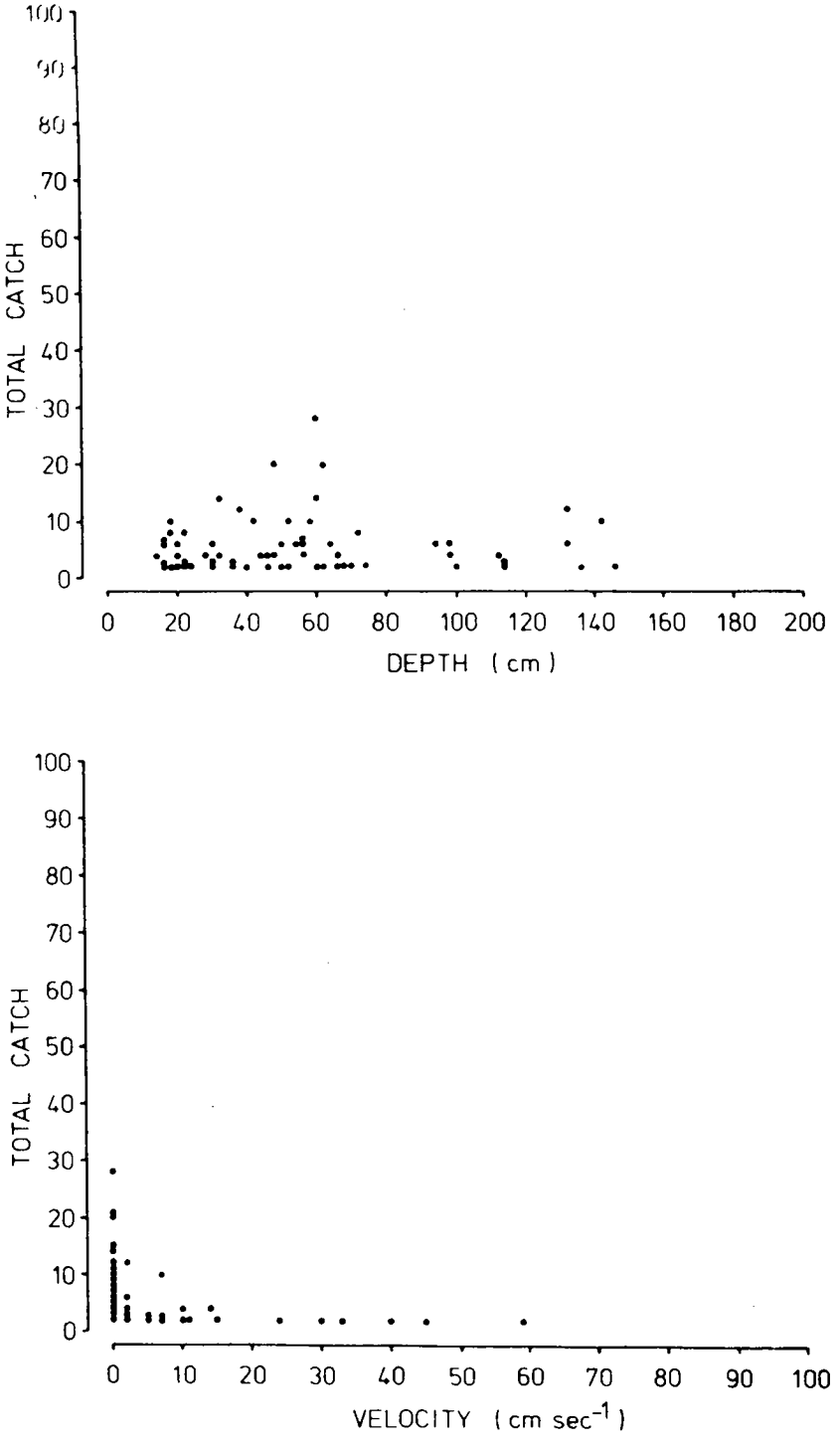
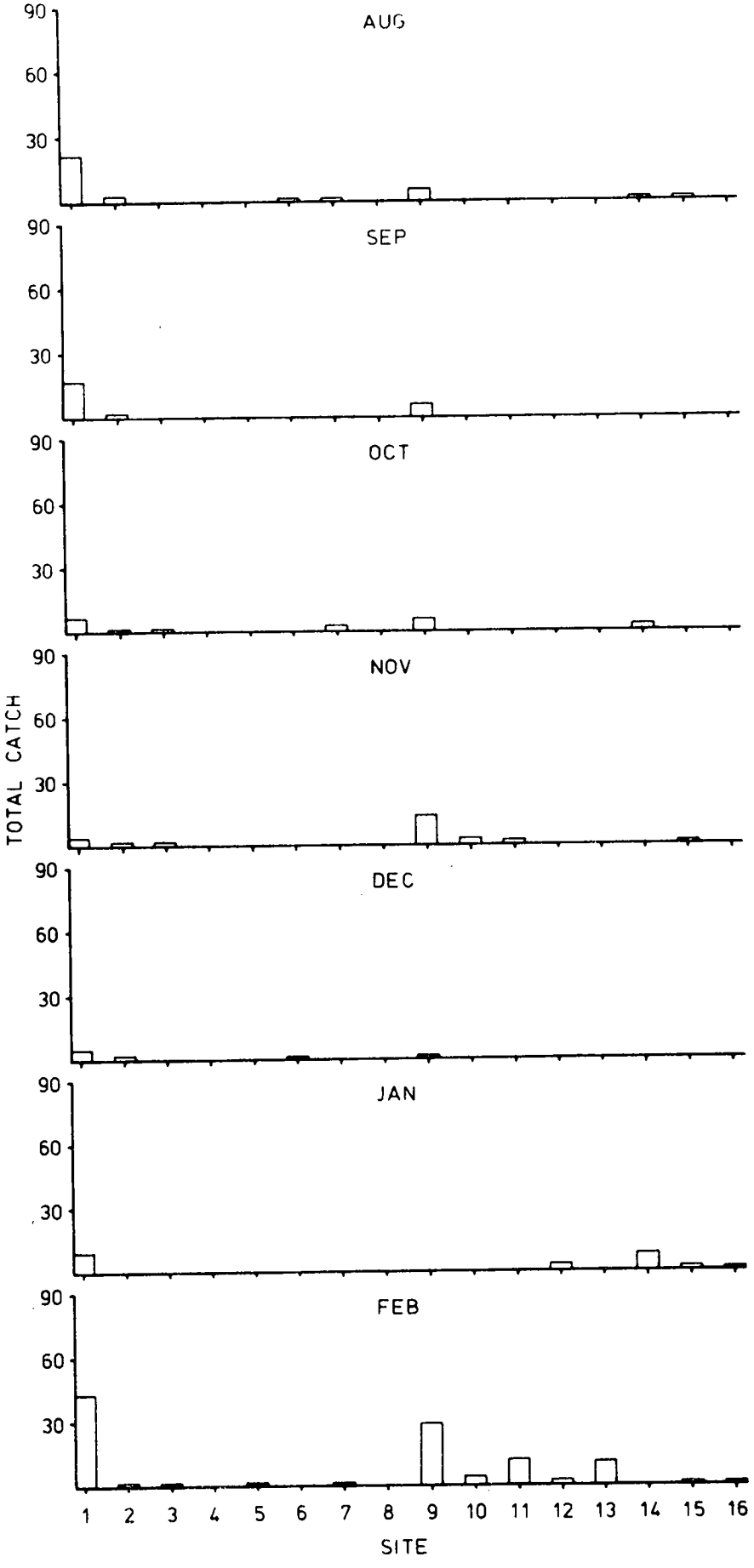


Fig. 16. Total catch of *M. novae-hollandiae* versus depth and surface velocity at each site on each sampling occasion. Zero catches have been omitted.


AUG
SEP
OCT
NOV
DEC
JAN
FEB
90
60
30
TOTAL CATCH
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
SITE

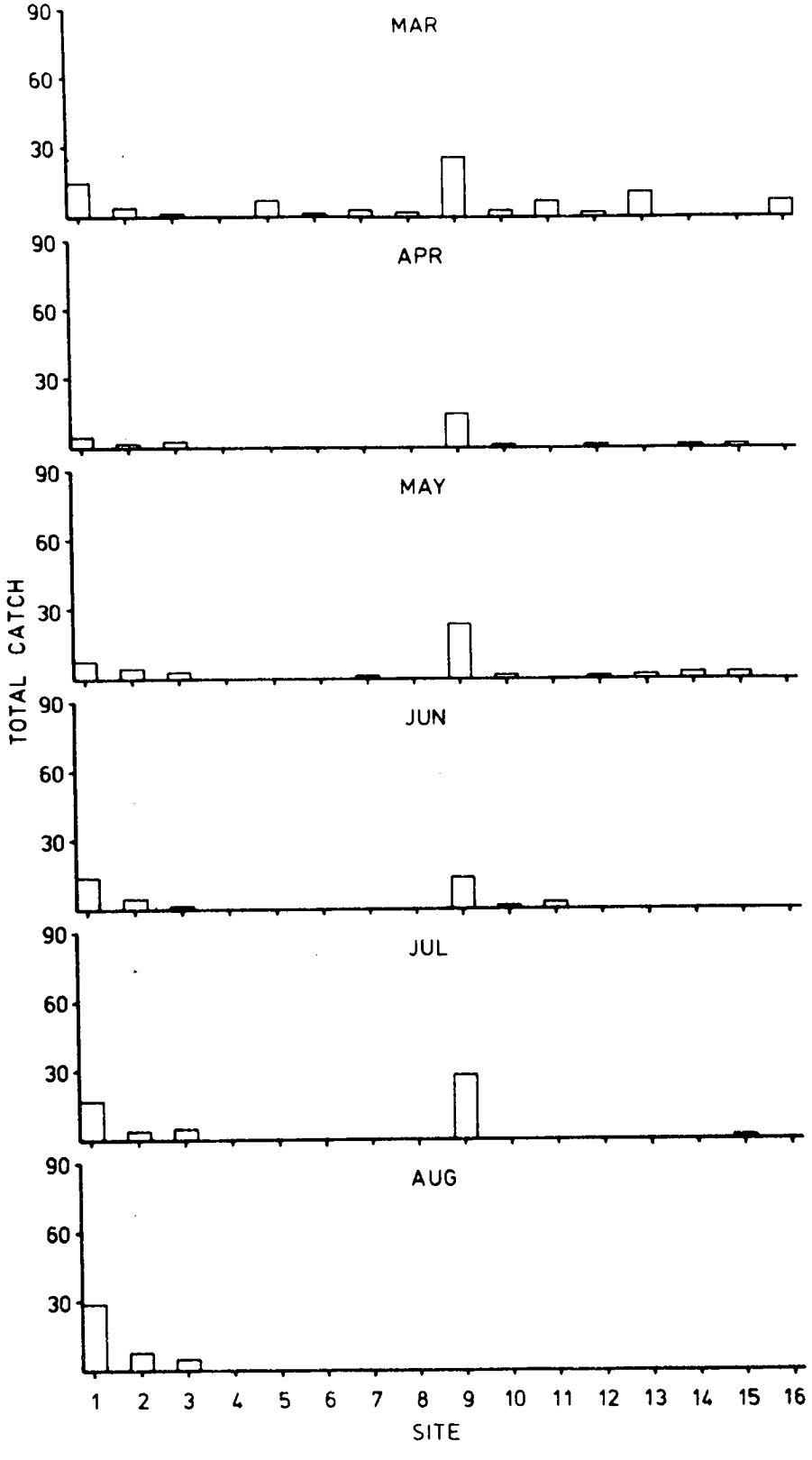


Fig. 17. Total catch of *M. tolmerum* at each site on each sampling occasion from August 1975 to August 1976.

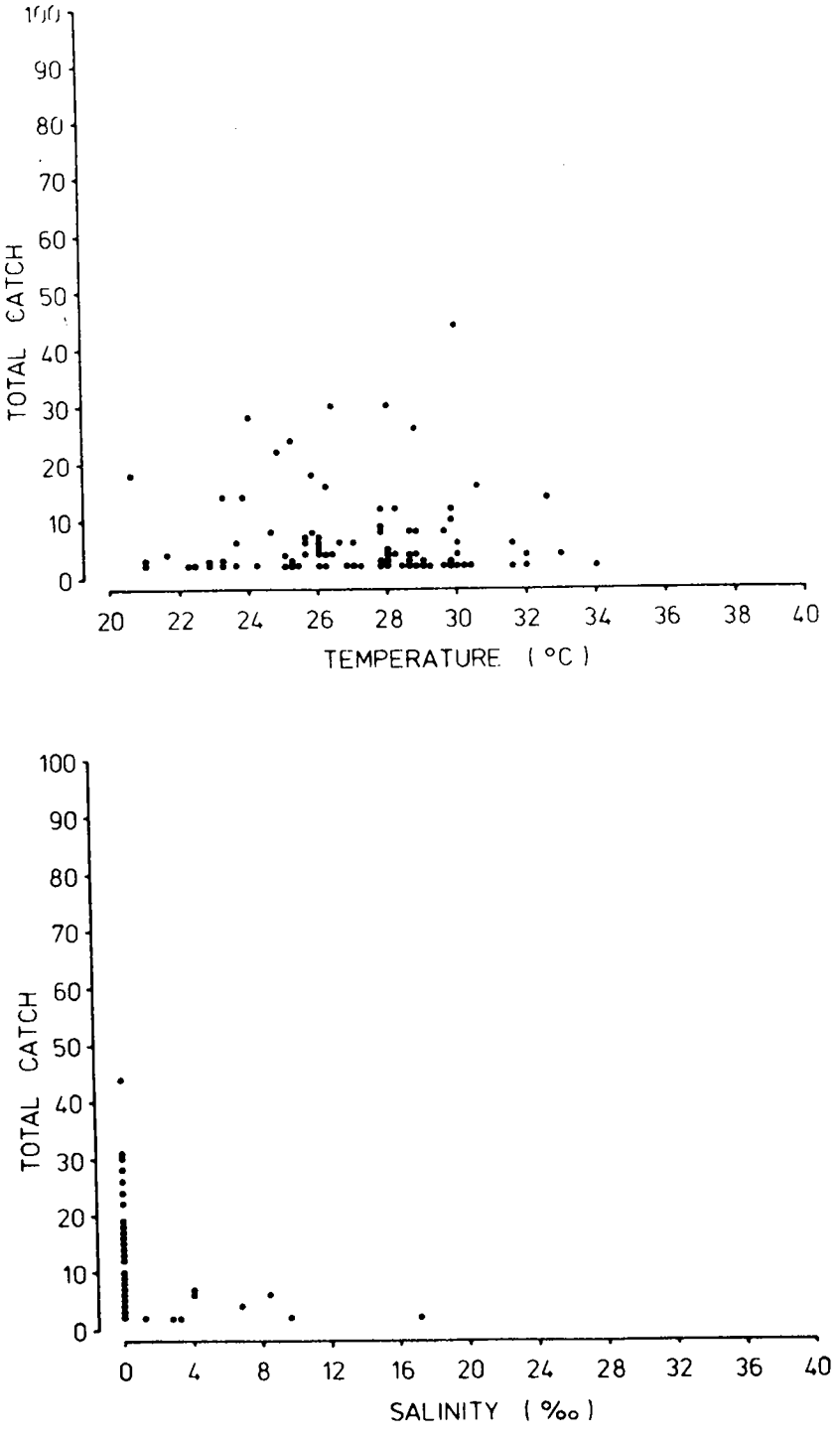


Fig. 18. Total catch of *M. tolmerum* versus temperature and salinity at each site on each sampling occasion. Zero catches have been omitted.

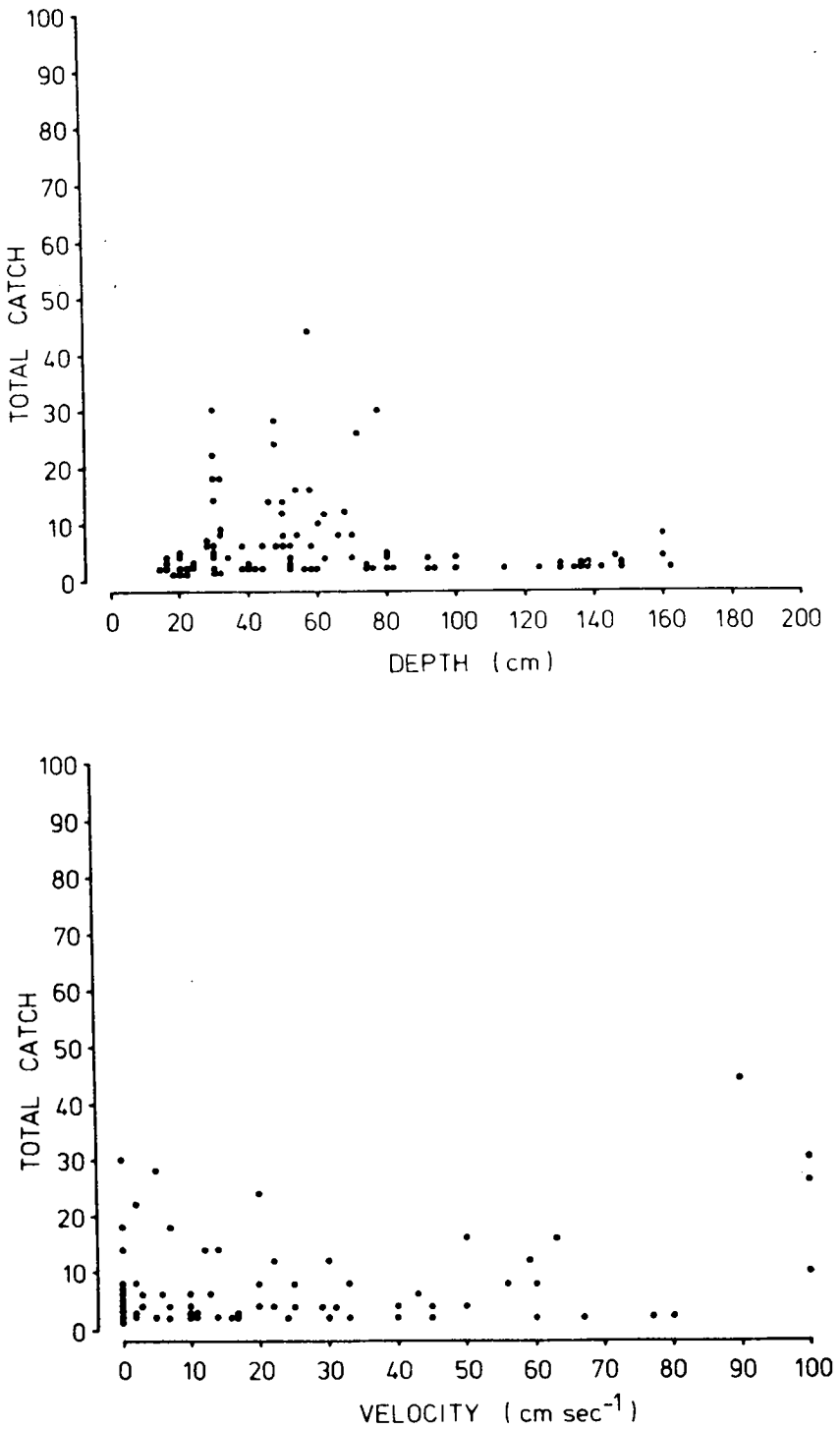
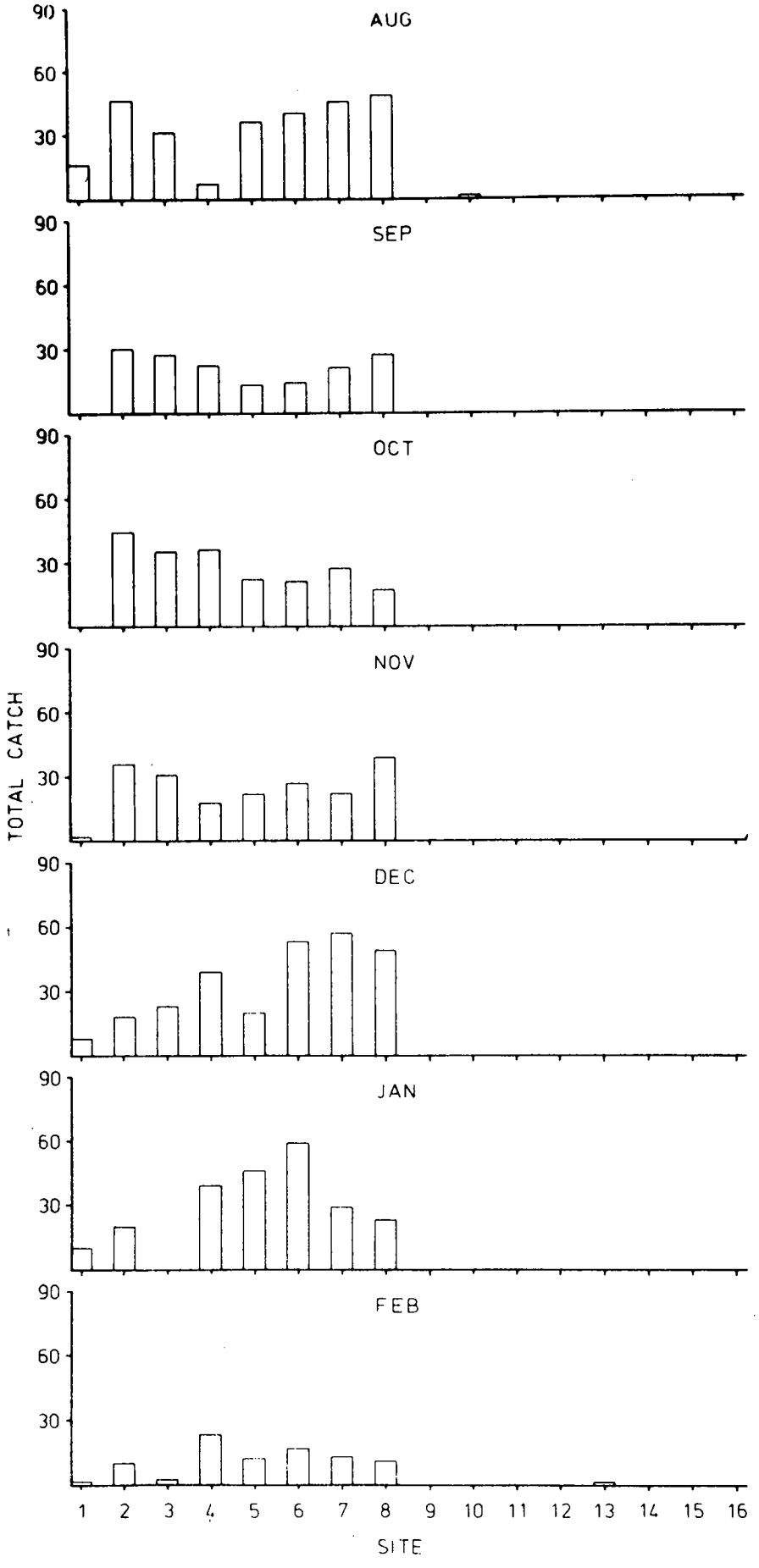


Fig. 19. Total catch of *M. tolmerum* versus depth and surface velocity at each site on each sampling occasion. Zero catches have been omitted.


AUG
SEP
OCT
NOV
DEC
JAN
FEB
90
60
30
TOTAL CATCH
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
SITE

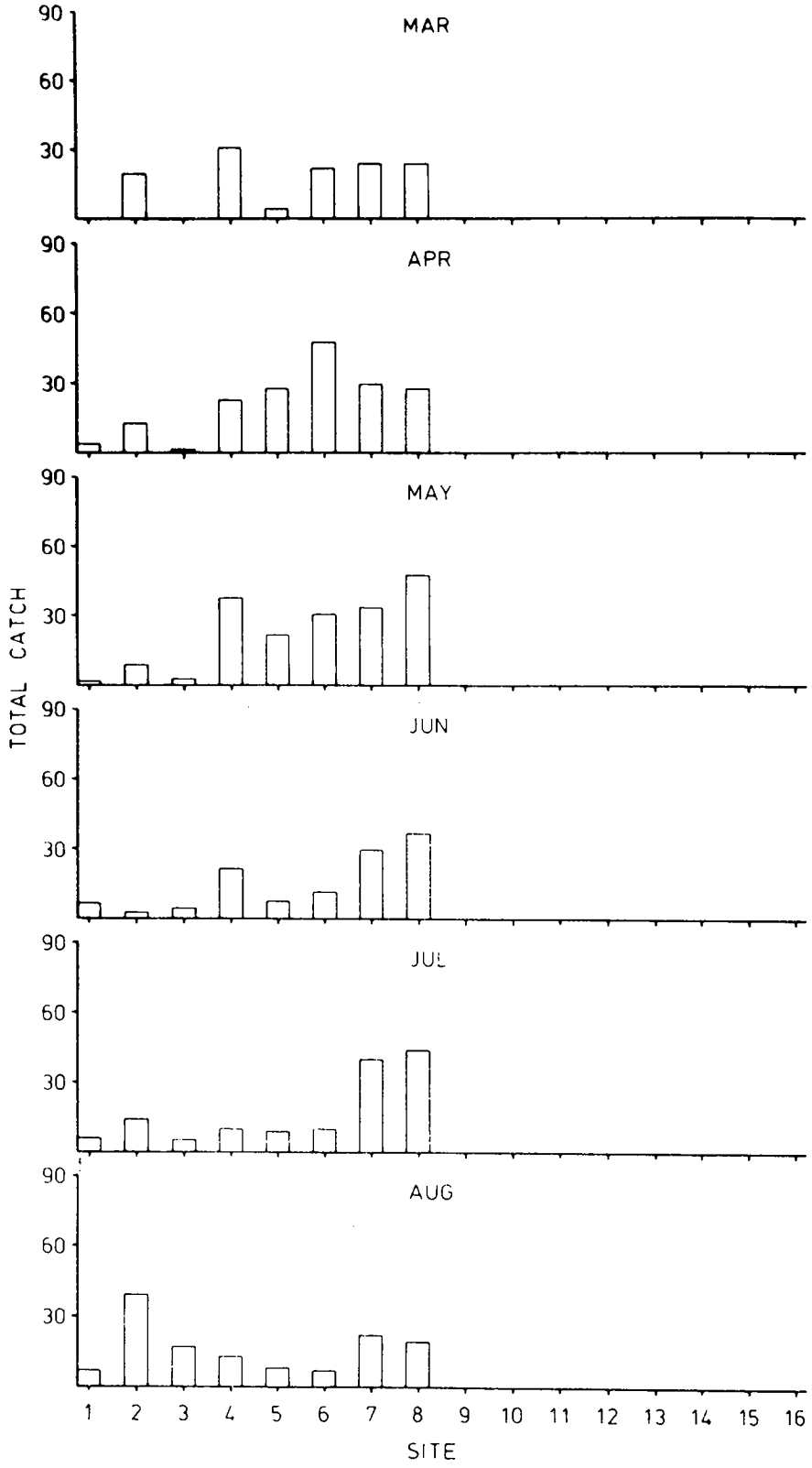


Fig. 20. Total catch of *M. australiense* at each site on each sampling occasion from August 1975 to August 1976.

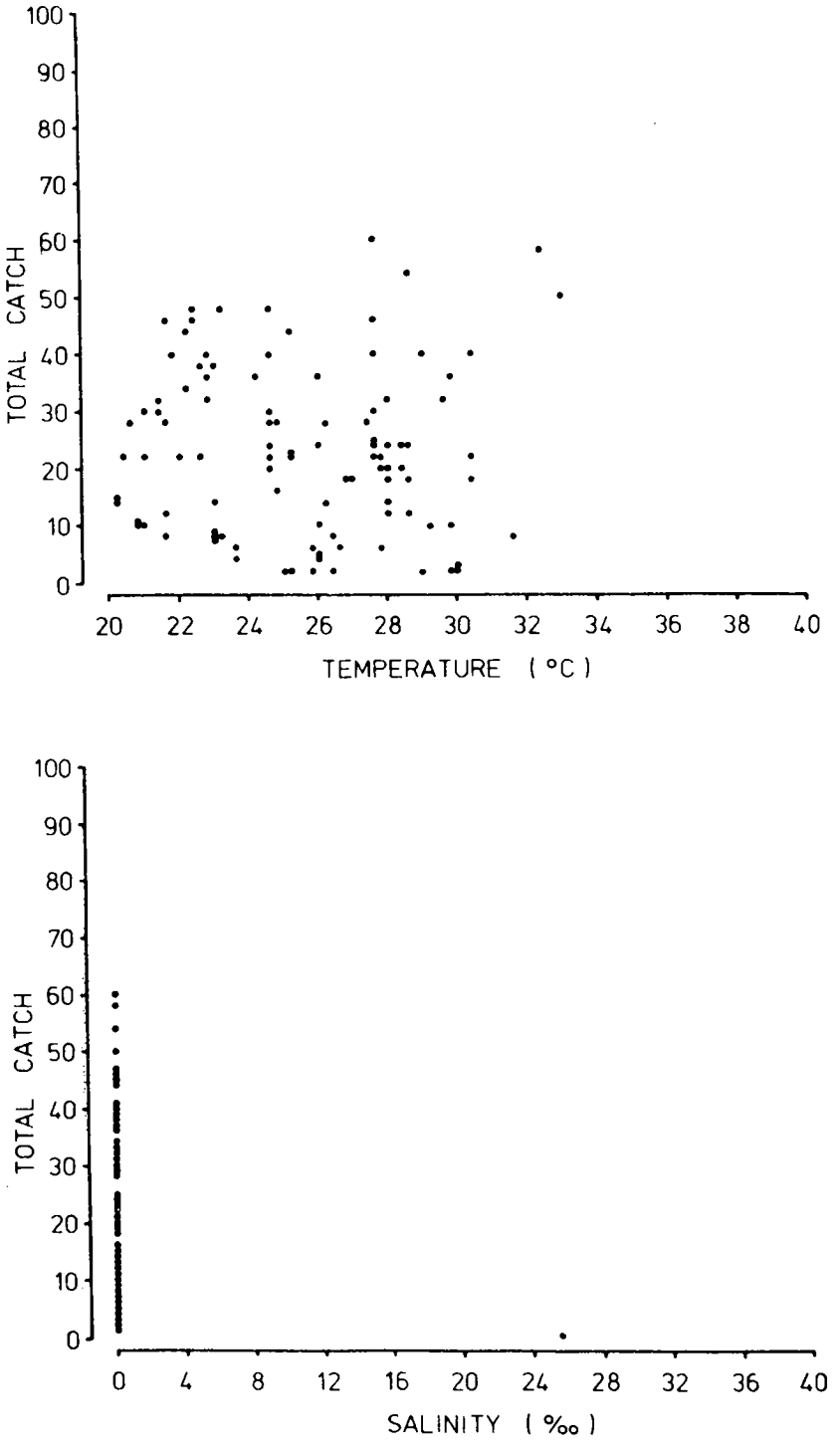


Fig. 21. Total catch of *M. australiense* versus temperature and salinity at each site on each sampling occasion. Zero catches have been omitted.

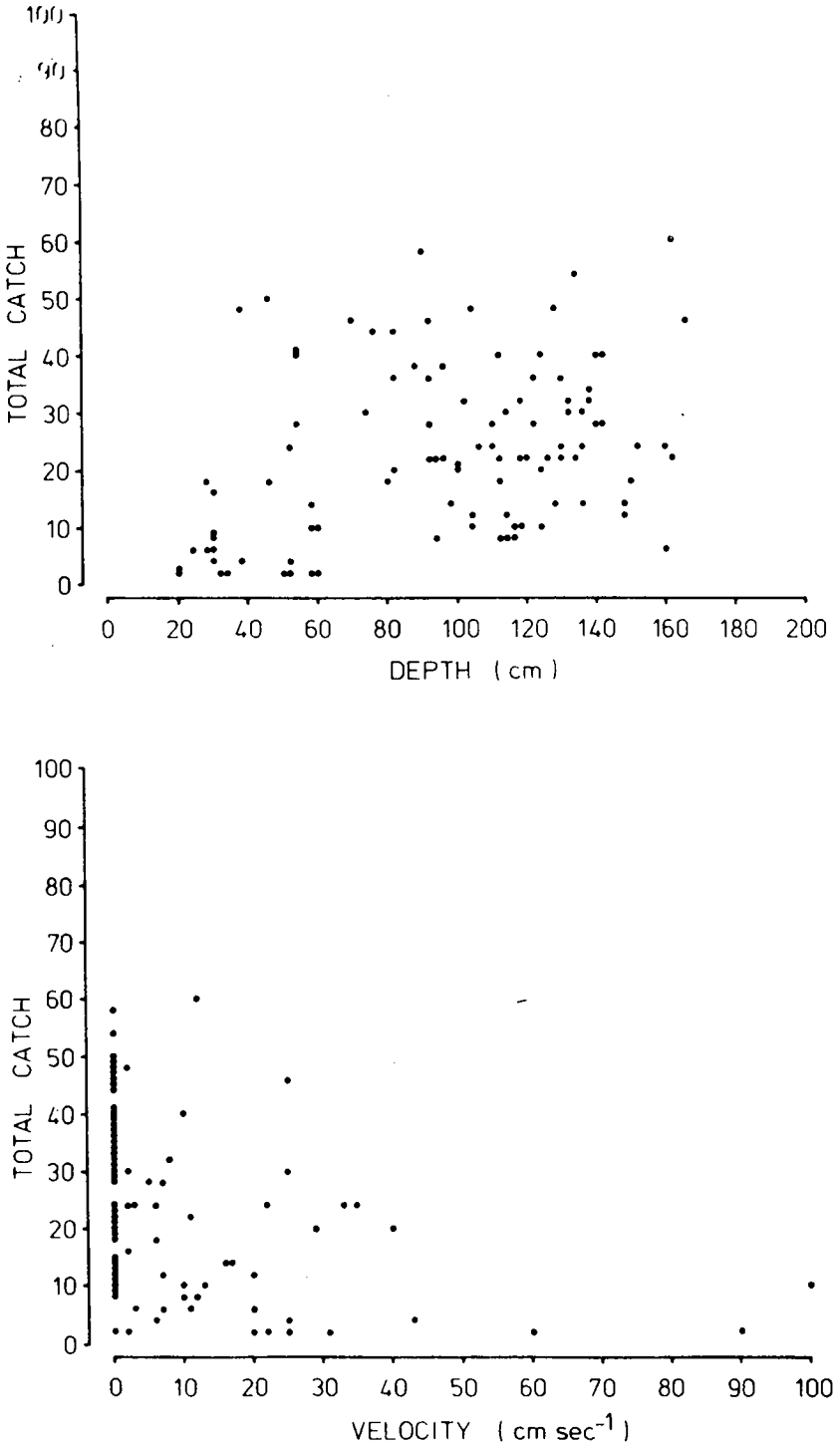
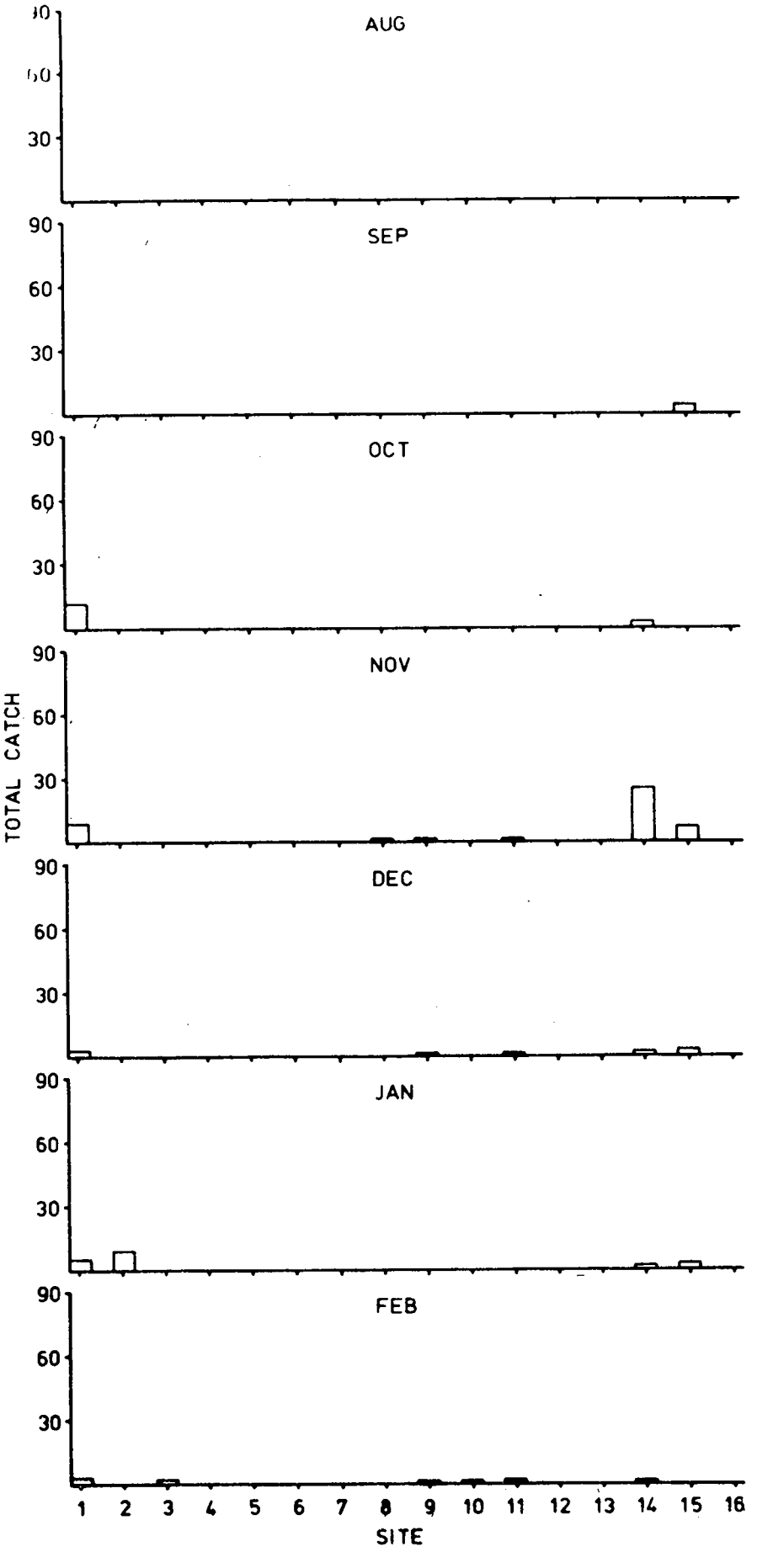


Fig. 22. Total catch of *M. australiense* versus depth and surface velocity at each site on each sampling occasion. Zero catches have been omitted.


AUG
SEP
OCT
NOV
DEC
JAN
FEB
90
60
30
TOTAL CATCH
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
SITE

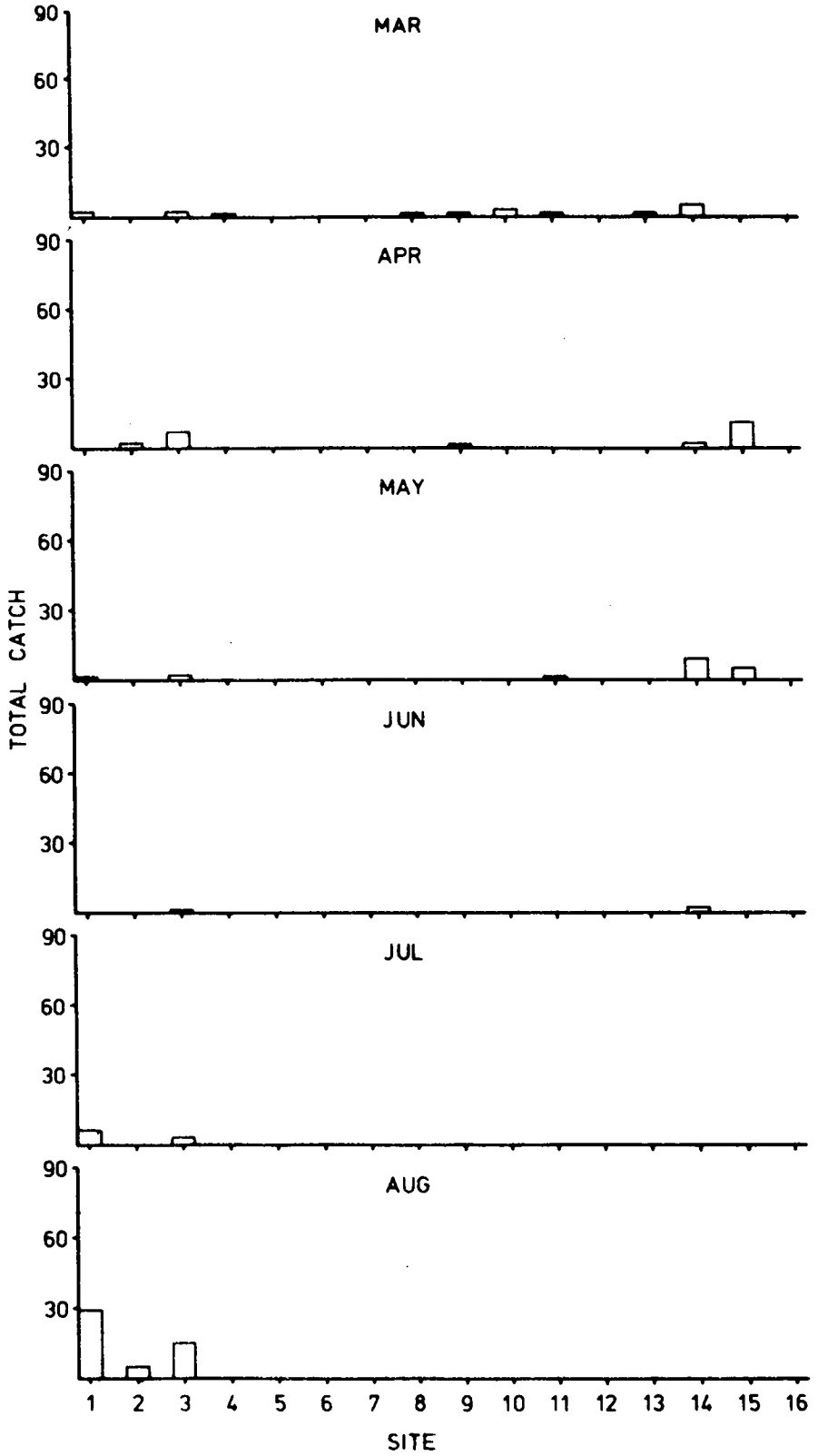


Fig. 23. Total catch of *M.* sp. A at each site on each sampling occasion from August 1975 to August 1976.

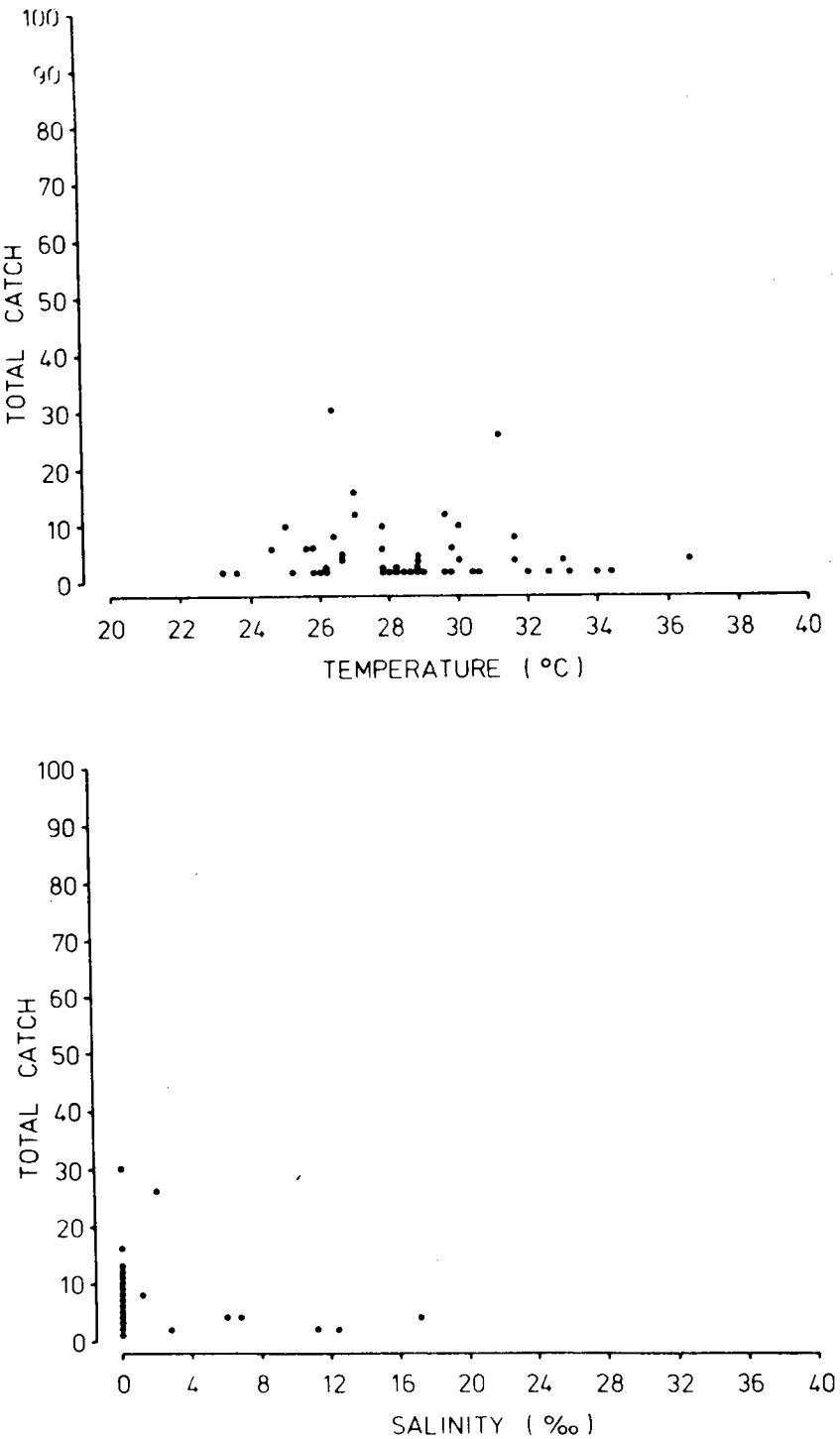


Fig. 24. Total catch of *M.* sp. A versus temperature and salinity at each site on each sampling occasion. Zero catches have been omitted.

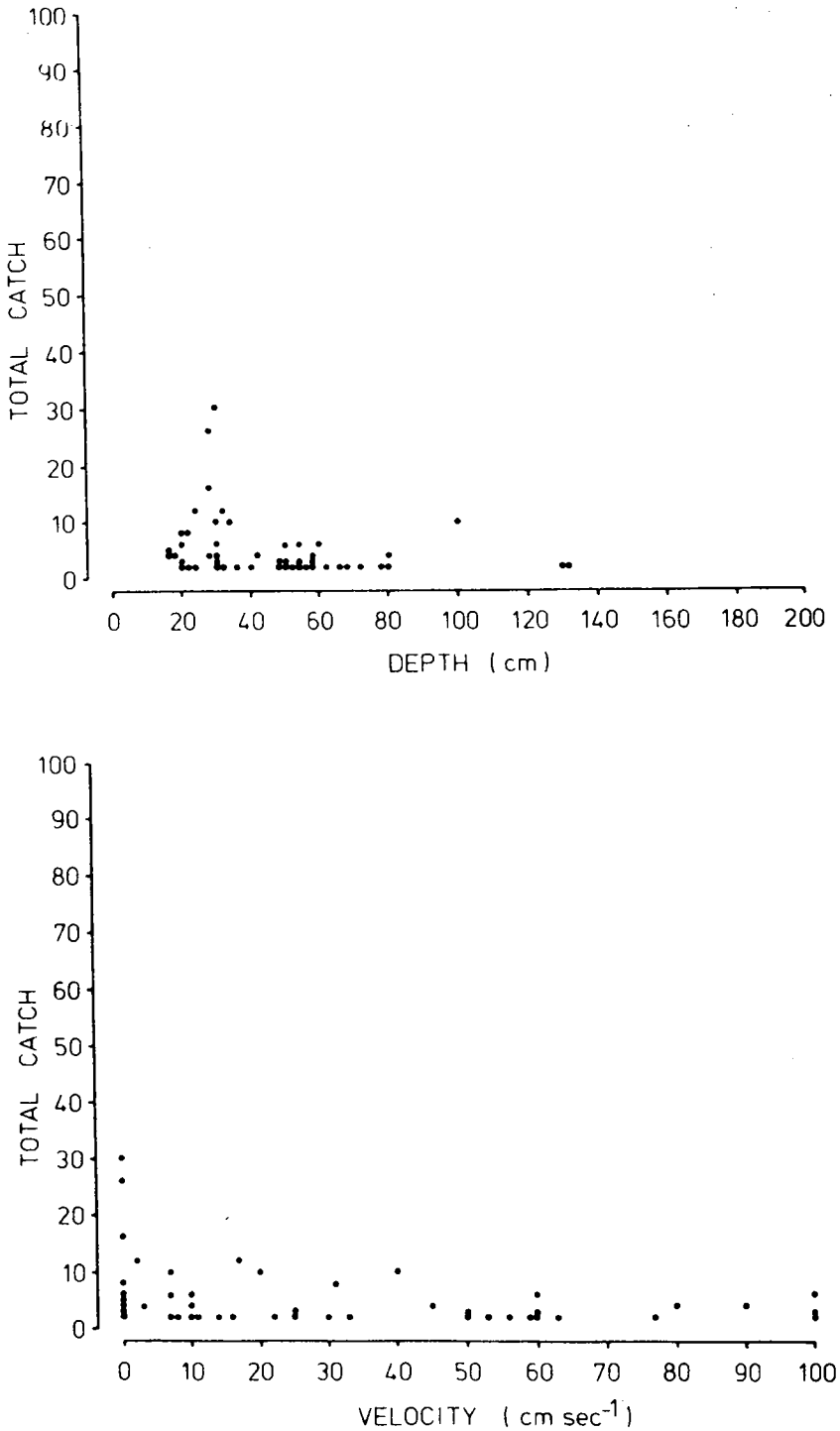


Fig. 25. Total catch of *M.* sp. A versus depth and surface velocity at each site on each sampling occasion. Zero catches have been omitted.

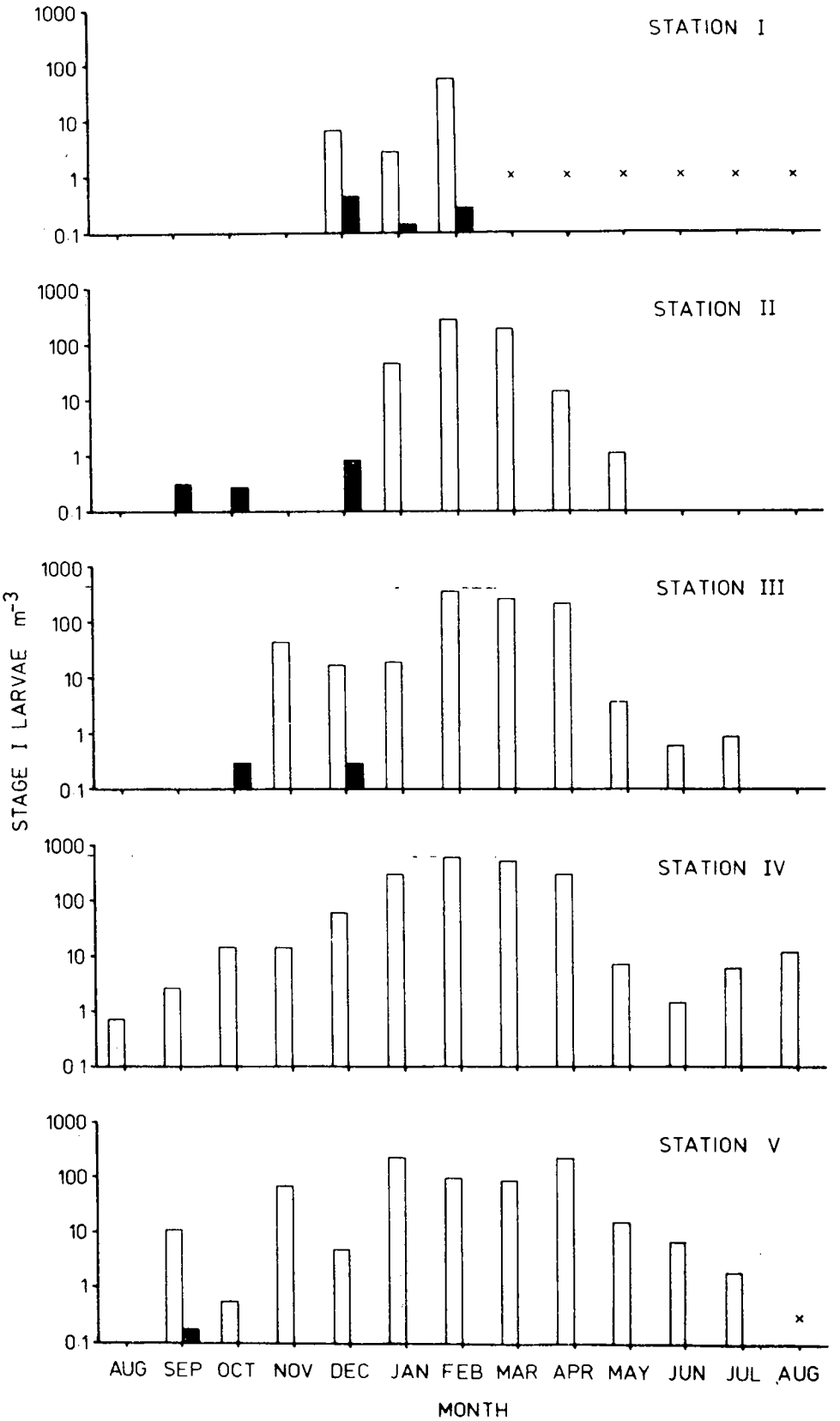
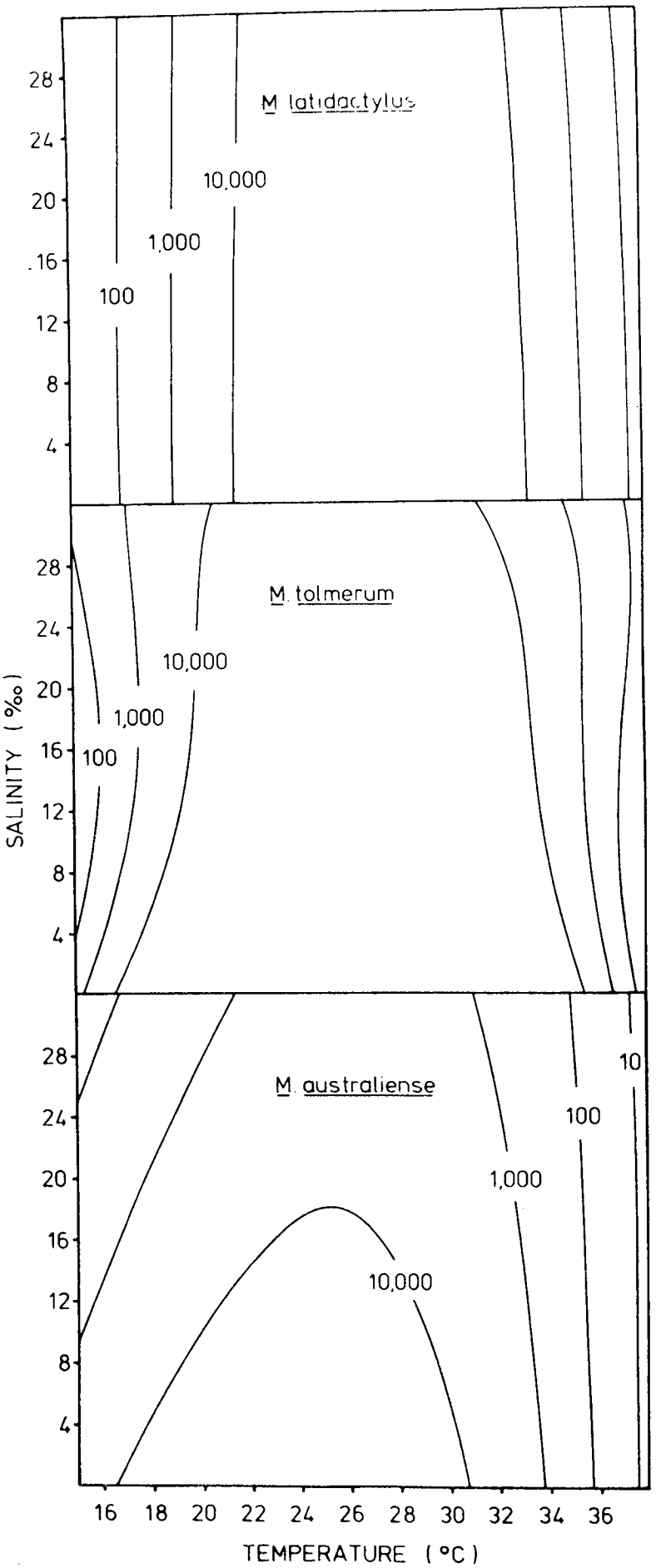


Fig. 26. Estimated density of stage I larvae of *M. australiense* (solid bars) and other *Macrobrachium* species (open bars) at each station on each sampling occasion. At stations I to III, 'other species' can be assumed to be *M. tolmerum* only.

Fig. 27. Fitted response of mean survival time (minutes) of adult male *M. latidactylus, M. tolmerum* and *M. australiense* to experimental temperature and salinity (based on data presented in Tables 17, 18 and 19).


M. latidactylus
10,000
1,000
100
M. tolmerum
10,000
1,000
100
M. australiense
10,000
1,000
100
10
SALINITY (‰)
TEMPERATURE (°C)
4
8
12
16
20
24
28
16
18
20
22
24
26
28
30
32
34
36

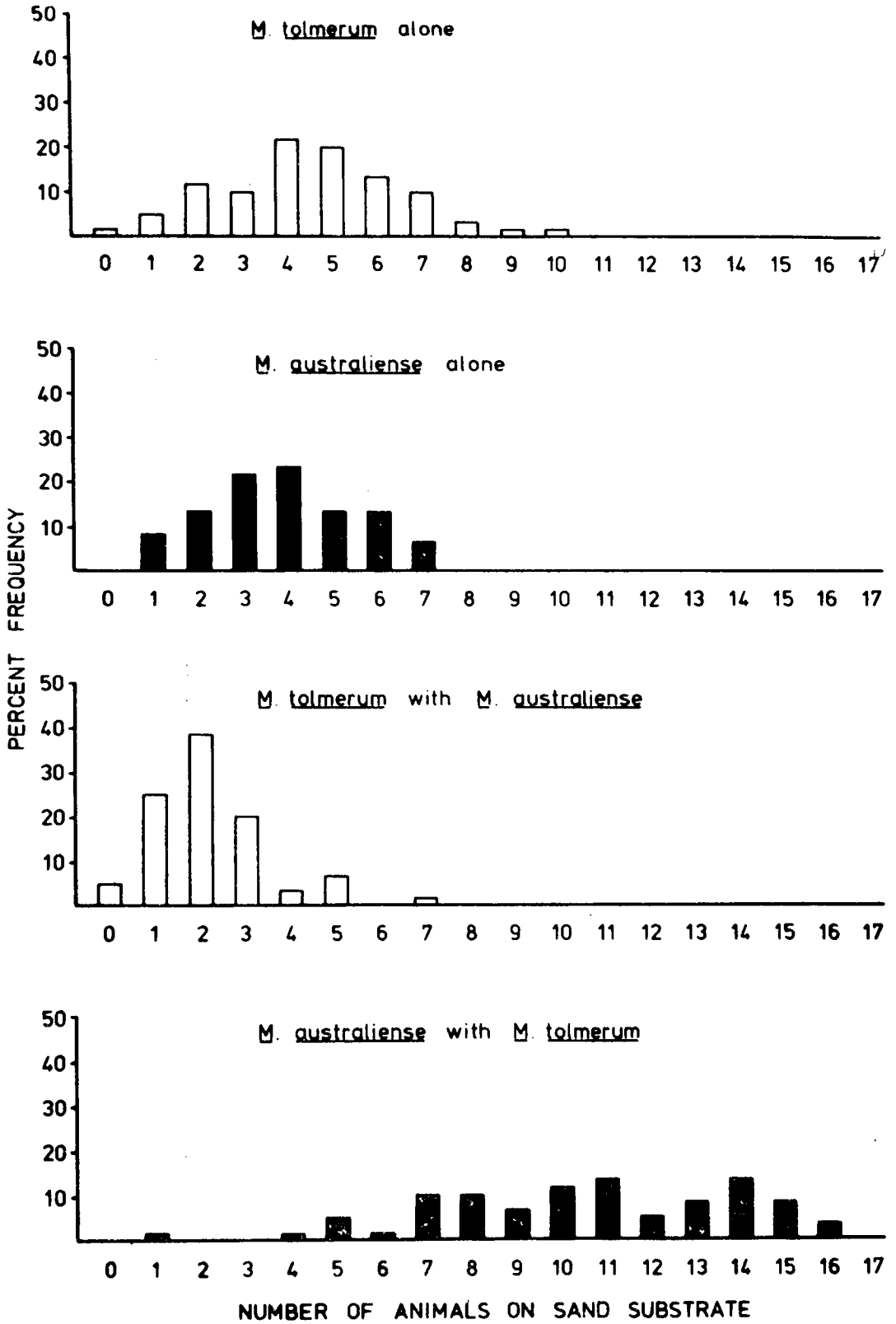


Fig 28. Substrate preference (sand/stones choice) in the absence of current. Results of three experiments are shown - *M. tolmerum* alone, *M. australiense* alone, and the two species together.

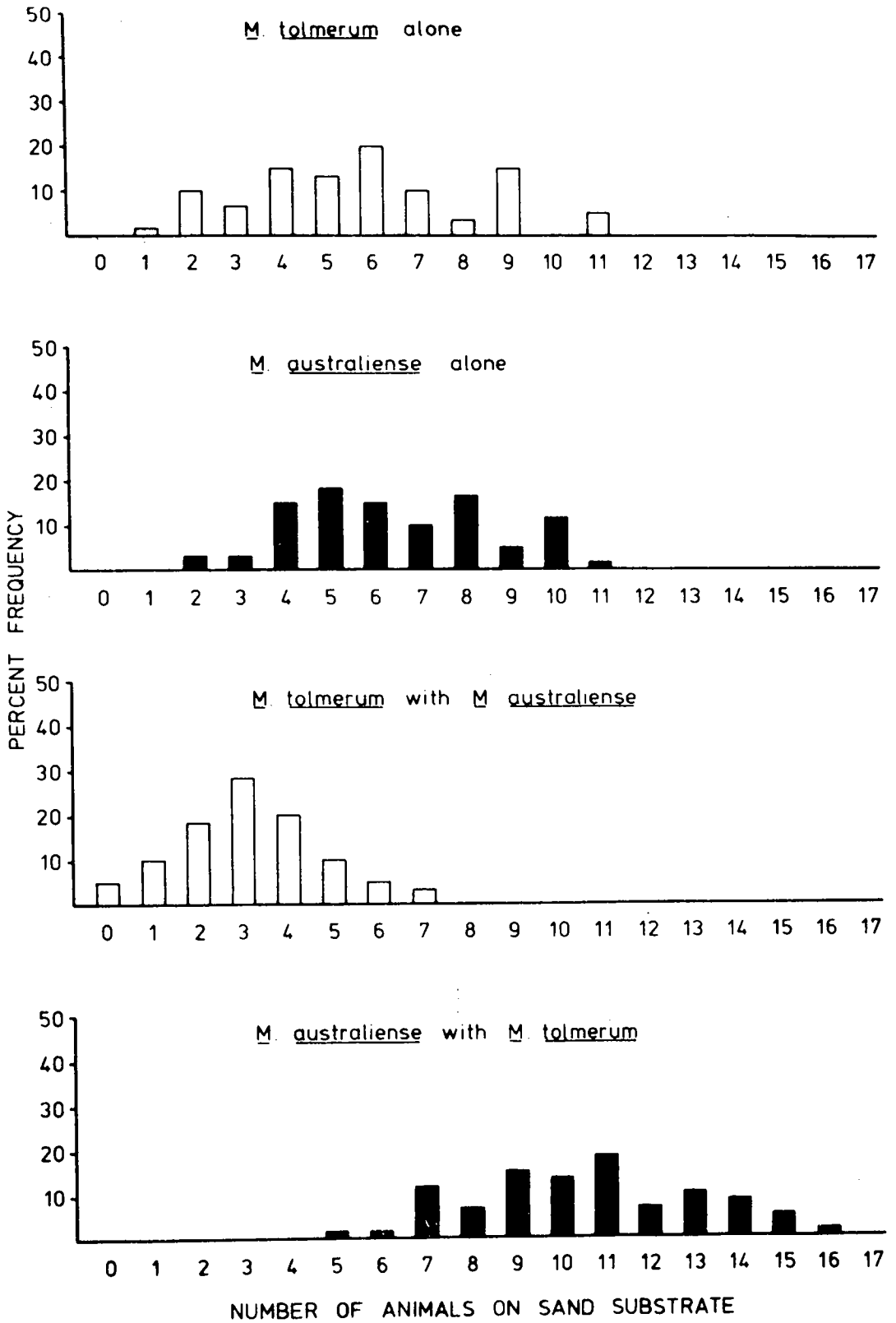


Fig. 29. Substrate preference (sand/leaf litter choice) in the absence of current. Results of three experiments are shown - *M. tolmerum* alone, *M. australiense* alone, and the two species together.

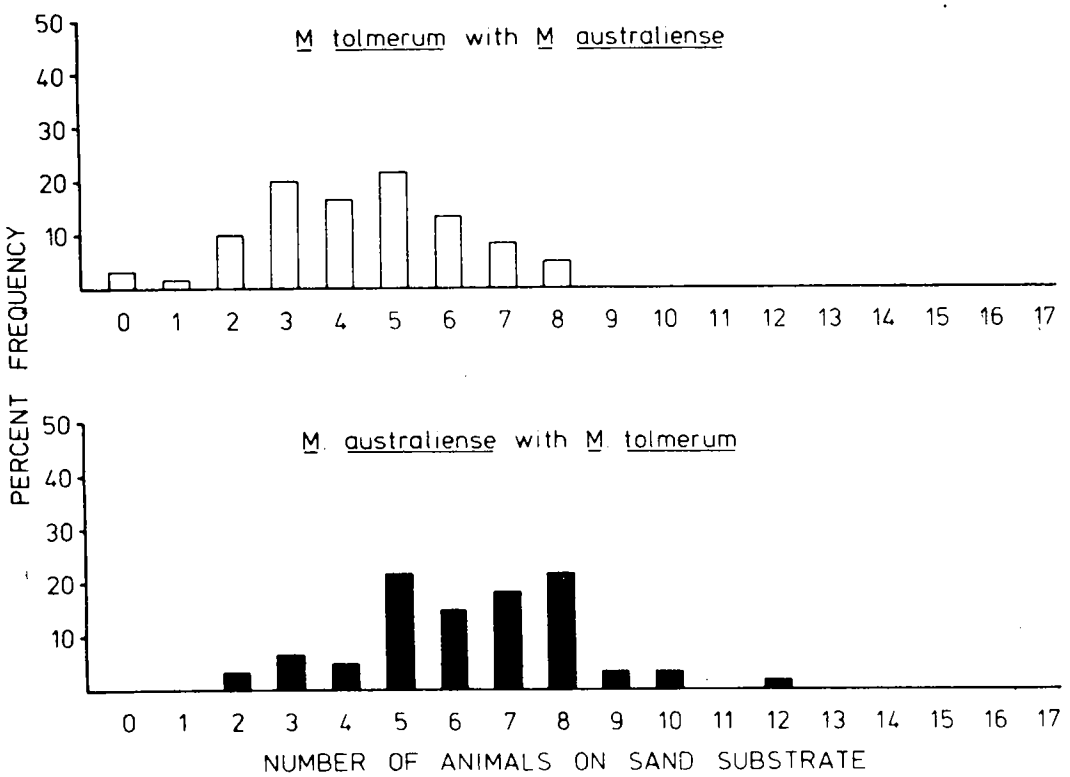


Fig. 30. Substrate preference (sand/stones choice) in the presence of current. The results of one combined species experiment are shown.

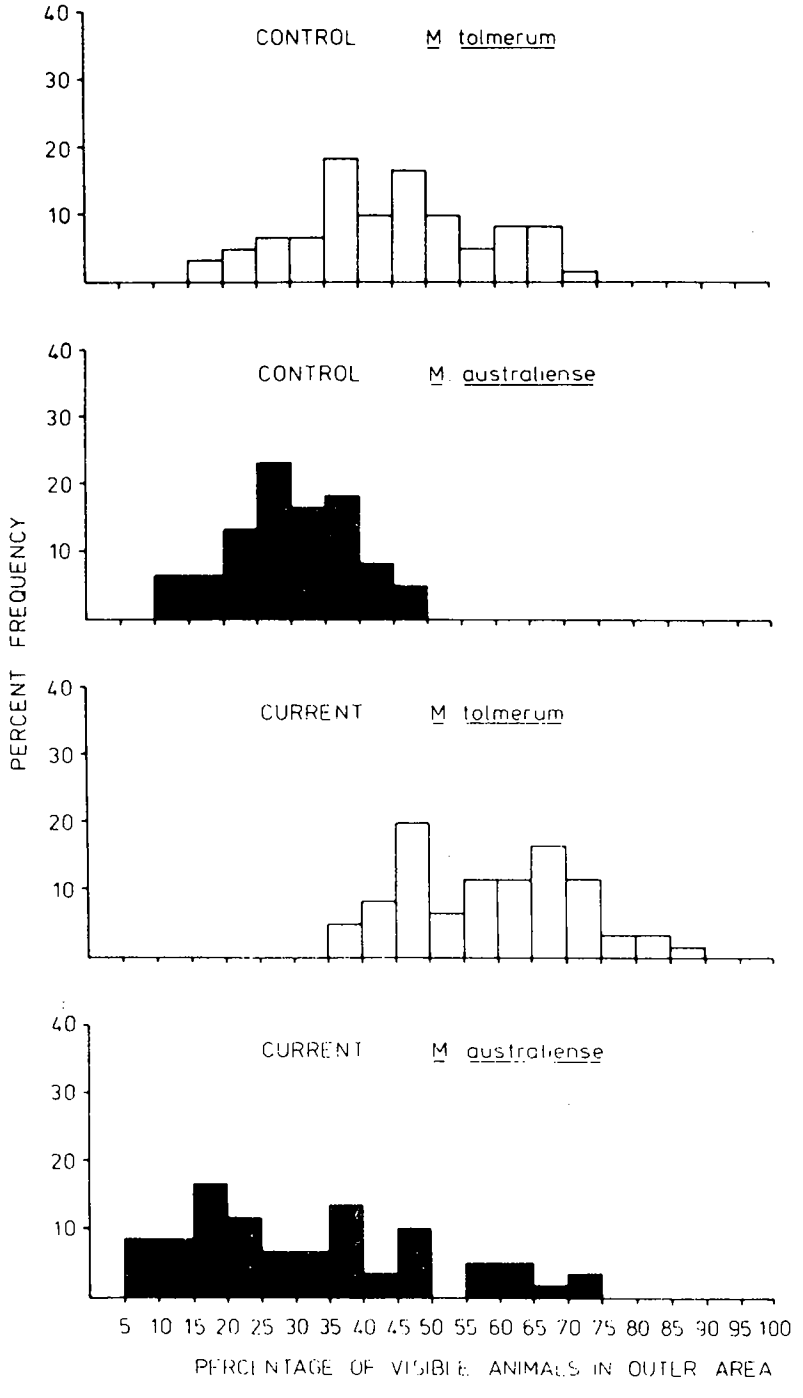
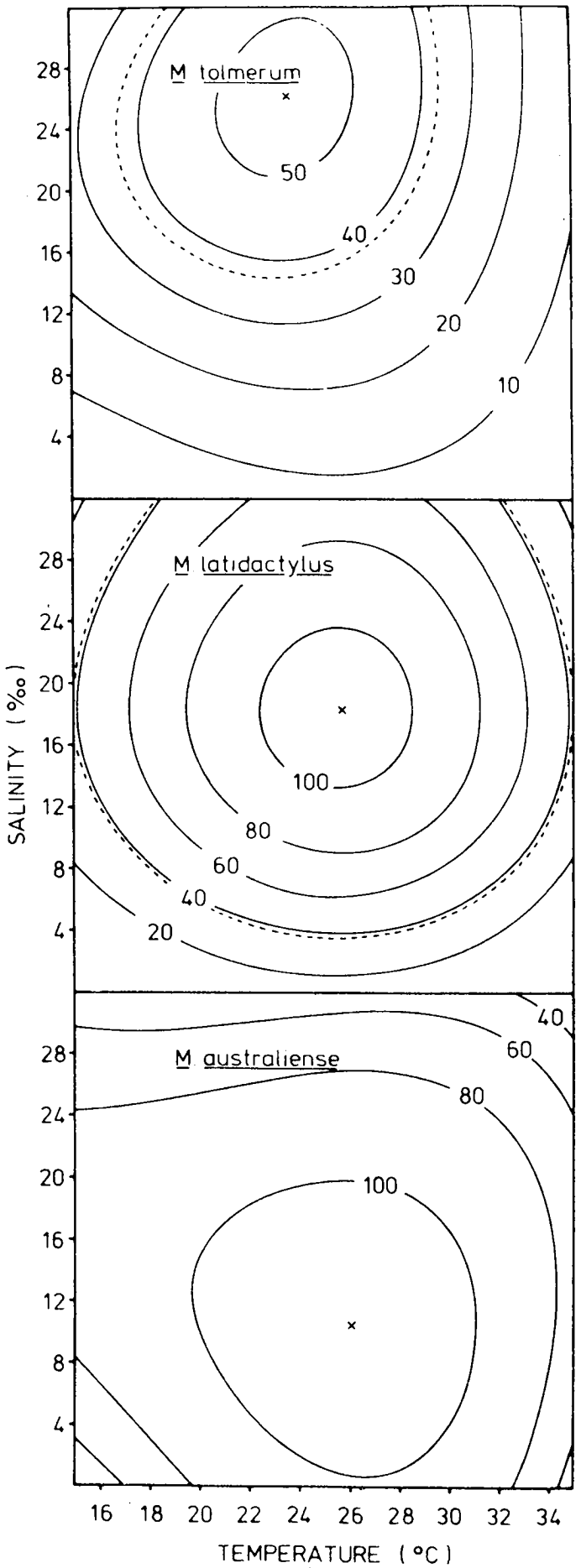


Fig. 31. Current preference of *M. tolmerum* and *M. australiense* in a combined species experiment with a choice of substrate (sand/stones).

Fig. 32. Fitted response of survivor days proportion (%) of *M. tolmerum*, *M. latidactylus* and *M. australiense* larvae to experimental temperature and salinity (based on data presented in Tables 29, 30 and 31). The isopleths represented by broken lines are at the mean survival times outside which there is little chance of survival to post-larvae (explanation in text).


M tolmerum
50
40
30
20
10
M latidactylus
100
80
60
40
20
M australiense
40
60
80
100
SALINITY (‰)
4
8
12
16
20
24
28
16 18 20 22 24 26 28 30 32 34
TEMPERATURE (°C)

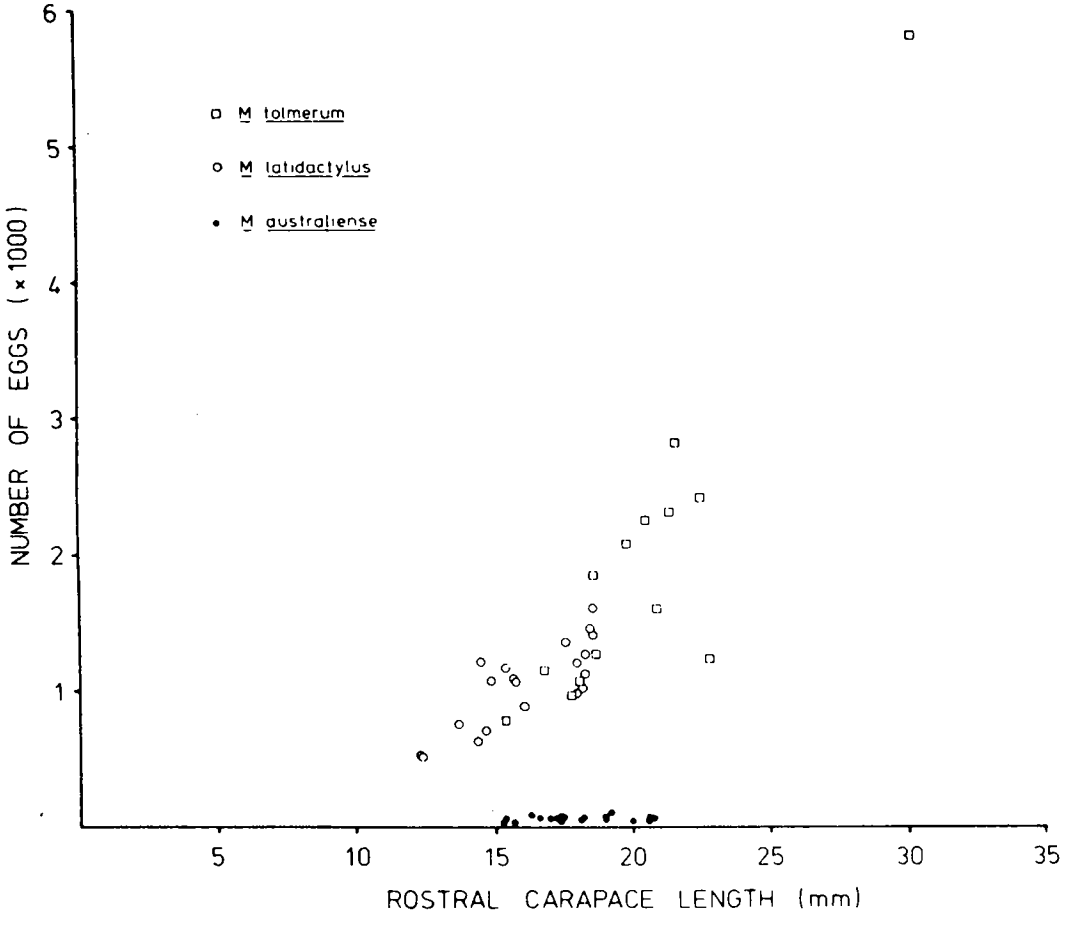
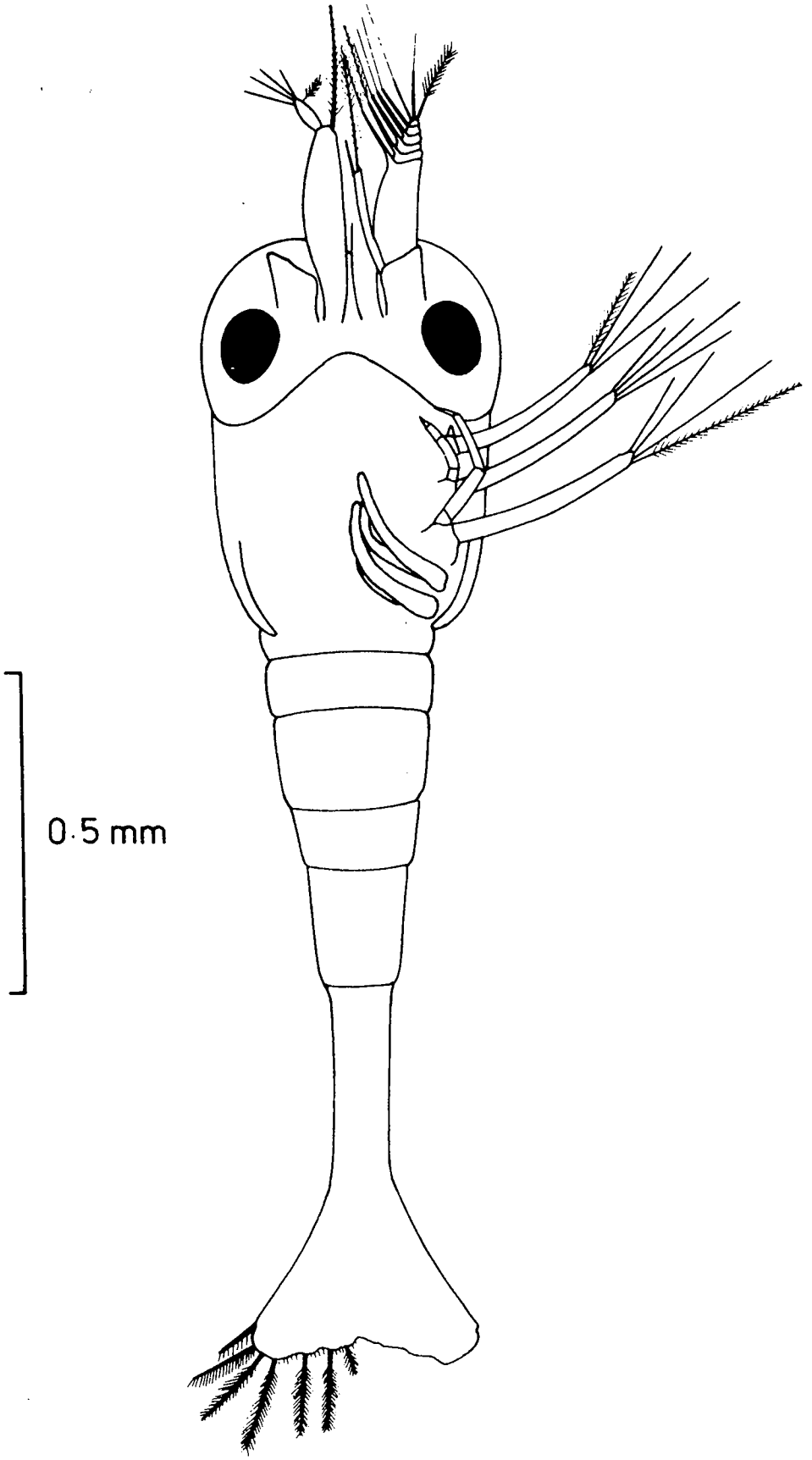


Fig. 33. The number of eggs per egg mass versus rostral carapace length of females of *M. tolmerum*, *M. latidactylus* and *M. australiense*.

Fig. 34. Gross morphology of stage I larva of *M. latidactylus*, ventral view.


0.5 mm

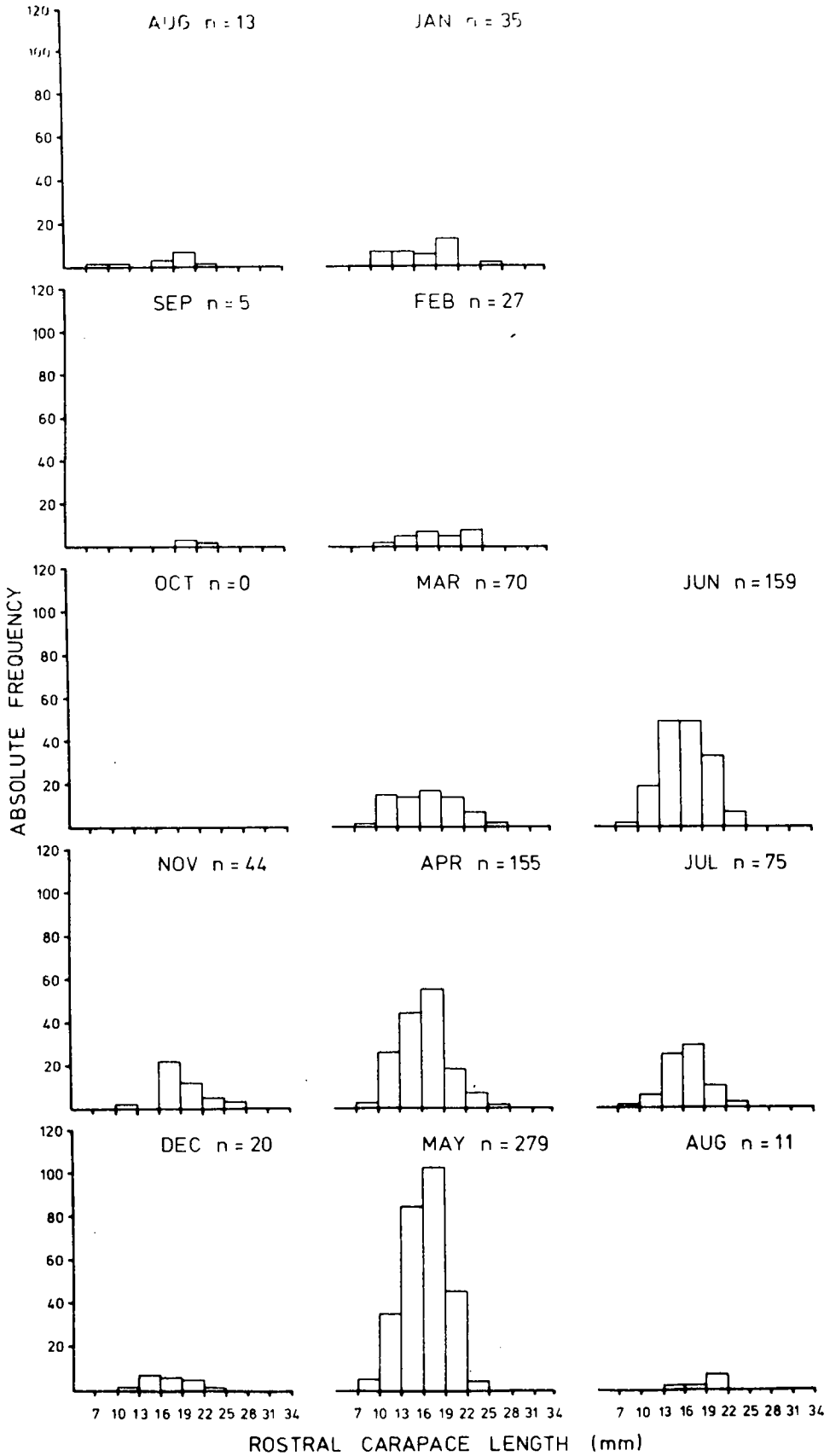


Fig. 35. Size frequency distributions of *M. latidactylus* taken on each sampling occasion from August 1975 to August 1976.

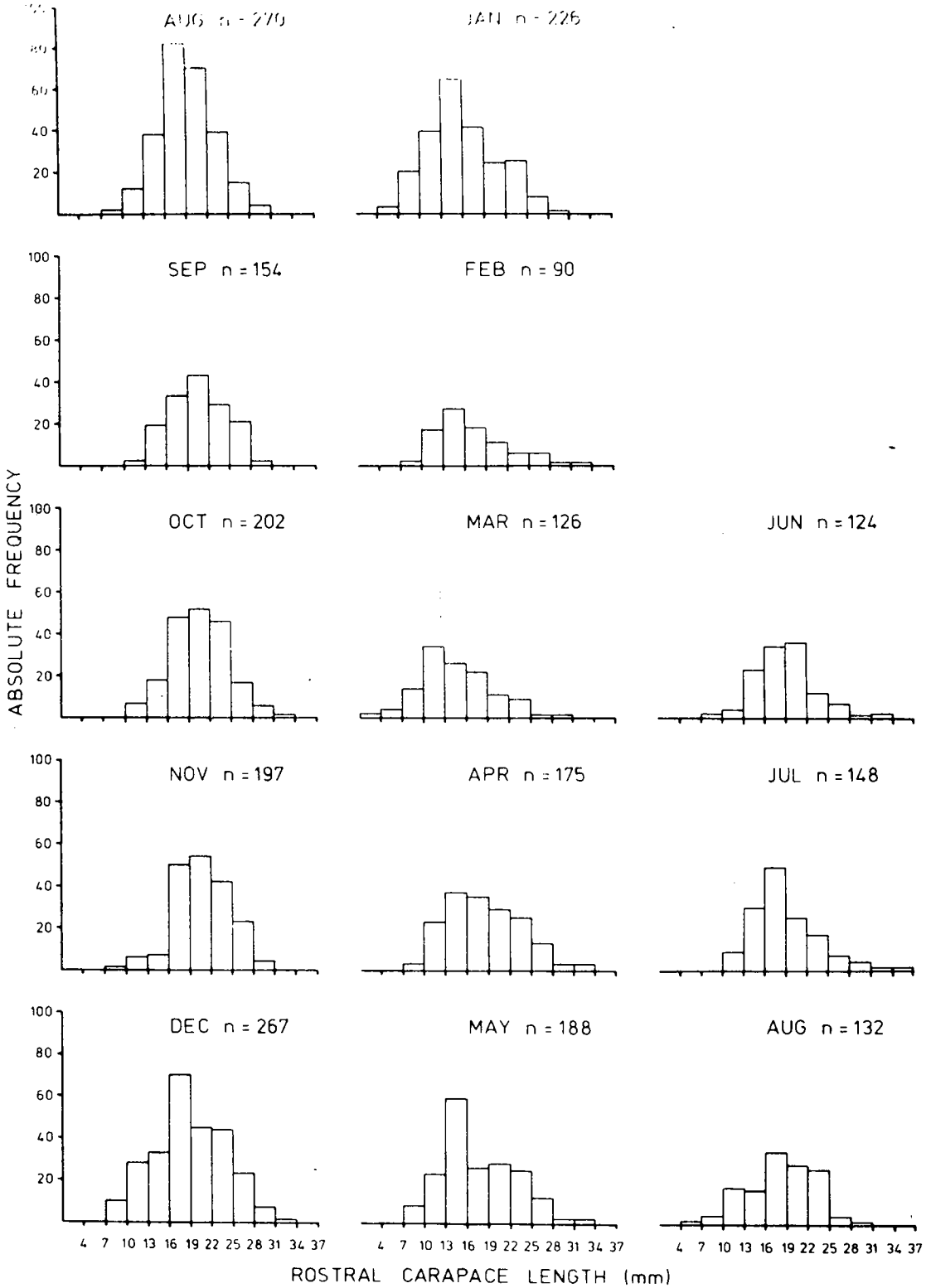


Fig. 36. Size frequency distributions of *M. australiense* taken on each sampling occasion from August 1975 to August 1976.

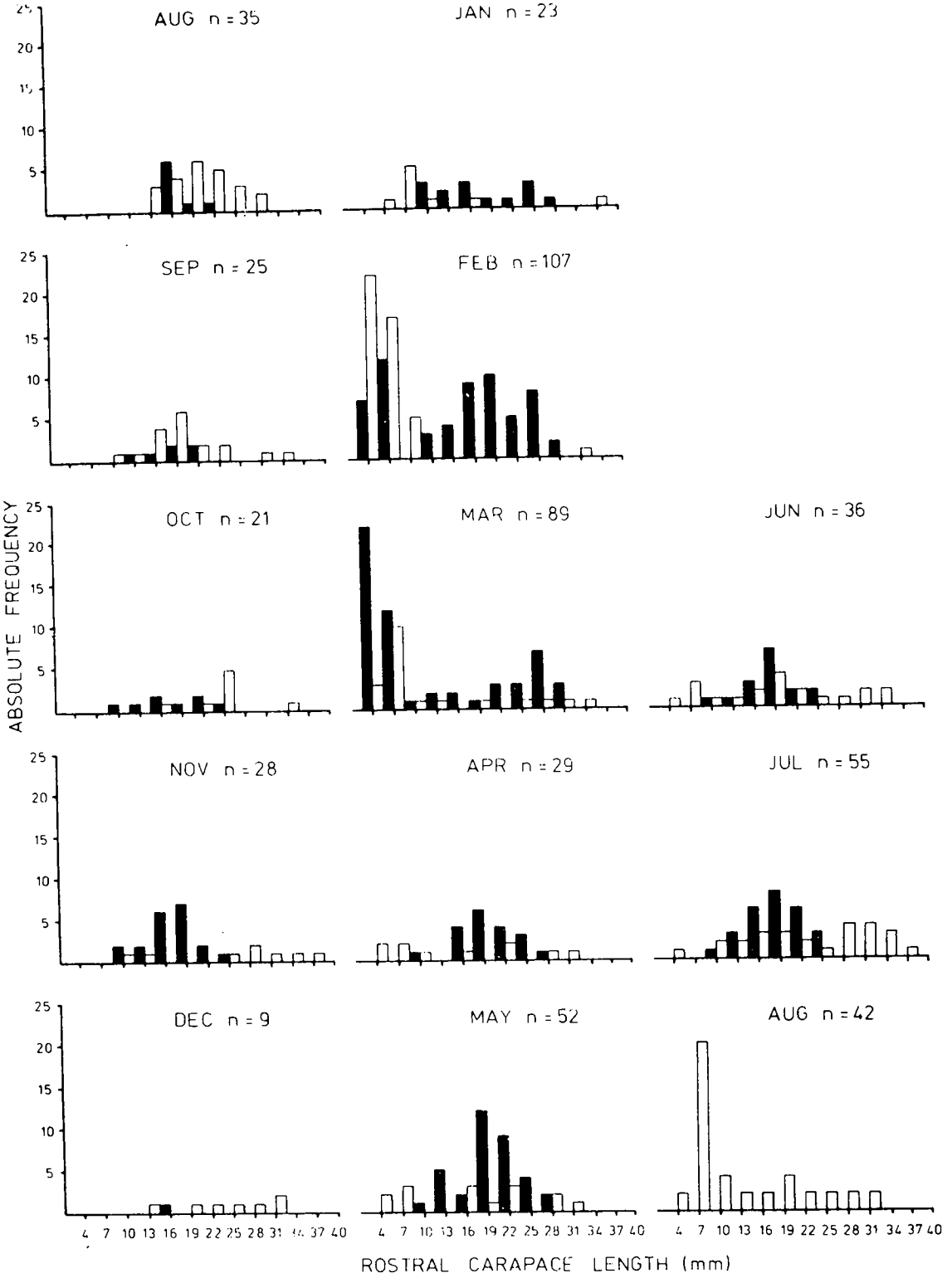


Fig. 37. Size frequency distributions of *M. tolmerum* taken at sites 1 to 8 (open bars) and sites 9 to 16 (closed bars) on each sampling occasion from August 1975 to August 1976.

Plate 1. Pine Creek at sampling site 1 (above) and Bluewater Creek in the vicinity of sampling sites 4, 5 and 6 (below).

Plate 2. Bluewater Creek in the vicinity of sampling site 9 (above) and sites 10 and 11 (below).

Plate 3. Bluewater Creek in the vicinity of sampling site 15 (above) and site 16 (below).

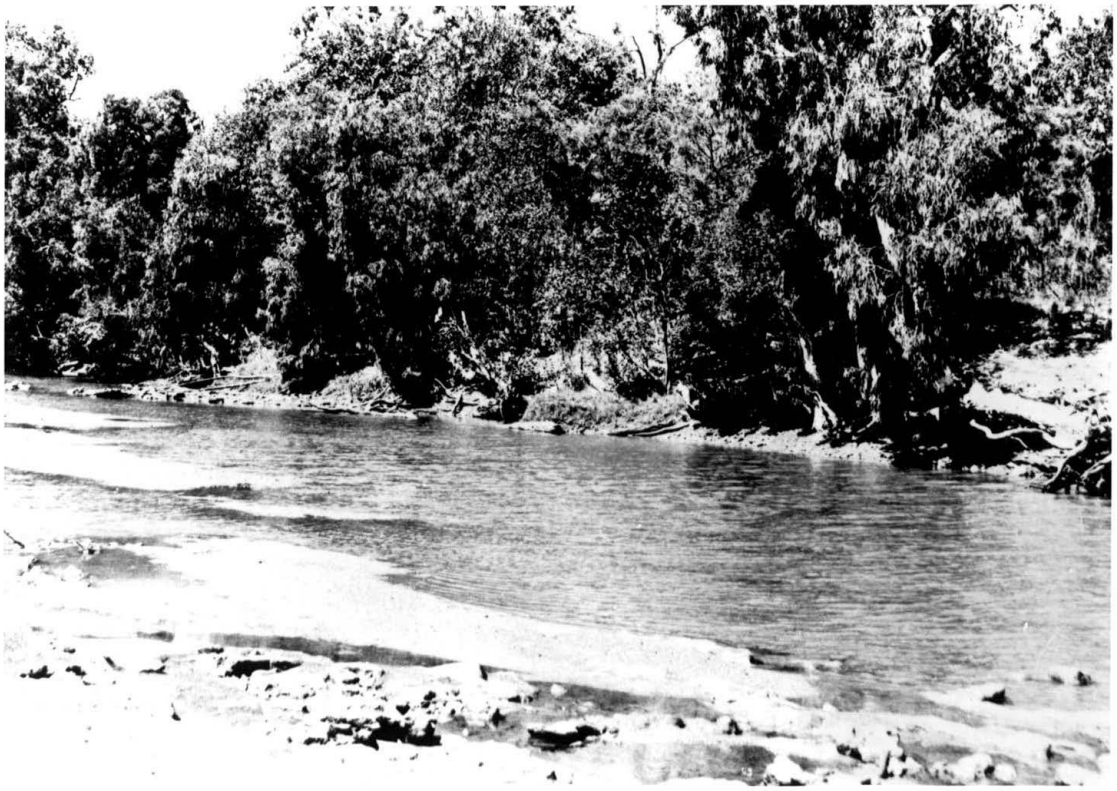
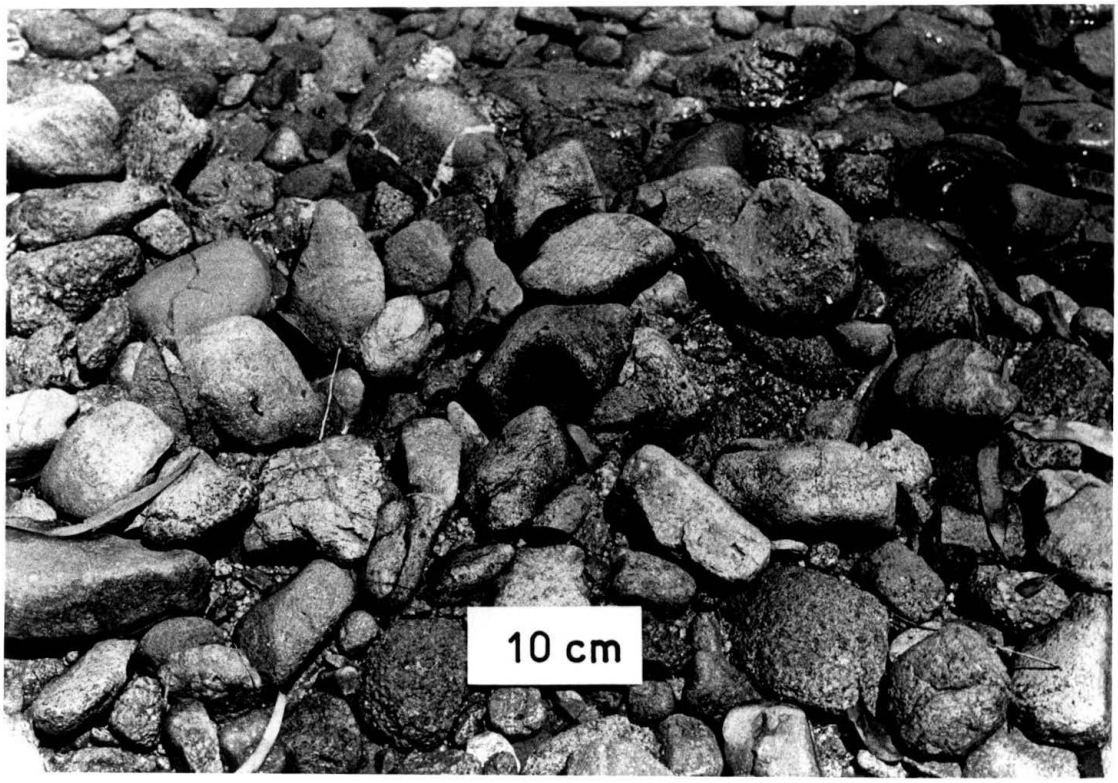


Plate 4. Typical stone substrate of Bluewater Creek.


10 cm

APPENDIX A

A STUDY OF MORPHOLOGICAL DIFFERENCES BETWEEN *MACROBRACHIUM TOLMERUM* RIEK AND *M.* SPECIES A (UNDESCRIBED).

INTRODUCTION

The type material of *Macrobrachium tolmerum* Riek, 1951 in the Australian Museum contains two morphological forms. Animals similar to both of these forms occur in the Bluewater Creek study area where they are substantially sympatric. The forms were visually distinguished on the basis of rostrum shape, the number of dorsal rostral teeth, patterns of body pigmentation and behaviour (see Section 3 of the main text).

A study of morphological differences between the two forms was undertaken in order to:-

(1) provide an objective assessment of the validity of separating the two forms;

(2) determine the extent of overall morphological difference, an important consideration in assigning taxonomic status to the forms;

(3) determine the smallest set of morphological variables which could be used to distinguish the two forms.

No conclusion as to the taxonomic status of the two forms is drawn in this Appendix, but they are referred to as *M. tolmerum* (= Group 1) and *M.* sp. A (= Group 2), since this facilitates reference to the Appendix by Section 3 of the main text.

MATERIAL AND METHODS

Because of the difficulty of obtaining sufficient females of *M.* sp. A the study was restricted to males. Animals were sampled by baited funnel trap (described in Section 4). All males above juvenile size (13 mm rostral carapace length) were included in the sample. Juveniles were present in some of the catches, but there were no

adults between 13 mm and 15 mm rostral carapace length of *M.* sp. A or between 13 mm and 21 mm rostral carapace length of *M. tolmerum*. The sample was therefore of mature males. Successive catches were added to the sample until 41 *M. tolmerum* were obtained. Further catches were necessary to obtain the same number of *M.* sp. A, and from the final catch, the required number of individuals were selected by random numbers. A further sample of 10 individuals of each form was obtained in the same manner; this was used as an independent sample for testing the allocation efficiency of discriminant functions.

Twenty two metric variables (Fig. A1) and two discrete variables, the number of dorsal rostral teeth (variable 1) and the number of ventral rostral teeth (variable 2), were used in the study. dimensions to 10 mm were measured with an ocular micrometer and dissecting microscope, while larger dimensions were measured with vernier calipers. All measurements were taken to 0.05 mm.

The following methods were used in the analysis:-

(1) Bivariate Scatter Diagrams.

Scatter diagrams of each variable against carapace length and other selected combinations were drawn. These were used to visually examine the nature of relationships between and within the groups and to check for data errors.

(2) Analysis of Ratios.

The ratio of each variable to carapace length was analysed in order to determine the significance of univariate differences between the two groups. Computations were carried out on the James Cook University PDP-10 using SPSS programs (Nie *et al*,

1975) and Statpack (Western Michigan Computer Centre).

(3) Discriminant Analysis.

Discriminant analysis involves multivariate techniques of potential predictive and inferential value aimed at the analysis of groups of data. Its purposes are:-

(a) on the basis of several variables, to test for overall differences between the groups and determine their degree of overlap;

(b) to derive allocation rules for classifying further cases into the groups; and

(c) to estimate the probability of correct classification using the rules derived.

In the present study, linear discriminant functions were used. Each linear discriminant function is a reduction of the multivariable space to a single dimension, derived by linear combination of the original discriminating variables. The coefficients of the variables are derived so that differences between groups along the discriminant function are maximised.

Mathematical treatments of the derivation of discriminant functions are given by Cooley and Lohnes (1971, pp. 243-250); Marriott (1974, Ch. 5) and Eisenbeis and Avery (1972, Ch. 1). The method used by SPSS maximises the ratio of the between groups to the pooled within groups deviation sums of squares of the discriminant function scores (Nie *et al.*, 1975). Various tests of significance are available for the difference between groups on the discriminant function axis (Porebski, 1966).

Following derivation of a discriminant function, a classification function for each group may be obtained. Each case to be classified is given a score on each classification function and then allocated to the group on whose function it has the highest score. In some simple two group instances such as that of the present study, it is not necessary to use separate classification functions in the classification phase. Where prior probabilities of group membership are equal and the centroids of the groups in reduced space are symmetrically placed about zero, allocation can be achieved according to the sign of the discriminant score. This method assumes prior evaluation of the scores of some test cases whose group membership is known.

The efficiency of classification functions can be empirically assessed from their performance on a further sample of cases of known group membership. In the present study, the sample used to derive a function is termed 'original sample' and the independent sample used to test classification efficiency is termed the 'test sample'.

Discriminant function analysis (also called canonical variate analysis in multi-group examples) has had extensive biological application in recent years. It has been used by Spain *et al.*(1976) and Grant *et al.* (1977) to investigate sexual dimorphism, while many workers have used it to investigate other sources of variation, particularly as a guide in taxonomic considerations, e.g. Clifford and Binet (1954), Delaney and Healey (1964), Ducker *et al.* (1965), Phillips *et al.* (1973), Atchley (1974), Campbell and Mahon (1974), Zimmermann and Ludwig (1974), Messieh (1975), Campbell (1976), Campbell and Saunders (1976), Johnston and Sharman (1976), Brown and Shipp (1977) and Taylor *et al.* (1977).

RESULTS

(1) Bivariate Scatter Diagrams.

Individuals of *M. tolmerum* taken in traps were on average, larger than those of *M.* sp. A and this was reflected by carapace length in the scatter diagrams. However, in assessment of the scatter diagrams, the overall size difference of individuals in the two groups was disregarded, and attention paid to differences in slope and intercept of the major axes of the groups of points. On this basis, the following variables showed differences between groups in their relationship with carapace length:-

Variable	1	number of dorsal rostral teeth
	3	rostrum length
	6	carapace width
	7	carapace depth
	15	posterior rostrum depth
	17	telson width
	20	telson distance 3
	21	carpus proximal width.

Of these, the most marked difference between groups was present in the scatter diagram of telson distance 3 against carapace length and the least difference by carapace width against carapace length. These two scatter diagrams are shown in Fig. A2. Even greater difference between groups was evident in the scatter diagram of the number of dorsal rostral teeth against rostrum length (Fig.A3). This scatter diagram gave almost complete separation of the groups.

The most obvious conclusions to be drawn from the examination of scatter diagrams are that for a given body size in mature males, *M. tolmerum* has fewer dorsal rostral teeth, a longer

rostrum and greater telson distance 3 than *M.* sp. A.

(2) Analysis of Ratios.

Mean, standard deviation and range for the ratio of each variable with carapace length are given in Table A1.

Significant skewness, kurtosis and inequality of variance between groups were shown by some of the ratios. Logarithmic transformation reduced but did not eliminate these problems. Consequently the Mann-Whitney U statistic was used to test for differences between groups in the ratios.

Twelve of the 23 variables were significantly different ($\alpha = 0.05$) between groups in their ratio with carapace length (Table A2). They were, in decreasing order of magnitude of difference

Variable	1	number of dorsal rostral teeth
	20	telson distance 3
	3	rostrum length
	17	telson width
	6	carapace width
	7	carapace depth
	21	carpus proximal width
	19	telson distance 2
	24	propus distal width
	15	posterior rostrum depth
	8	abdomen width
	16	ventral carapace width

(3) Discriminant Analysis.

Variables 1 and 2, being discrete and with a small number of possible values, were excluded from the analysis since

their population distributions could not be assumed to be normal.

Means, standard deviations and ranges of the variables are given in Table A3.

Significant skewness and kurtosis were shown by some of the untransformed variables and little overall reduction in the magnitude of these statistics was achieved by the logarithmic transformation. However, discriminant analysis is more sensitive to departures from equality of dispersion matrices than to minor departures from normality (Marriott, 1974). The data were therefore analysed as their natural logarithms, as this was expected to ensure approximate equality of dispersion. A test exists for equality of dispersion matrices, but it was not applied since it is more sensitive to departures from normality than the procedure in this instance being justified (Marriott, 1974).

Initially, a forward stepwise discriminant analysis was carried out using the SPSS program 'Discriminant'. At each step one further variable was introduced into the analysis, the variable chosen being that which maximised the increase in Rao's V, a generalised distance measure (Rao, 1948 pp. 66 - 67). Variables entered or removed at each step and the corresponding change in Rao's V are given in Table A4. Only 16 of the possible 22 variables were retained in the final discriminant function, since further variables would not have significantly improved group separation. Variables in the discriminant function with their coefficients and the classification function coefficients are given in Table A5. The most important contributing variables, as indicated by the absolute magnitude of their standardised coefficients were, in decreasing order, 24 (distal propus width), 3 (rostrum length), 5 (extent of dorsal rostral teeth),

15 (posterior rostrum depth), 10 (merus length) and 4 (carapace length). As indicated by opposite signs of coefficients, there was a contrast between distal propus width, rostrum length, posterior rostrum depth and merus length on the one hand and carapace length and extent of dorsal rostral teeth on the other. The square of the cononical correlation between the discriminant function and the group distinguishing dummy variable was 0.976 (Table A5), that is, 97.6% of variation on the discriminant function was explained by the groups.

Allocation of the 82 original cases and 20 test cases using the derived classification functions yielded 100% correct classification.

Because it cannot be assumed that the data strictly fulfil the requirements of normality and equality of dispersion matrices, significance tests cannot be rigorously applied. However, it is evident from the cononical correlation and efficiency of classification shown by this discriminant function, that complete separation of the groups was achieved.

Further analysis was carried out in order to determine the minimum subset of variables which could give 100% correct classification. To this end, a series of discriminant functions was derived, using increasing numbers of variables in the order of preference suggested by the initial stepwise analysis. The variables used in each function, their coefficients, and performance as measured by canonical correlation and allocation efficiency are given in Table A6. Classification functions associated with each of these discriminant functions are given in Table A7. Only five variables were needed in order to completely separate the groups, a further indication of the degree of distinction between the two morphological forms.

DISCUSSION

All three approaches used in the foregoing analysis suggested the two groups were discrete and recognisable on the basis of the variables considered. While the relative importance attached to each variable differed between approaches, this was inherent in the methods and is not seen as a contradiction. The scatter diagrams and analysis of ratios dealt with variables in pairs, while discriminant analysis dealt with all variables and their relationships to each other simultaneously.

Understandably, analysis of ratios by the Mann-Whitney test is a more powerful method than visual interpretation of scatter diagrams. Analysis of ratios resolved differences not apparent in the scatter diagrams and, furthermore, allowed the assignment of relative magnitude to differences between the groups. The scatter diagram approach was of value in that it allowed the dispersion of data points to be checked and permitted examination of the two discrete variables not included in the discriminant analysis.

Analysis of ratios, by demonstrating differences between groups in 12 of the 23 variables used, suggested considerable overall morphological difference between *M. tolmerum* and *M.* sp. A. It also gave some indication of which variables should be of most value in characterizing the two forms. The information obtained from this analysis however, is only of limited use in the classification of individuals of unknown group membership. That is, because there was overlap between groups on each ratio, it is possible that the whole series of ratios could be evaluated for an individual and still leave its group membership uncertain.

Discriminant analysis was a useful technique in this instance. It indicated complete separation of the groups when all the measured variables were considered, but that the separation could be achieved with a subset of five variables. The most useful variables of the set were thus identified. Allocation of further individuals to the groups can be carried out objectively by using the derived classification functions.

Theoretically, testing the allocation efficiency of a discriminant function on those cases from which it was derived would give biased results (Eisenbeis and Avery, 1972). However, in the present analysis, the independent sample of 20 cases was correctly classified by the discriminant function based on only three variables. A larger independent sample would be required to thoroughly test the functions, but these results suggest the five-variable function to be adequate.

Where group membership of the individuals is known, the classification phase of discriminant analysis is redundant except in testing the performance of the classification functions. However, its application obviously has potential in instances where only a subset of the group defining variables is available to the observer. For example, live animals often possess several distinguishing characters not present in preserved material. A discriminant function which uses morphometric variables only, but was derived using the certainty of group membership afforded by live animals, could be used to classify independent samples of preserved material.

From the present morphometric study, it has been possible to select those variables most suitable for characterizing and separating the *M. tolmerum* and *M.* sp. A groups. The scatter diagrams

and analysis of ratios suggested the number of dorsal rostral teeth to be of value. This character has been used extensively in the literature in the separation of *Macrobrachium* species. The minimum subset of measured variables giving a discriminant function which completely separated the forms consisted of telson distance 3, rostrum length, extent of dorsal rostral teeth, propus distal width and carpus proximal width. The position of spines on the telson has often been given in written descriptions but has not been used in keys to the species. Also, before this morphometric study, it was found that the second pereiopods could often be used successfully to allocate an individual to one of the forms without reference to other characters. However, this was in part due to colour patterns, and any differences in shape of these appendages was considered too subtle to be used as a reliable group separating feature. The discriminant analysis surprisingly gave high weightings to propus distal width and carpus proximal width. Subsequent examination of material showed that these differences could in fact be seen consistently: width of the propus increases slightly near the articulation of the dactylus in *M. tolmerum* whereas it does not in *M.* sp. A; the proximal end of the carpus tends to be wider for a given body size in *M.* sp. A than in *M. tolmerum*.

Separation of the two forms on morphometric grounds cannot be taken as indicative of their being species without the use of supporting evidence. It is possible for discriminant analysis to produce discrete groups from the degree of geographic variation found within a species. Atchley (1974) has given an example in a study of grasshoppers. In that instance there was no doubt as to the status of the groups, which had been confirmed by chromosome studies.

That this situation could arise in *Macrobrachium* is possible since the genus is recognised as having a high level of intra-specific variation.

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TABLE A1. Mean, standard deviation and range of the ratio of each morphological variable to carapace length for a sample of 41 males each of *M. tolmerum* and *M.* sp. A.

	M. tolmerum			*M.* sp. A		
VARIABLE NO.	MEAN	SD	RANGE	MEAN	SD	RANGE
1	0.585	0.091	0.435 - 0.821	0.898	0.179	0.623 - 1.340
2	0.210	0.054	0.130 - 0.353	0.234	0.061	0.118 - 0.412
3	0.666	0.057	0.589 - 0.852	0.574	0.039	0.491 - 0.651
5	0.922	0.061	0.843 - 1.124	0.928	0.039	0.842 - 1.019
6	0.614	0.023	0.566 - 0.659	0.585	0.032	0.507 - 0.648
7	0.648	0.031	0.586 - 0.710	0.618	0.027	0.562 - 0.657
8	0.505	0.019	0.474 - 0.565	0.492	0.027	0.447 - 0.560
9	0.577	0.033	0.499 - 0.667	0.572	0.028	0.512 - 0.643
10	0.836	0.172	0.542 - 1.131	0.765	0.141	0.489 - 1.007
11	1.096	0.288	0.670 - 1.735	1.140	0.285	0.610 - 1.625
12	1.225	0.348	0.457 - 1.869	1.248	0.325	0.566 - 1.819
13	0.561	0.081	0.406 - 0.706	0.564	0.114	0.381 - 0.775
14	0.161	0.011	0.137 - 0.181	0.161	0.014	0.135 - 0.197
15	0.125	0.008	0.113 - 0.148	0.119	0.008	0.106 - 0.134
16	0.294	0.030	0.229 - 0.366	0.278	0.049	0.211 - 0.381
17	0.183	0.007	0.168 - 0.201	0.169	0.006	0.158 - 0.185
18	0.225	0.013	0.204 - 0.255	0.219	0.011	0.198 - 0.245
19	0.127	0.014	0.084 - 0.172	0.118	0.010	0.095 - 0.139
20	0.146	0.013	0.107 - 0.172	0.115	0.010	0.095 - 0.138
21	0.103	0.011	0.080 - 0.123	0.117	0.016	0.085 - 0.144
22	0.170	0.017	0.139 - 0.208	0.167	0.028	0.103 - 0.210
23	0.161	0.014	0.110 - 0.183	0.163	0.025	0.103 - 0.199
24	0.178	0.017	0.145 - 0.213	0.159	0.024	0.103 - 0.199

TABLE A2. Tests for differences between groups in location of the ratio of each variable to carapace length. The Mann-Whitney U - statistic, its standard normal transformation (z) and the associated probability of a more extreme value of z are given.

VARIABLE NO.	U	z	P
1	1,624.5	7.27	0.000
2	1,050.5	1.95	0.051
3	1,566.0	-6.73	0.000
5	984.0	1.33	0.184
6	1,295.0	-4.22	0.000
7	1,285.5	-4.13	0.000
8	1,109.5	-2.49	0.013
9	934.5	-0.87	0.384
10	1,025.0	-1.71	0.087
11	920.0	0.74	0.459
12	879.5	0.36	0.719
13	850.0	-0.08	0.928
14	841.0	0.00	0.999
15	1,190.0	-3.24	0.002
16	1,082.0	-2.24	0.025
17	1,542.0	-6.51	0.000
18	1,043.5	-1.88	0.060
19	1,235.5	-3.66	0.000
20	1,610.0	-7.14	0.000
21	1,264.5	3.93	0.000
22	842.0	-0.01	0.992
23	940.5	0.93	0.352
24	1,216.0	-3.48	0.000

TABLE A3. Mean, standard deviation and range of each of 22 variables for 41 males each of *M. tolmerum* and *M.* sp. A.

	M. tolmerum			*M. sp.* A		
VARIABLE NO.	MEAN	SD	RANGE	MEAN	SD	RANGE
3	11.379	1.683	8.30 - 15.40	7.816	1.033	6.00 - 10.00
4	17.160	2.658	12.85 - 23.00	13.707	2.241	9.70 - 18.30
5	15.750	2.226	11.90 - 20.80	12.676	1.867	9.10 - 16.40
6	10.528	1.597	7.90 - 14.15	7.993	1.220	6.00 - 10.30
7	11.111	1.671	8.00 - 15.00	8.462	1.416	5.90 - 11.20
8	8.655	1.303	6.30 - 11.80	6.737	1.084	4.70 - 8.65
9	9.878	1.489	7.20 - 13.80	7.828	1.219	5.40 - 9.70
10	14.472	4.259	8.20 - 24.85	10.538	2.868	6.10 - 17.45
11	18.959	6.275	9.25 - 33.50	15.773	5.227	7.70 - 27.70
12	21.322	7.670	6.65 - 36.35	17.282	5.959	7.70 - 30.45
13	9.654	2.196	5.80 - 16.15	7.746	2.109	4.05 - 12.45
14	2.750	0.421	1.80 - 3.80	2.194	0.312	1.70 - 2.80
15	2.144	0.303	1.60 - 2.80	1.623	0.240	1.25 - 2.05
16	5.035	0.835	3.40 - 6.90	3.787	0.823	2.45 - 5.90
17	3.133	0.499	2.40 - 4.30	2.324	0.396	1.60 - 3.10
18	3.848	0.565	2.90 - 5.10	2.996	0.445	2.20 - 3.80
19	2.177	0.366	1.10 - 3.05	1.615	0.240	0.95 - 2.00
20	2.498	0.395	1.40 - 3.50	1.563	0.239	1.10 - 2.00
21	1.767	0.363	1.10 - 2.60	1.605	0.377	0.90 - 2.55
22	2.918	0.560	2.00 - 4.40	2.300	0.576	1.30 - 3.70
23	2.751	0.472	1.90 - 4.20	2.221	0.465	1.25 - 3.40
24	3.055	0.532	2.10 - 4.40	2.173	0.433	1.30 - 3.25

TABLE A4. Summary of stepwise discriminant analysis indicating the order of entry or removal of variables and their respective effects on separation of the groups as reflected by the change in Rao's V.

STEP NO.	VARIABLE ENTERED	VARIABLE REMOVED	CHANGE IN RAO'S V	SIGNIFICANCE OF CHANGE
1	20		175.46	0.000
2	4		75.59	0.000
3	3		98.27	0.000
4	5		213.65	0.000
5		4	-0.22	1.000
6	24		122.02	0.000
7	21		233.74	0.000
8	15		71.75	0.000
9	14		83.17	0.000
10	22		49.81	0.000
11	9		58.45	0.000
12	6		89.37	0.000
13	4		32.02	0.000
14	23		40.63	0.000
15	11		55.27	0.000
16		20	-15.88	1.000
17		22	-20.79	1.000
18	10		99.23	0.000
19	22		50.30	0.000
20	12		30.62	0.000
21	18		25.89	0.000
22	20		28.25	0.000

TABLE A5. Standardized and unstandardized coefficients, classification function coefficients, canonical correlation and classification efficiency of the discriminant function derived by stepwise analysis of the full set of variables.

	DISCRIMINANT FUNCTION		CLASSIFICATION FUNCTIONS	
VARIABLE	STANDARDIZED	UNSTANDARDIZED	GROUP 1	GROUP 2
3	-0.882	-3.764	-169.525	-320.631
4	0.415	2.112	1067.213	1152.000
5	0.601	3.311	1145.740	1278.691
6	-0.302	-1.474	504.393	445.232
9	0.208	1.070	-99.886	-56.934
10	-0.423	-1.321	-88.034	-141.058
11	0.275	0.793	152.866	184.704
12	0.110	0.287	25.305	36.822
14	0.284	1.537	168.918	230.627
15	-0.468	-2.329	-858.686	-952.188
18	-0.157	-0.811	-930.665	-963.227
20	-0.111	-0.390	-396.958	-412.604
21	0.278	1.224	-479.378	-430.217
22	0.268	1.044	-435.830	-393.900
23	0.120	0.539	1.647	23.278
24	-0.885	-3.435	485.822	347.901
Constant		-2.465	-2366.565	-2465.536

Canonical correlation	0.976	
% correct classification	original sample	100.00
	test sample	100.00

TABLE A6. Standardized coefficients, unstandardized coefficients (in brackets), canonical correlation and success of allocation by discriminant functions derived from subsets of the original set of variables.

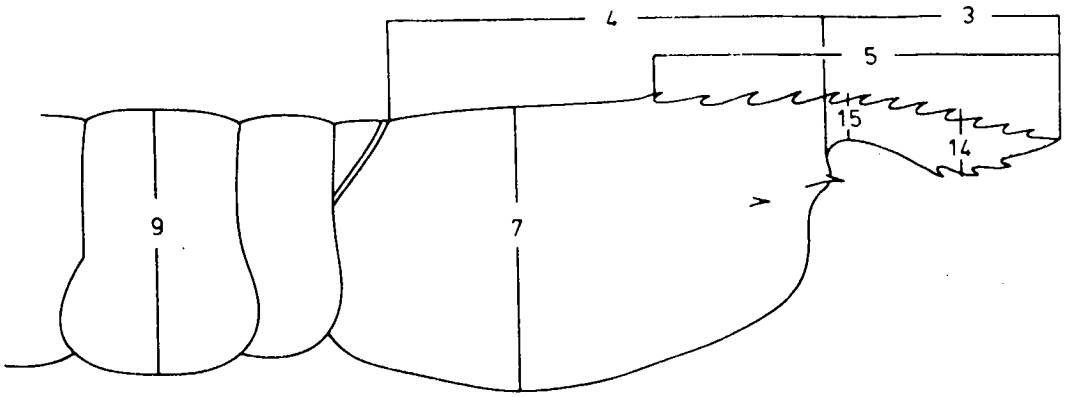
	DISCRIMINANT FUNCTION					
VARIABLE	1	2	3	4	5	6
20	1.477 (5.207)	0.859 (3.030)	0.531 (1.874)	-0.332 (-1.172)	-0.209 (-0.737)	-0.167 (-0.588)
4	-0.608 (-3.098)	-0.880 (-4.483)				
3		0.872 (3.723)	1.651 (7.050)	-1.742 (-7.435)	-1.180 (-5.033)	-1.093 (-4.666)
5			-1.372 (-7.561)	1.493 (8.232)	0.841 (4.636)	0.969 (5.340)
24				-0.262 (-1.018)	-0.679 (-2.637)	-0.678 (-2.631)
21					0.487 (2.151)	0.503 (2.218)
15						-0.270 (-1.342)
Constant	4.937	1.837	2.942	-3.373	0.888	-1.103
Canonical correlation	0.871	0.902	0.936	0.946	0.959	0.962
% correct classification						
original sample	96.34	97.56	98.78	98.78	100.00	100.00
test sample	90.00	100.00	100.00	100.00	100.00	100.00

TABLE A7. Classification function coefficients for each of the discriminant functions derived from subsets of the original set of variables.

VAR.	FUNCTION 1		FUNCTION 2		FUNCTION 3		FUNCTION 4		FUNCTION 5		FUNCTION 6	
	GP 1	GP 2	GP 1	GP 2	GP 1	GP 2	GP 1	GP 2	GP 1	GP 2	GP 1	GP 2
20	-192.290	-229.124	-225.597	-254.394	-203.218	-230.874	-187.693	-208.503	-214.153	-231.474	-181.030	-195.884
4	269.528	291.447	183.824	226.425								
3			146.610	111.231	-22.489	-126.536	-85.974	-218.016	-190.308	-308.592	-184.918	-302.801
5					337.125	448.723	415.551	561.734	697.829	806.788	1046.189	1181.090
24							-40.983	-59.055	291.927	229.954	231.624	165.162
21									-383.265	-332.724	-309.422	-253.383
15											-455.354	-489.262
Const.	-294.738	-329.667	-335.895	-353.358	-344.156	-387.576	-359.460	-419.354	-687.312	-666.441	-1002.873	-1030.750

Fig. A1. Measured dimensions.

VARIABLE NO.	DESCRIPTION
3	Rostrum length
4	Carapace length
5	Extent of dorsal rostral teeth
6	Carapace width at third pereiopod
7	Carapace depth at second pereiopod
8	Abdomen width mid second segment
9	Abdomen depth mid second segment
10	Merus length, larger second pereiopod
11	Carpus length, larger second pereiopod
12	Palm length, larger second pereiopod
13	Dactylus length, larger second pereiopod
14	Anterior rostrum depth
15	Posterior rostrum depth
16	Ventral carapace width
17	Telson width
18	Telson distance 1
19	Telson distance 2
20	Telson distance 3
21	Carpus proximal width, larger second pereiopod
22	Carpus distal width, larger second pereiopod
23	Propus proximal width, larger second pereiopod
24	Propus distal width, larger second pereiopod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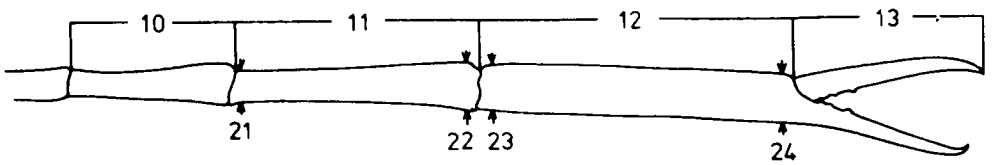
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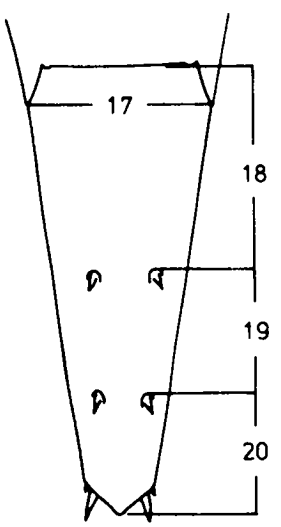
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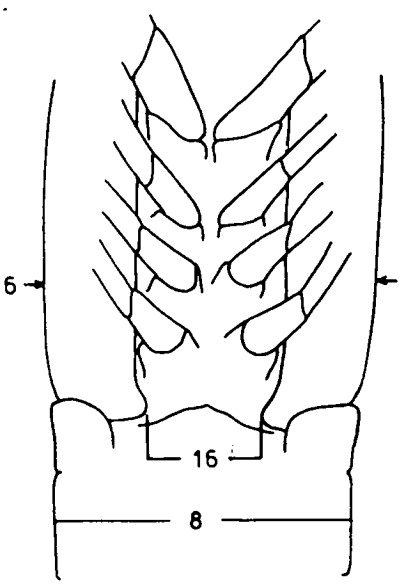
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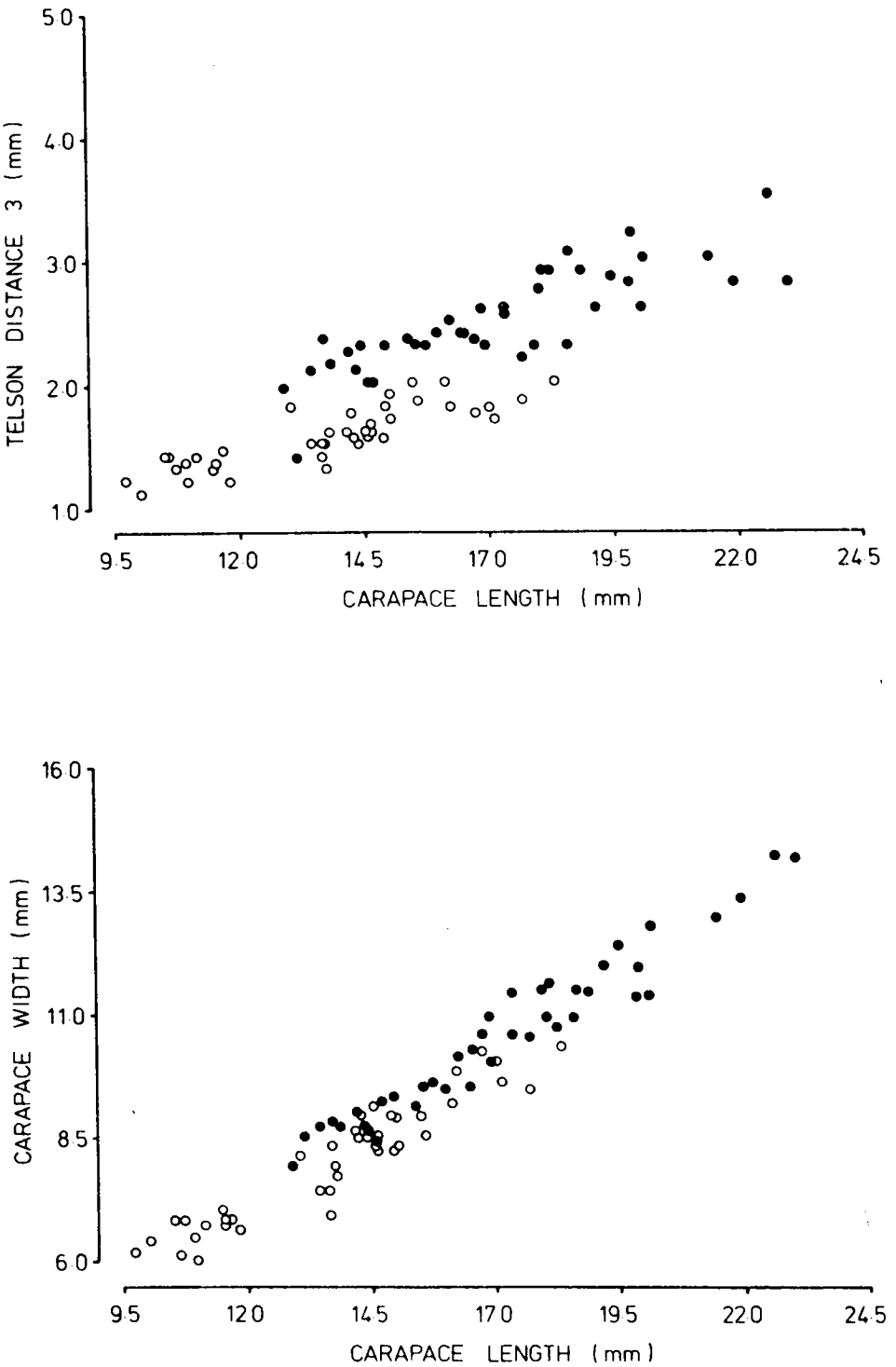

Fig. A2. Scatter diagrams of telson distance 3 and carapace width versus carapace length for samples of 41 males each of *M. tolmerum* (closed symbols) and *M.* sp. A (open symbols).

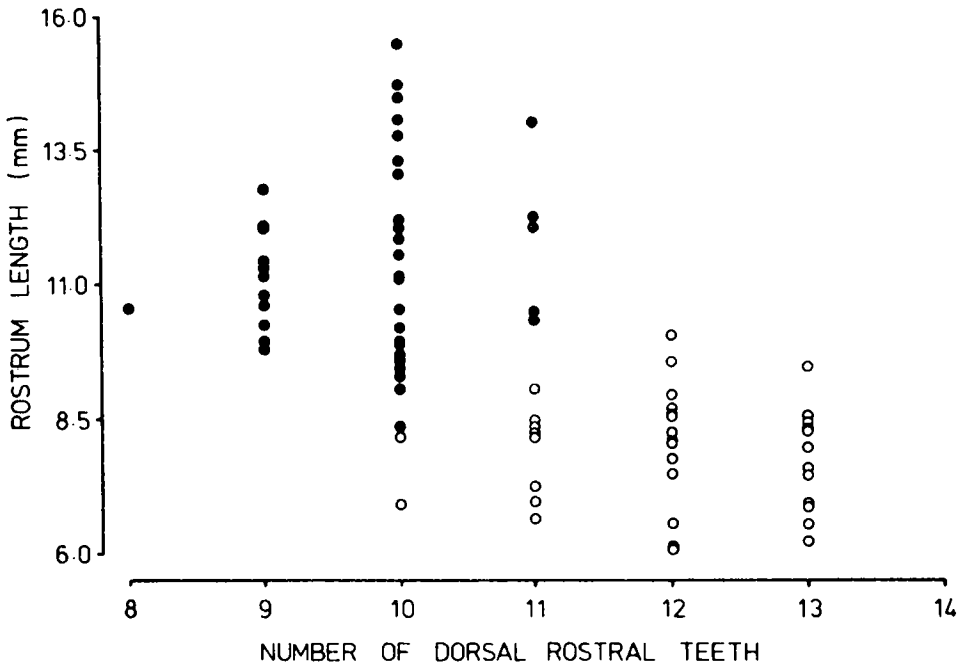

Fig. A3. Scatter diagram of rostrum length versus the number of dorsal rostral teeth for samples of 41 males each of *M. tolmerum* (closed symbols) and *M.* sp. A (open symbols).

APPENDIX B

TABULATION OF *MACROBRACHIUM* CATCH DATA BY SITE, MONTH, SPECIES AND REPRODUCTIVE CATEGORY.

AUGUST 1975

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile				1	2	3	5	3									14
	Male	11	27	16	4	17	24	15	21									135
	Female Non Ovig.	3	4	4		3	5	11	3		1							34
	Female Ovig.	2	15	11	2	14	8	14	21									87
M. tolmerum	Juvenile																	
	Male	21	3				1			1					1	1		28
	Female Non Ovig.	1								5								6
	Female Ovig.							1										1
M. sp. A	Juvenile																	
	Male																	
	Female Non Ovig.																	
	Female Ovig.																	
M. latidactylus	Juvenile										1				1			2
	Male											3				2		5
	Female Non Ovig.											2		1		1		4
	Female Ovig.										2							2
M. novae-hollandiae	Juvenile										4	1						5
	Male									1	8	2	10			3		24
	Female Non Ovig.										2		1		1			4
	Female Ovig.											2	1	1		2		6
	TOTAL	38	49	31	7	36	41	46	48	7	18	10	12	2	3	9		357

SEPTEMBER

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile		1			1												2
	Male		18	23	14	6	7	11	21									100
	Female Non Ovig.		10	2	5	5	4	8	5									39
	Female Ovig.		1	2	3	1	3	2	1									13
M. tolmerum	Juvenile	1								1								2
	Male	13	2							3								18
	Female Non Ovig.									2								2
	Female Ovig.	3																3
M. sp. A	Juvenile															4		4
	Male																	
	Female Non Ovig.																	
	Female Ovig.																	
M. latidactylus	Juvenile														2	2		4
	Male																	
	Female Non Ovig.														1			1
	Female Ovig.																	
M. novae-hollandiae	Juvenile									1								1
	Male									2	5	3	4		1	3		18
	Female Non Ovig.												1					1
	Female Ovig.											1				3		4
	TOTAL	17	32	27	22	13	14	21	27	9	5	4	5		4	12		212

OCTOBER

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile			2	1		1	3										7
	Male		28	21	19	16	16	15	12									127
	Female Non Ovig.		9	5	8	4	3	5	4									38
	Female Ovig.		7	7	8	2	1	4	1									30
M. tolmerum	Juvenile									1					1			2
	Male	7	1	1				3		3					2			17
	Female Non Ovig.									2								2
	Female Ovig.																	
M. sp. A	Juvenile	1																1
	Male	10													2			12
	Female Non Ovig.	1													1			2
	Female Ovig.																	
M. latidactylus	Juvenile																	
	Male																	
	Female Non Ovig.																	
	Female Ovig.																	
M. novae-hollandiae	Juvenile										1	1			1			3
	Male										4	6	2		1	5		18
	Female Non Ovig.											2	1			2		5
	Female Ovig.															2		2
	TOTAL	19	45	36	36	22	21	30	17	6	5	9	3		8	9		266

NOVEMBER

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile					1	5	1	3									10
	Male	2	22	14	14	15	16	13	21									117
	Female Non Ovig.		7	5	1	3	1	1	3									21
	Female Ovig.		7	12	3	3	5	7	12									49
M. tolmerum	Juvenile			1						3	1							5
	Male	4	2	1						5	1					1		14
	Female Non Ovig.									6	1	2						9
	Female Ovig.																	
M. sp. A	Juvenile														7	2		9
	Male	7							1			1			17	5		31
	Female Non Ovig.	2								1					1			4
	Female Ovig.																	
M. latidactylus	Juvenile									1		1						2
	Male									4	6	2			2	5		19
	Female Non Ovig.									2	4	7			4	2		19
	Female Ovig.									3		1						4
M. novae-hollandiae	Juvenile										2	2	3	5		1		13
	Male										13	6	1		3	4		27
	Female Non Ovig.										4	2	4	1		1		12
	Female Ovig.										1		1	1		1		4
	TOTAL	15	38	33	18	22	27	22	40	25	33	24	9	7	34	22		369

DECEMBER

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile				2	7	8	10	11									38
	Male	4	15	11	25	5	27	25	17									129
	Female Non Ovig.	1	3	7	7	7	9	18	17									69
	Female Ovig.	3		5	5	1	9	4	4									31
M. tolmerum	Juvenile																	
	Male	2	1							1								4
	Female Non Ovig.	3	1				1											5
	Female Ovig.																	
M. sp. A	Juvenile															1		1
	Male	3								1		1			2	2		9
	Female Non Ovig.																	
	Female Ovig.																	
M. latidactylus	Juvenile											1						1
	Male									1		6			2	3		12
	Female Non Ovig.											1				1		2
	Female Ovig.									1	1	3						5
M. novae-hollandiae	Juvenile									1	9	8	3	3	2	2		28
	Male									3	12	7	1	1	4	4		32
	Female Non Ovig.									1	5	4		1		1		12
	Female Ovig.										1							1
	TOTAL	16	20	23	39	20	54	57	49	9	28	31	4	5	10	14		379

JANUARY 1976

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile	10	4		3	11	11	12	11									62
	Male		9		21	20	18	10	9									87
	Female Non Ovig.		4		10	6	18	2	1									41
	Female Ovig.		3		5	9	12	5	2									36
M. tolmerum	Juvenile	6													3			9
	Male	2											1		3	2		8
	Female Non Ovig.	1											1		2		1	5
	Female Ovig.												1					1
M. sp. A	Juvenile		8												1	1		10
	Male	5	1													2		8
	Female Non Ovig.														1			1
	Female Ovig.																	
M. latidactylus	Juvenile													2			5	7
	Male												2	3			8	13
	Female Non Ovig.												4	1			3	8
	Female Ovig.												1	2			4	7
M. novae-hollandiae	Juvenile												1					1
	Male																	
	Female Non Ovig.																	
	Female Ovig.																	
	TOTAL	24	29		39	46	59	29	23				11	8	10	5	21	304

FEBRUARY

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile	1		1	3	5	3	2	3					1				19
	Male		10	1	10	3	7	2	3									36
	Female Non Ovig.				7	3	5	6	3									24
	Female Ovig.				3	1	2	3	2									11
M. tolmerum	Juvenile	43		1						9	1	3		9				66
	Male		1							8	1	1	1			1		13
	Female Non Ovig.									6	1	4	1	1				13
	Female Ovig.					1		1		6	1	4		1			1	15
M. sp. A	Juvenile			1														1
	Male	2		1							1	2			1			7
	Female Non Ovig.	1																1
	Female Ovig.									1								1
M. latidactylus	Juvenile																2	2
	Male										3		2	1			8	14
	Female Non Ovig.										1		2	1			1	5
	Female Ovig.												2				4	6
M. novae-hollandiae	Juvenile																1	1
	Male											1						1
	Female Non Ovig.													1				1
	Female Ovig.																	
	TOTAL	47	11	5	23	13	17	14	11	30	9	15	8	15	1	1	17	237

MARCH

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile		4		10	3	12	10	15									54
	Male		6		13	2	7	7	4									39
	Female Non Ovig.		9		7		2	6	3									27
	Female Ovig.		1		1		1	1	2									6
M. tolmerum	Juvenile	11	3			5	1	3	2	12	1	7		10			7	62
	Male	3	1	1		1				5			1					12
	Female Non Ovig.	1				1				9	2		1	1				15
	Female Ovig.																	
M. sp. A	Juvenile			1											2			3
	Male	2		1	1				1	1	3	1		1	3			14
	Female Non Ovig.																	
	Female Ovig.																	
M. latidactylus	Juvenile											1	7	3			5	16
	Male										3		7	10	1		12	33
	Female Non Ovig.										1		1	1			6	9
	Female Ovig.												1	5			6	12
M. novae-hollandiae	Juvenile												1					1
	Male												1	1				2
	Female Non Ovig.																1	1
	Female Ovig.																	
	TOTAL	17	24	3	32	12	23	27	27	27	10	9	20	32	6		37	306

APRIL

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile		1		11	3	8	2	1									26
	Male		5	1	5	13	30	20	17									91
	Female Non Ovig.	4	7		7	12	10	8	10									58
	Female Ovig.																	
M. tolmerum	Juvenile	1	2	2						1								6
	Male	3								5								8
	Female Non Ovig.	1		1						7	1		1		1	1		13
	Female Ovig.									2								2
M. sp. A	Juvenile			1														1
	Male		2	6						1					2	10		21
	Female Non Ovig.															1		1
	Female Ovig.																	
M. latidactylus	Juvenile										6	3	2	11	3	2	1	28
	Male										8	8	10	37	14	8	2	87
	Female Non Ovig.										8	3	5	10	3			29
	Female Ovig.									1	1	1	2	5		1		11
M. novae-hollandiae	Juvenile												2	1				3
	Male										2	1		5			1	9
	Female Non Ovig.							1						3			2	6
	Female Ovig.																	
	TOTAL	9	17	11	23	28	48	31	28	17	26	16	22	72	23	23	6	400

MAY

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile			1	5	8	6	1	9		1							31
	Male	1	4	1	22	8	11	22	19									88
	Female Non Ovig.	1	5	1	11	6	14	11	20									69
	Female Ovig.																	
M. tolmerum	Juvenile	4		1						4					1	1		11
	Male	2	2	2				1		9	2		1	2		2		23
	Female Non Ovig.	2	3							11					2			18
	Female Ovig.																	
M. sp. A	Juvenile														3			3
	Male	1		2								1			5	5		14
	Female Non Ovig.														1			1
	Female Ovig.																	
M. latidactylus	Juvenile										9	6	6	8	10	1		40
	Male									3	24	21	17	21	52	16	1	155
	Female Non Ovig.										11	7	13	13	16	6		66
	Female Ovig.										2	1	1		10	4		18
M. novae-hollandiae	Juvenile												2					2
	Male										1	1	4	9	2			17
	Female Non Ovig.													2		3		5
	Female Ovig.																	
	TOTAL	11	14	8	38	22	31	35	48	27	50	37	44	55	102	38	1	561

JUNE

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile		1				5											6
	Male	1	1	3	15	2	6	19	15									62
	Female Non Ovig.	6	1	2	6	5	1	9	18									48
	Female Ovig.				1	1		2	4									8
M. tolmerum	Juvenile	5								2								7
	Male	8	5	1						8	1							23
	Female Non Ovig.	1								4		1						6
	Female Ovig.																	
M. sp. A	Juvenile														1			1
	Male			1											1			2
	Female Non Ovig.																	
	Female Ovig.																	
M. latidactylus	Juvenile									3	16	1		1				21
	Male									3	21	21	2	21	19	5		92
	Female Non Ovig.										4	8	1	11	7	1		32
	Female Ovig.										1	1		2	6	4		14
M. novae-hollandiae	Juvenile									1			1	1				3
	Male										2	1	4	2	2	1		12
	Female Non Ovig.									2	2		1					5
	Female Ovig.																	
	TOTAL	21	8	7	22	8	12	30	37	23	47	33	9	38	36	11		342

JULY

SPECIES	REPRODUCTIVE CATEGORY	TOTAL 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile		3	1		1	3		1									9
	Male	2	12	1	3	1	4	24	16									63
	Female Non Ovig.	2	6	3	4	2	1	6	1									25
	Female Ovig.	2	3		3	5	2	10	26									51
M. tolmerum	Juvenile	2		1						4								7
	Male	13	4	4						15						1		37
	Female Non Ovig.	2								9								11
	Female Ovig.																	
M. sp. A	Juvenile	1		2														3
	Male	5																5
	Female Non Ovig.			1														1
	Female Ovig.																	
M. latidactylus	Juvenile									3	3	1						7
	Male									18	3	12	1		11	2		47
	Female Non Ovig.									1	1	5			3			10
	Female Ovig.									1	2	4			4			11
M. novae-hollandiae	Juvenile										1			4			1	6
	Male											1	1	6	1	3	1	13
	Female Non Ovig.												1	2				3
	Female Ovig.													2				2
	TOTAL	29	28	13	10	9	10	40	44	51	10	23	3	14	19	6	2	311

AUGUST

SPECIES	REPRODUCTIVE CATEGORY	SITE 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
M. australiense	Juvenile	2	6		5	3	3	2	1									22
	Male	3	15	10	3	1	1	11	11									55
	Female Non Ovig.	1	15	6	2	1	1	4	3									33
	Female Ovig.	1	3	1	3	3	2	5	4									22
M. tolmerum	Juvenile	18	3	5														26
	Male	8	3															11
	Female Non Ovig.		2															2
	Female Ovig.	3																3
M. sp. A	Juvenile	10	1	5														16
	Male	17	4	9														30
	Female Non Ovig.	2		1														3
	Female Ovig.																	
M. latidactylus	Juvenile																	
	Male														6	2		8
	Female Non Ovig.														1			1
	Female Ovig.															2		2
M. novae-hollandiae	Juvenile													1				1
	Male													5		2		7
	Female Non Ovig.																	
	Female Ovig.																	
	TOTAL	65	52	37	13	8	7	22	19					6	7	6		242