ASPECTS OF THE ECOLOGY OF THE SHRIMP PALAEMON PACIFICUS (STIMPSON) (DECAPODA, PALAEMONIDAE) IN THE BUSHMANS RIVER ESTUARY

by

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PART 3: TEMPERATURE AND SALINITY TOLERANCE OF P. PACIFICUS

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ABSTRACT

The recruitment of Palaemon pacificus to the Bushmans River estuary was studied over a 12 month period. The dynamics of a population of shrimps in a small, tidal channel in the lower reaches of the estuary was investigated over a similar time span. Temperature and salinity tolerances of various stages and sizes of shrimps were compared in controlled experiments and are discussed in the light of the distribution and general ecology of the shrimp.

Stage 6 zoeae and post-larvae entered the estuary on nocturnal flood tides throughout the year with peak recruitment occurring in March/April. The population of shrimps in the study site was predominantly juvenile for most of the year, with peak sub-adult numbers occurring in midsummer. The sex ratio was female-biased throughout the year except for short bursts of male predominance in February and April. Average growth rate was 0,043 mm carapace length per day. Maximum residence time in the study site was estimated to be four months and in the estuary at least six months. Flooding of the estuary resulted in a considerable reduction in juvenile numbers in the study site and some loss of sub-adults.

Shrimps tolerated a temperature range of 4,3 to 30,9°C for 144 hours. Their long term tolerance range is probably narrower (10 to 28°C) because of the effects of temperature related factors such as starvation and disease. Their distribution in South Africa (Olifants River to Kosi Bay) is consistent with this tolerance range.

Sub-adults tolerated salinities of 1 to 79 ^{o}/oo and post-larvae 2 to 60 ^{o}/oo at 15°C for 144 hours. Low moulting success (low and high salinities) and starvation (high salinities) would probably reduce these tolerance ranges to 2 to 56 ^{o}/oo (sub-adults) and 4 to 56 ^{o}/oo (post-larvae). Higher and lower temperatures (10 and 20°C) reduced the tolerance of post-larvae to low salinities, but sub-adults were only affected at 30°C. Stages 4 and 5 and stage 6 zoeae were intolerant of salinities below 14 ^{o}/oo. The development of salinity tolerance with age is consistent with the retention of a marine breeding phase. It also explains the high loss of juveniles from the study site following the flood. It is postulated that recovery of the population after a flood would be fairly rapid except in extreme cases when estuarine vegetation is severely affected.

NOMENCLATURE

There is apparently considerable confusion surrounding the use of the terms 'prawn' and 'shrimp'. In the present work, no clear cut distinction has been made, although there has been a tendancy to use 'shrimp' for the smaller species and 'prawn' for the larger ones. The term 'shrimp' has been used for *Palaemon pacificus*.

Generic and specific names of many of the natant decapods have undergone several changes which has also led to considerable confusion. Nomenclature in the present work follows that of Holthuis (1980). Where reference is made to a paper in which an old name is used, the old name is given with the current name in brackets on the first occasion on which it is mentioned. Thereafter the current name is used.

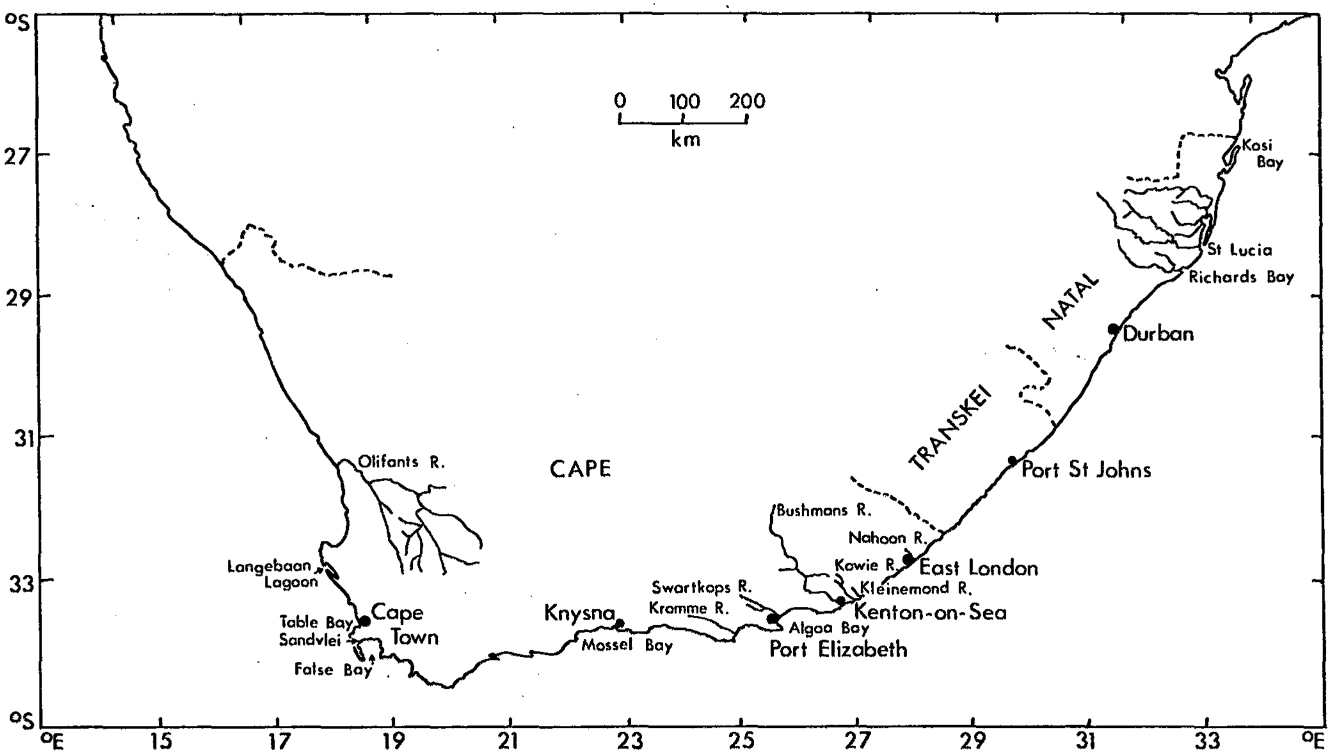

Figure 1. Map of South Africa showing places referred to in text.

PART 1

INTRODUCTION

Although some research has in the past been directed towards studies of South African penaeid prawns (Joubert and Davies, 1966; Champion, 1970, 1976), caridean prawns or shrimps have received little attention until recently. Of the marine species found in South Africa, *Palaemon pacificus* (Stimpson) is probably the most abundant and certainly the most widespread. It occurs in coastal waters and estuaries from the Olifants River on the west coast to Kosi Bay on the east coast (Day, 1981a)(Figure 1).

Although these shrimps are too small to be of commercial value (maximum total length ± 64mm - Emmerson, in press b), they are a major component of the faunal community associated with *Zostera* beds in estuaries (Hanekom, 1982). They form an important link in the food chain between the phytoplankton, detritus and associated bacteria on which they feed, and the fish species which prey on them (Emmerson and Baird, 1982; Day *et al*, 1954; Millard & Harrison, 1954).

Emmerson (1983) suggests that the life history of *P. pacificus* involves both an offshore and an inshore phase. Spawning and larval development are thought to take place offshore after which young shrimps migrate into the more sheltered and highly productive waters of estuaries and tidal pools which they use as nursery areas. This life cycle is typical of most species of penaeid prawns (Kutkuhn, 1966; Allen, 1966) as well as several species of caridean prawns e.g. Crago (=Crangon) franciscorum and C. nigricauda (Israel, 1936) and Leander (=Palaemon) serratus (Forster, 1951).

The aim of the first part of this study was to investigate the estuarine phase in the life history of Palaemon pacificus with emphasis on patterns of immigration and subsequent growth within the estuary. Two 24 hour sampling programmes conducted by Emmerson (1983) in the mouth of the Swartkops River estuary (Figure 1), revealed a net movement of young P. pacificus into the estuary on flood tides. A regular sampling programme was therefore initiated near the mouth of the Bushmans River estuary (Figure 1) to establish, if possible, a seasonal pattern of migration of young shrimps into the estuary. A population of shrimps in a selected site in the Bushmans River estuary was also studied over a 12 month period and changes in the structure of the population related to recruitment, growth and loss due to mortality and/or migration.

The extensive coastwise distribution of P. pacificus and the success with which it has invaded estuaries, indicate a wide range of temperature and salinity tolerance. The retention of an offshore breeding phase suggests, however, that the earlier stages are less well adapted to cope with the extreme and fluctuating conditions typical of estuaries. The second part of this study is a comparison of the temperature and salinity requirements of post-larval and sub-adult shrimps to determine whether the tolerance limits of these shrimps increases with age. Tolerance to low salinities of stages 4, 5 and 6 zoeae was also briefly investigated. Heavy rains towards the end of the study period created a natural experiment to determine the effect of flooding on the shrimp population, thus enabling predictions made in the laboratory to be tested under natural conditions.

The results of both the field and laboratory studies are discussed in the light of our present knowledge of the life history and distribution of P. pacificus.

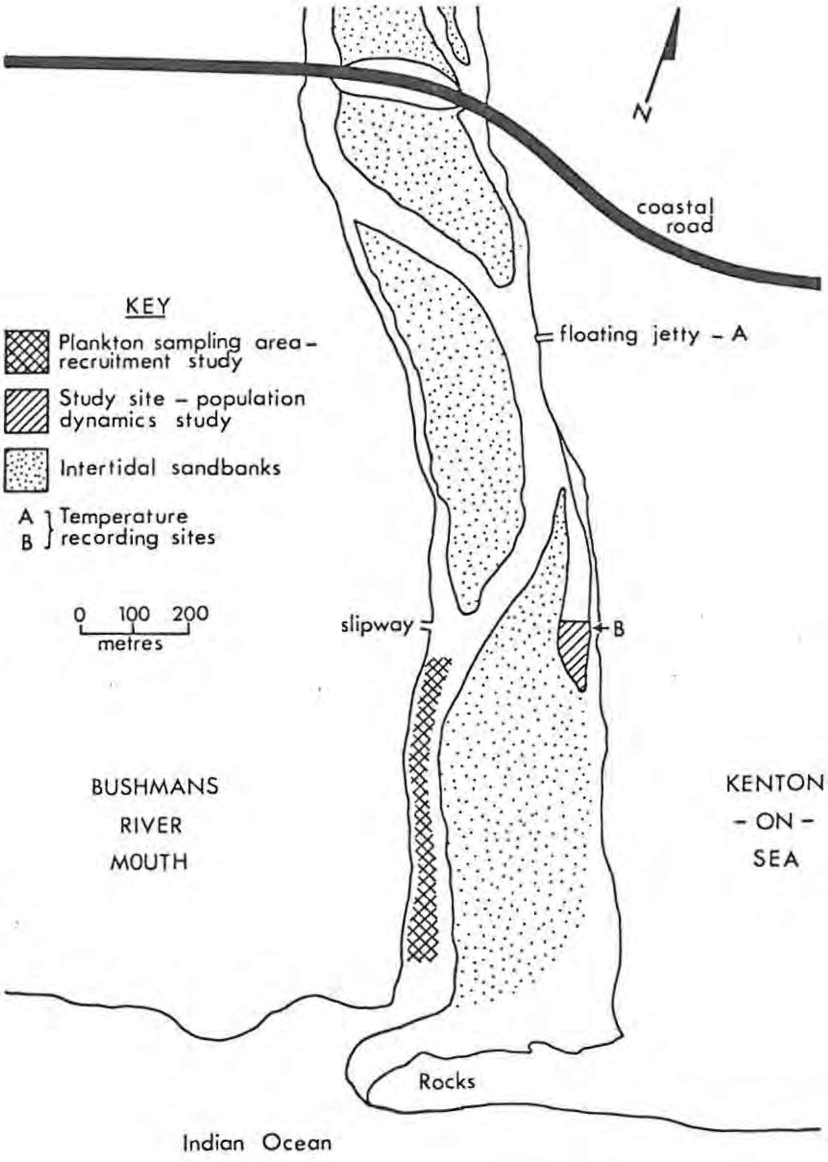

Figure 2. Lower reaches of Bushmans River estuary at low tide showing sampling area and temperature recording sites.

PART 2

THE ESTUARINE PHASE IN THE LIFE CYCLE OF *P. PACIFICUS*.

2.1 DESCRIPTION OF ESTUARY AND STUDY SITE

The Bushmans River estuary opens into the Indian Ocean between the villages of Kenton-on-Sea and Bushmans River Mouth at $33^{o}42'$S and $26^{o}40'$E (Figure 1). The mouth of the estuary is constricted by a rocky outcrop on the east bank and a sand spit on the west bank (Figure 2). In the lower reaches of the estuary the channel meanders between intertidal sandbanks, the edges of which support fairly extensive meadows of *Zostera capensis* Setchell. *Spartina maritima* (Curtis) grows on the more exposed areas.

The estuary extends as far as 40 km inland during the dry months and has a catchment area of 2718 km^2 (Bushmans-Kariega Trust, 1975). The only major impoundment affecting the river is formed by the New Years River Dam situated on the New Years River tributary which joins the Bushmans River some 130 km from the mouth. The river is thus subjected to frequent flooding which results in extensive mud deposition on the intertidal sandbanks.

The migration of young shrimps into the estuary was monitored in the main channel between the mouth and the slipway on the west bank (Figure 2). The seaward end of a small channel along the east bank approximately 0,8 km from the river mouth (Figure 2) was the site chosen for the investigation of the dynamics of an estuarine

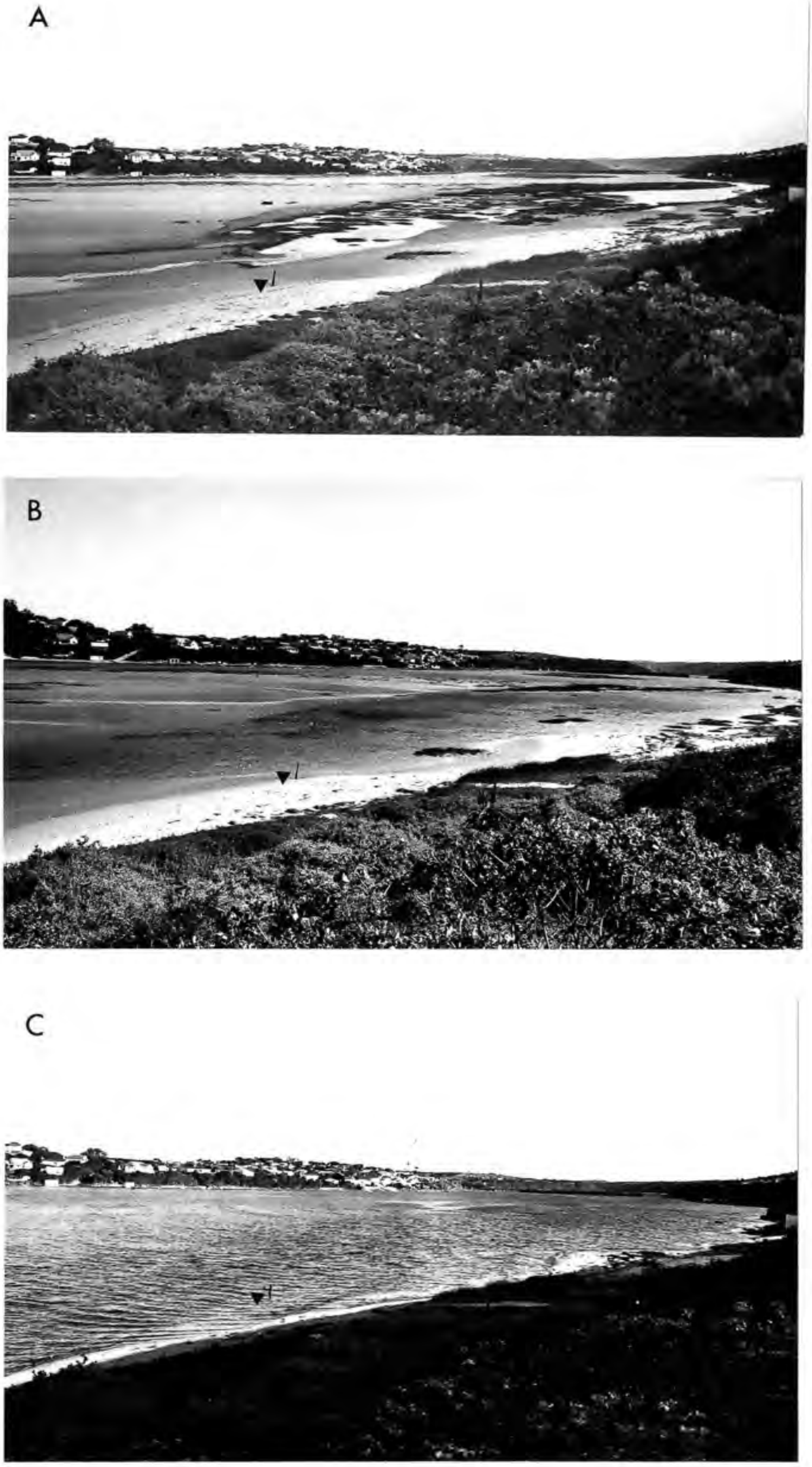

Figure 3. Study site on Bushmans River estuary, photographed from east bank, looking upstream towards coastal road bridge. Arrow indicates reference pole. A) Low tide (springs and neaps) B) Mid-tide, when sampling was done C) High tide (springs).

population of shrimps. Zostera capensis covers most of this area (hereafter referred to as the study site) although the length and density of the grass varies considerably.

At low tide of springs and neaps, the study site is separated from the main channel of the estuary by a large sandbank, the only connection between the two being through a narrow opening at the upstream end of the small channel (Figure 2). The study site then consists of a series of interconnected pools (maximum depth ± 200 mm) and much of the Zostera is exposed (Figure 3A). At high tide of springs, the area is completely flooded (Figure 3C). During neap tides, the sandbank may remain exposed throughout a tidal cycle and changes in water depth in the study site are then very slight.

2.2. MATERIALS AND METHODS

a. Temperature and salinity measurements

Temperature was measured in the field with a mercury in glass thermometer and salinity with an optical refractometer (American Optics Corporation). If salinities were low ($< 1{,}0\ ^{o}/oo$) or the water muddy, samples were returned to the laboratory and chlorinity determined on a chloride titrator (Radiometer, Copenhagen). Chlorinity was converted to salinity using the expression

$$S\ ^{o}/oo = 0{,}03 + 1{,}805\ Cl^{-}\ ^{o}/oo \qquad \text{(Harvey, 1955)}$$

Water samples below the surface were collected using a Frascati bottle.

Temperature and salinity of surface and bottom water were measured at stations along the length of the navigable portion (± 30 km) of the Bushmans River estuary on four occasions during a 12 month period. Severe drought conditions which existed in the eastern Cape were partially broken by five days of heavy rain from 24 to 28 July 1983. During this time the Bushmans River came down in flood. Two of the surveys (10.7.82 and 12.4.83) were conducted before, and a third (13.8.83) about two weeks after, the flood. A fourth, less detailed survey was conducted on 27.8.83 to monitor further recovery of the estuary after the flood.

Weekly maximum and minimum water temperatures were measured in the lower reaches of the estuary from November 1982 to November 1983 with a maximum and minimum thermometer attached to a floating jetty on the east bank (A in Figure 2). The thermometer was suspended about 20 cm below the surface of the water in the shade of the jetty. Minimum water depth at that point was about 0,7m.

An early attempt to obtain continuous records of temperature in the study site itself failed when the equipment was tampered with and irreparably damaged. Water temperatures were, however, recorded on each sampling trip, and, from February to October 1983, early morning (06h00 to 07h30) and late afternoon (17h30 to 18h30) temperatures were recorded daily in the study site (B in Figure 2) by a local resident.

Since temperature data during the early part of the field study were scanty, temperature records at both sites were continued after sampling had stopped to give some idea of conditions in the estuary during winter and spring.

b. Distribution of *P. pacificus* in estuary

In addition to the physical data collected during the survey of the Bushmans River estuary on 10.7.82, the distribution of *P. pacificus* along the length of the estuary was also investigated.

Three nets were used for sampling. A long handled scoop net (diameter 30 mm; mesh size 0,280 mm) was used to sample amongst the reeds. A square framed net (mouth 370 X 180 mm; mesh size 1,3 mm) and a D net (base length 450 mm; maximum height 250 mm; mesh size 0,475 mm), both mounted on aluminium skids and fitted with tickler chains, were used for hauling along the bottom. The D net was more suitable in muddy areas as the mouth of the net was raised slightly off the bottom, thus preventing it from digging into the mud.

No attempt was made to quantify the sampling during this survey, the main objective being to determine whether or not shrimps were present at each station and, if so, their size distribution.

Shrimps collected at each station were counted and carapace length measured with the aid of a dissecting microscope fitted with a micrometer eyepiece. The definition of carapace length followed that of Hart (1981) and was taken as the distance, laterally, between the anterior margin of the carapace behind the insertion of the eyestalk, and the most posterior margin.

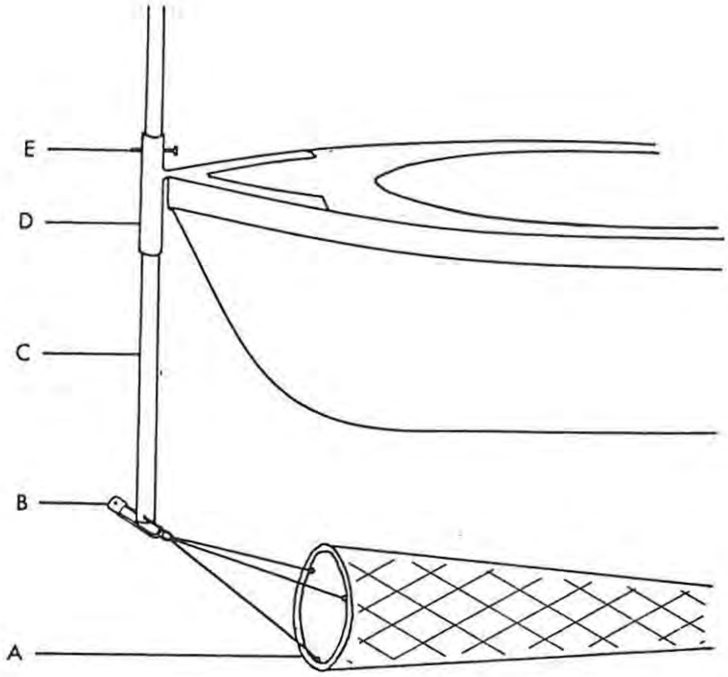

Figure 4. Apparatus used for plankton hauls. The plankton net (A) is connected by means of a bicycle lock (B) to the end of a galvanized iron rod (C) attached to the boat by means of a metal sleeve (D). The net is lowered to the required depth and the rod held in position by a retaining pin (E).

c. Monitoring of shrimp recruitment into estuary

Young & Carpenter (1977) found that recruitment of *Penaeus plebejus* post-larvae to nursery areas in Moreton Bay, Queensland, occurred predominantly at night on an incoming tide. A similar trend was found for *P. pacificus* moving into the Swartkops River estuary (Emmerson, 1983). Sampling in the present programme was therefore restricted to nocturnal flood tides. Nights on which high tide occurred between 22h00 and 24h00 were selected as this ensured at least four hours of sampling under the required conditions. These conditions were always met at neap tides.

The sampling apparatus (Figure 4) was the same as that used by Read (1982) for collecting *Macrobrachium petersi* larvae. A plankton net (A) (diameter 300 mm; mesh size 0,475 mm) was attached to the end of a galvanized iron rod (B) which was free to slide within a metal sleeve (D) mounted on the bow of a 3m glass fibre dinghy. The dinghy was powered by a 3,5 h.p. outboard motor. The net could be set at the required depth within the water column by lowering or raising the rod within the metal sleeve.

A plankton haul consisted of a 2,5 minute trawl against the current followed immediately by a 2,5 minute trawl with the current with the net sampling 0,5 m below the surface of the water. An estimated 30 kℓ of water was filtered during each haul. (For details of calculation, see Appendix A.)

On each sampling trip, two five minute hauls were carried out every

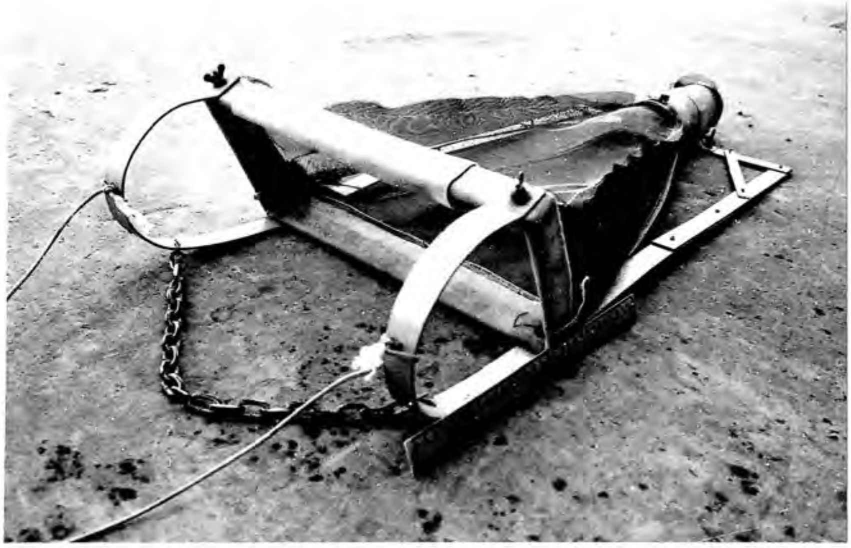

Figure 5. Net used for sampling in study site. Dimensions are: net opening 370 x 180 mm; mesh size 1,3 mm; net length 570 mm; diameter of cod end 80 mm.

hour, beginning at dusk and continuing until about one hour after the predicted high tide for that stretch of coast. This coincided approximately with slack water in the estuary.

Samples were either returned to the laboratory immediately and frozen, or, if return to the laboratory was delayed, they were preserved with formalin. All P. pacificus were removed from the sample, the stages identified and carapace length of each shrimp measured.

d. Sampling of shrimp population in study site

The net (Figure 5) used for sampling in the study site was mounted on an aluminium frame to allow smooth passage through the Zostera. The tickler chain activated shrimps sitting on the bottom and the downward tilt of the net opening minimized escape over the top of the net. To empty the net, the circle of gauze clamped over the distal opening of the cod end was removed and the contents washed into a basin.

A 70m length of graduated rope was attached to the net so that it could be drawn across a transect without the operator disturbing the section being sampled. The area sampled by the net during each transect was recorded.

To avoid errors due to concentration or dilution of the population, sampling was always done when the water in the study site reached a set depth during the ebb tide (Figure 3B). The ebb tide was chosen since water levels changed more gradually than during flood tides. Tides found to be most suitable for sampling were between two and five days after the full or new moon when the required water depth was reached between 08h30 and 10h30 (approximately three hours after high water).

On each sampling day (every ± 14 days) two randomly chosen transects were sampled. The contents of the net were preserved with formalin (final concentration ± 4 %) and returned to the laboratory for sorting. Shrimps from both transects were counted, combined and the number of shrimps per 40 m^2 (mean area sampled per trip) calculated. A random subsample of ± 300 shrimps was then taken using a Y-shaped plankton splitter. The carapace length (CL) of each shrimp in the subsample was measured and grouped into 0,5 mm size classes e.g. shrimps of CL 1,5 to 1,9 mm formed the first size class with median CL 1,7 mm. The following developmental stages were also recognized:

Stage 6 zoeae - last larval stage - identified after description of Han & Hong (1978)
Post-larvae - CL $< 2,5$ mm but not stage 6 zoeae (size classes 1 and 2)
Juveniles - CL $\geq 2,5$ mm but $< 4,0$ mm; sex distinction not possible (size classes 3 to 5)
Subadults - CL $\geq 4,0$ mm (size classes 6 and upwards)
    Males - *appendix masculina* on second pleopod
    Females - no *appendix masculina*

There is no clear morphological difference between post-larvae and juveniles. The above distinction was made for convenience and based purely on size differences. Since no berried females were found in

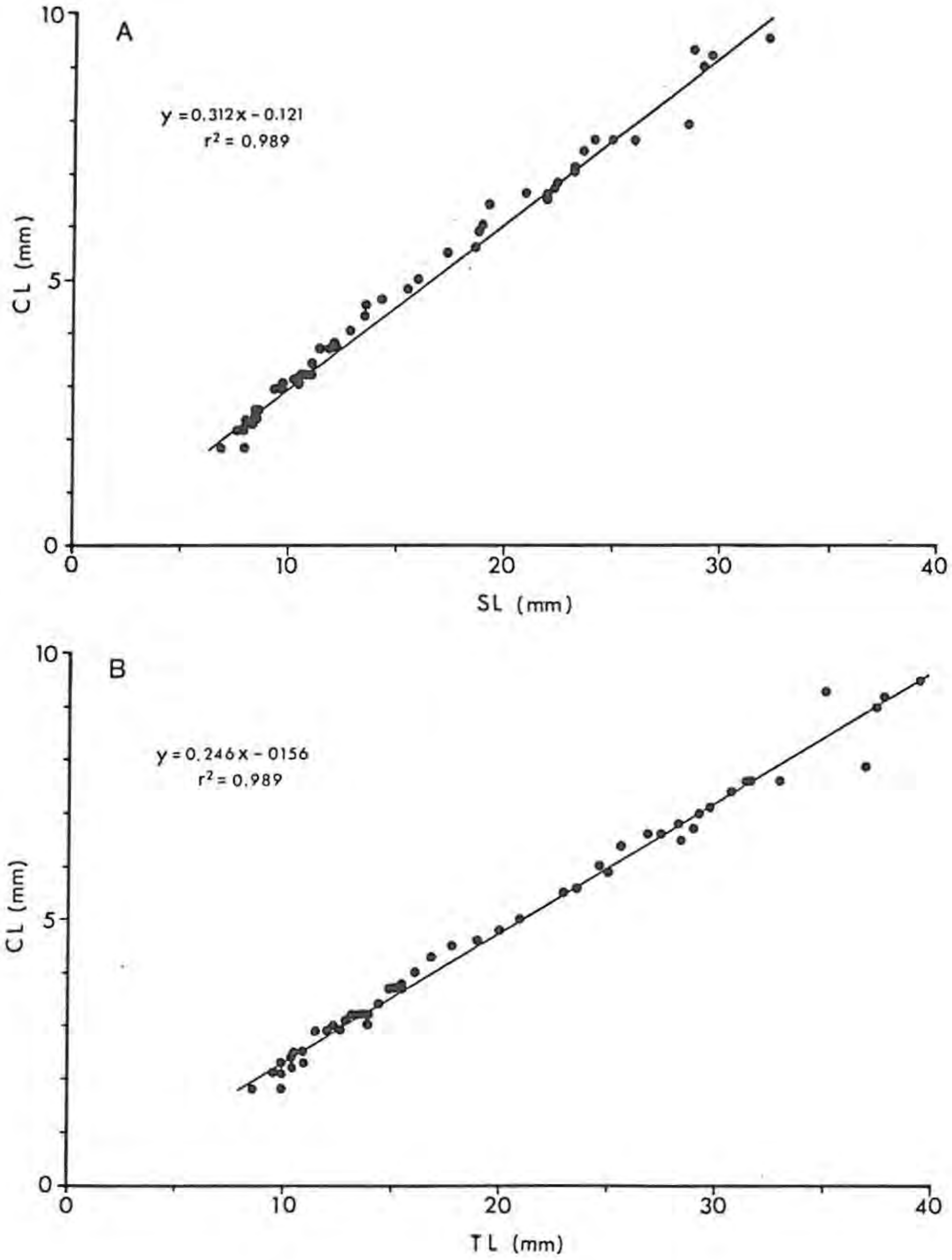

Figure 6. Relationship between A) standard length (SL) and carapace length (CL) and B) total length (TL) and carapace length of *P. pacificus*.

the estuary and no attempt was made to determine whether or not shrimps were sexually mature, all shrimps of distinguishable sex were termed sub-adults. The distinction between juveniles and sub-adults was made at 4,0 mm CL because this was the smallest size at which males could be positively identified.

e. Conversion of measurements

In the present study, carapace length was used to express shrimp size. Cook & Achituv (in press) used standard length (SL = distance from base of eyestalk to tip of telson) and Emmerson (in press a and b) used total length (TL = distance from tip of rostrum to tip of telson) in their measurements of *P. pacificus*. To enable comparisons to be made, the relationship between each of these measurements and carapace length was established.

Carapace length, standard length and total length were determined on 54 shrimps covering the size range found in the study site. Carapace length was measured as described above (page 7). Vernier calipers were used to determine standard and total lengths.

The relationships between carapace length and standard length and carapace length and total length were both found to be linear in the size range 1,8 to 9,5 mm CL (Figure 6A and B). The data used to establish these relationships are tabulated in Appendix B. The equations of the fitted regression lines were:

$$CL = 0{,}312\ SL - 0{,}121 \qquad (r^2 = 0{,}989)$$

$$CL = 0{,}246\ TL - 0{,}156 \qquad (r^2 = 0{,}989)$$

11a

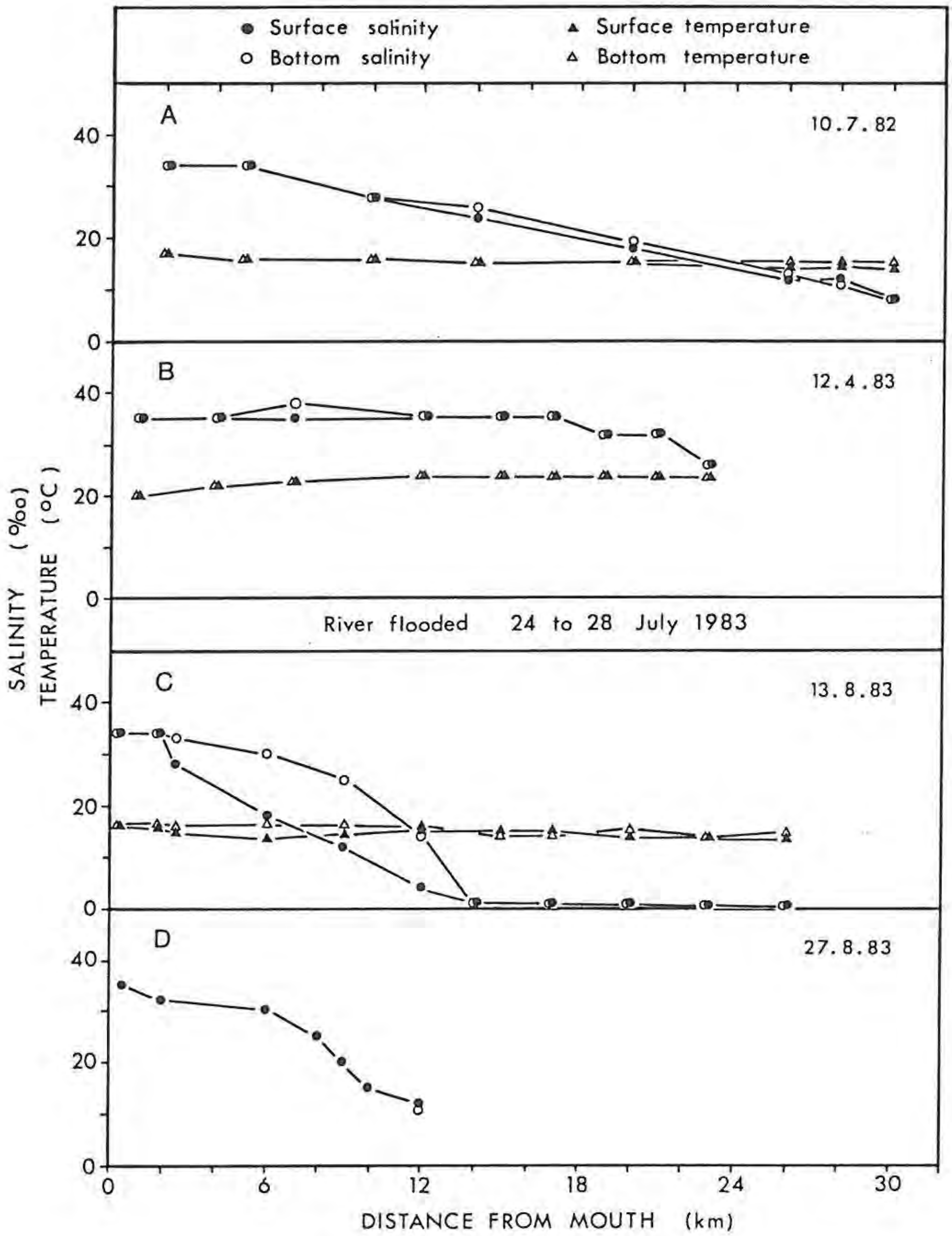

Figure 7. Water temperatures and salinities recorded during four surveys of the Bushmans River estuary, A and B before, and C and D after July 1983 flood. Surveys conducted on following tides:

A : High tide to high tide (between springs and neaps)
B : High tide (springs)
C : Ebb tide (neaps)
D : low tide (between springs and neaps)

2.3. RESULTS

a. Temperature and salinity records

Temperature and salinity recorded during four surveys of the Bushmans River estuary are shown in Figure 7. Surface and bottom temperatures were almost identical except on 13.8.83 (Figure 7C) when very slight differences were apparent. The moderating influence of the sea is evident from the slightly higher (Figure 7A) and lower (Figure 7B) temperatures at the mouth compared with the rest of the estuary in winter and summer respectively. Apart from this, temperature varied very little with distance from the mouth. Winter temperatures ranged from 13,5 to 17°C and summer temperatures from 20 to 24°C.

Predictably, rainfall had a marked influence on the salinity regime within the estuary. Salinities in the middle and upper reaches of the estuary rose considerably between July 1982 and April 1983 (Figure 7A and B), a period of low rainfall. In April 1983, salinities of 32 $^{o}/oo$ were recorded as far as 21 km from the mouth. Salinity differences within the water column were very slight (Figure 7B).

During this period of low rainfall, surface salinities measured at the slipway (Figure 2) every ± 14 days were never below 34 $^{o}/oo$, even at low tide. Two days after the heavy rains in July 1983, however, surface water at the slipway was completely fresh (S = 0,35 $^{o}/oo$) on the outgoing tide. Four days later, surface and bottom salinities were measured in the channel opposite the slipway on an incoming tide (Figure 8). At low tide, surface and bottom salinities were both low

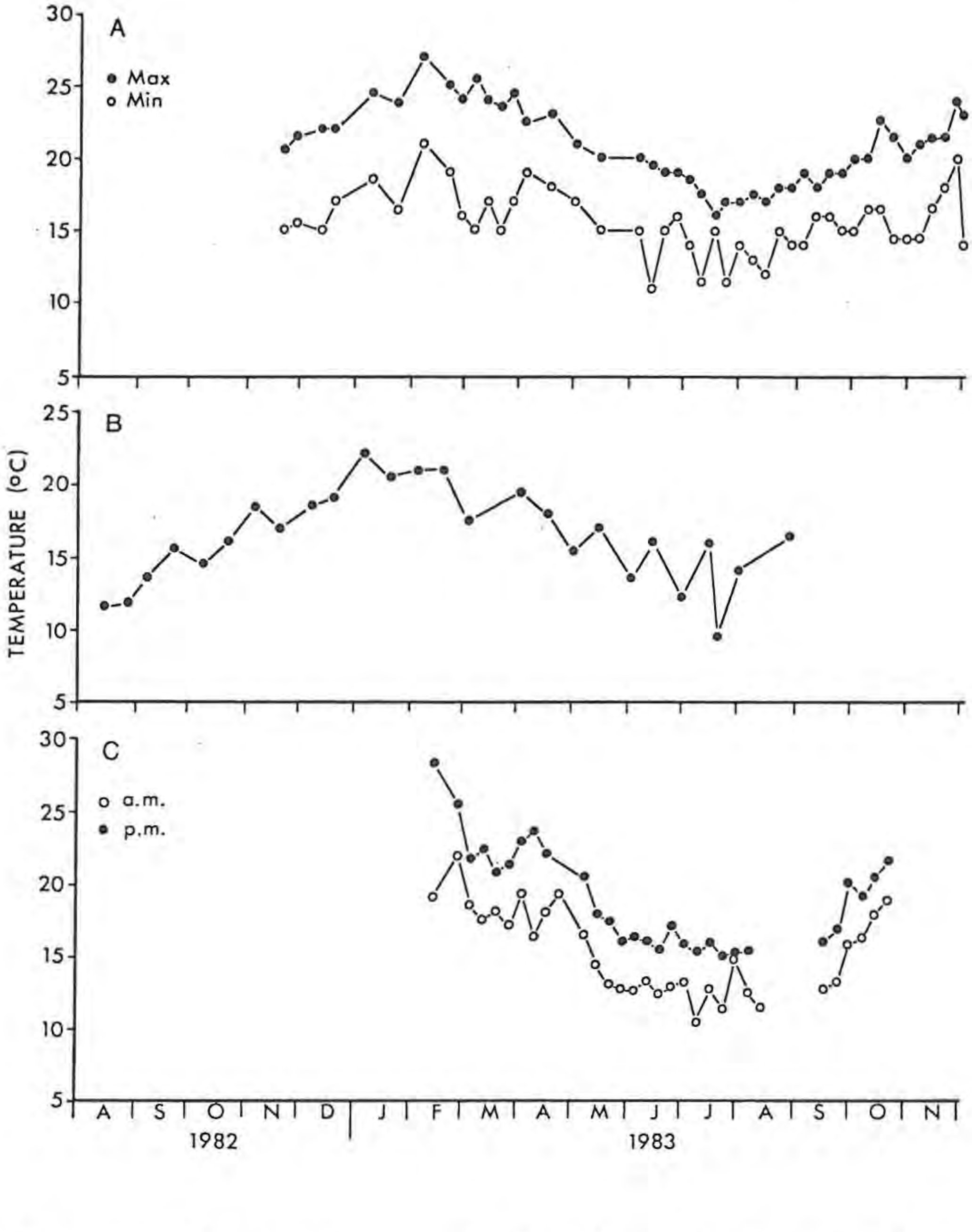

Figure 9. Temperature records from lower reaches of Bushmans River estuary.

A : Maximum and minimum temperatures at jetty (A in Figure 2). Temperatures recorded every 1 to 2 weeks.

B : Temperature of water in study site at 08h30 on each sampling day (mid-tide, 2 to 5 days after springs).

C : Weekly means of early morning (06h00 to 07h30) and late afternoon (17h30 to 18h30) temperatures recorded in study site (B in Figure 2) daily.

(< 20 ^{o}/oo) but layering was evident. At high tide the entire water column was full strength sea water. Water depth was between three and four metres.

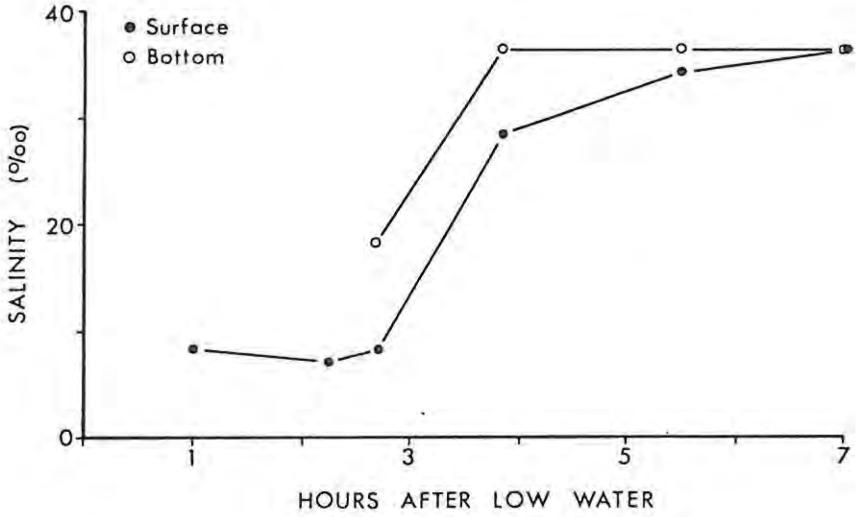

Figure 8. Salinity changes in main channel of Bushmans River estuary about 0,8 km from mouth, during incoming tide on 3.8.83. River flooded between 24 and 28.7.83.

About two weeks after the flood (13.8.83) salinities in the middle and upper reaches of the estuary (⩾14 km from the mouth) were low (< 1 ^{o}/oo) and a salinity gradient was evident as far as 12 km from the mouth (Figure 7C). After a further two weeks (Figure 7D) the estuary showed signs of recovery with salinities of surface water being considerably higher.

Weekly maximum and minimum temperatures recorded in the lower reaches of the Bushmans River estuary (A in Figure 2) over a 12 month period, are shown in Figure 9A. Highest temperatures were recorded during January and February and lowest temperatures during July and August.

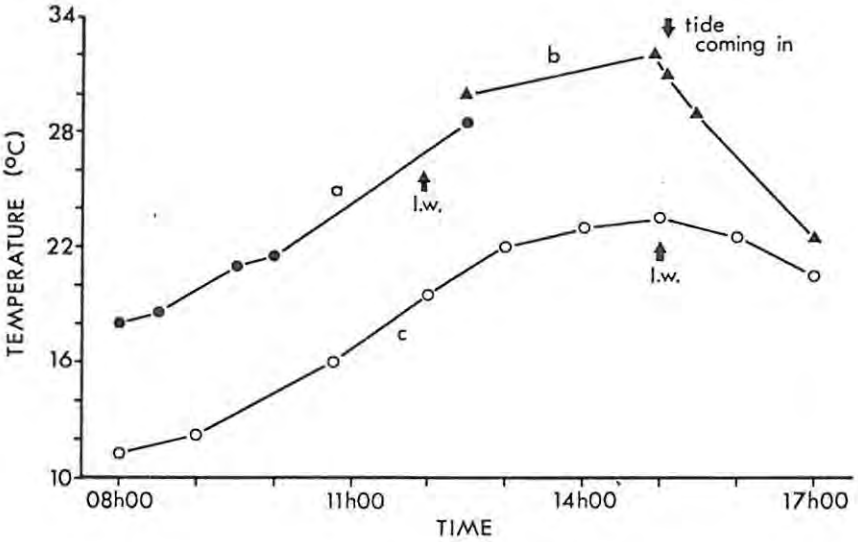

Figure 10. Temperature changes in study site on selected days (l.w. = low water).
a) 5.11.82 : outgoing tide, 4 days after springs
b) 16.3.83 : incoming tide, 2 days after springs
c) 26.8.82 : outgoing tide, neaps

Both maximum and minimum temperatures dropped suddenly during April and May.

Temperatures recorded in the study site at 08h30 every ± 14 days throughout the study period are plotted in Figure 9B, and Figure 9C shows weekly means of early morning and late afternoon temperatures recorded over a period of nine months. The sudden drop in temperature during April and May is very obvious in Figure 9C.

Because of the tidal nature of the study site and its shallowness at low tide, considerable fluctuations in temperature occurred over short periods of time. Figure 10 shows changes in temperature recorded in the study site on representative days in winter and early and late summer.

Temperatures in summer may rise rapidly as the tide recedes (Figure 10a) and high temperatures (28 to 30°C) may persist for several hours (Figure 10b). The incoming tide is accompanied by a sudden drop in temperature (Figure 10b). In winter, the water may also warm by 10 to 12°C during the day on an outgoing tide (Figure 10c) and temperatures of 20°C and higher are not uncommon. At night the water temperature may drop as low as 8,0°C at low tide.

b. Distribution of *P. pacificus* in estuary

The size frequency distribution of shrimps collected during a survey of the Bushmans River estuary on 10.7.82 is shown in Figure 11. Temperature and salinity data recorded during this survey have already

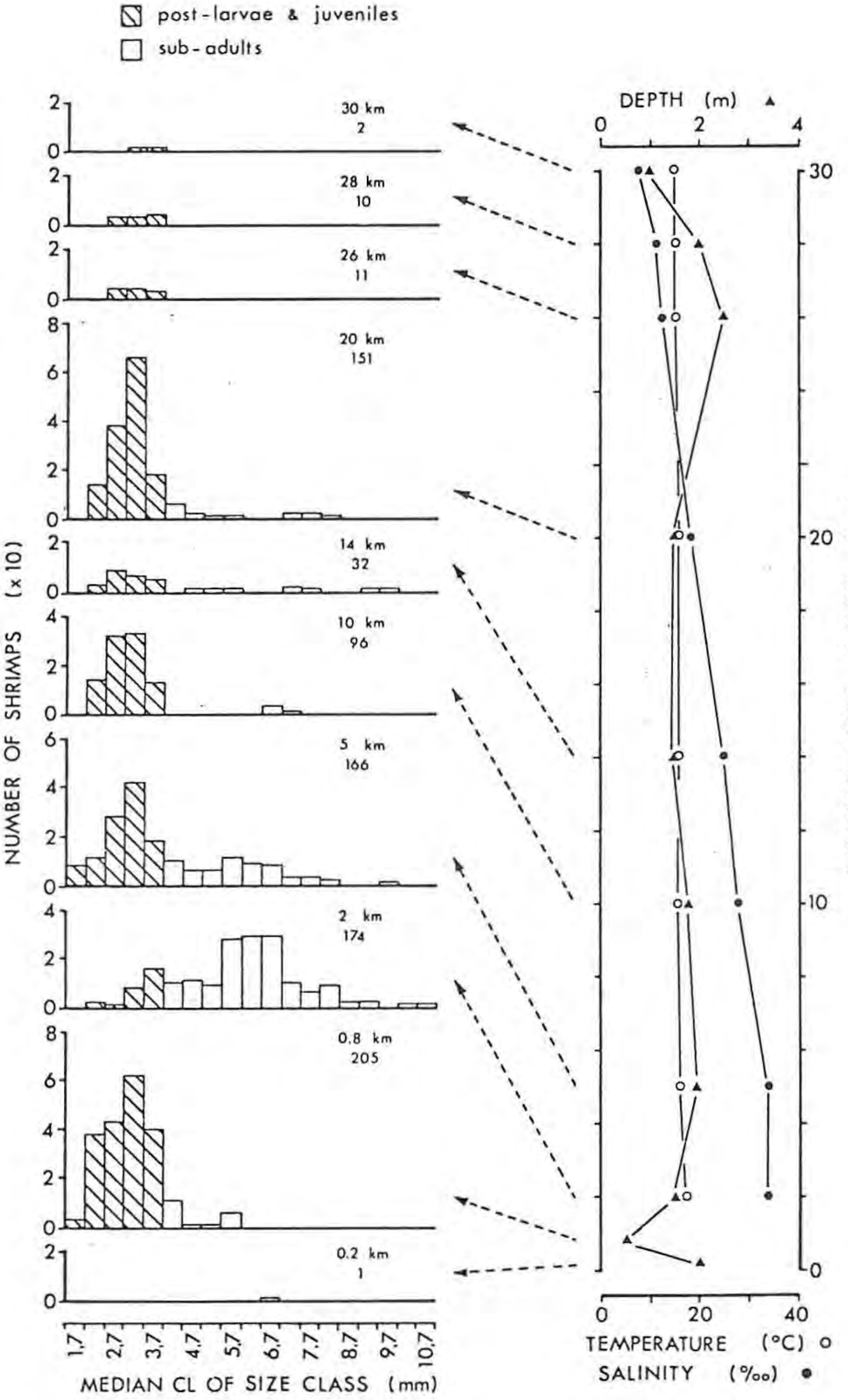

Figure 11. A) Size frequency distribution of P. pacificus in Bushmans River estuary on 10.7.82. Distance from mouth and number of shrimps collected at each station is shown. Size classes not labelled on X-axis are 2,2 mm, 3,2 mm, 4,2 mm etc..
B) Water temperature, salinity and depth at each station during survey.

been discussed under Figure 7A, but are reproduced for ease of reference.

Dense beds of Potamogeton prevented navigation beyond 30 km from the mouth and impeded sampling at the top two stations (30 and 28 km from the mouth respectively). The population was predominantly juvenile (CL < 4,0 mm) throughout the estuary except at 2 km from the mouth where the modal size class was considerably larger than at any other station (Figure 11). The reason for this is not clear but it may represent a congregation of larger shrimps prior to emigration. The minimum carapace length of shrimps decreased towards the mouth, probably reflecting growth as they moved up the estuary.

The sample at 0,8 km from the mouth was collected in the study site. Many post-larvae and juveniles were present but large sub-adults were absent, probably on account of the shallowness of this area. Samples from the study site may thus be expected to give a good indication of the juvenile population throughout the estuary, but are probably less representative of the sub-adult population.

c. Study of shrimp recruitment and population dynamics

i. Recruitment

Plankton hauls undertaken in the mouth of the estuary at about two weekly intervals from September 1982 to August 1983, caught only two stages of P. pacificus in significant numbers; stage 6 zoeae (CL 1,3 to 2,2 mm; mean 1,8 mm) and post-larvae (CL 1,4 to 2,3 mm;

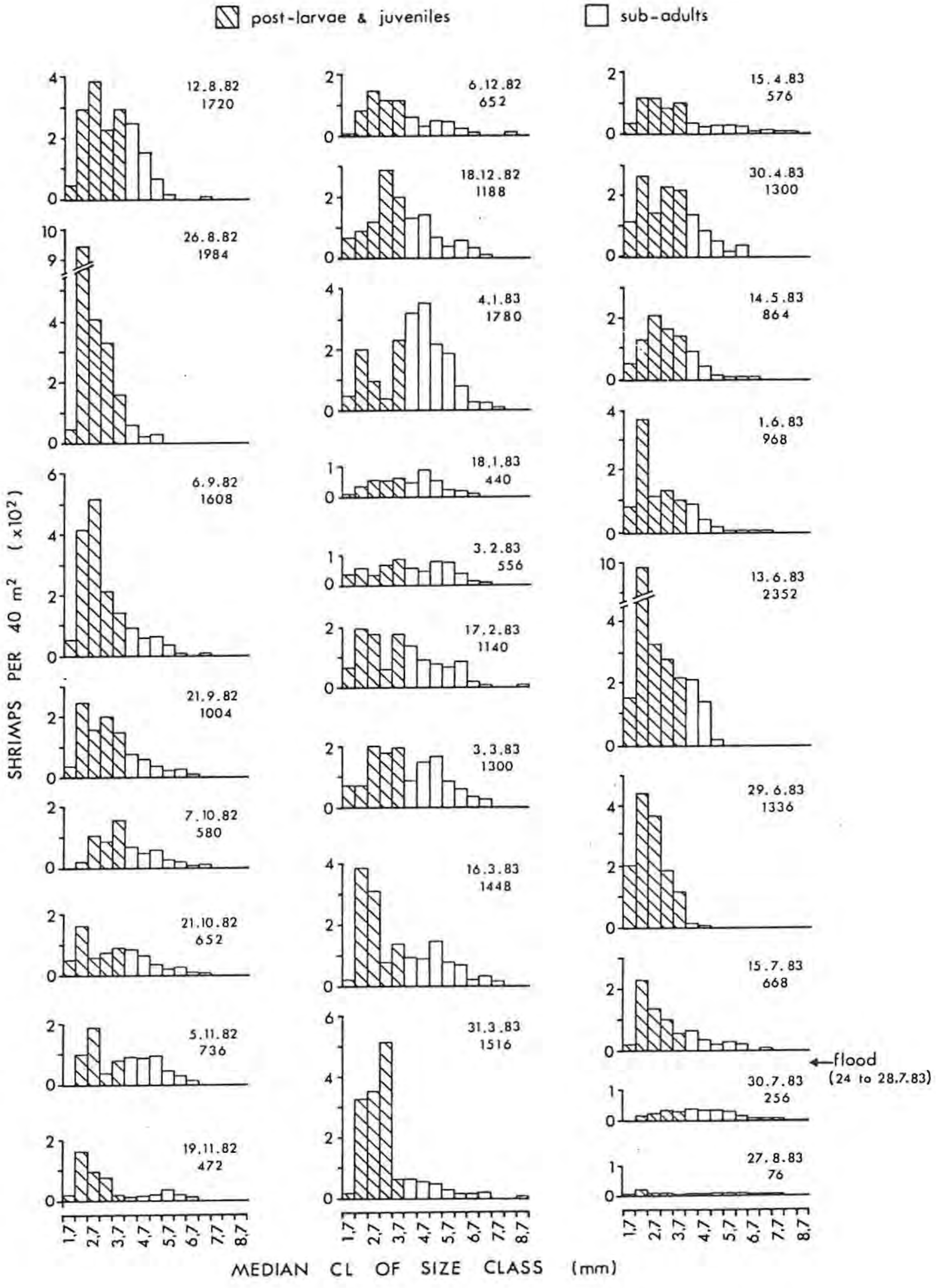

Figure 13. Size frequency distribution of P. pacificus collected from study site in Bushmans River estuary from August 1982 to August 1983. Total number of shrimps caught per 40 m² is given below sampling date. Size classes not labelled on X-axis are 2,2 mm, 3,2 mm, 4,2 mm etc.

mean 1,9 mm). Both stages were present throughout the year but in varying proportions (Figure 12). Peak numbers occurred in March/April with smaller peaks evident in October, December/January and June.

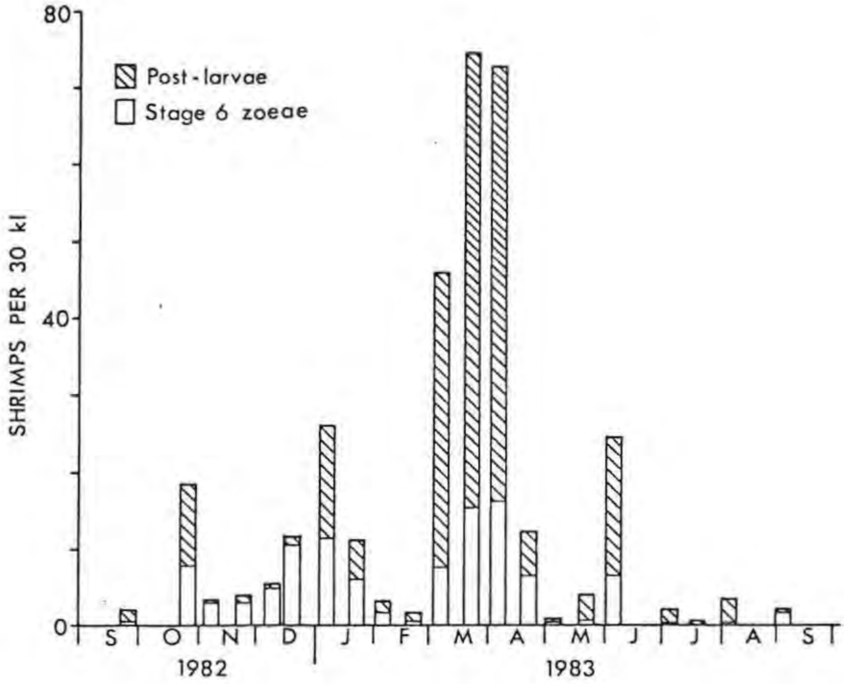

Figure 12. Numbers of *P. pacificus* stage 6 zoeae and post-larvae caught during bi-weekly plankton hauls near mouth of Bushmans River estuary.

The size frequency distribution of shrimps collected from the study site over a 12 month period (August 1982 to July 1983) is shown in Figure 13. Very few stage 6 zoeae were found in the samples, but large numbers of post-larvae were present for most of the year. The size range of post-larvae in the study site (CL 1,5 to 2,4 mm) was very similar to that of post-larvae caught in the plankton hauls indicating that the recruiting stages settled in feeding sites in the estuary immediately after entry.

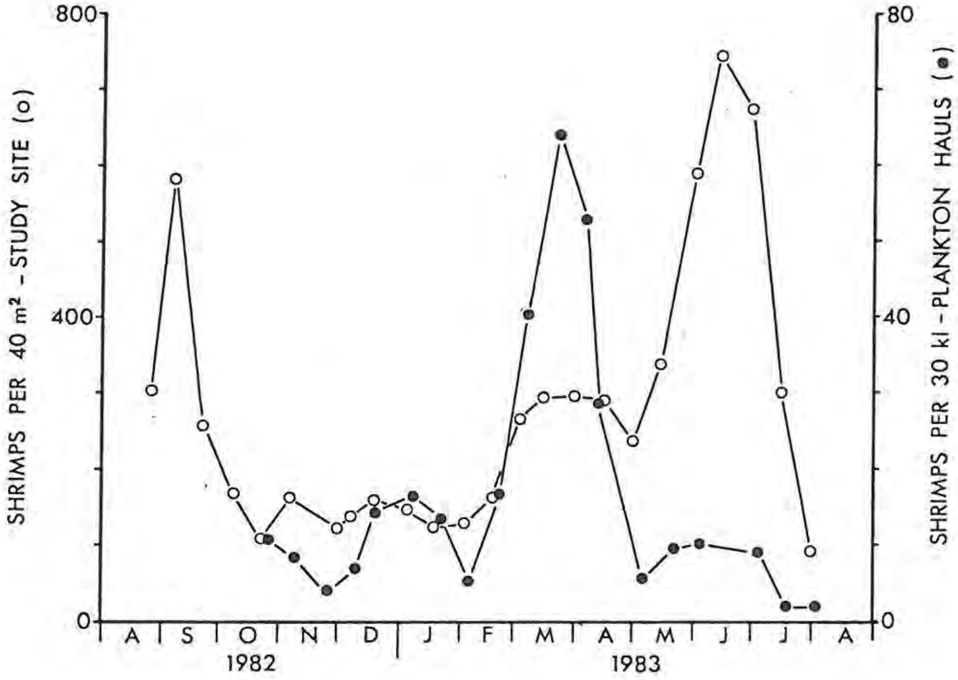

Figure 14. Three sample running means of numbers of stage 6 zoeae and post-larvae collected in plankton hauls near the mouth, and numbers of the same stages collected in the study site in the Bushmans River estuary.

If this were the case, high numbers of post-larvae in the study site should coincide with periods of peak recruitment into the estuary. This was investigated, using a three sample running mean to smooth out random fluctuations (Figure 14). Three periods of peak recruitment were evident, coinciding in time but not in magnitude with three peaks of post-larval abundance in the study site. The slightly elevated numbers in the plankton hauls in October probably represent the tail end of a peak coinciding with the late winter peak of post-larvae in the study site.

Many post-larvae were present in the study site in May/June at a time when very few of these shrimps were collected in plankton hauls. This probably represents an accumulation of small shrimps in the study site resulting from a period of slower growth following the sudden drop in estuarine temperatures during this period (Figure 9C).

Post-larval numbers in the study site dropped sharply following the flooding of the estuary in July 1983.

ii. Identification of cohorts

The shrimp population in the study site was made up predominantly of post-larvae and juveniles (CL <4,0 mm) throughout the year except for a few weeks in midsummer when sub-adult numbers were high (Figure 13). To establish the reason for this, the population was divided into cohorts and the history of each cohort followed.

Since recruitment to the estuary occurred continuously with waves of

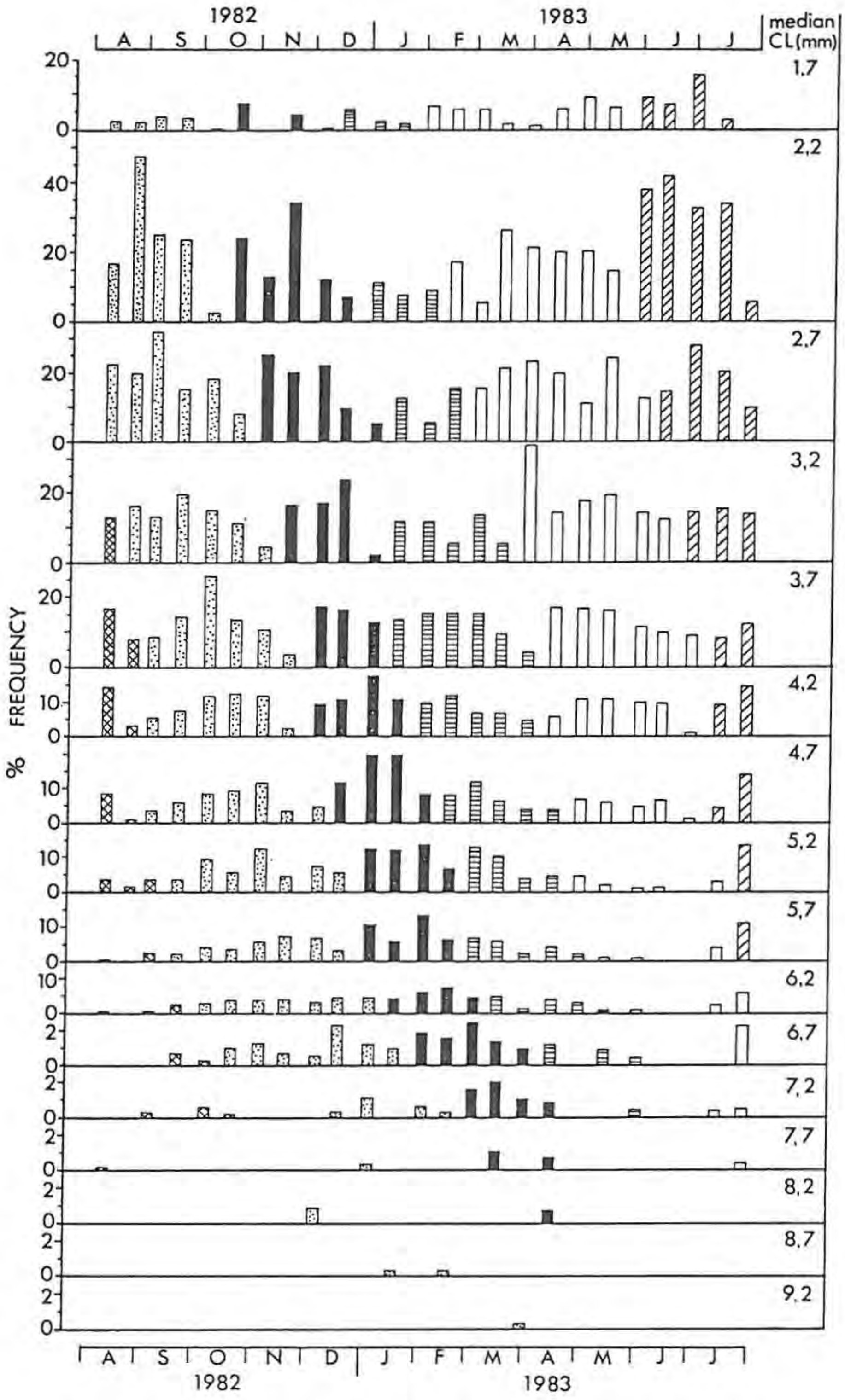

Figure 15. Temporal changes in relative frequency of shrimps in each size class collected from study site in Bushmans River estuary. Note that scale of Y-axis has been expanded in last six size classes as numbers were very low. Cohorts distinguished as follows:

░ A ■ B ☰ C □ D ▨ E

peak recruitment following each other in fairly close succession (Figure 14), separation of cohorts was difficult. Each wave of new individuals settling in the study site was therefore treated as the start of a new cohort and its growth followed through the size classes.

To do this, absolute data presented in Figure 13 were converted to relative frequencies and plotted for each size class over the year (Figure 15). Relative frequencies here refer to the number of shrimps in each size class on each sampling day expressed as a percentage of the total number of shrimps collected on that sampling day. They were used in preference to absolute numbers to correct for random differences between total sample sizes.

In this series of graphs, cohorts are spread over a period of time rather than over a series of size classes. The movement of a cohort is followed through successive size classes. Overlap between adjacent cohorts made definition of cohort limits difficult and somewhat arbitrary at times. An attempt was made to use the graphical method of Harding (1949) and Cassie (1954) to separate cohorts, but the choice of cohort boundaries by this method also tended to be rather subjective and the little that was gained in objectivity did not merit the long and tedious calculations required to achieve it.

Five cohorts were identified from Figure 15. In the post-larval size classes (median CL 1,7 and 2,2 mm respectively) these cohorts coincide fairly closely with the peaks of post-larval abundance apparent in Figure 14. There was some doubt as to whether B and C should be

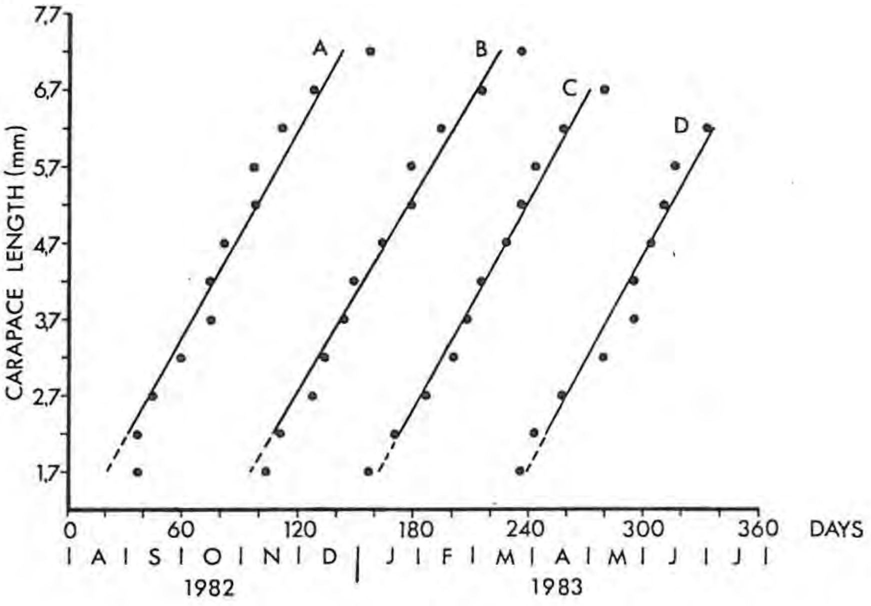

Figure 16. Growth curves of shrimps in cohorts A to D from study site in Bushmans River estuary. Curves fitted by linear regression (for equations see Table 1). Points corresponding to size class 1,7 mm CL not used in fitting regression line.

considered separate cohorts, but further analysis indicated that this distinction was merited. On the other hand, cohort D appeared to begin with two peaks which later merged into one. This may represent two strongly overlapping cohorts with different growth rates, the second growing more rapidly than, and finally merging with, the first. Cohort E was incomplete and was markedly affected by the floods in July 1983.

iii. Growth rates

The growth rate of each cohort was calculated in the following way. Within a size class each cohort is spread over several samples (Figure 15). The date on which the median sample in each cohort was collected was plotted on the X-axis with the corresponding median carapace length of the size class on the Y-axis. This was repeated for each size class and for each cohort. If the cohort was spread over an even number of samples, the date midway between the collection dates of the two central samples was used. The results are shown in Figure 16. To facilitate interpretation, actual dates have been replaced by number of days, with 31.7.82 being arbitrarily chosen as day 0. Cohort E was omitted as the data were insufficient.

Although it is unlikely that growth is constant throughout the shrimp's life, linear regressions were fitted to each set of points. In fitting the regression lines, the point corresponding to the first size class was omitted in each case. This was done because size differences between this class and the next did not necessarily represent growth within the sampling site as both size classes immigrated simultaneously. The larger size classes (>7,2 mm median CL) could also not be used for estimation of growth rate since very few shrimps of this size were found and the median sample could not be estimated accurately. The equation of each regression line is shown in Table 1 together with the coefficient of determination, r^2. Growth rate is represented by the slope of the line, b, in the generalized equation $y = a + bx$.

Table 1. Equations describing growth of shrimps in study site.

Cohort	Equation	r^2
A	$y = -0,194 + 0,045x$	0,951
B	$y = -3,191 + 0,042x$	0,971
C	$y = -6,556 + 0,045x$	0,981
D	$y = -10,325 + 0,046x$	0,940

Growth rates for the four cohorts (A to D) were very similar with a mean (harmonic) of 0,043 mm CL per day.

iv. Survivorship curves

Shrimp numbers declined with increasing age (Figure 13). Losses from the population may result from either death or emigration and no definite distinction can be made between the effects of these two factors from the available data.

Following the method outlined by Krebs (1972), life tables were constructed and survivorship curves (reflecting survivors of both

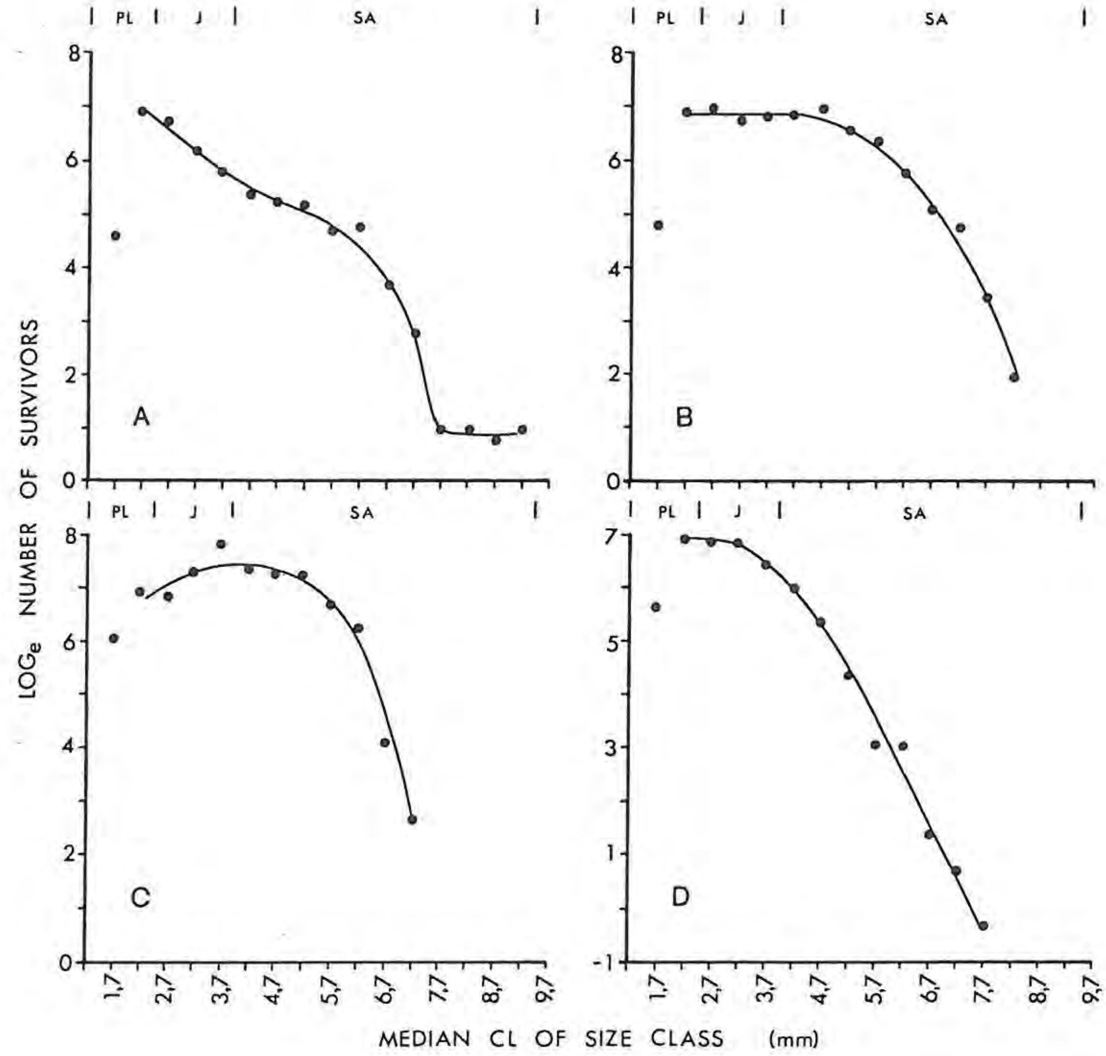

Figure 17. Survivorship curves of shrimps in cohorts A to D. Curves fitted by eye. Size classes not labelled on X-axis are 2,2 mm, 3,2 mm, 4,2 mm etc. PL = post-larvae J = juveniles SA = sub-adults.

mortality and migration) plotted for each cohort as follows. The number of shrimps in each size class was tabulated for each cohort. There were always more shrimps in the first post-larval size class (1,7 mm median CL) than in the second (2,2 mm median CL). This is because the latter represents shrimps which have grown from the previous size class as well as newly recruited individuals. Taking the number of shrimps in the second post-larval size class as equivalent to 1000 in each case, the numbers in each of the other size classes were adjusted proportionately. The natural logarithms of these values were then plotted against the median carapace length of each size class. Natural logarithms were used in preference to absolute numbers since it is the rate of loss rather than absolute loss which is of interest. Curves were fitted to the data by eye and are shown in Figure 17. The abscissa is plotted as a size scale rather than a time scale to enable the loss rate per size class to be compared between cohorts. If desired, the size scale could be converted to time using the calculated growth rate for each cohort. Since these growth rates were so similar, the time scale would vary little between cohorts.

Cohorts A and D showed a high loss of juveniles compared with cohorts B and C (Figure 17). Only 22 % and 39 % of the original numbers of post-larvae (size class 2,2 mm median CL) in cohorts A and D respectively survived through to the first sub-adult size class (4,2 mm median CL). Comparable figures for cohorts B and C are 94 and 100 % respectively. Examination of Figure 15 suggests the possibility of an incorrect choice of division between cohorts C and D in the second and third size classes, which may explain the increase in numbers in cohort C and the corresponding decrease in cohort D. Adjustment of the boundary between these two cohorts did not alter the curves significantly, however, and the original boundaries were therefore maintained. The reason for the increase in numbers in cohort C is therefore not known.

Loss of sub-adults began gradually in cohorts A, B and C, but increased in the later size classes (Figure 17). In cohort D, loss occurred at a constant rate from all sub-adult classes. These survivorship curves offer an explanation for the large numbers of sub-adults present in the study site in summer, compared with other times of the year (Figure 13).

The majority of sub-adults present in spring and early summer (September to December) were derived from cohort A (Figure 15). Because of high juvenile loss from this cohort (Figure 17A), the number of sub-adults present at this time of the year was low (see Figure 13). The later summer population (January to March) was comprised largely of shrimps from cohorts B and C which showed very low rates of juvenile loss (Figure 17 B and C), hence the large numbers of sub-adults present. Adults present from April onwards belonged mainly to cohort D with a few of the larger shrimps being part of cohort C. Juvenile loss from cohort D was also high and sub-adults disappeared fairly rapidly as well. This resulted in low numbers of sub-adults, especially in the larger size classes.

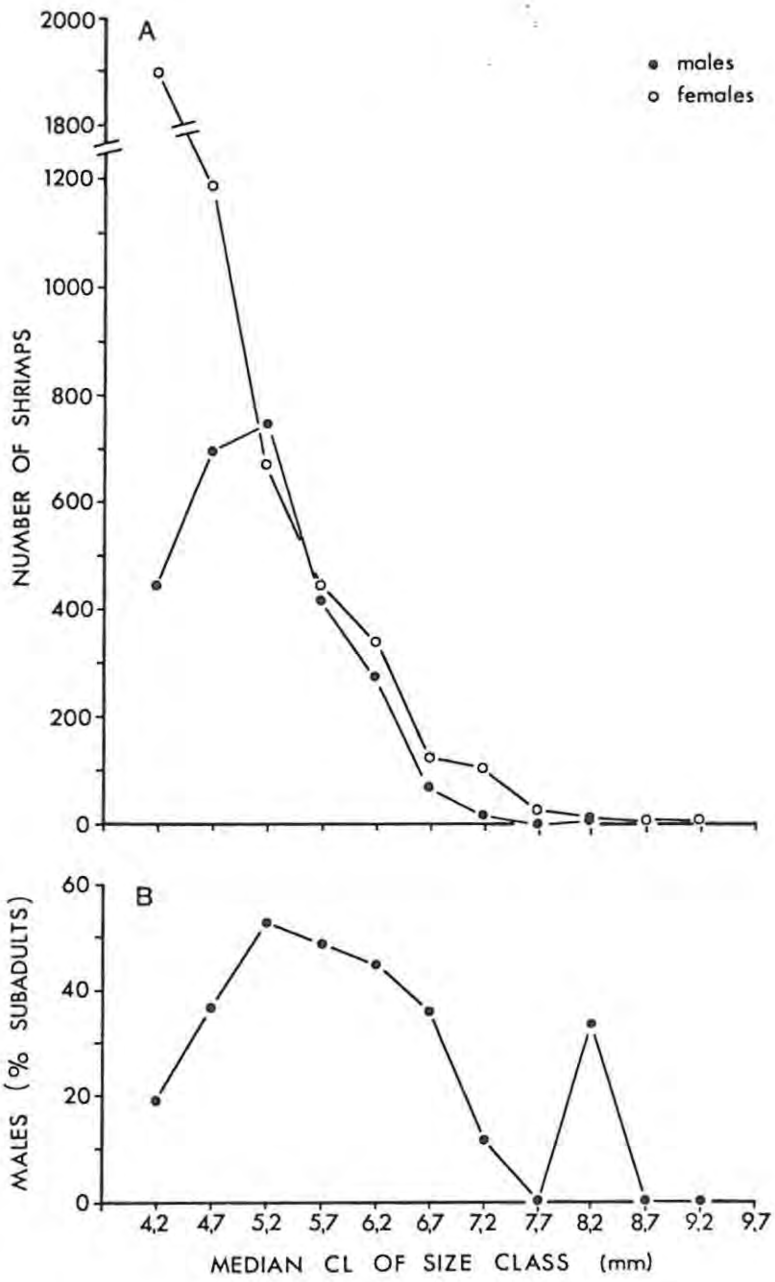

Figure 18. A) Total numbers of males and females and B) percentage males in each sub-adult size class collected from study site during sampling period (August '82 to August '83).

iv. Sex ratios

Size frequency data for P. pacificus over the entire sampling period was combined and the total number of males and females in each sub-adult size class calculated (Figure 18A). The percentage of males making up the sub-adult population in each size class was then estimated (Figure 18B). The low proportion of males in the first and, possibly, also the second size class, is probably an artefact caused by the late appearance of the appendix masculina in many male shrimps. This explanation is further supported by the fact that male numbers increased markedly between the first and third size classes (Figure 18A). Thereafter the proportion of males declined steadily.

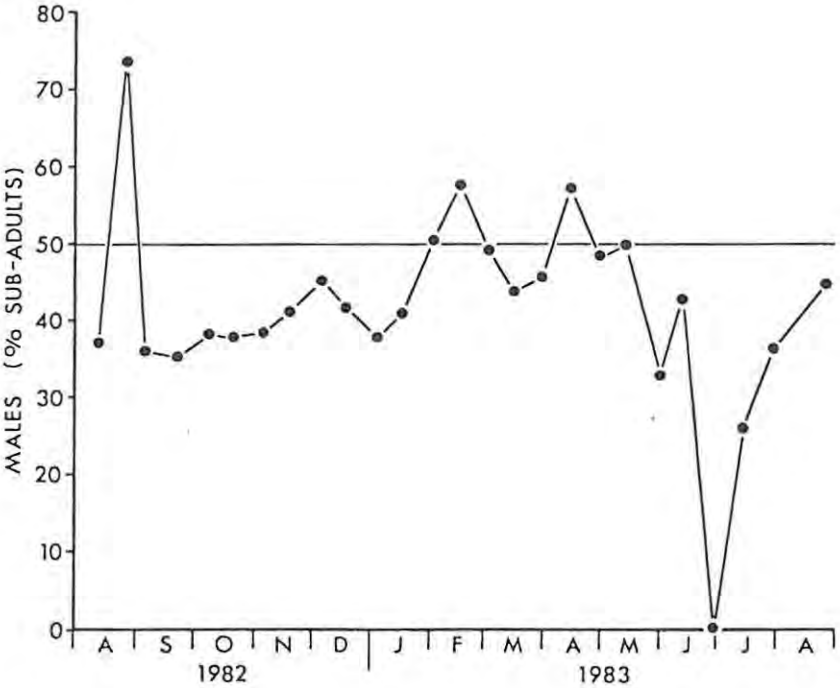

Figure 19. Temporal changes in percentage males comprising sub-adult population in study site in Bushmans River estuary.

Table 2. Records of berried females of P. pacificus in South African waters.

LOCATION	TIME OF YEAR	SOURCE	COMMENTS
	Coastal waters		
Langebaan Lagoon	October, November	Achituv, 1983 pers. comm.	
Table Bay	July, November	Barnard, 1950	
False Bay (St James)	January, February	Barnard, 1950	
Mossel Bay	March, July	Barnard, 1950	
Knysna	August,	Barnard, 1950	
Port Elizabeth	November	Barnard, 1950	
Algoa Bay	July - January	Emmerson, in press b	
Kenton-on-Sea	January	Present	1 specimen
East London	April, July, September	Barnard, 1950	
	Estuaries		
Muizenberg vlei (Sandvlei)	October, November	South African Museum	
Kleinemond	June	Hill, 1983 pers. comm.	3 specimens mouth closed ?
Kowie	June	Hill, 1983 pers. comm.	1 specimen East Lagoon
Nahoon (East London)	?	Barnard, 1950	14 specimens
Richards Bay	Winter, January	Millard & Harrison, 1954	
St Lucia	Winter	Day *et al*, 1954	large numbers

Temporal changes in the proportion of males comprising the sub-adult population are shown in Figure 19. Because of the large female bias in the first sub-adult size class, shrimps of this size were excluded from the calculations. Females were predominant for most of the year. Male numbers peaked in February and April. The high male to female ratios on 26.8.82 and 29.6.83 were based on very few animals and are therefore of doubtful significance. No berried females were found.

2.4 DISCUSSION

a. Breeding and recruitment

The absence of berried females and early larval stages from the Bushmans River estuary and the presence of late larval and post-larval stages near the mouth of the estuary during flood tides support the proposal of an offshore breeding phase. Berried females of P. pacificus have, however, been observed in at least six estuaries in South Africa in the past (Table 2). In at least three of these, Kleinemond, Kowie and Nahoon, very few shrimps were found, and their presence in the estuary may have been related to difficulties in reaching the sea. Female Scylla serrata normally migrate to sea to breed, but if cut off from the sea by closure of the estuary mouth, they will occasionally extrude their eggs while still in the estuary (Hill, 1975). Hill found that, although eggs extruded by crabs trapped in the Kleinemond River estuary were viable, the larvae apparently did not survive since no recruitment of juveniles to the population was detected.

In St Lucia and Richards Bay, large numbers of berried females of *P. pacificus* were found, leading to the conclusion that breeding occurred in estuaries and that the shrimps were non-migratory (Day et al, 1954; Millard & Harrison, 1954). An alternative explanation is suggested by the work of Kunju (1955). He found berried females of *Leander* (=*Exopalaemon*) *styliferus* in areas of reduced salinity in the River Hooghly, but always in low numbers, and the eggs they carried were never in an advanced stage of development. He concluded that the prawns probably migrate seawards at the end of their period of egg carriage to release their young. A similar occurrence was observed for *Palaemon mirabilis* (=*Macrobrachium mirabile*) in the River Hooghly (Rajyalakshmi, 1961) and *Crangon vulgaris* (=*crangon*) in the Bristol Channel and Severn River estuary (Lloyd & Yonge, 1947). The possibility that a seaward migration prior to larval release may occur in the case of *P. pacificus* is supported by Emmerson's (in press a) observation that no larval stages were found in tidal pools in which berried females of this species had previously occurred. Thus eggs may be extruded in estuaries and tidal pools, but there is no evidence that larval release occurs in these environments.

The presence of post-larvae in the Bushmans River estuary throughout the year suggests that *P. pacificus* is a perennial breeder. Recruitment did not occur at a constant rate, however, but in waves or pulses of increased activity (Figure 14). Peak recruitment occurred between February and April 1983.

Considerable care should be taken in interpreting and extrapolating the above observation. Firstly, the study covered only one seasonal cycle and it is not known to what extent patterns of recruitment may vary annually. Staples (1979) studied the pattern of post-larval migration of Penaeus merguiensis in 20 rivers in the Gulf of Carpentaria, Australia, over a four year period and found considerable year to year variation in the timing of post-larval ingress in most cases. In nine of the rivers there was at least one year when no larval immigration was recorded at all.

Secondly, patterns of recruitment observed in P. pacificus in the Bushmans River estuary do not necessarily represent typical behaviour patterns of these shrimps, since these are likely to be affected by geographical variations in environmental conditions. The most important factors influencing recruitment are probably temperature and ocean currents.

Mean sea temperatures change quite rapidly as one moves up the east coast of South Africa from Port Elizabeth to Port St Johns (Christensen, 1980). Beckley (1983) has shown that large temperature differences may occur in the waters around prominent coastal headlands such as Cape Recife near Port Elizabeth. Considerable variations in recruitment patterns could therefore be expected to occur over a short stretch of coastline. Thus, Emmerson (in press a) reports continuous recruitment of P. pacificus to tidal pools in the Port Elizabeth area, but, in contrast to the present results, he found peak activity to occur in November with a smaller peak in winter. This difference may of course represent annual as well as geographical variations.

Work by Staples (1979), Crocos & Kerr (1983) and Rothlisberg et al (1983) on Penaeus merguiensis in the Gulf of Carpentaria, has demonstrated the influence that currents may have on patterns of post-larval recruitment. Staples (1979) found that, in addition to the occurrence of year to year differences, patterns of post-larval recruitment of Penaeus merguiensis during any one year could vary considerably between estuaries in the Gulf of Carpentaria. He divided the Gulf into four major areas, each characterized by its own pattern of larval recruitment. He then proposed that two peaks of spawning occurred each year throughout the Gulf and that differences in the seasonal pattern of immigration of post-larvae in the different areas of the Gulf is a reflection of both geographical and yearly differences in the fate of larvae produced during these two spawning periods.

A more thorough investigation of the spawning periods in the Gulf by Crocos & Kerr (1983) confirmed Staples' proposal and demonstrated further that periods of peak post-larval recruitment in the estuaries did not necessarily follow the spawning period of greatest reproductive output. Rothlisberg et al (1983) provide evidence that the offshore transport of larvae by currents during certain spawning periods accounts for the low level of post-larval recruitment to estuaries in the Gulf at these times.

The Agulhas Current and related circulatory systems which characterize the waters of the east coast of southern Africa, are extremely complex and have been the subject of numerous investigations (Lutjeharms, 1983). Although the core of the Current follows the continental shelf some 30 to 70 km offshore (Gründlingh, 1983), inshore waters are also greatly affected by its presence. Periodic deflections in the Current have been implicated in the creation of inshore turbulence and current reversals off the Natal coast (Gründlingh, 1974) and in the occurrence of upwelling off the coast south of East London (Harris et al, 1978).

The Agulhas Current is known to have a profound influence on the distribution and migration of marine organisms occurring in east coast waters (Macnae, 1962; Heydorn et al, 1978). The recruitment of planktonic stages of P. pacificus into estuaries is no doubt similarly affected. Thus, patterns and intensity of recruitment may not necessarily reflect patterns and intensity of spawning in the area. This view is supported by Emmerson's (in press a) observation that, although juvenile recruitment of P. pacificus to tidal pools was continuous, berried females were only present in the area between June and January.

Thus, the most reliable indicator of spawning activity in an area appears to be the presence of berried females, although, as has already been pointed out, even these stages may undergo limited migrations before releasing their young. Table 2 summarizes published reports of the occurrence of berried females of P. pacificus in South African waters. Many of these reports are probably the result of an isolated collection or casual observation and can in no way be considered to represent the complete breeding period of P. pacificus. An interesting trend does, however, emerge.

In the western Cape (Langebaan Lagoon, Table Bay, False Bay, Sandvlei) berried females were mostly observed in the warmer months (October to February) with one report from Table Bay in July. Along the Natal coast (Richards Bay, St Lucia), winter breeding is reported with some berried females occurring in January. Along the south and south-east coasts (Mossel Bay to East London), breeding apparently occurs at various times of the year. On the strength of these reports and the present observations on recruitment patterns in the Bushmans River estuary, I propose that P. pacificus is a perennial breeder with peak spawning activity occurring in summer in the cold temperate zone of the western Cape, in winter along the subtropical Natal coast and at various times of the year along the warm temperate south and east coasts. Further confirmation is, however, required.

In penaeid prawns, recruitment to estuarine nursery areas occurs at the post-larval stage (Baxter & Renfro, 1967; Munro, 1968; Young & Carpenter, 1977; Staples, 1980). This also appears to be the case for the palaemonid prawns, Crangon franciscorum and C. nigricauda (Israel, 1936). The fact that stage 6 zoeae and post-larvae of P. pacificus were collected in plankton hauls near the mouth of the Bushmans River estuary (Figure 12) indicates that, in this species, both of these stages immigrate. This contrasts with Emmerson's (1983) view that P. pacificus invades estuaries as stage 6 zoeae and not as post-larvae. His proposal was based on the results of only two 24 hour sampling programmes in the mouth of the Swartkops River estuary, the second of which produced very few shrimps. This discrepancy may thus be an artefact caused by limited sampling, but, on the other hand, it may represent a geographical variation in recruitment.

b. Growth rates

The method used to estimate growth rates in the present study (i.e. by following the growth of a wave of newly recruited individuals through a series of size classes) proved to be a useful method of obtaining an average growth rate for a population in which recruitment is continuous and the identification of cohort boundaries difficult. It is not as sensitive to temperature changes as is the usual method in which a cohort is followed through a series of successive samples. This is because each cohort identified by the former method tends to span a considerable period of time, sometimes several months, within each size class (Figure 15). The effect of environmental conditions during this period is thus averaged out in the calculation of growth rate, resulting in smaller differences between individual cohorts.

It is nevertheless surprising that growth rates estimated for the four cohorts were so similar (Table 1). Had it been possible to estimate the growth rate of cohort E, which experienced winter conditions, it is likely that more variation would have been obtained. The similarity in growth rates of cohorts A to D may be partly attributable to the high daytime temperatures experienced by shrimps in the study site in both winter and summer (Figure 10). Cook & Achituv (in press) found temperatures of 20 to 25°C to be optimal for growth of P. pacificus with higher temperatures (28°C) retarding growth. Daytime warming of the water in the study site would often produce optimal conditions for growth in the cooler months ($\geqslant$20°C) but unfavourable conditions for growth in summer ($\geqslant$28°C) (Figure 10). This would tend to accelerate an otherwise slower growth rate in the cooler months and retard the summer growth, thus reducing the difference between the two rates.

The mean growth rate estimated for cohorts A to D (0,043 mm CL per day) is very similar to that calculated from the data of Cook & Achituv (in press) for shrimps held at 20°C (0,045 mm CL per day - from their Table III). Mean annual growth rates calculated by Emmerson (in press a) for shrimps in six tidal pools in and around Algoa Bay, were all lower than these values, the highest being 0,035 mm CL per day (0,167 mm TL per day in Emmerson's Table 5).

c. Mortality and emigration

The high loss of post-larvae and juveniles from the population in spring and autumn (cohorts A and D) (Figure 17) indicates that young shrimps may be susceptible to low temperatures. Emmerson (in press b) found considerable mortality (85,3 %) during the post-larval to juvenile stages in shrimps reared in the laboratory, showing this to be a critical period in the life history of these shrimps. Seasonal changes in loss of young shrimps from the study site may also reflect seasonal fluctuations in their upstream migration in response to temperature changes. The validity of these hypotheses will be discussed in Part 3 in the light of salinity and temperature tolerances of these shrimps.

Emigration would be expected to be a major cause of loss of larger shrimps in view of their seaward migration for the purpose of breeding. Very few shrimps in size classes >7,2 mm median CL were found in the study site (Figure 15). This size was attained about four months after the arrival of these shrimps as stage 6 zoeae and post-larvae (Figure 16). Thus the residence time of most shrimps in the study site was less than four months.

This probably does not reflect the maximum residence time of shrimps in the estuary. Large shrimps appear to move out of shallow areas such as the study site into deeper water as they grow (Figure 11), a tendancy which Israel (1936) observed in Crangon franciscorum and C. nigricauda. The largest shrimps found in the estuary measured 10,5 mm CL. Using the growth curves in Figure 14, and assuming linear growth, these shrimps would be about 6 to 6,5 months old. This is probably an underestimate of their age since growth generally tends to slow down in older animals. The maximum residence time in the estuary is therefore probably in the region of seven to eight months.

d. Sex ratios

Temporal changes in sex ratio have been reported in other species of caridean shrimps e.g. Crangon franciscorum (Israel, 1936), Palaemonetes pugio (Alon & Stancyk, 1982), and have also been found in P. pacificus occurring in tidal pools (Emmerson, in press a). Israel (1936) found that female C. franciscorum were most abundant in San Francisco Bay during the breeding season and males just before the breeding season.

Changes in sex ratio in P. pacificus may also be related to breeding. Emmerson (in press a) has found that P. pacificus males mature earlier than females, the smallest mature individuals occurring in tidal pools being 25 mm TL (6,0 mm CL) and 41 mm TL (9,9 mm CL) respectively. Males may therefore be expected to migrate seaward at a smaller size than females. This view is consistent with the decline observed in the proportion of males in successive size classes in the study site (Figure 18B). Further investigation is obviously required since other factors such as differential mortality or differential growth rates may also be responsible for changes in sex ratio.

The effect of flooding in the shrimp population will be discussed in Part 3 in the light of the salinity tolerance of *P. pacificus*.

PART 3

TEMPERATURE AND SALINITY TOLERANCE OF *P. PACIFICUS*

3.1. MATERIALS AND METHODS

a. Collection and maintenance of shrimps

i. Stage 4 zoeae

A single berried female was collected from a rock pool near the mouth of the Bushmans River estuary on 5.11.82. The shrimp was transferred to an aquarium containing aerated full strength sea water (temperature 18 to 21°C) and held there under natural photoperiod conditions until the larvae hatched on 21.11.82. While incubating the eggs, the female was fed on a mixture of fishmeal and maizemeal bound by gelatin.

Larvae were held under the same conditions as the female but were fed on algae (*Chlorella* sp.) and *Artemia salina* nauplii (dead and living). Larvae were identified according to the descriptions of Han & Hong (1978). Stage 4 zoeae began emerging on 2.12.82 and the experiment was commenced the following day. Each larva was checked under the microscope to ensure that only stage 4 zoeae were used, before being transferred to the test solution. Experiments on this stage were limited by the small number of animals available.

ii. Stage 6 zoeae

Stage 6 zoeae were collected from the Bushmans River estuary. Some were collected in plankton hauls near the mouth of the estuary, using the method described in Part 2 for monitoring recruitment into the estuary. Others were collected from shallow pools around exposed sandbanks at low tide using a small hand net.

The larvae were returned to the laboratory in buckets containing aerated sea water and held overnight at room temperature before being used. Many of the larvae moulted during the night which considerably reduced the number of simultaneous tests which could be undertaken.

iii. Post-larvae and sub-adults

These shrimps were collected from the study site using the net shown in Figure 5, and returned to the laboratory in buckets containing aerated sea water. They were held in the laboratory for at least 24 hours before being used.

Shrimps to be used the following day were sorted into size classes and transferred to plastic basins containing about 4 ℓ of aerated sea water. They were fed on fishmeal-maizemeal mix and left under natural photoperiod conditions until the next day.

If experiments could not be conducted immediately, the shrimps were transferred to several large plastic tanks containing sea water (34 to 35 $^{o}/oo$). Water from the tanks was continuously circulated through a closed system, which included a biological filter and a common reservoir from which the sea water was returned to the tanks. The system was set up under natural photoperiod conditions and temperature was not controlled. The shrimps were fed regularly.

b. Experimental details

This section describes the apparatus and general procedures used in most of the experiments. Any departures from these methods will be discussed in the 'Results' section under the particular experiment in question.

i. Acclimation

Aziz & Greenwood (1981) found it necessary to acclimate Metapenaeus bennettae juveniles first to temperature and later to salinity to avoid heavy mortalities associated with simultaneous acclimation to more than one factor. In the present study, the acclimation temperature of 20°C was well within the range of temperatures naturally encountered by the shrimps, and so temperature and salinity acclimation were carried out simultaneously.

Shrimps required for acclimation experiments were returned to the laboratory and transferred to a Constant Environment Room (C.E.Room) set at 20°C. Shrimps were gradually acclimated to 5 $^{o}/oo$ over a period of 7 days by exposure to the following salinities: 28 $^{o}/oo$ (1 day), 21 $^{o}/oo$ (1 day), 10 $^{o}/oo$ (2 days) and 5 $^{o}/oo$ (2 days). Because

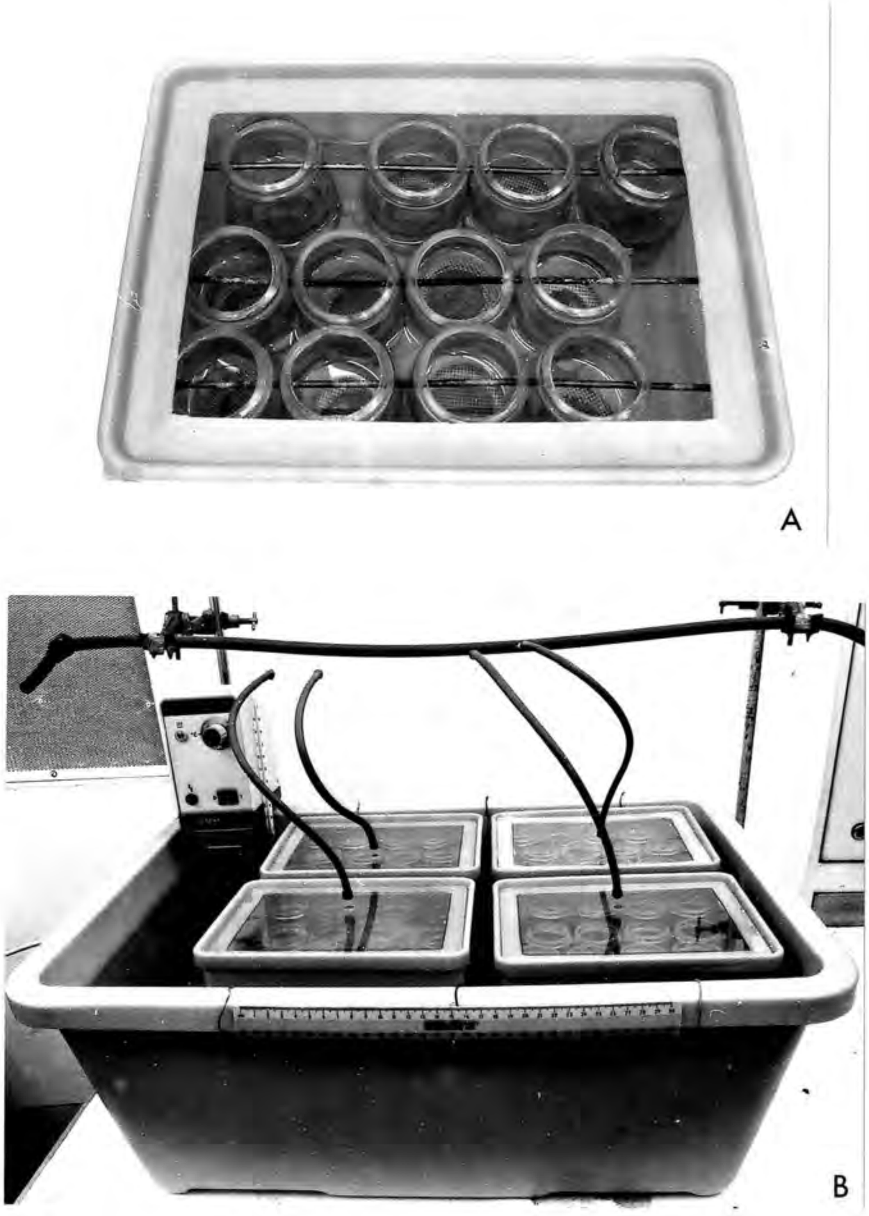

Figure 20. Apparatus used in temperature and salinity tolerance experiments. A) One shrimp was placed in each bottle and 12 bottles suspended in a plastic trough containing water at the required salinity. B) The troughs were placed in water baths at the required temperature. An aeration tube passed through the lid of each trough.

of the large volumes of water required, low salinity water for this purpose was obtained by diluting sea water with tap water. Glass distilled water was used for preparing test solutions since greater accuracy was required and volumes were smaller. The water was aerated and the shrimps fed daily.

ii. Experimental apparatus and procedures

Shrimps were isolated under test conditions to prevent cannibalism. They were placed individually in plastic bottles (diameter 40 mm; height 65 mm), the bottoms of which had been replaced by nylon gauze (mesh size 1,3 mm). The bottles were suspended in plastic test troughs (200 mm X 140 mm X 100 mm), containing water of the required salinity (Figure 20A). A clearance of about 10 mm between the bottles and the bottom of the trough ensured free exchange of water between the bottles. Each trough was covered with a perspex lid through which an aeration tube was passed, and placed in a water bath pre-heated to the required temperature by means of a heater-stirrer. Each water bath could accommodate four test troughs (Figure 20B). The water baths were held in a C.E.Room set at a temperature just below that of the coolest bath.

The lowest temperature which could be reached in the C.E. Room was ±10°C. Experiments requiring temperatures below 10°C were carried out in a refrigerated incubator or a refrigeration water bath. The latter was cooled by metal coils containing 'Freon' gas circulated from a refrigeration system.

Photoperiods were chosen to match as closely as possible conditions which, in the field, would coincide with temperatures to which the shrimps were being exposed. Thus, salinity tolerance experiments were carried out in a 12 hour light/12 hour dark regime. A 15 hour light/9 hour dark regime was used for the remainder of the trials except the cold tolerance experiments. The latter were conducted under conditions of continuous dark owing to an absence of suitable lighting in the refrigerated incubator.

Oxygen tension of aerated water in experimental troughs was checked over a range of temperature/salinity combinations. A mean value of 6,7 $mg\ell^{-1}$ O_2 (range 5,2 to 8,0 $mg\ell^{-1}$) was obtained.

Two replicates of 12 shrimps each of a particular size class were exposed to each treatment unless otherwise specified under 'Results'. Shrimps of similar size were arbitrarily transferred to the bottles described above which were wired together in groups of four. Each group of four shrimps was then randomly assigned to a treatment using the method of Allanson & Noble (1964). No discrimination was made between the sexes since sexing of live shrimps is very difficult.

Shrimps were transferred directly from their overnight salinity (either 5 or 35 $^{0}/oo$) to the test salinity. Temperature changes were gradual as shrimps were transferred to water at the same temperature as their overnight medium and then placed in a pre-set water bath or refrigerated incubator and the water allowed to adjust to the test temperatures. Temperatures of 10°C and higher were usually reached within one hour but at lower temperatures (<10°C) this took between 7 and 11,5 hours depending on the test temperature.

In experiments involving a salinity change, time 0 was taken as the time at which the shrimps were transferred to the test salinity. When a temperature change only was involved, the exposure time was commenced when the test temperature was reached.

iii. Maintenance under test conditions

Shrimps under test conditions were fed at one to three day intervals on living *Artemia* nauplii. Because of the difficulty of warming or cooling water to a range of temperatures, water in the test troughs was only changed during those experiments in which all the tests were done at the same temperature. The shrimps were transferred in their bottles from the test trough into a spare trough containing water of the same temperature and salinity. The test trough was emptied, rinsed and refilled with clean water at the correct temperature and salinity, and the shrimps replaced.

The temperature of the water in each test trough was recorded at each examination using a mercury in glass thermometer graduated in 0,1°C. The salinity of test solutions was also checked regularly using a chloride titrator, and evaporative losses were made good by adding distilled water.

iv. Examination of shrimps and criterion for death

In most experiments, shrimps were examined at 1 to 1,5 hour intervals for the first 12 hours, at 6 hour intervals for the next 24 hours and every 12 hours thereafter. More frequent checks were made when necessary. In cold tolerance experiments, checks were made every 12 hours throughout the experiment to minimize loss of cold air through opening of the incubator door.

At each examination dead shrimps were removed, measured, and, in the case of shrimps of CL ⩾4,0 mm, sexed. All experiments were terminated after six days.

Onset of death was usually characterized by shrimps collapsing onto their backs or sides. In this position, they would beat their pleopods rapidly for long periods of time, gradually slowing down as death approached. If the pleopods were not beating, a gentle prod with a blunt probe would start them moving again if the animal was still alive. If the shrimp did not respond, it was regarded as dead and removed. This criterion was used in all experiments except in the low temperature tolerance experiments.

Temperatures below 10°C retarded activity to such an extent that all movement of limbs appeared to stop long before the animals were actually dead. Cessation of scaphognathite beat as used by Hill & Allanson (1971) was therefore taken as the criterion for death in these experiments. Since this required examination of the shrimps under a microscope, it was not used in the other experiments where death was more rapid and scaphognathite beat ceased soon after the pleopods had stopped moving.

c. Analysis of data

The number of shrimps alive at each examination was converted to a percentage of the number of shrimps originally exposed to each treatment. Probits of percentage survival were then plotted against a logarithmic time scale and a line fitted to the points by eye as recommended by Finney (1971). Median times of survival (MTS = time for which 50 % of the population survives a given set of conditions) were determined from the curves.

Many of the probit lines showed a distinct break or split which complicated the determination of MTS values. Split probits have been obtained in temperature tolerance experiments by several authors (Brett, 1952; Gibson, 1954; Hill and Allanson, 1971; Hart, 1983) and are generally thought to indicate that more than one lethal factor is operating.

Another problem which arose was that, under the set of conditions chosen for the experiments, 50% mortality was often not reached within the experimental period of 144 hours. A second index of comparison was therefore used, namely the percentage of shrimps alive at the end of the experiment (hereafter referred to as percentage survival). This dose-response method was not considered sufficiently reliable to be used on its own because of the low number of experimental animals, but, when considered in conjunction with MTS, gave valuable additional

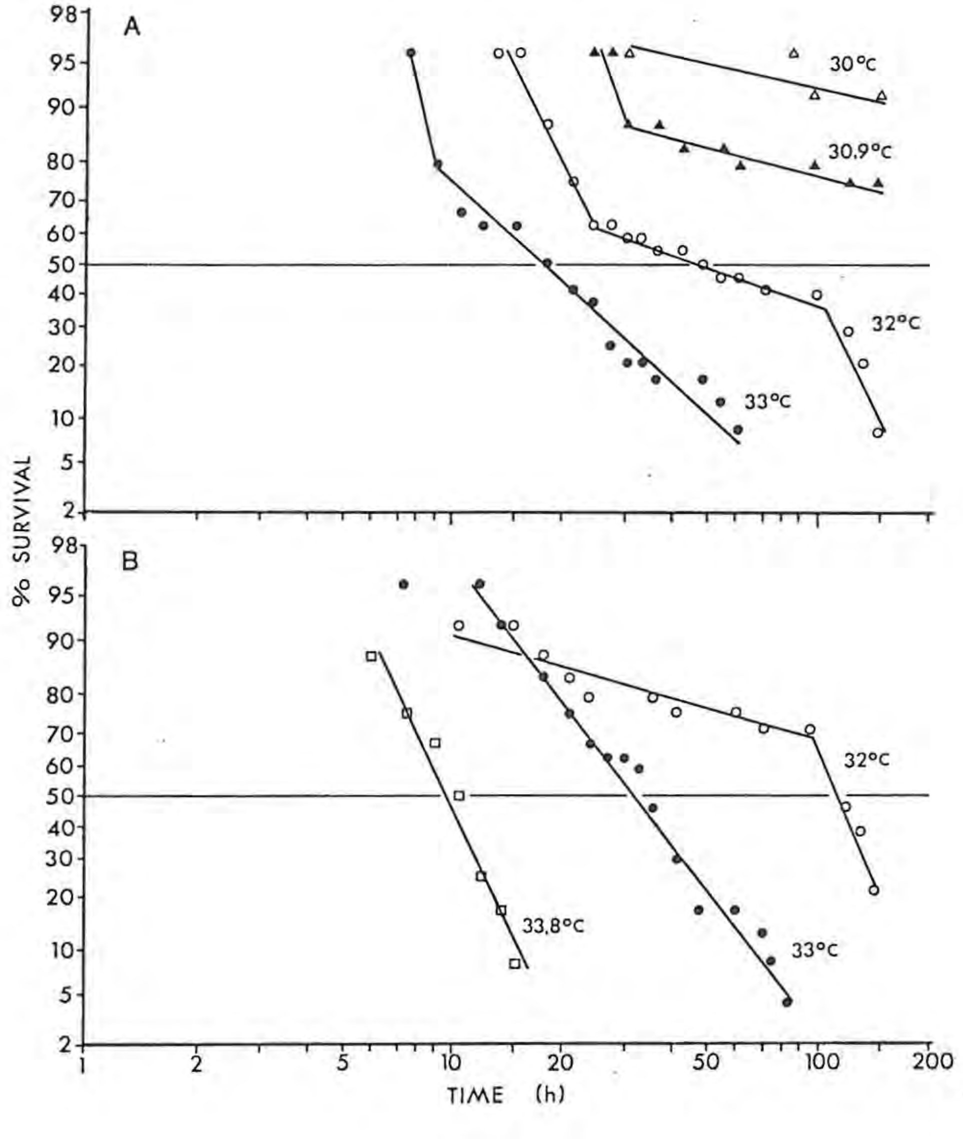

Figure 21. Survival of A) post-larval and B) sub-adult shrimps at high temperatures (salinity = 35 °/oo). Percentage survival plotted on probit scale. Sub-adults at 30 and 30,9°C all survived.

information.

Shrimps were considered to have tolerated experimental conditions if their MTS was >144 hours (i.e. less than 50 % died within 144 hours).

3.2. RESULTS

a. Tolerance to high temperatures

Tolerance to high temperatures of large (mean CL ± s.d. = 6,3 ± 0,6 mm) and small (CL 2,2 ± 0,3 mm) shrimps collected early in March (i.e. summer acclimated) was tested by exposing them to temperatures approximating 34, 33, 32, 31, 30, 28 and 26°C. The actual mean temperatures were as follows:

large shrimps - 33,8; 33,0; 32,0; 30,9; 30,0°C
small shrimps - 33,0; 32,0; 30,9; 30,0; 28,0; 26,1°C

Controls were kept at room temperature (18 to 21,5°C, mean 19,5°C).

The results are shown in Figure 21 and Table 3. Post-larvae and sub-adults were both intolerant of temperatures of 32°C and higher. Post-larvae died earlier than sub-adults at 32 and 33°C. There was no sub-adult mortality at 30 or 30,9°C whereas some post-larvae died at both of these temperatures. All post-larvae survived at 28°C and below. Thus, although both size groups tolerated temperatures below 32°C, mortality rates indicate that post-larvae are more susceptible to high temperatures than sub-adults. There was no mortality amongst the controls.

Table 3. Median times of survival (MTS) and percentage survival (after 144 hrs) of post-larval (PL) and sub-adult (SA) shrimps exposed to high temperatures (salinity = 35 ^{0}/oo). ∞ = no mortality.

Temp (°C)	MTS (hrs)		% survival	
	PL	SA	PL	SA
26,1	∞	-	100	-
28,0	∞	-	100	-
30,0	>144	∞	91,7	100
30,9	>144	∞	75,0	100
32,0	47,9	114,8	8,3	20,8
33,0	17,0	31,6	0	0
33,8	-	9,7	-	-

b. Tolerance to low temperatures

In a pilot experiment to determine the effect of low temperatures on shrimps, 72 post-larvae, previously acclimated to 20°C for nine days, were placed in test troughs containing full strength sea water and then transferred to a refrigerated water bath which reduced the water temperature from 16,7 to 0°C in 6,5 hours. Batches of six shrimps were removed at various temperatures, transferred to a recovery tank at room temperature and checked for survival after 12 hours.

At 6°C the shrimps were largely inactive and at 3°C most were lying on their backs. At 2°C they showed no response to touch, but the six shrimps transferred from this temperature to the recovery tank had all revived after 12 hours. At 1,5°C, five out of six shrimps recovered, at 0,5°C, six out of six and at 0°C, four out of six survived.

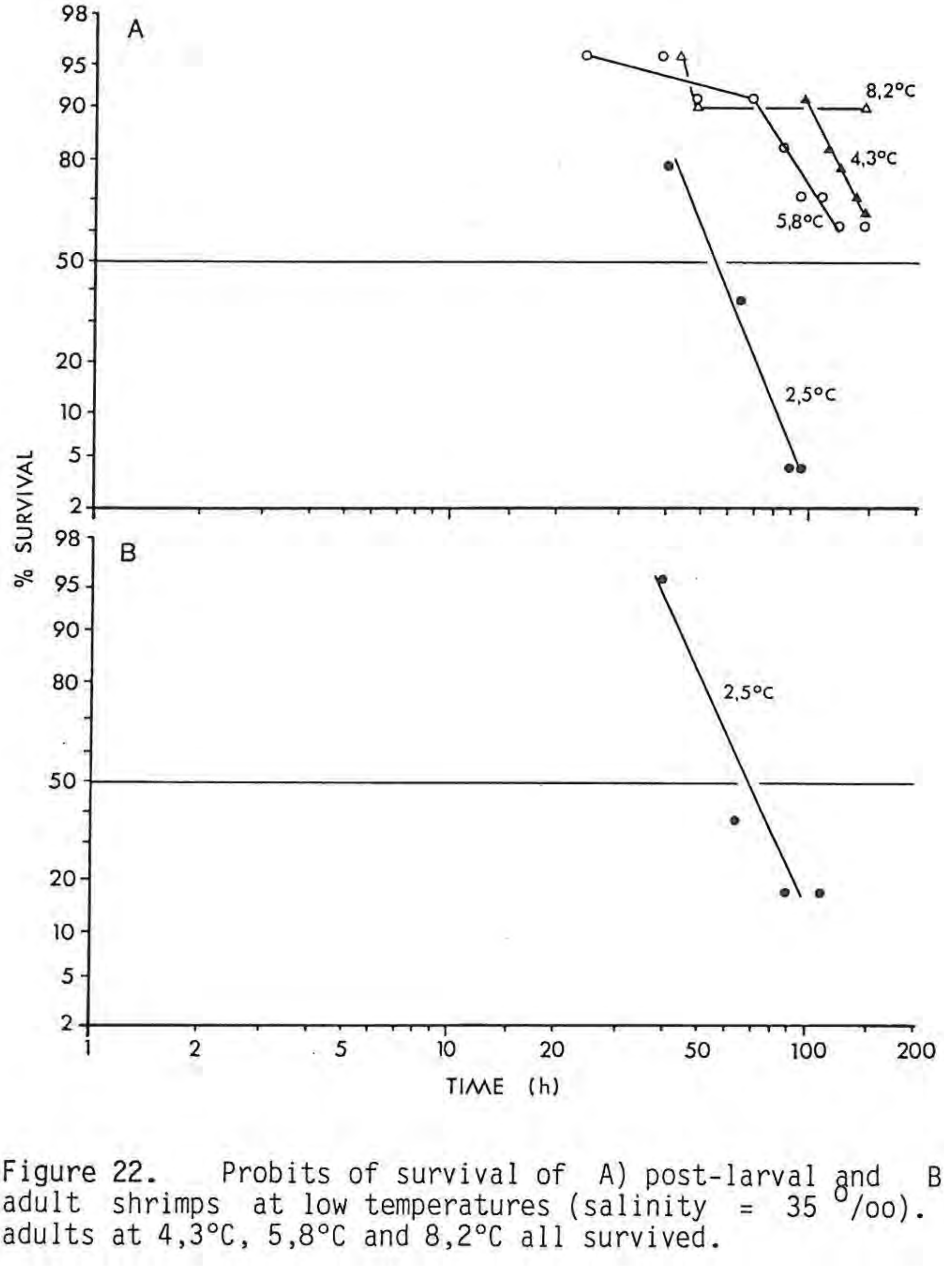

Figure 22. Probits of survival of A) post-larval and B) sub-adult shrimps at low temperatures (salinity = 35 ^{0}/oo). Sub-adults at 4,3°C, 5,8°C and 8,2°C all survived.

P. pacificus can clearly withstand low temperatures for short periods of time. To determine how long they can survive these conditions, samples of post-larvae (CL 2,2 ± 0,2 mm) and sub-adults (CL 6,1 ± 0,6 mm) were exposed to temperatures of 2,5, 4,3, 5,8 and 8,2°C. Shrimps used in the experiment were collected in July (winter acclimated) and kept in holding tanks at room temperature until used (maximum holding time = 1 month). Temperatures in the holding tanks varied between 13 and 16°C. The experiments were carried out in a refrigerated incubator. Since only one such incubator was available, experiments at the various temperatures had to be carried out in succession.

The results are shown in Figure 22 and Table 4. Shrimps were largely inactive and very few fed at these low temperatures. Both post-larvae and sub-adults were intolerant of 2,5°C. Post-larvae died earlier than sub-adults at this temperature (MTS 55 and 70 hours

Table 4. MTS and percentage survival (after 144 hrs) of post-larvae and sub-adults exposed to low temperatures (salinity = 35 ^{o}/oo).

Temp (°C)	MTS		% Survival	
	PL	SA	PL	SA
2,5	55	70	4,2*	12,5*
4,3	>144	∞	66,6	100,0
5,8	>144	∞	62,5	100,0
8,2	>144	∞	91,6	100,0
10,0**	>144	∞	54,2	100,0

* percentage survival at 96 hrs when this particular experiment was terminated.

** these shrimps previously acclimated to 20°C.

respectively). Sub-adults all survived at temperatures of 4,3°C and higher, whereas some mortality occurred amongst post-larvae at 4,3°C, 5,8°C and 8,2°C. Post-larvae are thus less tolerant of cold than are sub-adults.

The MTS and percentage survival of a batch of post-larvae and sub-adults previously acclimated to 20°C and then transferred to 10°C has been included in Table 4. The high mortality (46 %) suffered by the post-larvae demonstrates the adverse effect on them of a sudden drop in temperature. Sub-adults were apparently not affected by this temperature change.

c. Tolerance to high salinities

Tolerance of shrimps to high salinities was determined by exposing them to slowly increasing salinities. Twenty-four post-larval (CL 2,2 ± 0,2 mm) and 24 sub-adult (CL 5,7 ± 0,5 mm) shrimps were placed in water at 34 $^{o}/oo$ held at 15,5°C in a water bath. The test troughs were not covered and an electric fan was used to accelerate evaporation. Salinity was allowed to increase at a mean rate of 3,6 $^{o}/oo$ per day. Controls were kept in sea water (34 to 36 $^{o}/oo$). The water in each trough was replaced with clean water of the same salinity every three days.

At salinities above 52 $^{o}/oo$, shrimps became very quiescent, but still responded with a violent flick of the abdomen when touched. Very few fed above this salinity.

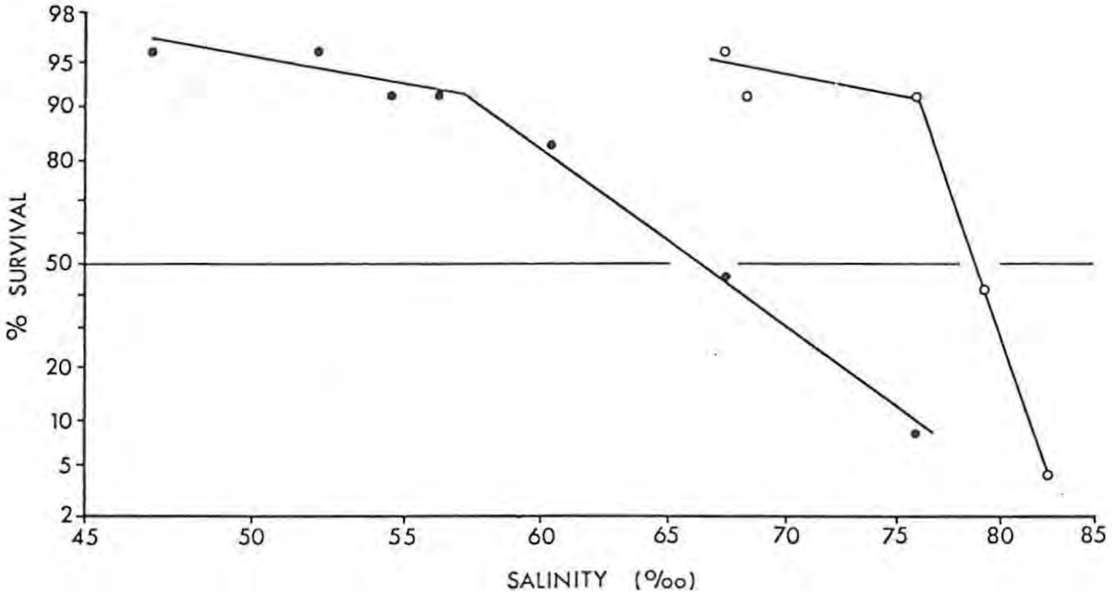

Figure 23. Survival of post-larval (●) and sub-adult (○) shrimps at slowly increasing salinities (temperature= 15,5°C). Percentage survival plotted on probit scale.

The percentage of shrimps alive at each examination was plotted on a probit scale against the log of the salinity of the water at that time (Figure 23). The median lethal salinity (i.e. the salinity required to kill 50 % of the population) was 66 $^{0}/oo$ for post-larvae and 78 $^{0}/oo$ for sub-adults. Thus sub-adults were considerably more resistant to high salinities than post-larvae.

d. Tolerance to low salinities

i. Stage 4 and 5 zoeae

Salinity tolerance experiments on stage 4 and stage 5 zoeae were carried out in 500 mℓ glass beakers at room temperature (19 to 23°C) under natural photoperiod conditions. The water was aerated and the beakers covered with plastic to reduce evaporation. Shrimps were fed *Artemia* nauplii and the water was changed on the third day. Ten shrimps were used in each trial.

Initially 10 stage 4 zoeae each were exposed to 20, 14 and 10 $^{0}/oo$. After 24 hours, no deaths had occurred at 20 or 14 $^{0}/oo$. These shrimps (still stage 4) were then transferred to 10 and 5 $^{0}/oo$ respectively. Thus the 24 hours spent at the higher salinities may be regarded as acclimation periods. The shrimps were examined under a microscope periodically and the experiment terminated when stage 6 zoeae began appearing in the beakers.

The results are shown in Figure 24. More than 50 % of shrimps exposed to 10 $^{0}/oo$ without prior acclimation, died within the first 10

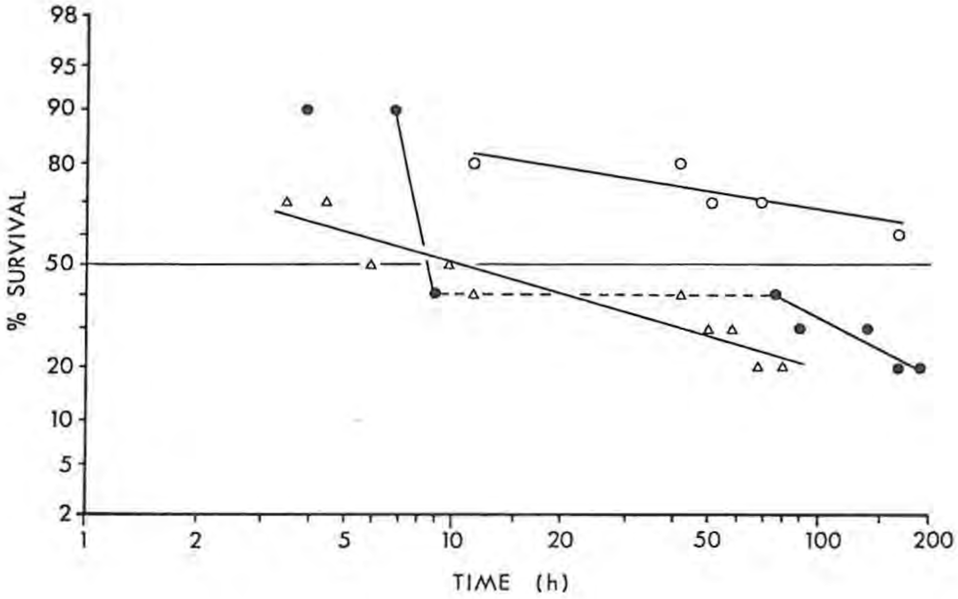

Figure 24. Probits of survival of stage 4 zoeae transferred directly from sea water to 10 ^{0}/oo (●), acclimated to 20 ^{0}/oo for 24 hrs and then exposed to 10 ^{0}/oo (o), or acclimated to 14 ^{0}/oo for 24 hrs and then exposed to 5 ^{0}/oo (△) (temperature 19 to 23°C) .

hours, after which mortality was gradual. All surviving shrimps at 91,5 hours were still stage 4 zoeae, but after 193 hours, the remaining two shrimps had moulted to stage 5.

Shrimps previously acclimated to 20 ^{o}/oo for 24 hours fared better in 10 ^{o}/oo. Six of the seven shrimps surviving through to 70,5 hours were stage 5 zoeae and after 173 hours, all seven shrimps were still alive and had moulted through to stage 6. Stage 4 zoeae exposed to 5 ^{o}/oo following acclimation to 14 ^{o}/oo had an MTS of 10,7 hours (Figure 24). The two shrimps alive after 70,5 hours were both still stage 4.

A further batch of 16 stage 4 zoeae was transferred to 14 ^{o}/oo and left for eight days after which the 11 surviving shrimps had all moulted through to stage 6. Thus, at 14 ^{o}/oo, 70 % of the shrimps developed successfully from stage 4 to stage 6 zoeae. At 10 ^{o}/oo, mortality was high and development retarded, but, if larvae were previously acclimated to 20 ^{o}/oo for 24 hours, their tolerance was similar to that of larvae in 14 ^{o}/oo. At 5 ^{o}/oo, even after previous acclimation, mortality was high and development severely retarded.

ii. Stage 6 zoeae

Stage 6 zoeae were collected in summer and tested immediately. Between 15 and 24 shrimps each were exposed to 5, 10 and 14 ^{o}/oo at a temperature of 15°C. Controls were held in 35 ^{o}/oo at the same temperature. The ability of the larvae to survive lowered salinities and to moult to the post-larval stage is shown in Table 5.

Table 5. Tolerance of stage 6 zoeae to low salinities (temperature = 15°C).

Salinity (^{o}/oo)	% shrimps which: died without moulting	died immediataly after moulting	moulted successfully
5	100,0	0	0
10	43,5	30,4	26,1
14	6,7	0	93,3
35	0	4,2	95,8

Most of the control shrimps moulted to post-larvae within 24 hours of the start of the experiment, the last ones moulting within 48 hours. Seventy-one percent of those exposed to 14 ^{o}/oo moulted within 24 hours, the remainder within the following 52 hours.

At 10 ^{o}/oo, moulting was delayed considerably with the last moult occurring at 115 hours. Only 26,1 % of these moults were successful (Table 5). All shrimps exposed to 5 ^{o}/oo were dead within three hours. Stage 6 zoeae are thus very susceptible to salinities of 10 ^{o}/oo and lower but appear able to tolerate 14 ^{o}/oo and above. Their salinity tolerance is similar to that of stage 4 and stage 5 zoeae.

iii. Post-larvae and sub-adults

Tolerance to low salinities of post-larval shrimps (CL 2,3 ± 0,2 mm)

4.29

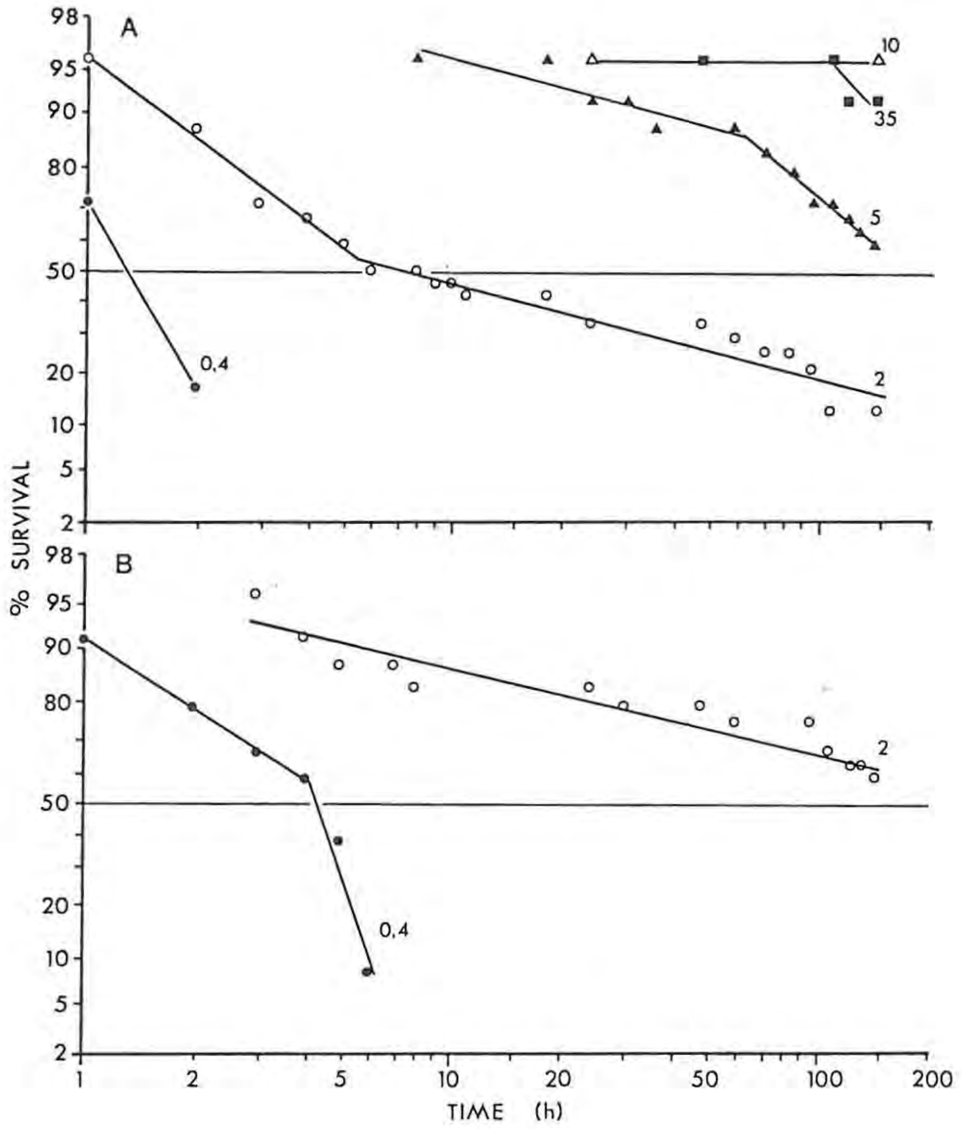

Figure 25. Probits of survival of A) post-larval and B) sub-adult shrimps at low salinities (no acclimation; temperature = 15°C). Salinity in °/oo shown against each curve. Sub-adults at 5 °/oo and higher all survived.

was compared with that of a mixture of juveniles and sub-adults (CL 4,8 ±0,5 mm). Although mixing of the latter two stages was unintentional, it was not considered a problem since the only morphological distinction between juveniles and sub-adults appears to be the presence of an *appendix masculina* in the males. The important factor in the comparison is the size difference. For convenience, the group of larger shrimps will be referred to as sub-adults.

Shrimps were collected in spring and held in the aquarium at temperatures of 17 to 18°C for about 10 days before being tested. They were then exposed to salinities of 0,4 (freshwater), 2, 5, 10 and 14 $^{o}/oo$ respectively at a temperature of 15°C. Controls were held in 35 $^{o}/oo$ at the same temperature.

Table 6. MTS and percentage survival (after 144 hrs) of post-larvae (PL) and sub-adults (SA) at low salinities (temperature = 15°C). FW = fresh water.

Salinity ($^{o}/oo$)	MTS (hrs)		% survival (144 hrs)	
	P.L.	S.A.	P.L.	S.A.
0,4 (FW)	1,3	4,3	0	0
2,0	7,4	>144	12,5	58,3
5,0	>144	∞	58,3	100
10,0	>144	∞	95,8	100
14,0	∞	∞	100,0	100
35,0	>144	∞	91,7	100

The results are shown in Figure 25 and Table 6. Post-larvae all died within three hours and sub-adults within seven hours of transfer to freshwater (0,4 $^{o}/oo$). Sub-adults tolerated a salinity of 2 $^{o}/oo$, but post-larvae only tolerated 5 $^{o}/oo$ and higher. There was little or no mortality in either size group at salinities above 5 $^{o}/oo$.

e. Effect of temperature and acclimation on tolerance to low salinity.

The response of an organism to levels of salinity may be greatly affected by the levels of temperature to which it is simultaneously exposed (Kinne, 1963; 1964). To determine the effect of temperature on the ability of P. pacificus to tolerate low salinities, shrimps were exposed to combinations of these two factors within the temperature range that the shrimps are likely to encounter naturally.

Estuarine animals are not normally subjected to such sudden changes in salinity as were the shrimps in the previous experiment, except under flood conditions. The more usual situation would be for shrimps to move down a salinity gradient as they move further up the estuary. Shrimps used in this experiment were therefore gradually acclimated to a salinity of 5 $^{o}/oo$ (as described under 'Methods') before being exposed to a temperature/salinity combination. Temperature was held constant at 20°C during acclimation.

Table 7. Design of experiment to test the tolerance of post-larvae (PL) and sub-adults (SA) to combinations of temperature and salinity.

Part	C.L. of shrimps	Test salinity ($^{o}/oo$)	Test temp. (°C)
1	2,2 ± 0,2 mm (PL)	1, 2, 4	10, 15, 20
2	2,9 ± 0,6 mm (PL)	1, 2, 4	21, 25, 30
3	5,5 ± 0,5 mm (SA)	1, 2, 4	10, 15, 20
4	5,3 ± 0,4 mm (SA)	1, 2, 4	20, 25, 30

The experiment was conducted in four parts as shown in Table 7. The acclimation temperature (20°C) was included in each part as a control. In the second part (Table 7), this temperature rose to 21°C owing to malfunction of the C.E. Room. To determine the effect of temperature *per se* on the shrimps, a batch of each size class was exposed to 35 ^{o}/oo at each temperature. Data from these shrimps were only used to aid interpretation of the results at low salinities and were not included in the data analysis.

Since 50 % mortality was not reached in most of the experiments involving sub-adults, MTS values could not be used as a basis for comparison. Percentage survival therefore had to be used. To increase the reliability of this method, percentage survival after 24, 72 and 144 hours was considered. These values are shown in Figures 26 and 27 for each temperature/salinity combination. Contours enclosing 50 % and 90 % survival have been drawn in to facilitate interpretation.

The two sets of data at ± 20°C show close agreement except at 1 ^{o}/oo where differences are greater particularly in the post-larval group. This indicates that 1 ^{o}/oo is a critical salinity; any slight variation in salinity around this point affects survival markedly.

Acclimation improved the tolerance of both post-larval and sub-adult shrimps to low salinity. Only 12,5 % and 58,3 % of post-larvae and sub-adults, respectively, survived a salinity of 2 ^{o}/oo (T=15°C) for 144 hours without previous acclimation (Table 6). Corresponding figures for acclimated shrimps are 50 % and 87,5 % (Figures 26C and

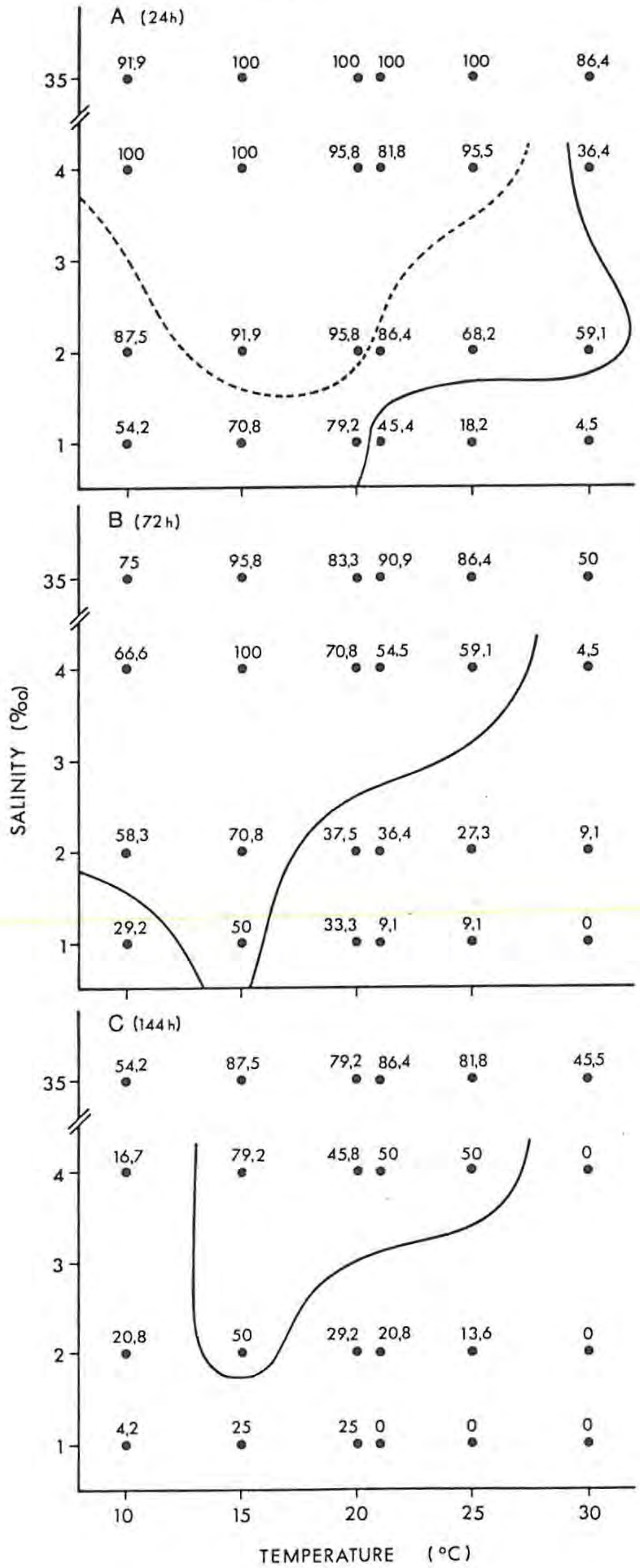

Figure 26. Percentage survival of post-larval shrimps at combinations of temperature and salinity after A) 24 hrs B) 72 hrs and C) 144 hrs. Shrimps previously acclimated to 5 ^{o}/oo at 20°C. Contours enclosing 50 % (——) and 90 % (---) survival are shown.

27C). Sub-adults even tolerated a salinity of 1 ^{0}/oo following acclimation.

An analysis of variance was carried out to determine the significance of temperature and salinity effects individually on the shrimps, and to ascertain whether there was a significant interaction between these two factors. The results of the analysis are shown in Table 8.

Table 8. Analysis of variance on effects of temperature (T) and salinity (S) combinations (Table 7) on survival of post-larvae and sub-adults previously acclimated to 5 ^{0}/oo at 20°C (based on percentage survival after 24, 72 and 144 hrs).

Source (^{0}/oo)	DF	F statistic					
		Post-larvae			Sub-adults		
		24 hr	72 hr	144 hr	24 hr	72 hr	144 hr
T	4	19,4	27,5	20,7	1,9*	8,3	13,7
S	2	41,0	24,1	22,6	18,7	16,2	17,7
TXS	8	2,9	1,6*	3,2	1,9*	1,5*	0,5*
Error	15						

* not significant ($p > 0{,}05$)

In post-larvae, temperature and salinity both affected survival significantly ($p < 0{,}001$). Interaction between temperature and salinity had a significant effect at 24 hours ($p < 0{,}05$) and 144 hours ($p = 0{,}025$) (Table 8). These shrimps were intolerant of a combination of high temperature and low salinity even for short periods of time (24 hours) (Figure 26A). Low temperature (10°C) combined with low salinity ($\leqslant$ 4 ^{0}/oo) resulted in high mortality after 144 hours

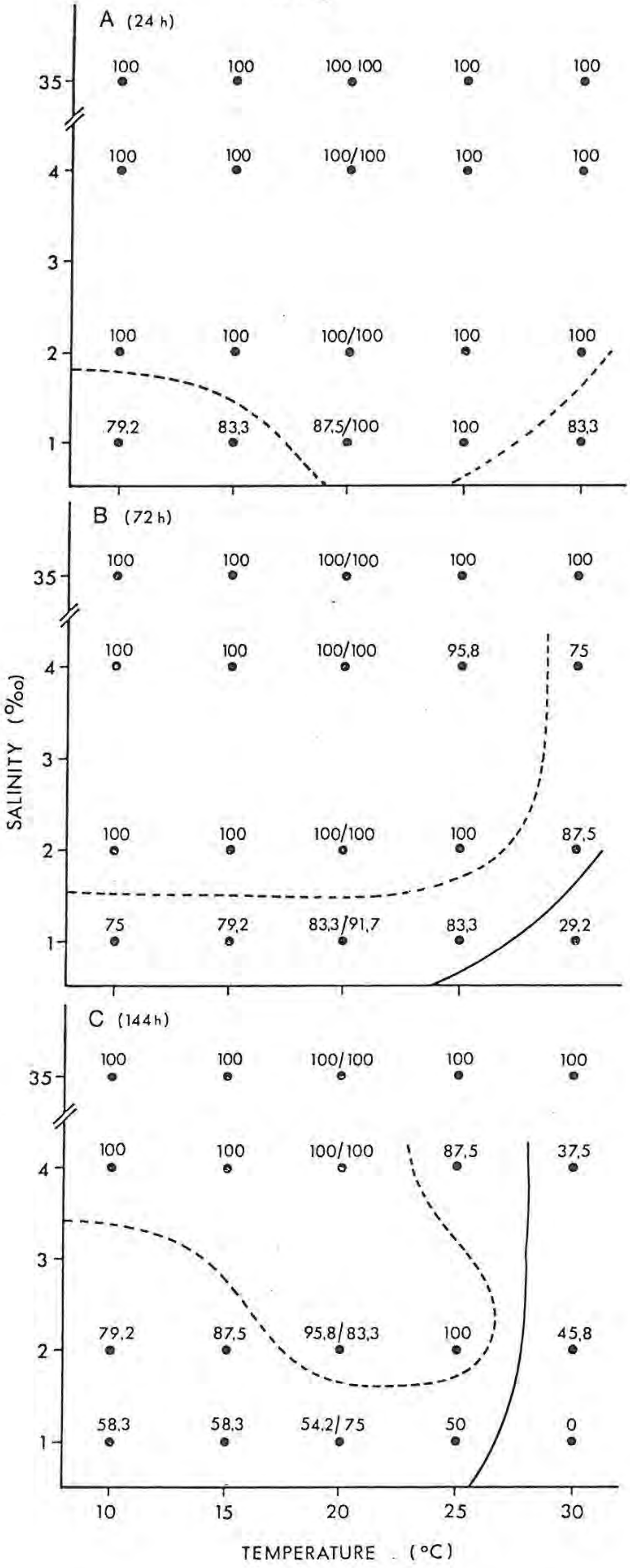

Figure 27. Percentage survival of sub-adult shrimps at combinations of temperature and salinity after A) 24 hrs B) 72 hrs and C) 144 hrs. Shrimps previously acclimated to 5 °/oo at 20°C. Contours enclosing 50 % (——) and 90 % (---) survival are shown.

(Figure 26C). Survival in the control group at 10°C was also low (54,2 %) compared with that of shrimps at higher temperatures. Survival at low salinities was best at 15°C (Figure 26C).

Sub-adults were tolerant of wide temperature and salinity ranges, but were unable to withstand a combination of high temperature and low salinity for extended periods of time (Figure 27C). Both temperature and salinity had a significant effect on the shrimps, although temperature was not important in the early stages of the experiment ($p > 0,1$ at 24 hours) (Table 8). There was no significant interaction between temperature and salinity at any stage during the experiment.

f. Effect of temperature and salinity on moulting

Although the effect of temperature and salinity on moulting was not directly investigated, any moults which occurred during tolerance experiments were recorded and these data were collated to see whether any significant trends became apparent. The number of shrimps moulting in each treatment or control group during an experiment was used as an indicator of moulting frequency under those conditions. Moulting frequency of shrimps in an experiment will depend not only on the conditions of the experiment, but also on the time which has lapsed since their previous moult. Moulting frequencies should therefore not be compared between experiments without first comparing moulting frequency of the controls in each experiment.

Since test animals were isolated, the subsequent fate of each newly moulted individual could be recorded and the success or failure of each moult determined. Hill (1971) found that *Upogebia africana* were still extremely sensitive to low salinities 24 hours after moulting, probably due to increased permeability to water during the moult phase. Lockwood & Inman (1973) report increased permeability to water in the amphipod *Gammarus duebeni* and the isopod *Idotea linearis* during the moult phase, but found that it began to decline after 24 to 48 hours. The success of a moult in the present experiments was therefore determined by the ability of a shrimp to survive for at least 48 hours after moulting. If an animal showed ill effects within 48 hours and subsequently died without recovering, the moult was considered unsuccessful.

Table 9. Effect of temperature on frequency and success of moulting in post-larval and sub-adult shrimps (Salinity = 35 $^{0}/oo$). % success = % survival after attempted moult; C = control

Temp (°C)	Post-larvae		Sub-adults	
	% moult	% success	% moult	% success
2,5	8,3	0	0	-
4,3	4,2	100	0	-
5,8	4,2	100	4,2	100
8,2	12,5	100	8,3	100
19,7 (C)	54,2	100	45,8	100
26,1	70,8	100	-	-
28,0	58,3	100	-	-
30,0	37,5	88,9	45,8	100
30,9	54,2	92,3	62,5	100
32,0	37,8	70,0	41,7	60
33,0	12,5	66,7	12,5	33,3
33,8	-	-	0	-

Frequency of moulting was considerably reduced in both post-larvae and

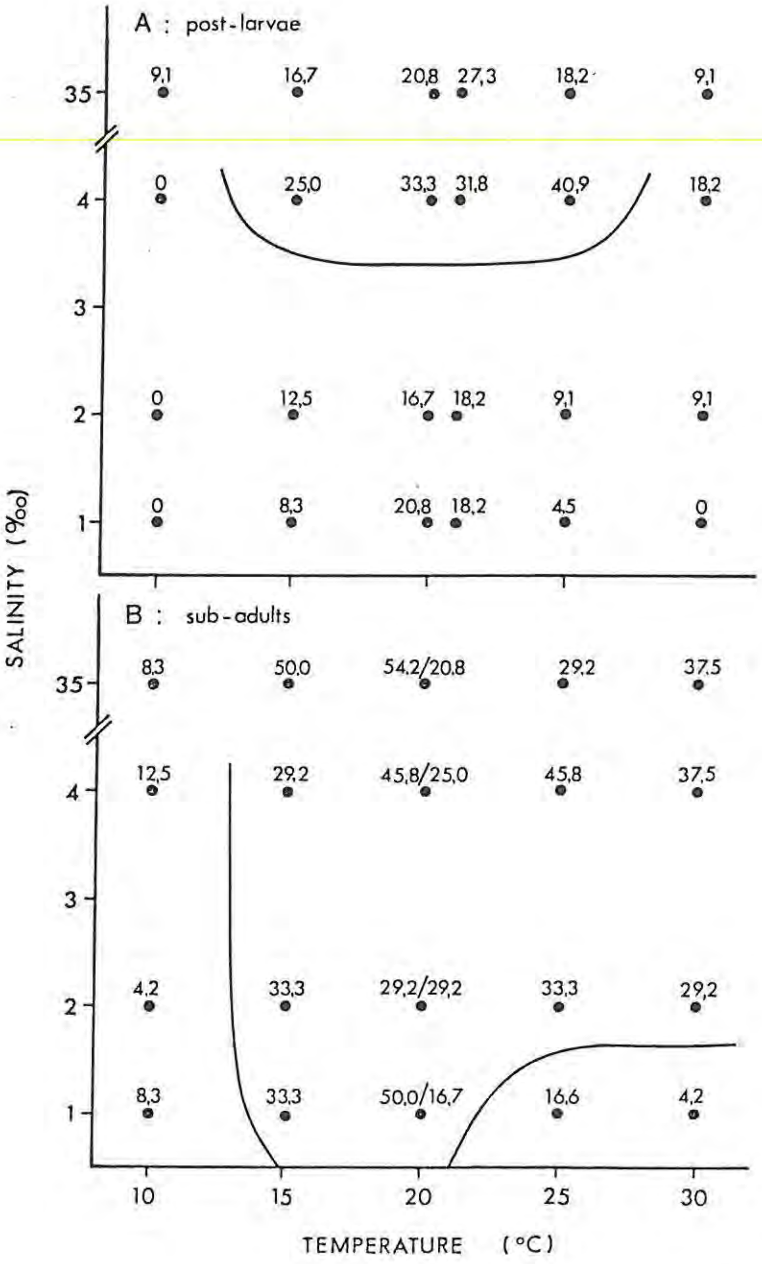

Figure 28. Percentage A) post-larval and B) sub-adult shrimps which moulted at combinations of temperature and salinity. Shrimps previously acclimated to 5 ‰ at 20°C. Contours enclosing 20 % moulting frequency are shown.

sub-adults at high (≥33°C) and low (≤8°C) temperatures (Table 9). At high temperatures the number of shrimps moulting was reduced by the early mortality of the shrimps. Those shrimps which did moult at low temperatures survived, whereas moulting success was reduced at high temperatures (≥32°C).

The effect of low salinity on the moulting of non-acclimated shrimps is shown in Table 10. At salinities of 0,4 and 2 ^{o}/oo (15°C), moulting was inhibited in post-larvae and reduced in sub-adults. Sub-adults which did moult died. Moulting frequency in post-larvae at 5 ^{o}/oo was similar to that of the controls (35 ^{o}/oo) but success was low (43,8 %)(Table 10). All sub-adults that moulted at 5 ^{o}/oo survived. Above this salinity frequency and success of moulting in both size classes were similar to that of the controls.

Table 10. Effect of salinity on frequency and success of moulting in post-larval and sub-adult shrimps (temperature = 15°C). FW = fresh water.

Salinity	Post-larvae		Sub-adults	
(^{o}/oo)	% moult	%success	% moult	% success
0,4 (FW)	0	-	4,2	0
2,0	0	-	16,7	0
5,0	66,6	43,8	20,8	100
10,0	62,5	100,0	37,5	100
14,0	58,3	100,0	45,8	100
35,0	58,3	100,0	41,7	100

Sub-adults exposed to slowly increasing salinities moulted successfully up to 56,3 ^{o}/oo. One further moult was recorded at

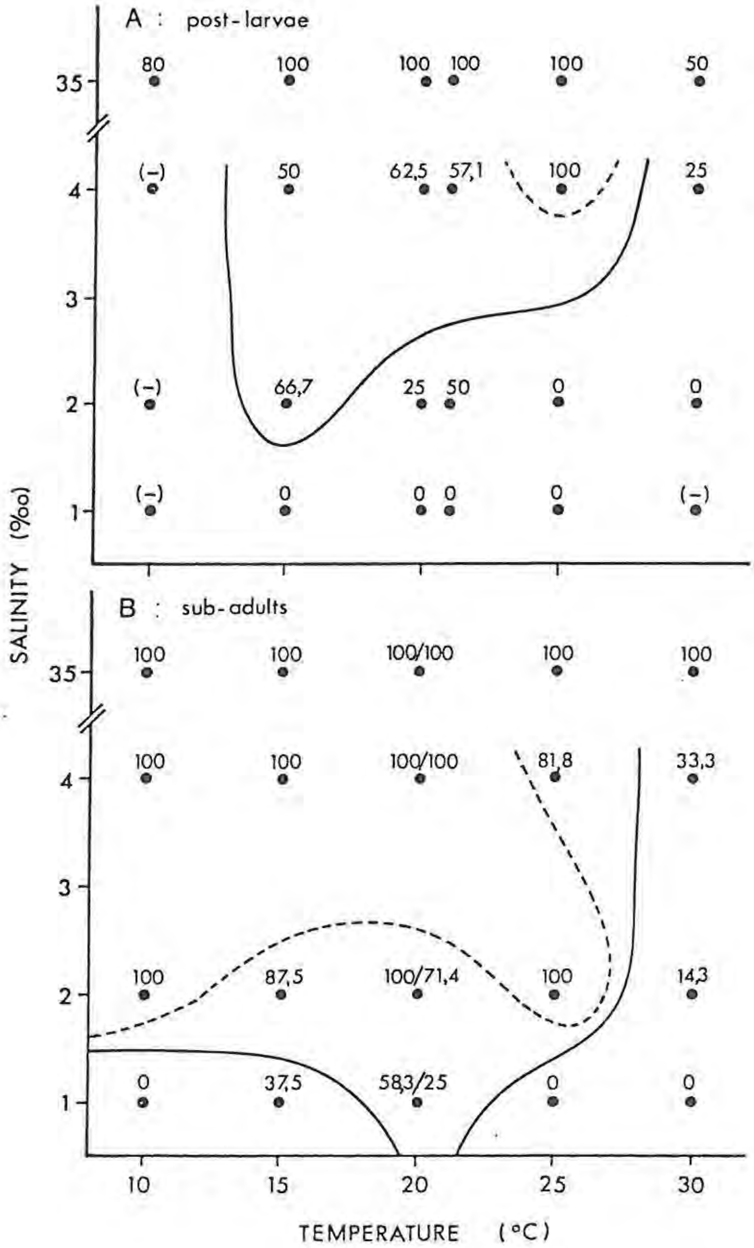

Figure 29. Percentage moults successful at combinations of temperature and salinity: A) post-larvae B) sub-adults. Shrimps previously acclimated to 5 ‰ at 20°C. Contours enclosing 50 % (——) and 90 % (---) success shown.

62,5 ^{o}/oo, but the shrimp died immediately. Moulting occurred successfully in post-larvae up to 54,6 ^{o}/oo. Several shrimps moulted after this but all died. The last moult occurred at 60,5 ^{o}/oo.

The combined effects of low salinities and a range of temperatures on frequency of moulting and moulting success in shrimps previously acclimated to 20°C and 5 ^{o}/oo are shown in Figures 28 and 29 respectively. Acclimation appeared to improve moulting success since acclimated post-larvae and sub-adults both moulted successfully at 15°C and 2 ^{o}/oo (Figures 29A & B) although moulting frequency was reduced (Figure 28A & B).

In post-larvae, moulting was completely inhibited under conditions of low temperature and salinity (10°C : 1, 2 and 4 ^{o}/oo) and was considerably reduced at high temperatures and low salinities (25 and 30°C : 1 and 2 ^{o}/oo) (Figure 28A). While low salinities appeared to inhibit moulting of post-larvae, it is interesting to note that moulting frequency at 35 ^{o}/oo was consistently lower than at 4 ^{o}/oo. The reason for this is not known. Moulting was never completely inhibited in sub-adults but was also considerably reduced when low salinities were combined with low or high temperatures (10°C : 1, 2 and 4 ^{o}/oo; 25 and 30°C : 1 ^{o}/oo) (Figure 28B).

Moulting success in control groups was high (Figure 29), except in post-larvae at 30°C. The 50 % moulting success contours shown in Figure 29A & B are similar to the 50 % and 90 % survival contours in Figures 26C and 27B respectively. It appeared from this that the ability of shrimps to tolerate unfavourable conditions may be largely

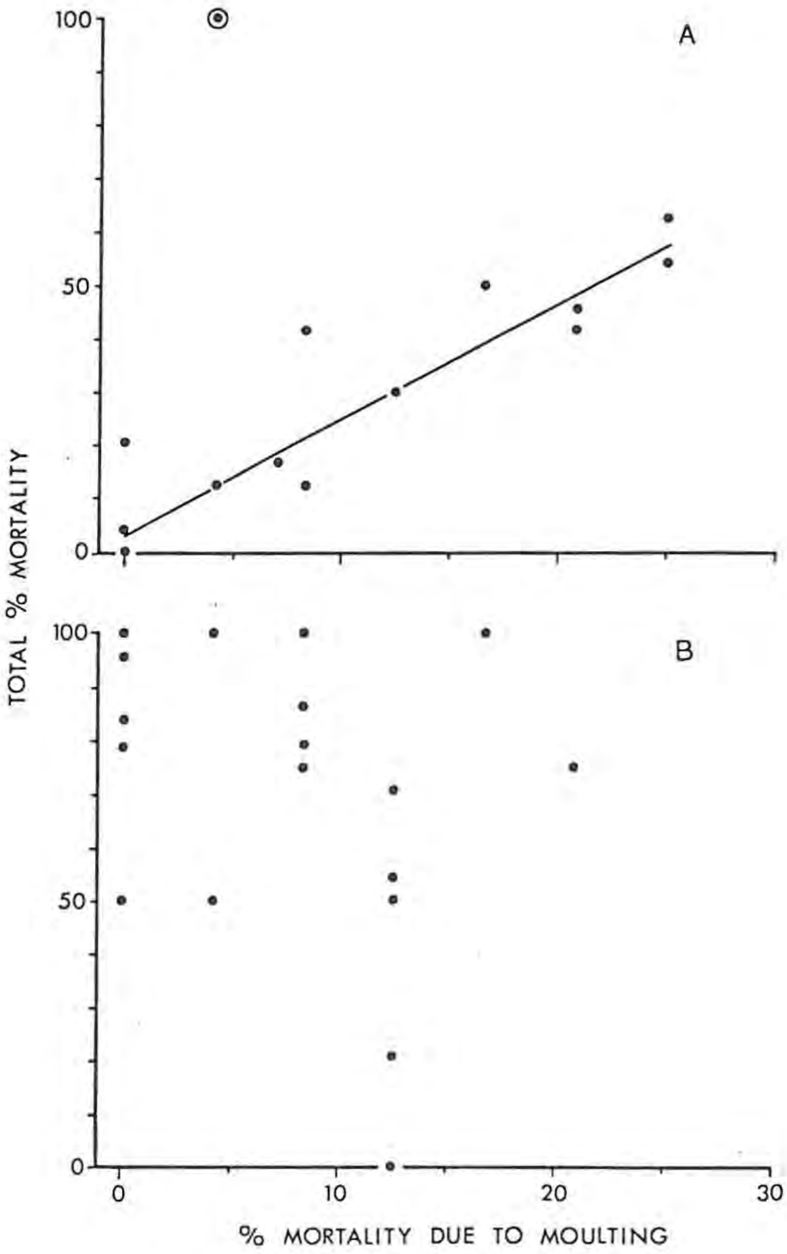

Figure 30. Correlation between total percentage mortality and mortality due to moult in shrimps at combinations of temperature and salinity: A) sub-adults B) post-larvae.

dependent on their ability to moult successfully. This idea was tested by plotting mortality due to moulting (as a percentage of the number of shrimps in each treatment) against the total mortality after 144 hours for each temperature/salinity combination. Correlation curves were fitted to the data and are shown in Figure 30A & B. The point representing sub-adults exposed to 30°C and 1 ^{o}/oo (circled in Figure 30A) is an obvious outlier and was omitted from the calculations.

There was a strong correlation ($r=0,926$; $p < 0,001$) between percentage sub-adults that died as a result of moulting and total sub-adult mortality under each set of conditions. The coefficient of determination ($r^2=0,858$) (Figure 30A) indicates that 85,8 % of the total mortality in the sub-adult populations can be attributed to unsuccessful moults. No such correlation existed in the post-larval populations (Figure 30B). Post-larvae are apparently very susceptible to adverse conditions of temperature and salinity, even in the intermoult phase. Although most sub-adults were able to withstand these conditions in the intermoult phase they were not able to survive a moult. Under the extreme conditions of 30°C and 1 ^{o}/oo, moulting was severely inhibited and sub-adult deaths were due to other causes.

An interesting observation arising from this study of moulting behaviour is that *P. pacificus* is able to delay moulting under adverse conditions (Figure 28, Tables 9 and 10). McLusky (1967) found that moulting frequency in the amphipod *Corophium volutator* was reduced at salinities below 5 ^{o}/oo and above 46 ^{o}/oo, and Hill (1971) reports a similar delay in moulting in *Upogebia africana* exposed to low salinities. This is obviously advantageous since animals are very susceptible to physiological stress during the moult phase.

Moulting cannot, however, be delayed indefinitely and, although animals may survive for extended periods under adverse conditions, if moulting cannot occur successfully, they will be prohibited from living under those conditions. Thus, McLusky (1967) found that the salinity tolerance range of C. volutator was reduced from 2 to 50 ^{0}/oo, to a range of 5 to 46 ^{0}/oo by inhibition of moulting at high and low salinities. Hill (1971) reports that, although U. africana can survive a salinity of 1,7 ^{0}/oo for a long time (MTS = 420 hours), it is not able to survive a moult at this salinity.

Distribution of animals within the estuary may thus be limited by the conditions required for successful moulting. This is thought to be the case for Crangon vulgaris (Hagerman, 1973) and Gammarus duebeni (Lockwood & Inman, 1973) and is probably also true for P. pacificus.

3.3. DISCUSSION

Maximum and minimum temperatures recorded in the Bushmans River estuary over an annual cycle (Figure 9A) were well within the range of temperatures tolerated by both post-larval and sub-adult shrimps (Figures 21 and 22). Temperatures of 30 to 32°C recorded in the study site at times may be stressful, particularly to post-larvae. The influx of cooler sea water during flood tides or the drop in air temperatures in the evening would ensure, however, that these conditions did not last longer than six to ten hours.

Although winter acclimated post-larvae survived well at 8,2°C (Figure 22), if transferred directly from 20°C to 10°C they suffered high mortalities (Table 4) indicating a susceptibility to sudden changes in temperature. Thorp & Hoss (1975) found that, at a salinity of 35 $^{0}/oo$, survival of Palaemonetes pugio and P. vulgaris was significantly lower in a cyclic regime (7 to 13°C) than in a constant 7°C regime. Shrimps in the study site are subjected to regular and often rapid temperature changes (Figure 10). This may explain the high loss of post-larvae and juveniles from the study site during the cooler months (Figure 17) since low temperature per se does not appear to be a problem.

The long term temperature tolerance range of P. pacificus under natural conditions is probably narrower than that observed under experimental conditions. Their sluggishness at temperatures below 10°C would render them easy prey and, since they did not feed at these low temperatures, they would eventually die of starvation. Cook & Achituv (in press) found that sub-adult P. pacificus did not feed at 10°C and report high mortalities amongst shrimps exposed to this temperature for 8 weeks. Sub-adults in the present study survived at 30,9°C, but the above workers report heavy losses of sub-adult shrimps held at 28°C for 15 weeks. They suggest that, at high temperatures, shrimps may become susceptible to other factors such as bacterial infection which would affect their survival rather than temperature alone.

The coast-wise distribution of *P. pacificus* in South Africa (Olifants River to Kosi Bay) is probably closely related to its temperature tolerance. On the west coast, inshore temperatures range from 13 to 16°C but may drop as low as 10°C when upwelling occurs (Day, 1974; Christensen, 1980). In west coast estuaries, winter temperatures of 10 and 11°C have been recorded (Day, 1981b). These temperatures are within the short-term tolerance range of *P. pacificus* although a sudden drop in temperature as a result of upwelling may cause mortalities especially amongst smaller individuals. If very low temperatures persist, heavy mortalities will probably result. Cook & Achituv (in press) report low numbers of *P. pacificus* in tidal pools on the west coast. In Langebaan lagoon they have found large numbers of shrimps in summer, but in winter they are scarce.

P. pacificus is reported to be common on the Natal coast (Day & Morgans, 1956) where summer temperatures range from 25 to 28°C (Christensen, 1980). This species has also been found in parts of the Kosi Bay system (Broekhuysen & Taylor, 1959), and large numbers have been reported in St Lucia (Day *et al*, 1954) and Richards Bay (Millard & Harrison, 1954) where summer temperatures of 28 to 30°C are common. These temperatures are approaching the lethal limit as determined for *P. pacificus* in the present study, but gradual acclimation to high temperatures would probably increase their upper tolerance limit. Shrimps, being nektonic, could migrate to deeper water when temperatures in the shallows become excessive, but no evidence of this is available.

From this study it is apparent that *P. pacificus* is also able to tolerate a wide range of salinities. The upper limits of their salinity tolerance were 66 ^{o}/oo (post-larvae) and 79 ^{o}/oo (sub-adults), but in view of the fact that feeding stopped at about 52 ^{o}/oo and that no successful moults occurred at salinities above 56 ^{o}/oo, it is doubtful that these shrimps would survive long periods at salinities higher than 56 ^{o}/oo.

In Lake St Lucia, where reversed salinity gradients occur periodically, *P. pacificus* may be expected to occur in areas of high salinity. Millard and Broekhuysen (1970), however, give its recorded salinity range in St Lucia as 28 to 37,6 ^{o}/oo. Factors other than salinity appear to be limiting its distribution in this system.

Although sub-adults tolerated salinities as low as 1 ^{o}/oo following acclimation to 5 ^{o}/oo and 20°C (Figure 27C), low moulting success (Figure 29B) would preclude them from living at this salinity. Moulting success at 2 ^{o}/oo was considerably higher and this probably represents the lower limit of salinity tolerance of sub-adults.

Post-larvae were less tolerant of low salinities than sub-adults. Their survival at 1 ^{o}/oo was low (Figure 26C) and they were unable to survive a moult at this salinity (Figure 29A). Post-larvae only tolerated salinities of 4 ^{o}/oo and lower at temperatures of about 15°C (Figure 26C). They would therefore be better able to penetrate the upper reaches of the estuary during the cooler months than in summer. This could be partly responsible for the seasonal changes in juvenile loss from the study site (Figure 17).

P. pacificus collected during the survey of the Bushmans River estuary (Figure 9) were therefore well within their range of salinity tolerance and sub-adults are probably able to live even further up the estuary than recorded here. P. Jackson and R. Liversidge (unpublished data) report finding *P. pacificus* at Ebb and Flo in the Bushmans River estuary during a survey conducted in 1950, and Grindley (1976, in Grindley, 1981) found these shrimps in plankton samples throughout the Swartkops River estuary. Water salinities and shrimp sizes are unfortunately not known in either case.

Zoeal stages 4 to 6 are unable to tolerate low salinities (< 10 ^{o}/oo). It is highly likely that the earlier larval stages are even more susceptible to low salinities, since tolerance was found to improve with age. Thus, if breeding did occur in the estuary, it would be limited to the lower reaches. This has been found to be the case for *Callianassa kraussi* (Forbes, 1978). Although a population of this species has been found at a salinity of 1 ^{o}/oo, larval stages require salinities greater than 20 ^{o}/oo for their development. Breeding is therefore restricted to high salinity areas in the estuary. The first zoeal stage of *Scylla serrata* is susceptible to salinities of 17,5 ^{o}/oo or lower. Breeding in this species, however, occurs at sea (Hill, 1974), as appears to be the case for *P. pacificus*.

A flood in the Bushmans River estuary in July 1983 had a marked effect on the shrimp population in the study site (Figure 13) and, presumably, in the rest of the estuary. Post-larvae were affected more than sub-adults. This is not surprising since the latter are more tolerant of low salinities than post-larvae, especially when the salinity change is sudden (Table 6). After the flood, salinities of 0,4 $^{0}/oo$ and lower were measured in the study site and in the main channel opposite the slipway. These salinities have been shown to be lethal even to sub-adults (Figure 25, Table 6). The presence of a salt wedge in the channel and the slight elevation of salinities in the study site during flood tides obviously enabled some shrimps to survive. In view of the low salinities (± 1 $^{0}/oo$) recorded throughout the water column in the middle and upper reaches of the estuary on 13.8.83 (Figure 7C), it is doubtful whether any shrimps in these areas survived.

It was unfortunately not possible to monitor the recovery of shrimps in the study site after the flood. Although a salinity gradient was soon restored in the estuary (Figure 7C and D), salinity is not the only factor which affects estuarine animals. Palmer (1980) suggests that recolonization of the Bushmans River estuary by _Nassarius kraussianus_ following severe flooding in 1979, was probably related to the recovery of the substratum and vegetation rather than to salinity or temperature.

While the nature of the sediments would be less important to a nektonic animal such as _P. pacificus_, there is evidence that vegetation is important to this species. Hanekom (1982), comparing the abundance of various nektonic organisms occurring in _Zostera_ beds with the abundance of these same species over a bare, muddy substratum in the Kromme River estuary, found that 97 % of the total number of _P. pacificus_ collected were from the _Zostera_ beds (calculated from his

Table 5.2). After the flood of July 1983 (present study), Zostera in the study site in the Bushmans River estuary was almost completely covered by a layer of soft mud. Even though salinities in the study site had returned to normal (35 $^{o}/oo$) by 27.8.83, P. pacificus numbers were even lower then than they were immediately after the flood (30.7.83) (Figure 13) when salinities were very low (0,41 to 5 $^{o}/oo$). Thus conditions other than salinity were apparently still unfavourable in the study site. Severe floods having long term effects on the estuarine vegetation may thus have long term effects on the shrimp population.

The retention of a marine breeding phase could be advantageous to an animal such as P. pacificus. Sensitive larval stages are assured of a stable environment in which to emerge and develop, and breeding animals are protected from decimation by a crisis such as a flood. Replenishment of the estuarine population after such a crisis would then be effected by recruitment from the marine environment rather than survivors in the estuary being responsible for re-establishing the population. Perennial breeding would, of course be an added advantage as this ensures a continual supply of recruiting stages.

The ubiquity and sheer abundance of P. pacificus in South African waters bear witness to the fact that it is a highly successful species. Its ability to use both the stable marine environment and the fluctuating but highly nutritious estuarine environment to its advantage, has no doubt contributed to this success. While studies to date have tended to focus on the estuarine or inshore phase of its life cycle, little is known about the marine phase. Future work could profitably be directed towards investigations of spawning activity and larval dispersal and the way in which these factors determine estuarine recruitment patterns.

APPENDIX A

The volume of water filtered during each 5 minute trawl was calculated as follows. If the net was fixed in the water column, the volume of water filtered would be the product of the area of the net opening, the velocity of the water and the time for which the net was in the water:

i.e. $V = II\ r^2 \times s \times t$ ....(1)

where V = volume of water filtered

r = radius of net

s = water velocity

t = time

Since the net was pushed through the water during sampling, an additional factor came into operation, namely boat speed. The term 's' in the above equation is therefore affected by 2 factors, boat speed (b) and current speed (c). If the boat is moving against the current, then the velocity of the water in relation to the net will be the sum of the boat speed and current speed. When the boat is moving with the current, the velocity of the water in relation to the net will be the difference between the boat speed and the current speed:

i.e. $s = b + c$ (boat moving against current)

$s = b - c$ (boat moving with current)

Thus, applying these to equation 1:

$V = IIr^2t(b+c)$ (boat moving against current) 2

or $V = IIr^2t(b-c)$ (boat moving with current) 3

Since current speed varies with state of the tide, depth, wind etc. it was preferable to eliminate this variable from the equation. This was done as follows. If, during a single trawl, the net was pushed for a time against the current and then turned and pushed with the current, the total volume of water filtered would be the sum of the volume filtered against the current and the volume filtered with the current i.e. from equations 2 and 3

$$V\ (\text{total}) = (IIr^2t_a(b+c))+(IIr^2t_w(b-c))$$

where t_a = trawling time against current

t_w = trawling time with current

Now, if the trawling time with and against the current are made equal

i.e. $t_a = t_w = t$

then

$$\begin{aligned} V\ (\text{total}) &= IIr^2(t(b+c)+t(b-c)) \\ &= IIr^2(tb+tc+tb-tc) \\ &= 2IIr^2tb \ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 4 \end{aligned}$$

The only unknown in the above equation is boat speed (b). To measure this, two markers were set up 100m apart. The time taken to cover the distance between the markers was then measured with the throttle of the motor at a fixed setting and the net at various depths. Fifteen trawls were made with the current and fifteen against. The total distance travelled was then divided by the total travelling time to obtain the mean boat speed. This worked out to be 83,4 mmin^{-1} for the particular throttle speed chosen (this throttle speed was used in all subsequent trawls). If trawling time was 5 minutes (2,5 minutes each way) and radius of the net opening 0,15 m, then, from equation 4:

$$V\ (\text{total}) = 2 \times \frac{22}{7} \times 0{,}15^2 \times 2{,}5 \times 83{,}4$$

$$= 29{,}5\ \text{m}^3$$

i.e. the total volume of water filtered per 5 minute trawl (2,5 minutes in either direction) is about 30 kl.

APPENDIX B

Measurements of carapace length (CL), standard length (SL) and total length (TL) of *P. pacificus* used to derive equations to describe the relationship between the respective measurements.

CARAPACE LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL LENGTH (mm)
1,8	6,8	8,7
1,8	7,9	10,0
2,1	7,6	9,7
2,1	7,9	10,0
2,2	8,3	10,5
2,3	8,0	10,0
2,3	8,5	11,0
2,4	8,4	10,3
2,5	8,4	10,6
2,5	8,6	10,9
2,9	9,3	11,6
2,9	9,3	12,1
2,9	9,7	12,7
3,0	9,7	12,4
3,0	10,5	13,9
3,1	10,2	12,9
3,2	10,5	13,3
3,2	10,7	13,8
3,2	10,7	13,8
3,2	10,8	13,5
3,2	10,8	13,7
3,2	11,0	13,5
3,4	11,1	14,4
3,7	11,4	15,5
3,7	11,9	15,2
3,7	12,1	14,9
3,8	12,1	15,5
4,0	12,8	16,1
4,3	13,4	16,8
4,5	13,4	17,8
4,6	14,3	19,0
4,8	15,5	20,0
5,0	16,0	20,9
5,5	17,3	22,9
5,6	18,6	23,7
5,9	18,7	25,0
6,0	18,8	24,6
6,4	19,2	25,7
6,5	21,9	28,3
6,6	20,8	27,4
6,6	21,9	26,8
6,7	22,2	28,9
6,8	22,3	28,2
7,0	23,2	29,2
7,1	23,2	29,7
7,4	23,6	30,7

Appendix B (continued)

CARAPACE LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL LENGTH (mm)
7,6	24,1	31,3
7,6	24,9	31,4
7,6	25,8	32,8
7,9	28,4	36,8
9,0	29,0	37,3
9,2	29,4	37,7
9,3	28,7	35,0
9,5	32,2	39,3

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