A STUDY OF THE BURROWING SANDPRAWN *CALLIANASSA KRAUSSI* STEBBING

(CRUSTACEA : DECAPODA : THALASSINIDEA)

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INTRODUCTION

Estuarine studies in southern Africa have attained increasing importance in recent years for a number of reasons. Biologically they are rich areas having both a resident fauna and also providing feeding grounds and nurseries for many marine species. From a human point of view they are significant because of their roles in the life cycles of economically important fish and crustacea and because of their use for recreational purposes. At the same time they are vulnerable to over-exploitation of their resources, to uncontrolled development and to pollution.

Investigation of estuaries in southern Africa was begun about 25 years ago by the Zoology Department of the University of Cape Town under Professor J.H. Day who in 1951 produced a review of conditions prevailing in southern African estuaries. More detailed studies followed and these surveys eventually covered the area from the Orange River between the Cape Province and South-West Africa (Brown, 1959) around the south and east coasts as far as Morrumbene estuary in Mocambique (Day, 1973). These studies included non-estuarine areas of sheltered water, of which the most important were Langebaan Lagoon (Day, 1958) and Durban Bay (Day & Morgans, 1956). Invaluable information was gained on the types of estuaries, the conditions in different areas and the variations and geographical range of the fauna.

In recent years studies have tended to become more specific and have concentrated on the biology of certain species or groups of species. One of the most important of these groups in our estuaries, in terms of both numbers and biomass are the burrowers. These consist mainly of thalassinid prawns, followed to a very much lesser degree by the bivalves (McLachlan 1973). The thalassinid prawns are extremely abundant. There are two common species, Upogebia africana studied by Hill (1968, 1971a, 1971b) and the equally abundant Callianassa kraussi.

C.kraussi is a familiar species in those areas where it occurs due to its popularity as bait among fishermen and is known by a variety of names in the different areas ranging from "wit kapper" in the southern Cape Province, "sand prawn" in the south-eastern and eastern Cape to "cracker" in the Transkei and Natal and "kafoof" in Mocambique. Despite this widespread distribution and familiarity, biological information was restricted to comments and occasional records in the general estuarine surveys mentioned above and further investigations of this species was justified for a number of reasons.

C.kraussi is a member of a world-wide genus which apparently only occurs in large numbers in South Africa and on the eastern coast of Australia (Hailstone & Stephenson 1961). The abundance of C.kraussi in South Africa thus provided an opportunity to contribute to knowledge of a little known group. Basic biological information on features such as distribution, densities, breeding and growth and the factors affecting these features would ultimately also be of importance in an assessment of the role of these prawns in estuaries.

As might be expected, C.kraussi is also little known physiologically, a feature it shares with most other species in the genus. General reviews have considered this species an osmoconformer although possessing some tolerance to low salinities. The only physiological studies are those of Thompson & Pritchard (1969) on the Californian C.californiensis and the New Zealand C.filholi which confirmed the above assumption. The distribution of C.kraussi in southern African estuaries however and the wide range of salinities over which it was found indicated a marked degree of euryhalinity (Day 1951) and it was therefore decided to investigate the physiological basis of this ability.

C.kraussi was known to occur in both conventional open and in the peculiar closed estuaries which are a feature of much of the South African coast. These closed estuaries are isolated from the sea for varying periods by sand-bars across their mouths. Unlike *U.africana*, *C.kraussi* is capable of surviving in these closed estuaries and it was hoped to clarify the means by which *C.kraussi* is able to survive under these conditions and also the effects of long term isolation from the sea.

Biological studies were also related to a second aspect of this species in southern Africa, viz. its recent increasing importance as a bait species for anglers. This aspect had come to the attention of the Department of Nature Conservation of the Cape Province of South Africa and regulations were promulgated to control collection of *C.kraussi*. These regulations and restrictions however were not based on any detailed knowledge of the biology of this species and consequently many of the observations and investigations made during this study were directed towards an assessment of existing bait regulations and the framing of adequate measures for conserving this species.

The scope of this investigation was thus necessarily broad, including aspects of distribution, the life cycle, physiology and conservation.

PART I

DISTRIBUTION OF CALLIANASSA KRAUSSI IN SOUTHERN AFRICA

A. General observations.

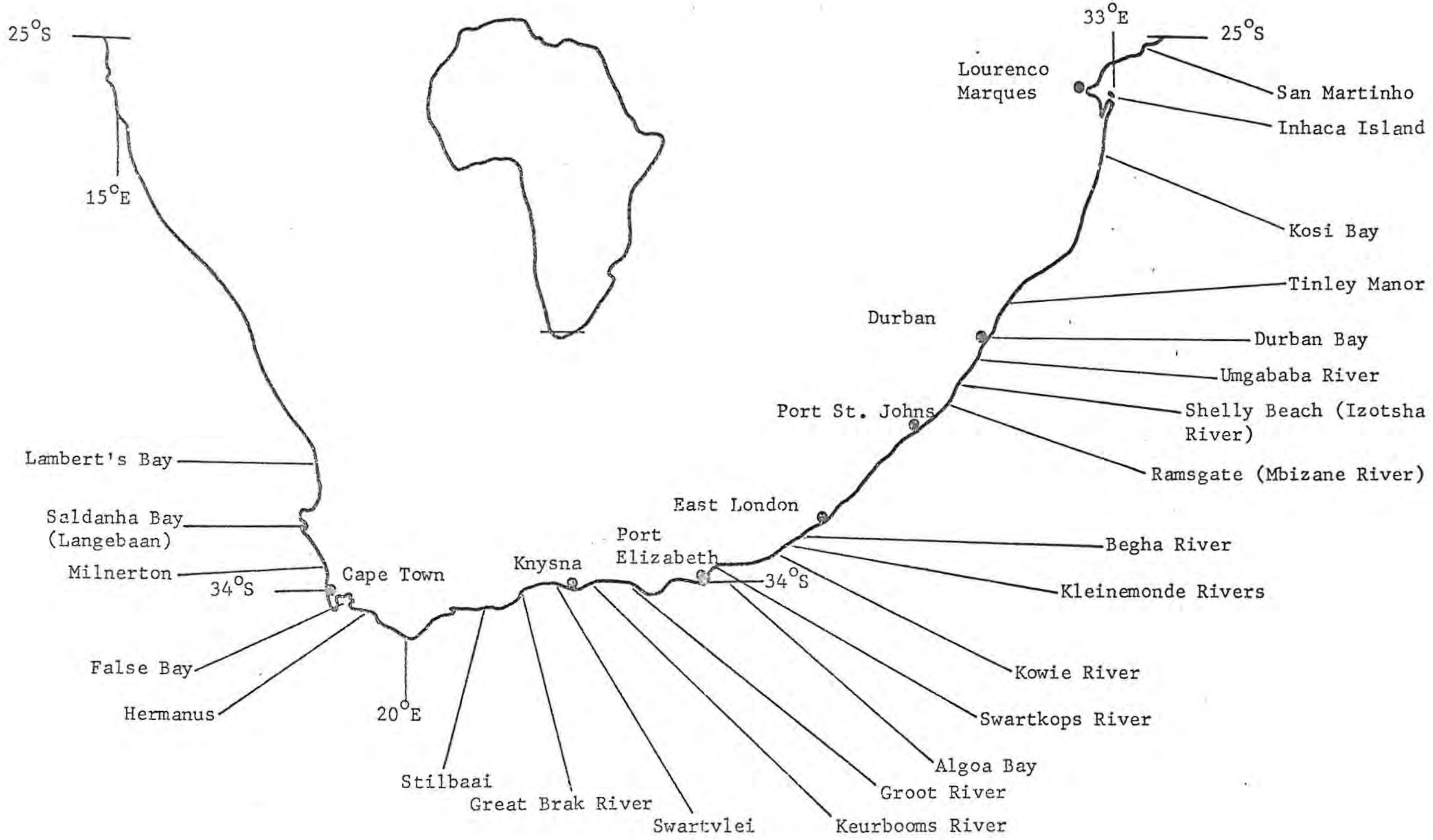
Barnard (1950) recorded the presence of *C.kraussi* in 15 localities along the southern African coast from Saldanha Bay on the west to Kosi Bay in northern Natal (Fig. 1). Day (1969) extended the known range of this species to Lamberts Bay on the west coast and Inhaca Island off Lourenco Marques in Mozambique. These published records show that *C.kraussi* occurs most commonly in estuaries but that it is also found in sheltered bays such as Langebaan, False Bay and Durban Bay.

During the course of the present survey as many areas as possible along the southern African coast were visited and the presence or absence of *C.kraussi* recorded. This clarified the general distribution of the species and also established distribution patterns within the areas from which it had been recorded. It also allowed comparison of different habitats and of features such as population structure and breeding.

Methods

During the survey 59 areas were visited and records obtained, both published and unpublished, for an additional 16 areas. A full list of all the areas is given in Appendix 1. Samples of *C.kraussi* were collected using a prawn pump, an instrument similar to that described by Hailstone & Stephenson (1961). This instrument is commonly used in South Africa for collection of this species by anglers for use as bait. Notes were made on the nature of the habitat, i.e. bays or estuaries

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



and whether the estuary was open to the sea or closed off by a sand-bar, the type of substrate and amount of shelter from waves and tidal currents. Temperatures were measured using a mercury in glass thermometer. Salinities were first determined by chloride titration using an American Instruments Co., Automatic Chloride Titrator and subsequently with an American Optical Co. Optical Salinometer. Oxygen records from Swartvlei estuary were obtained from Robarts (1973).

Results

The survey extended the known range of C.kraussi northwards on the east coast as far as San Martinho in Mozambique (Fig. 1) but was mainly of value in indicating the type of conditions under which C.kraussi occurred. This led to experimental investigations of some of the factors apparently affecting the distribution of this species.

Several important points emerged from the survey. The most obvious feature was that C.kraussi is predominantly a species of sheltered water away from wave action. The areas where C.kraussi was recorded or collected in this or other studies were mainly estuaries, both open and closed, or else very sheltered bays such as Durban Bay or Langebaan Lagoon. Unpublished records from the University of Cape Town show that C.kraussi occurs in the sea in Lamberts Bay and False Bay. In the present survey C.kraussi was also obtained in Algoa Bay at depths down to 9 m. Very little is known of these populations except that all records are from beyond the surf zone indicating a tendency to avoid areas of strong water movement. Although depths would thus not appear to be an immediately limiting factor in estuaries it was found that the numbers of burrows decreased at depths greater than 6 m in Swartvlei lake (Figs 1 and 2) and were absent beyond 8 m. These depths in

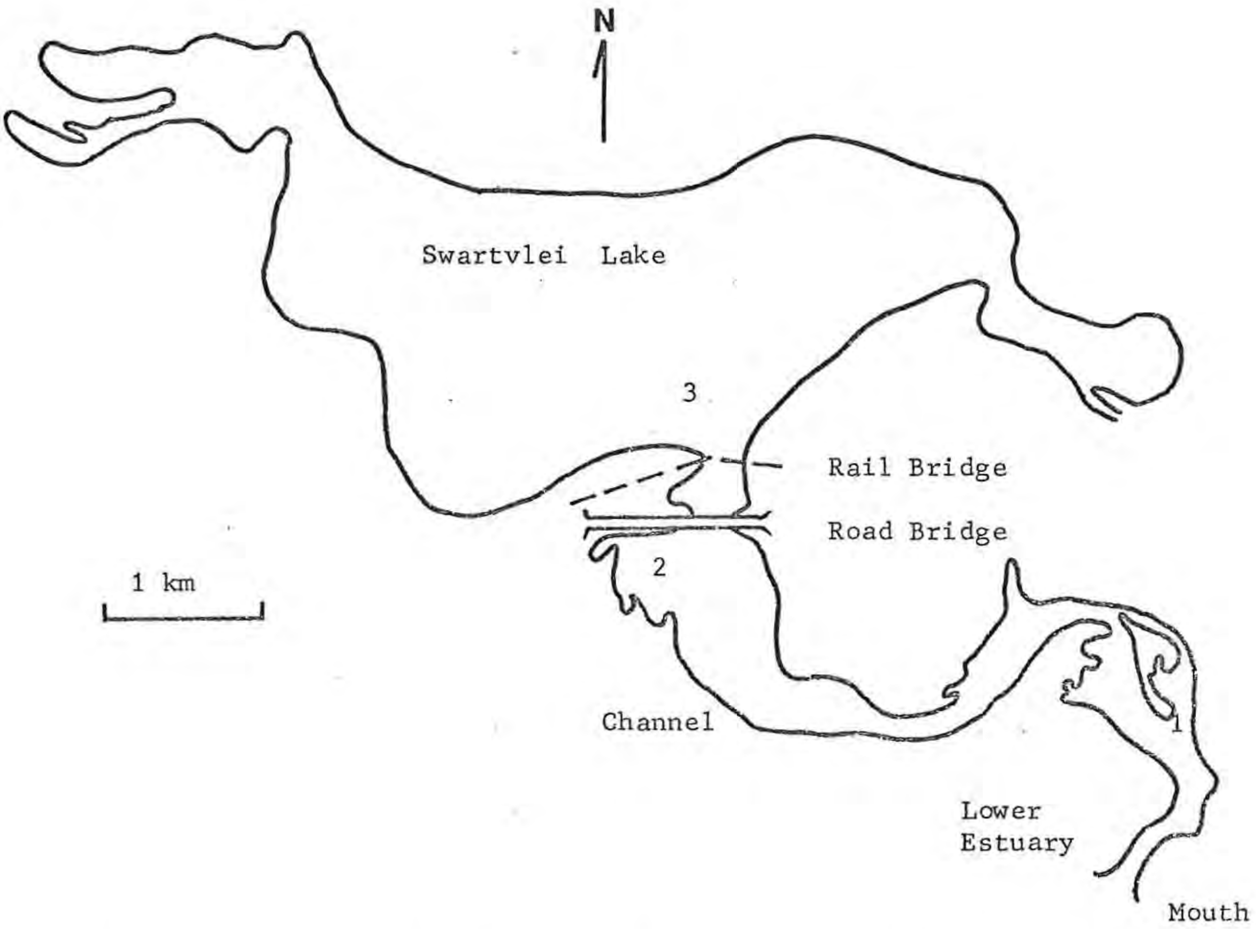


Figure 2. Sketch map of the Swartvlei system showing areas (1, 2 and 3) in the lower estuary, channel and lake where C.kraussi was collected.

Swartvlei were associated with a marked decrease in the oxygen tension as shown in Fig. 3, suggesting that low oxygen can be limiting. It is also apparent that C.kraussi is not dependent on access to the sea. Estuaries which had been closed for 2-3 years still had large populations of this species.

The survey also showed that C.kraussi is extremely tolerant of a

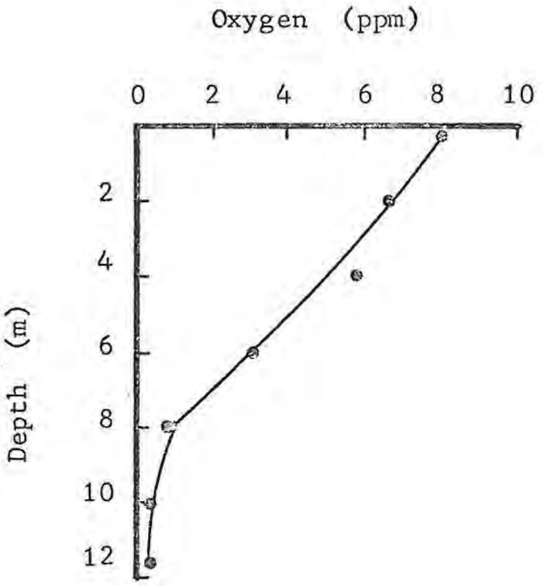


Figure 3. Decrease in oxygen concentration with depth in Swartvlei lake, from Robarts, 1973.

variety of physical conditions, occurring over a wide range of temperatures, salinities and substrates. Records showed that populations in the West Kleinemonde estuary (Fig. 1) tolerated an annual temperature range of 14-26°C. Winter inshore temperatures on the west coast drop to 9-10°C (Day 1958) while summer temperatures in estuaries on the northern Natal and Mozambique coasts reach over 30°C. Comparison with results from the west Kleinemonde and Swartkops estuaries indicated that extreme transient surface temperatures in both areas would be moderated by the substrate.

Salinities recorded from areas inhabited by C.kraussi indicated a marked degree of euryhalinity. C.kraussi was found in salinities varying from sea water (35^{o}/oo) in bays and the lower reaches of estuaries down to 6-7^{o}/oo in Swartvlei lake (Fig. 2) and 1^{o}/oo in the upper reaches of the Keurbooms estuary (Fig. 1). These results suggest that low salinities do not inhibit the spread of C.kraussi up estuaries.

In addition C.kraussi was able to survive in a variety of substrates and was found burrowing in substrates ranging from clean sand through muddy sand to mud silt and clay.

The above observations indicate a wide degree of tolerance to a variety of estuarine conditions. It was noticeable however that C.kraussi rarely occurred in similar numbers throughout an estuary. Thus in the closed Kleinemonde estuary the numbers decreased markedly near the sand bar. In Swartvlei estuary the numbers of C.kraussi decreased steadily as one moved into the lake away from its connection with the sea (Fig. 2). In addition C.kraussi appeared to be excluded from areas occupied by another common burrowing southern African thalassinid Upogebia africana. This is an extremely abundant species (Hill, 1968) found in most open southern African estuaries. Both species burrow into mudbanks but mixed populations are extremely rare (Macnae, 1957, Millard & Scott, 1953). These apparent anomalies in distribution suggested that a variety of factors affect the distribution and abundance of C.kraussi in southern Africa. It was not possible to investigate all these factors and it was decided to concentrate on the effects and mode of action of substrates and currents, salinity and temperature on the species.

B. Selection of study areas.

Three areas were selected for detailed investigation. These were the west Kleinemonde, Swartkops and Swartvlei estuarine systems (Fig. 1). The first two are on the south-eastern Cape coast (Fig. 4a) and are shown in more detail in Figs 4b and 4c. The west Kleinemonde estuary is an example of a closed estuary. Closed estuaries are very common on the south-eastern and eastern coasts of southern Africa. The lower reaches of the west Kleinemonde are wide and shallow with a maximum depth of 2 m. On the seaward side of the bridge the bottom is mainly sandy but upstream of the bridge the substrate becomes muddier. Further upstream the river narrows and the banks become steeper while the depth increases to 3-4 m. The limit of marine influence is at a weir 5 km from the mouth. The catchment is small and lies in an area of erratic rainfall where long dry periods are punctuated by heavy downpours. These floods fill the river and it may then break out through the bar. This occurred in August 1970 and the mouth remained open until October 1970. It opened intermittently again over the period July-November 1971 after which it remained closed for the rest of the survey period (end of 1973). Closure of the mouth is due to the small tidal exchange, a usually small inflow of fresh water and the onshore winds which cause extensive sand movement and eventually block off the mouth. Some water occasionally enters from the sea when storm winds flatten the dunes across the bar and waves wash over at high tide. The Swartkops estuary is a large permanently open estuary near Port Elizabeth. It has been described in detail by Macnae (1957). The area around the mouth and immediately above the bridge is sandy but then becomes more muddy. The lower section has extensive mud flats and salt marshes but upstream becomes narrower and muddier with steeper banks. A causeway about 16 km from the mouth is the limit of tidal influence.

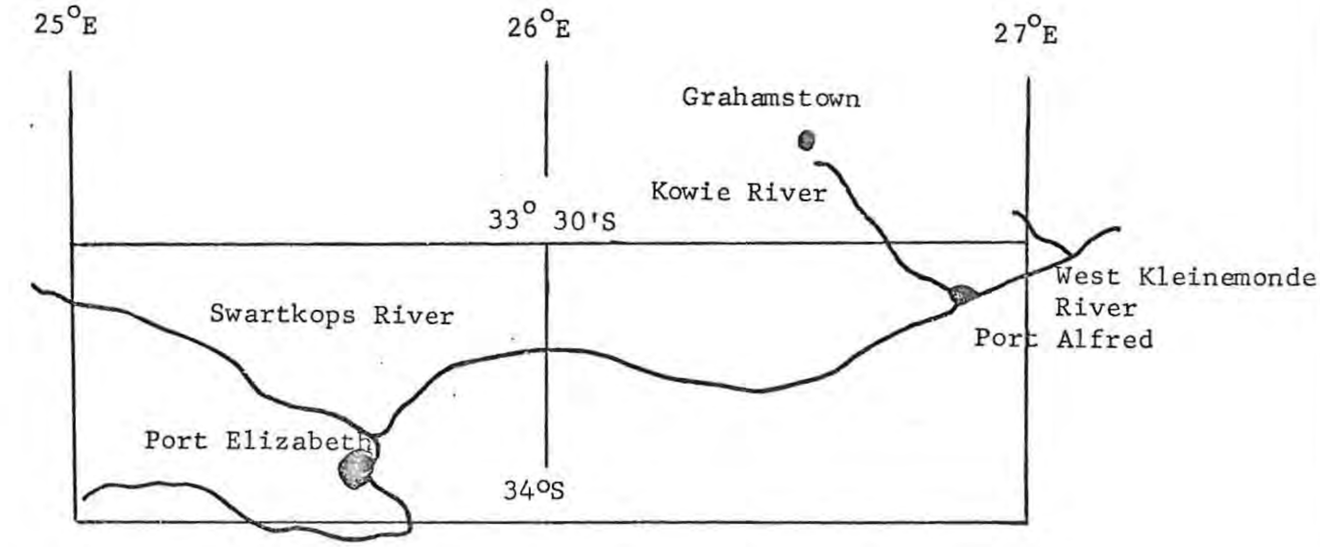


Figure 4a. Main study areas in the eastern Cape Province

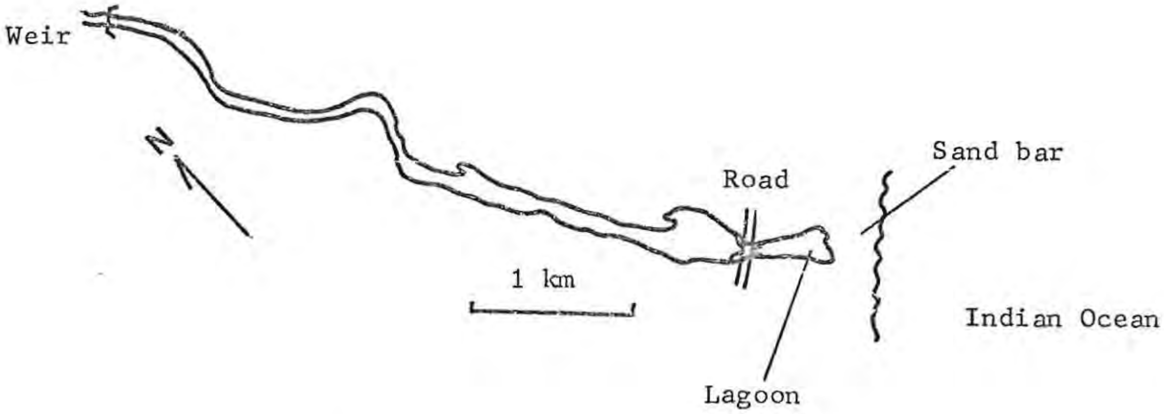


Figure 4b. Sketch map of west Kleinemonde River.

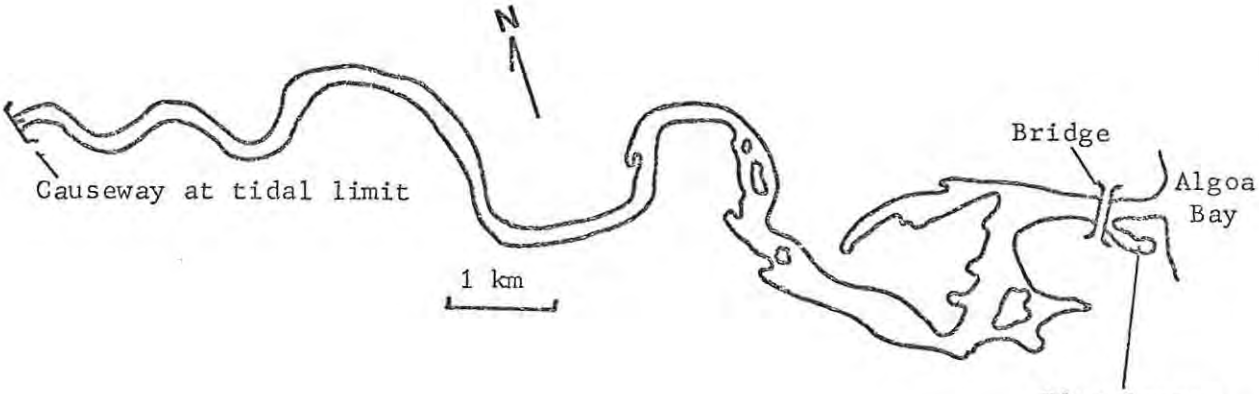


Figure 4c. Sketch map of Swartkops River.

These two areas were chosen as they were both in reasonable proximity to the laboratory, both were known to have large populations of *C.kraussi* and it was hoped that sampling of an open and a closed estuary would show up any possible effects of isolation from the sea on this species. Sampling in the Kleinemonde River was done in the area below the bridge (Fig. 4b) and especially in the shallow water near the sand bar at the closed off mouth. In the Swartkops estuary sampling was done in an area known as the "Blue Lagoon" near the mouth (Fig. 4c). The third sampling area was in the Swartvlei lake system on the southern Cape coast (Figs 1 and 2). This system differs from the other two estuaries in consisting of a 12 metre deep lake connected to the sea by a 1-2 m deep channel. Swartvlei was of interest because *C.kraussi* occurred throughout the channel leading into the lake but only had a limited distribution within the lake itself. The three sampling areas chosen to cover the salinity gradient in the system are shown by numerals on Fig. 2. Records dating from 1969 showed that the mouth could close at any time. This was usually followed by a gradual rise in the level of the lake over a period of months until the mouth burst out or was opened artificially to prevent flooding of low lying farmlands. The rise in the level was accompanied by a drop in salinities. The area thus provided information on a population of *C.kraussi* in a system where the salinity varied and in the main lake was frequently as low as $5-7^{0}/oo$ for 3-4 months at a time. Unfortunately this area was 450 km from the laboratory and thus could be visited only at two-monthly intervals. Special investigations were carried out at another open estuary, Knysna (Fig. 1 and Fig. 5) which is also on the south coast. These areas offered an almost complete range of the type of habitat under which *C.kraussi* was encountered and it was hoped that this would give an indication of the response of this species to different conditions.

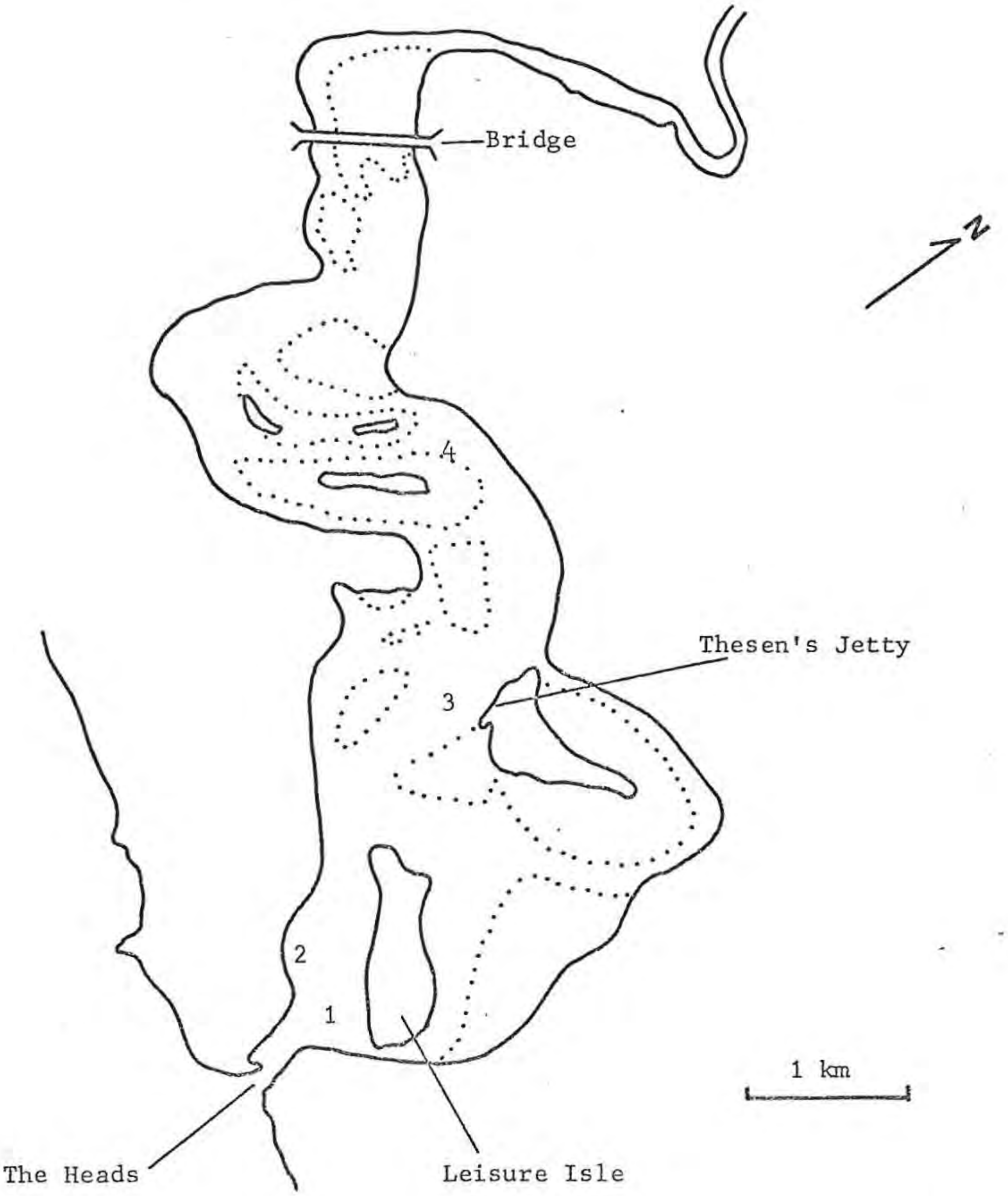


Figure 5. Sketch map of Knysna estuary showing areas where current speeds were measured or substrate samples taken. Dotted lines indicate tidal flats.

C. The nature of the burrow and its significance in the distribution of C.kraussi.

It has already been pointed out that C.kraussi lives in burrows which are usually the first indication of the presence in an area of this species. These structures play an extremely important part in the biology of burrowing prawns and the suitability of areas for burrow construction will be an important factor in determining the distribution of this species. Investigations of the burrow and burrowing were begun with studies of the nature of the burrow system in different areas. A more detailed investigation was then carried out into the effects of currents and substrates on the distribution of C.kraussi in estuaries.

Methods

Digging and burrow construction was observed in specimens kept in aquaria in the laboratory. In the field burrow distribution was noted and counts made using a metal frame 0.5 m square. Holes were counted in the west Kleinemonde estuary in the lagoon area below the bridge. In the Knysna estuary counts were made using SCUBA along a transect 31,5 m long at points 1,5 m apart and extending from 0,3 m into 1,8 m of water (Area 4 in Fig. 5). In Algoa Bay counts were done off a sandy beach using SCUBA from just beyond the surf zone at depths of 3, 5, 6 and 8 m. These three areas provided examples of a closed estuary, an open estuary and the open sea. The number of openings to a burrow system was determined by placing the prawn pump over an entrance to a burrow and gently depressing the plunger. The number of burrows through which water was expelled was then counted. The depth and form of burrows was investigated using a technique developed by Shinn (1968) and subsequently used by Farrow (1971) on Aldabra and by Rice & Chapman (1971) in work on Nephrops norvegicus and Goneplax rhomboides - both burrowing decapods. The method involves pouring polyester resin into the burrows and allowing it to set before digging it up again. It was found best to leave the cast to harden over a full tidal cycle. Exposure to water does not prevent hardening.

Substrate samples for analysis were taken in a number of areas inhabited by C.kraussi especially where the substrate appeared unusually fine or coarse as well as in areas from which C.kraussi was absent. Particle size analyses were carried out using the method described by Morgans (1956). Four sets of results were obtained from Wooldridge (1968) and from Hill (pers.comm.). In addition, the volume of silt was determined using a method described by Phillips (1971). Current speeds were measured using a Savonius Rotor current meter. (Hydro Products, California). Underwater observations were made using SCUBA. Experimental investigations into the limiting effects of water movement were made by determining burrowing ability in sand collected from an area subject to wave action near the Swartkops River mouth where C.kraussi had never been recorded. Sand was collected in this area in December 1972 and again in January 1973 and used in two separate experiments. The method was the same in each case. In each experiment 7 batches each of 10 similar sized prawns were used. Batch one consisted of 10 prawns in the size group 2-2,9 mm carapace; in batch two the size was 3-3,9 mm carapace. Successive batches fell into larger size groups with the seventh being 8-8,9 mm. Each batch was then placed in a bowl of diameter either 25 cm or 40 cm which had been filled with sand to depths ranging from 5-12 cm depending on the size of the prawns. The bowls were examined at intervals over a period of 3 days, both at night and during the day and a count kept of all prawns seen on the surface.

Results

Digging and burrow construction by C.kraussi are basically similar to that of C.californiensis (MacGinitie, 1934) and C.filholi (Devine, 1966). In all three species the second and third pereiopods are the most important digging appendages although some use is also made of the third maxillipeds and chelae. The importance of the chelae in C.kraussi declines with age especially in the males where this limb is proportionately far larger and more cumbersome than in females and young specimens. Both C.kraussi and C.filholi are able to bury themselves very rapidly in a sandy substrate and do not require to re-emerge except to push out loads of sand. MacGinitie observed that C.californiensis constructed a new burrow initially by digging and backing out with each load of sand until a depth equivalent to its own body length was reached. A turn-around was then constructed and the animal did not subsequently leave its burrow. By contrast, C.kraussi on a sand surface buries itself by pushing sand aside with its second and third pereiopods while in young animals the chelae are also used. At the same time the pleopods beat strongly, keeping the anterior part of the body pressed against the substrate. As soon as the prawn has managed to force the cephalothorax below the surface the abdomen is folded ventrally and the animal rapidly disappears.

In the field the appearance of areas inhabited by C.kraussi varies widely. In calm areas with a comparatively low burrow density such as Swartvlei lake at a depth of 3-4 m, the burrow openings may be surrounded by a cone of sand up to 15 cm high. In areas with a higher density of burrow openings but still in calm water, such as the area below the road bridge at Swartvlei, the burrowing activities of this species result in a very uneven surface. In areas where there is water movement, either due to tide or wind action such as in the Swartkops mouth area, these cones and uneven areas are usually more flattened out and there is less evidence of burrowing activity. This latter observation also appears to hold for both C.major (Lunz, 1937) and C.filholi (Devine, 1966). Both these species occur on open beaches, where the burrow openings are apparently not always clearly visible and may even lie in a slight depression.

It has been intimated above that the numbers of burrow openings varied in different areas and counts were therefore made in an attempt to account for these variations. Results of counts done in an offshore area in Algoa Bay are given in Table 1.

Table 1: Counts of burrow openings in an offshore area in Algoa Bay Four counts were done at each depth.

Depth (m)	Mean/ m^2	Range
3	1	0-4
5	64	24-148
6	364	276-404
8	320	184-524

The number of burrow openings clearly decreased in shallow water. This was probably related to increasing surf action with associated instability of the bottom through movement of sand.

The area surveyed at Knysna consisted of a bank which shelved fairly steeply at first and then flattened out. The counts obtained are given in Table 2.

Table 2: Counts of burrow openings at 1,5 m intervals along a transect at Knysna in 0,3 to 1,8 m depth of water.

Depth Range (m)	No. of counts	Mean/ m^2	Range
0-0,49	2	152	128-180
0,5-0,99	3	134	64-180
1-1,49	2	144	96-188
1,5-1,99	14	72	28-142

The initial slope followed by a flatter region is the reason for the greater number of counts beyond 1,5 m. The table shows that the number of burrow openings decreased below 1,5 m. This deeper section was in the channel and was an area of strong tidal currents with speeds up to 45 cm/sec. In the west Kleinemonde estuary where a large number of counts (n = 148) were done over the whole area below the bridge (Fig. 6) it was also found that there was a gradient in the density of the number of open burrows. In this case the number decreased towards the sand bar. All the Kleinemonde counts were done in shallow water (maximum about 50 cm). Near the bar there is more water movement due to wind action than in the areas sheltered by the dunes away from the bar. It appears that the number of open burrows generally declines in areas of greater water movement. Thus in Algoa Bay the number of burrow openings declined in areas of greater surf action; in Knysna the numbers declined with increasing depth in the channel where tidal currents were stronger and in the Kleinemonde the numbers decreased towards the sand bar where there was more water and sand movement. These observations lead to the question whether a decrease in the number of burrow openings reflects a decrease in population or merely a reduction in the number of openings per burrow.

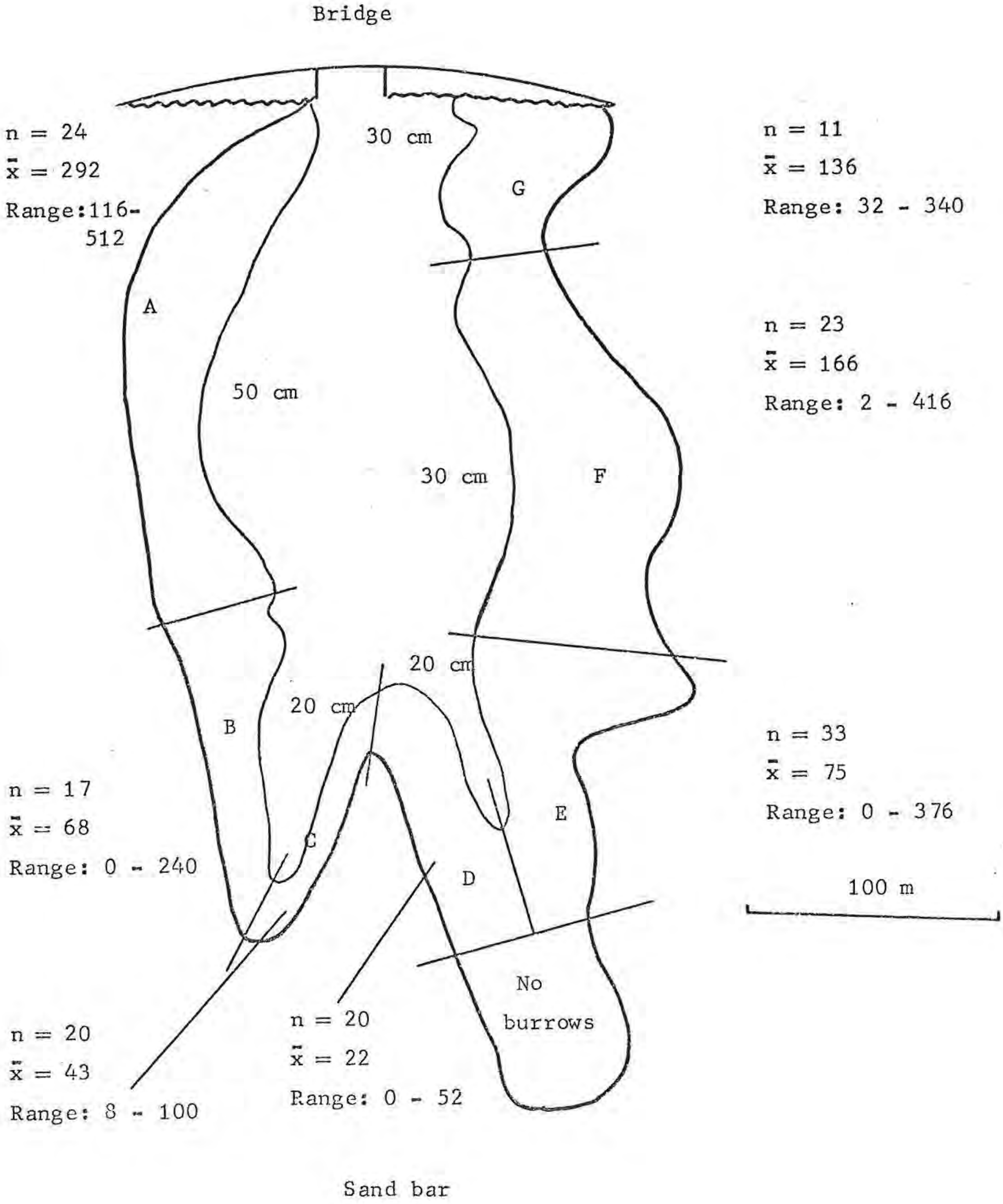


Figure 6. Sketch map of the lagoon area of the west Kleinemonde River. Figures refer to the number of counts made and the number of burrows per square metre in different areas.

Observations on the number of entrances or exits to a burrow were made in open and closed estuaries and in areas varying in their amount of shelter from wind and water movement. One of the first findings was that all openings to burrows were not permanently open. Forcing water into an open burrow frequently resulted in the expulsion of sand from openings which were previously closed off. During the investigation counts were made of both the number of open entrances to a burrow system and also of the total number of entrances both open or closed. The results are given in Table 3.

Table 3: The mean number of open entrances per burrow system and the mean number of total entrances (open and closed) per burrow system in different estuaries.

Area	No. of observations	Mean no. of open entrances per burrow	Mean no. of total entrances (open & closed) per burrow	Range of total no. of entrances (open & closed)
East Kleinemonde estuary (closed)	24	3	3	1-9
West Kleinemonde estuary (closed)	50	1,4	2,5	1-7
Swartkops estuary (open)	50	1	1,8	1-3

In the east Kleinemonde estuary where the area investigated was very sheltered from wind action all entrances to burrow systems remained open. In the west Kleinemonde counts were made along the sand bar where there was wind induced water and sand movement. In this area there was a reduction in the total number of openings as well as a high proportion (44%) of closed entrances. In the Swartkops estuary where there were both wind and tidal movements of water the trend to reduce the number of

Plate 1: A polyester resin cast of a burrow system of C.kraussi showing a thin connection between neighbouring burrows (arrow in lower left corner).

Plate 2: An enlargement of the central section of Plate 1 showing the positions of the two prawns (arrows) where they were trapped by the resin.

openings was carried still further although the same proportion (44%) of the entrances were closed. The number of open burrow entrances in any area will thus vary depending on water movement. This was supported by observations made using SCUBA in Algoa Bay. The counts given in Table 1 were made on a calm day. On subsequent dives in strong surf conditions very few open burrows were found and then only after a prolonged search. Phillips (1971) found similar fluctuations in the case of C.islagrande in Mississippi sound. Counts in the same area at different times of the year varied from 5 to 100 per square metre, and he suggested that this resulted from wind and surf action.

These observations were extended into the laboratory by counting the number of open burrows in two aquaria each containing twenty prawns. It was found that the number of burrows depended on whether or not the water was aerated (Fig. 7). In aerated conditions the total number of open burrows dropped as low as four, that is five prawns per opening, but if the aeration was stopped the number increased to give almost a 1 : 1 ratio with the prawns. A significant fact to emerge was that the number of open burrows never exceeded the number of prawns in the aquaria. As field observations often indicated more than one opening per burrow system this suggests that individuals of C.kraussi share burrows. Polyester resin casts of burrows of prawns kept in an aquarium in the laboratory showed that burrows were frequently joined by thin connections. Plates 1 and 2 show a burrow cast where two sections of a burrow system are joined by thin connections while a prawn has been trapped in each section by the resin. This suggests that while C.kraussi may share a burrow system each prawn remains in a specific part of the system. This separation has not been described in other species. Hailstone & Stephenson (1961) working in Australia simply record up to two specimens in a burrow system of C.australiensis. Devine (1966) referring to

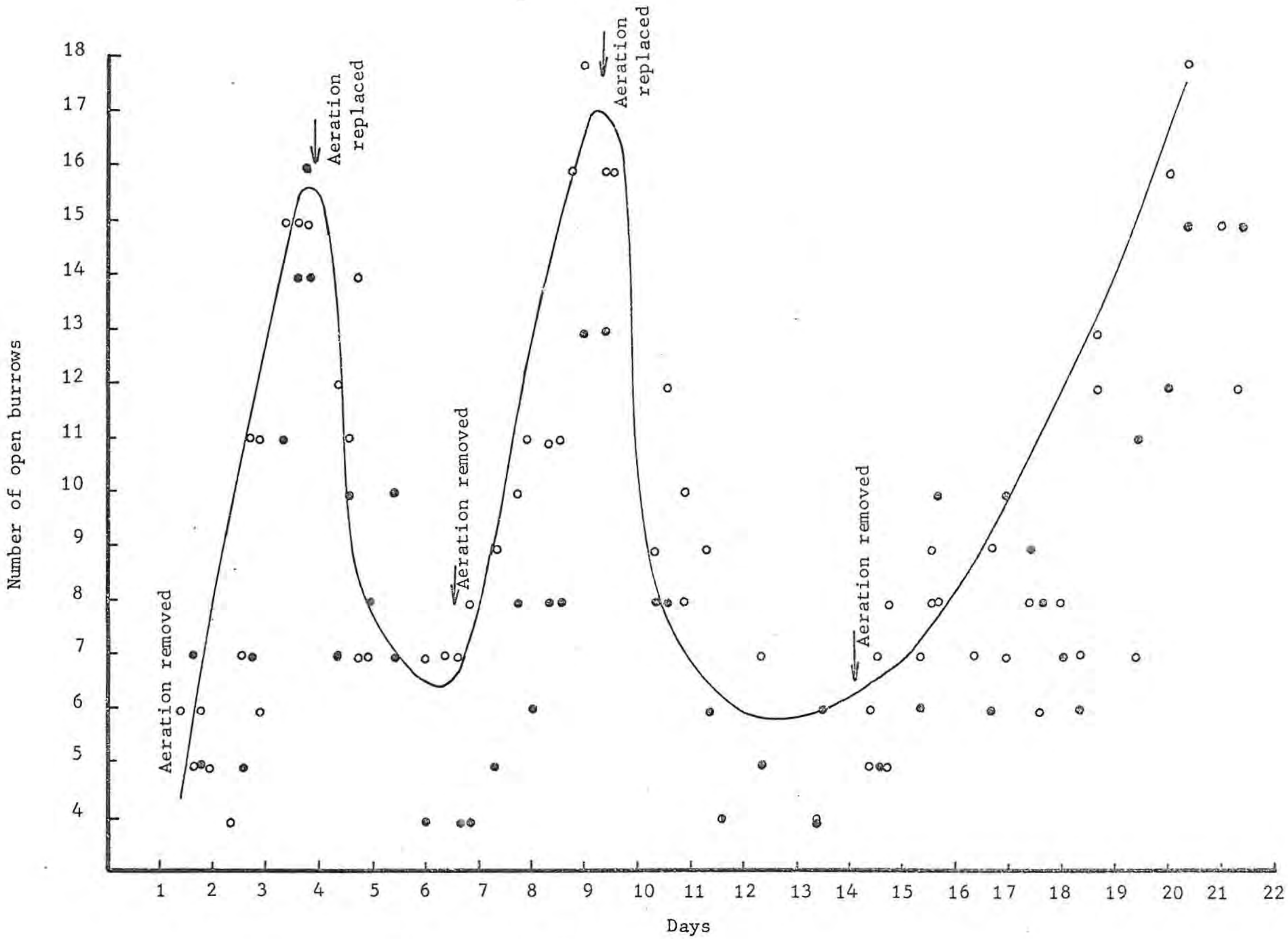


Figure 7. Effect of aeration on number of open burrows in two aquaria each containing 20 prawns.

Plate 3. Polyester resin cast of the more common type of burrow constructed by C.kraussi.

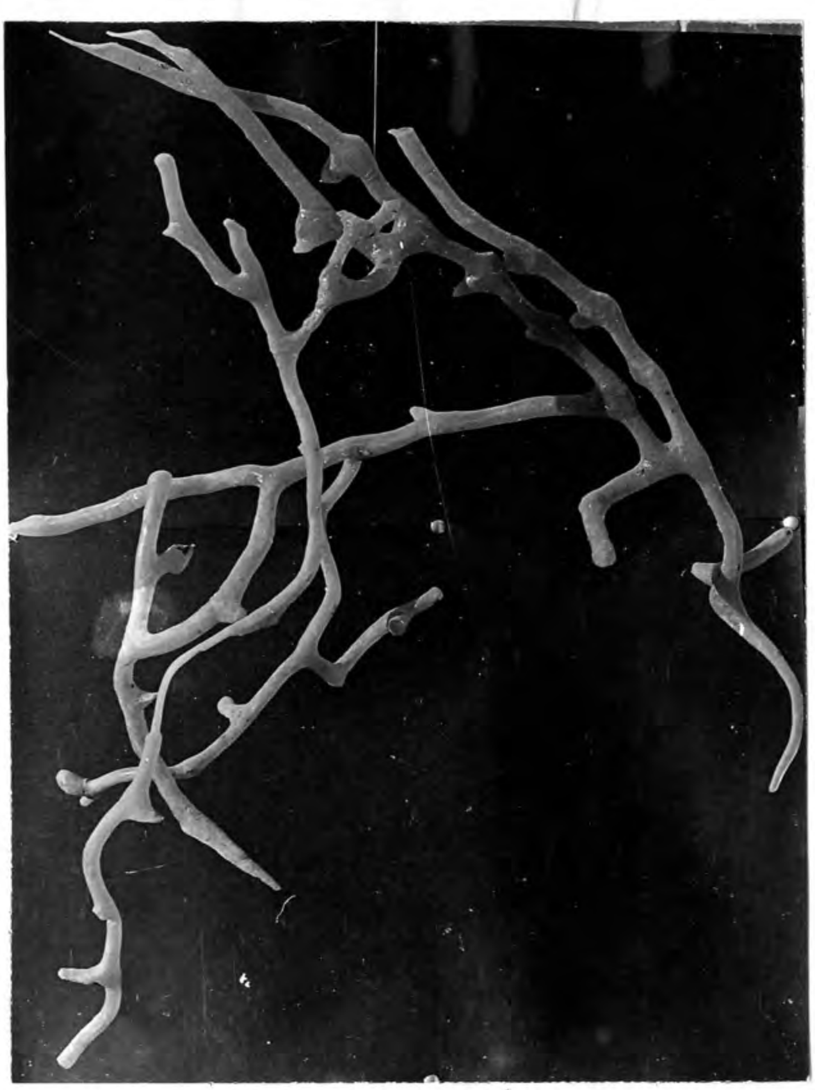


Plate 4. A polyester resin cast of an unusually complex burrow of C.kraussi. The thin connections to the surface were lost. Note the dilations used as turn-arounds.

C.filholi in New Zealand states that "groups of animals congregated together in a shared burrow system". On the other hand Phillips (1971) suggests that in *C.jamaicense louisianensis* burrows are occupied by single animals.

Polyester resin casts of the burrow of *C.kraussi* showed that it burrows to at least a metre depth. This is similar to depths recorded for other species, e.g. *C.californiensis* 0,75 m (MacGinitie, 1934); *C.major* 1,5 m (Lunz, 1937) and 1,46 m with a range of 0,6-1,2 m (Pohl, 1946) and *C.jamaicense louisianensis* 0,77 m with a range of 0,33-1,37 m (Phillips, 1971).

Most burrows of *C.kraussi* tend to be approximately vertical with varying numbers of side branches as shown in Plate 3. The photograph shows the way in which the burrow tapers off at the surface. This was also found by Lunz (1937) in *C.major*. Tapering was also found where burrows interconnected suggesting that the response to contact with the surface is similar to the response to contact with another burrow. Burrows may be extremely complex (Plate 4). This photograph also illustrates the dilations which are used as turn-arounds.

C.kraussi burrows were found in a variety of substrates. These ranged from the Keurbooms estuary where they were living in a coarse grit with a median phi value of less than 1 (Fig. 8) and a moderate silt content (Table 4) to fine mud with a median phi of 2,9 and 29% silt volume in the upper west Kleinemonde estuary.

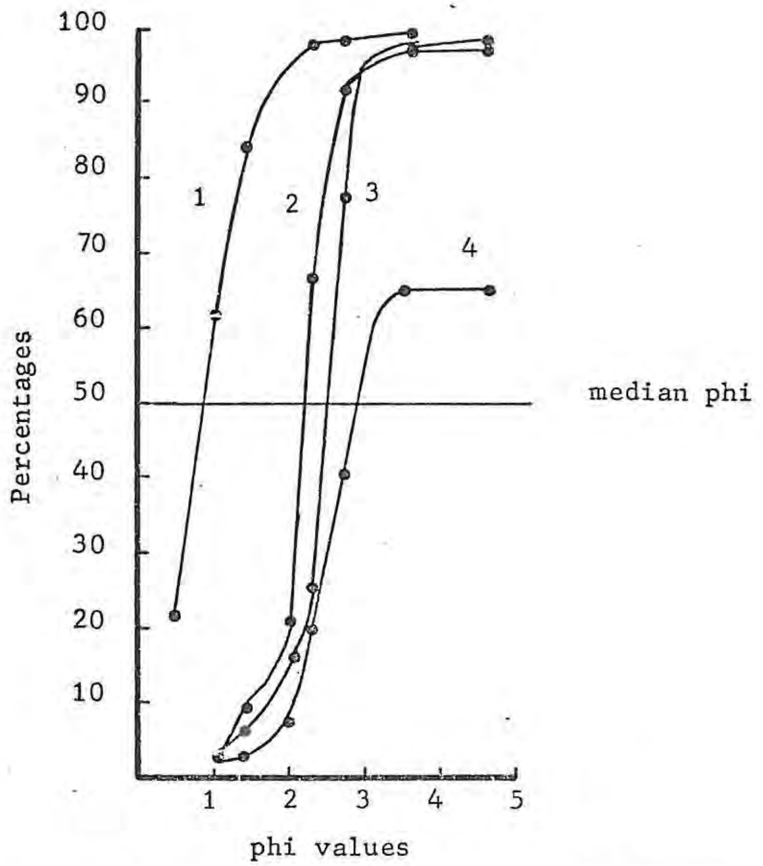


Figure 8. Analyses of substrates in which C.kraussi was found.
1) Keurbooms estuary; 2) Knysna area 4;
3) Langebaan lagoon and 4) Upper Kleinemonde estuary.

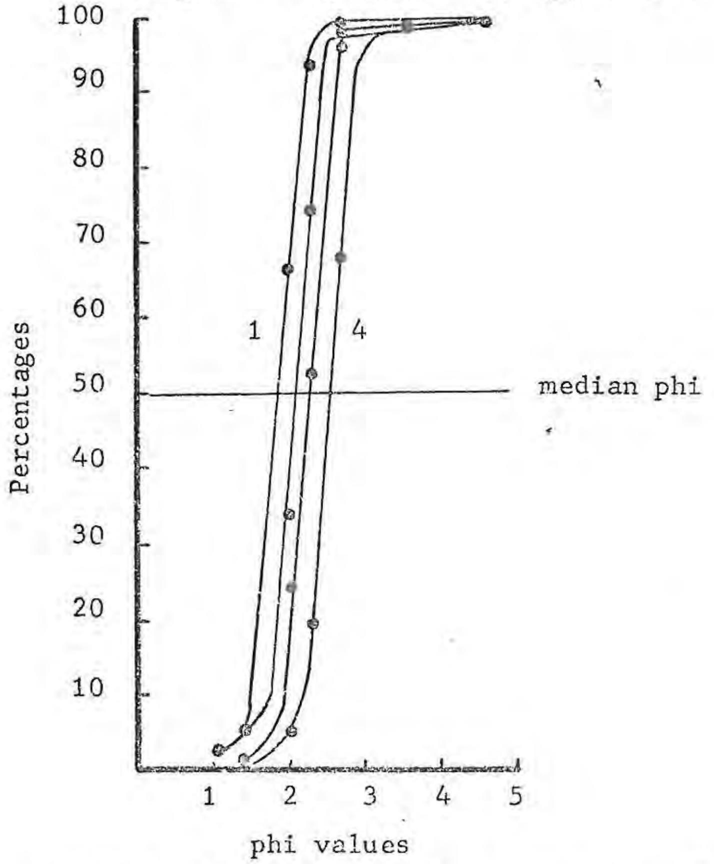


Figure 9. Analyses of substrates from areas where C.kraussi was absent or rare. From left: 1) Swartkops mouth; 2) Off Thesen's jetty, Knysna area 3; 3) Front Leisure Isle, Knysna area 1 and 4) Featherbed Bay channel, Knysna area 2.

Table 4: Silt volumes and median phi values of substrates in which burrows of C.kraussi were found.

Locality	Silt Volume %	Median phi
Knysna estuary	2	2,2
Langebaan lagoon	7	2,5
Keurbooms estuary	13	0,85
Upper Kleinemonde estuary	29	2,9

Despite this wide degree of tolerance C.kraussi was frequently absent from areas where the substrate appeared suitable for colonization. The substrate analyses from four such areas are shown in Fig. 9. The similarity of these substrates to those collected at area 6 in the Knysna estuary and at Langebaan is apparent.

The main difference between these two sets of localities lay in the amount of water movement to which they were subjected. The substrates inhabited by C.kraussi and analysed in Table 4 and Fig. 8 were either from quiet, sheltered waters in estuaries (Keurbooms, Knysna and Kleinemonde estuaries) or from a sheltered bay in the case of Langebaan lagoon. By contrast, the Swartkops river mouth and the front of Leisure Isle (area 1 on Knysna map) were both subject to wave action. In Featherbed Bay channel and off Thesen's jetty (areas 2 and 3 in the Knysna estuary) currents of 42 cm/sec and 23 cm/sec respectively were measured. SCUBA inspections of these latter two areas indicated large amounts of sand movement and sand ripples 15-20 cm high on the bottom.

Tests of the ability of C.kraussi to burrow in substrates collected in areas where they did not occur were made using sand from the Swartkops mouth. Results of the particle size analyses of samples

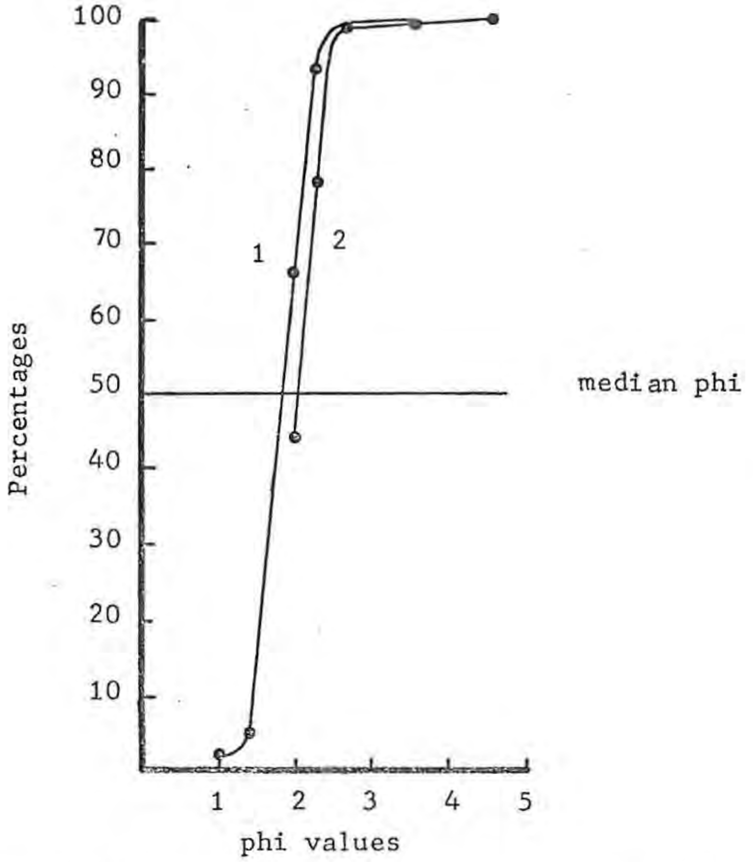


Figure 10. Analyses of substrates from Swartkops river mouth.

1) Collected in December, 1972

2) Collected in January, 1973

collected in December 1972 and January 1973 are given in Figure 10. The median phi values differed slightly, 1,85 in December and 2,05 in January. The December sample contained 6% coarse particles (phi value of 1,4 or less) which was not found in January.

All prawns burrowed immediately in sand collected in January 1973 and none re-appeared on the surface. Thus substrate composition was not excluding prawns from the area in January 1973, and the previous exposure of the sand to wave action had not made it in any way unsuitable for the prawns. Prawns had difficulty in burrowing in sand collected in December 1972, and varying numbers were counted on the surface over the three day duration of the experiment (Table 5).

Table 5: Number of prawns counted on the surface of the sand over 3 days.

Sizes (mm carapace length)	2-2,9	3-3,9	4-4,9	5-5,9	6-6,9	7-7,9	8-8,9
Mean no. on surface	0	1,3	2	5,4	5,4	7,7	5,4
Range	0	0-1	0-3	4-6	5-8	6-10	5-7
No. of observations	19	19	19	10	10	10	10

The results indicate that in December 1972 the different particle size composition could be contributing to the exclusion of larger prawns. Small prawns were clearly better able to cope with the coarse substrate.

Discussion

The number of C.kraussi burrow openings per square metre in southern Africa is comparable to figures given by Hailstone & Stephenson (1961) for C.australiensis. They report up to 500 openings per square metre in the case of large individuals (c. 60 mm total length) and up to 1,000 per square metre in the case of smaller specimens (c.40 mm total length). Results for other species are usually much lower. Figures for C.major on the east coast of North America are 30-40 per square metre on South Carolina beaches (Lunz, 1937) and only 11 per 25 square metres on North Carolina beaches (Pohl, 1946). These figures probably reflect lower population densities.

The number of openings per burrow system varies from "two to several" in the case of C.californiensis (MacGinitie, 1934) and up to six in

C.australiensis (Hailstone & Stephenson, 1961). Hailstone & Stephenson also attempted to determine the number of burrow openings/specimen so that burrow density could be converted to population density. They concluded that two to three burrow openings generally correspond with one individual. The fact that the number of burrow openings in aquaria containing C.kraussi did not exceed the number of prawns suggests that in quiet water the ratio is nearer 1:1, while in more turbulent conditions the number of open entrances decreases and the ratio becomes about 2:1. In extreme conditions such as were found in Algoa Bay under heavy surf all burrows will be closed off but this is only temporary.

If it is assumed that the population density of C.kraussi approaches a 1:1 density with that of the burrow openings, then the maximum population densities found were $400\text{-}500/m^2$ in parts of the west Kleinemonde estuary in February 1971 and off shore in Algoa Bay. The results from Algoa Bay are probably more accurate since surf action would close off burrows and only occupied burrows would be re-opened. In the west Kleinemonde estuary there was far less water movement and old or abandoned burrows would take longer to silt up thus giving erroneously high densities. These densities are extremely high; the only comparable area is the east coast of Australia where Hailstone & Stephenson (1961) recorded densities of up to $250/m^2$ for large individuals and up to $500/m^2$ for smaller specimens.

It has been shown that water movement can result in partial or complete obliteration of any sign of the burrows of C.kraussi. Does more powerful water movement exclude C.kraussi from certain areas despite the suitability of the substrate? Results have shown that C.kraussi can burrow in a wide variety of substrates (Fig. 8) while at the same time it is frequently absent from substrates (Fig. 9) which appear suitable.

In the case of Swartkops estuary prawns were able to burrow in sand collected at the mouth of the estuary from an area where they did not occur. This suggests that the nature of the substrate was not the excluding factor, and the most probable one was the amount of water movement.

Other workers have commented on this phenomenon. Scott, Harrison & Macnae (1952) noted the absence of *C.kraussi* from those areas in the Klein River estuary where "the sand is in almost constant motion with the tidal currents when the lagoon is open". Similar observations have been made on other species in the genus in other parts of the world. Hailstone & Stephenson (1961) consider *C.australiensis* "as definitely an estuarine form as it decreases in abundance at or beyond the mouth where there are shifting sand bars". Devine (1966), in discussing the factors limiting the distribution of *C.filholi* in New Zealand stresses the importance of the "instability of sand with respect to removal by wave action".

All these authors refer to the significance of water movement combined with sand movement and this is supported by the present results. High burrow opening counts were obtained in Algoa Bay despite wave action but this was probably associated with little sand transport. Open beaches, river mouths and channels in estuaries are all associated with strong water movement and sand transport and this is probably the limiting factor.

Wooldridge (1968) found experimentally that *C.kraussi* is capable of burrowing in substrates ranging from fine mud to coarse sand. Phillips (1971) reported that *C.jamaicense louisianensis* could only burrow efficiently in mud while *C.islagrande* could not tolerate silt and was thus excluded from muddy substrates. The burrowing ability of C.kraussi in sand collected in December 1972 at Swartkops mouth showed that increasing coarseness of the substrate was a limiting factor. There is thus a tendency for different species of Callianassa to be limited to a distinct range of substrates although C.kraussi is far more tolerant than either of the two species studied by Phillips (1971).

The substrate in the upper Keurbooms estuary is far coarser (Fig. 8) than that of any of the other areas investigated including the sand collected at the Swartkops river mouth in which the larger sizes of prawns were unable to burrow. This Keurbooms estuary substrate had a far higher silt content (Table 4) than Swartkops sand and this may assist in binding the substrate and so allow burrowing. Although adult prawns would have difficulty in establishing themselves in such a coarse substrate, the younger stages could do so. During growth they could easily extend their existing burrow and would not have to construct an entirely new one.

The limiting effects of coarser substrates are exerted differentially on the various sizes of C.kraussi. Adult prawns, especially the males with their very large chelae, are extremely clumsy when removed from their burrows and are less readily able to burrow again than the younger stages. It is thus apparent that mature prawns are far more dependent on their burrows than the younger stages. This could possibly account for the tendency shown by C.kraussi to avoid areas of strong water movement. If young prawns were washed out of their burrows by sand movement they could possibly re-establish themselves because of their ability to burrow rapidly. If adult prawns were washed out it is unlikely that they would be able to burrow again before being swept away. Such conditions are obviously drastic and would involve large scale sand movements. Less violent sand movement would still result in conditions such as were found in Algoa Bay when virtually no sign of any burrows could be found on a day when there was heavy surf. With even slight sand movement burrows tend to close up and all trace of burrows is obliterated. Under such conditions *C.kraussi* would not be able to survive for long periods. Thus it appears to be distinctly advantageous for *C.kraussi* to avoid areas of strong water movement and shifting substrates when selecting an area in which to burrow.

PART II

THE LIFE CYCLE OF CALLIANASSA KRAUSSI

Despite the world wide distribution of the genus Callianassa very few studies of breeding and growth have been carried out. This is probably due to their inconspicuous nature and the difficulty of obtaining regular large samples. On the east and west coasts of North America species of this genus are common and a number of ecological studies have been carried out (Lunz, 1937; MacGinitie, 1934 and Pohl, 1946) but the only population studies have been done in the southern hemisphere. Hailstone & Stephenson (1961) investigated C.australiensis which is abundant and readily obtainable along the coasts of New South Wales and Queensland. Devine (1966) did a similar study of C.filholi in New Zealand. No work has previously been carried out on the breeding and growth of C.kraussi in southern Africa despite its abundance (Day et al, 1952; Macnae 1957 and Day, 1958).

The work was concentrated in the three study areas described in Part 1, the open Swartkops estuary, the closed Kleinemonde estuary and the intermittently open Swartvlei system.

Methods

1. Breeding. Salinity and temperature effects on C.kraussi.

Sampling areas and techniques.

Collecting was carried out with a prawn pump in 0,5-1m depth of water. An assistant held a sieve (34 cm diameter with an 8 cm deep rim and a 2 mm bar mesh) and stood next to the pump operator. The pump was then pushed slightly into the substrate and the plunger pulled out vigorously. This action caused a mixture of substrate, water and prawns to be sucked into the barrel of the pump as it sinks down. The contents were then expelled into a sieve held partially underwater and agitated so that the substrate passed through and the prawns could be picked out. This method was successful in obtaining prawns as small as 10 mm total length. In order to avoid bias no attempt was made to place the pump directly over a burrow. A few pump strokes in an area soon caused the water to become cloudy with suspended matter which effectively obscured the bottom after which pumping was completely random. The sieving technique was used at Kleinemonde from March 1971 and 200 prawns were collected every month. At Swartkops the prawn pump was used from July 1971 until February 1972 and 100 prawns collected every month. After February 1972 the sieving technique was introduced and 200 prawns were collected every month. At Swartvlei samples were collected at a number of points in the channel and lower estuary (areas 1 and 2 on Fig. 2) over the period November 1970 to April 1972 using both pump alone and pump and sieve. From June 1972 samples were collected using pump and sieve in the lower estuary, channel and lake (Fig. 2). This more extensive sampling program was begun when apparent salinity dependent variations in the population began to develop. Samples of 200 animals were collected in the lower estuary and the channel but only 100 in the lake where collecting was more difficult due to the greater depth of water.

Treatment of samples

Samples of prawns were either formalised in the field or brought back alive to the laboratory in sea water in plastic bags in an insulated box. In the laboratory the carapace length of each specimen was measured. This was taken as the mid-dorsal length from the tip of the rostrum to the posterior end of the carapace - the area referred to by Biffar (1971) as the "dorsal oval". Prawns were then divided up into 1-1,9 mm, 2-2,9 mm, 3-3,9 mm etc. carapace length size classes. Females were examined for the presence of eggs and these were classified as eyed or non-eyed. The diameter of fresh eggs was measured using a graduated micrometer eyepiece. The number of eggs was counted in preserved specimens. It was usually possible to tell if a female had recently shed its eggs by the remains of egg cases on the pleopods. The state of development of the ovary was also noted; in C.kraussi this is easily visible through the transparent abdominal tergites. Specimens with a carapace length of 3 mm or less were difficult to sex and these were classified as unsexed juveniles.

Measurements of temperature and salinity in the field

The temperature of the surface water as well as that of the sand brought up in the pump was measured. Samples of water for salinity determinations were taken on the bottom, as this was the water in contact with the burrows. Temperatures and salinities were determined as described in Part 1.

Temperature tolerance of adults

The tolerance of adult prawns to temperatures of 10, 30, 33 and 35°C was determined. C.kraussi was collected at Kleinemonde at temperatures of 15-18°C. They were brought back to the laboratory and kept overnight in sea water (35°/oo) at 20°C. Experiments at the upper three temperatures were carried out in plastic basins containing 8 li of water and using Tecam heater stirrers. The low temperature experiment was done in a larger container with 20 li of water. A cooling coil connected to a refrigeration unit was used in conjunction with a heater stirrer to maintain a temperature of 10°C. A control experiment was set up in a constant temperature room at 20°C. In the case of the high temperatures, the temperature was raised from 20°C at a rate of 1,3-1,5° per minute. Twenty to twenty-five prawns were used in each experiment. Observations were made at increasing time intervals on a logarithmic scale for hours. Dead prawns softened and turned opaque rapidly. The percentage survivalship was converted to a probit following the method of Finney (1952).

Temperature and salinity tolerance of eggs and larvae

The temperature tolerance of eggs and the effect of high and low temperatures on development was determined experimentally by holding ovigerous females individually in plastic boxes containing 200-300 ml of sea water (35°/oo) at either 25 ± 3°C or 14 ± 1°C. Control females were kept at 20°C. Salinity tolerances of eggs were determined at salinities ranging from 10,4 to 35°/oo at 20°C. Controls were kept at 35°/oo.

The salinity tolerance of larval and post-larval stages was compared in individuals hatched in sea water (35°/oo). Batches of ten in triplicate were transferred to a salinity of 9°/oo at 20°C and left for 24 hours, after which the numbers alive or dead were counted. A control batch of both stages was kept in undiluted sea water.

2. Larval biology and dispersal.

The larvae.

Larval stages were reared in the laboratory and the biology of the larval stages both in the laboratory and in the field was investigated. After hatching larvae were transferred to glass dishes containing 50-60 ml of water and kept under the same conditions at which the eggs had developed so as to follow the further effects of temperature and salinity on development. The glass dishes allowed inspection for the presence of moulted exuvia.

Observations on larval behaviour under simulated natural conditions were carried out by allowing females carrying late stage eggs to burrow in narrow perspex containers (internal measurements 2 cm x 18 cm x 44 cm deep). After hatching it was usually possible to observe some larvae in the maternal burrow in areas where the burrow came in contact with the sides of the container.

Dispersal.

Attempts were made to collect larval and post-larval stages of *C.kraussi* in the plankton in the west Kleinemonde estuary. Initially a towed plankton net was used but subsequently a continuous sampling procedure using a water pump in a boat over a known prawn bed was employed. The intake consisted of a funnel 15 cm in diameter suspended 15-30 cm above the bottom and covered by wire mesh with 2 cm openings. The outlet pipe was placed in a plankton net suspended from the boat with the opening of the pipe placed below the surface of the water to lessen the force of the pump. The pump delivered about 4,000 li per hour. A monitoring system to catch migrating prawns was set up in the east Kleinemonde estuary. This consisted of four asbestos cement boxes 30 cm x 20 cm x 30 cm deep. These were filled to a few cm below the brim with sieved sand and buried in the estuary bed so that the sides just protruded above the sand. The boxes were left in position for 20 months during which time they were dug up every two months and the contents sieved. Any prawns that had moved in were preserved, measured and sexed.

3. Recruitment, growth and population density in different areas.

Rates of growth were determined from analyses of regular samples. After measurement and sexing of all the individuals in a sample, the numbers of juveniles were expressed as a percentage of the total numbers in the sample. A size frequency analysis of the adults was made. Males and females were considered separately as the males reached a greater maximum size. Growth rates were determined by inspection of the rate of progression of the modes in successive samples. Weighings of live prawns of different carapace lengths were done to establish a length/weight relationship and to determine whether this relationship differed between prawns from different areas. Samples collected in other areas during the general survey were also used, wherever possible, for comparison with the populations in the Kleinemonde, Swartkops and Swartvlei systems.

The relative growth of prawns in open and closed estuaries was compared in the east Kleinemonde and Kowie Rivers. Asbestos cement boxes, as already described, were filled with sieved sand from the west Kleinemonde estuary. Into each box were placed twelve 3 mm and sixteen 4 mm carapace prawns. Each box was then covered with a wire mesh lid which allowed water circulation but prevented the prawns from escaping. One box was placed in each estuary and left for 7 months, from 19/5/72 until 12/12/72. They were then lifted and the remaining prawns recovered, measured and weighed.

Attempts were made to assess population density independently of the techniques described in Part 1. Digging and sieving known volumes of sand was abandoned due to the difficulty of digging out a metre depth of sand under water. An attempt was made to develop an index of relative density, expressed as catch per unit effort. It was assumed that the efficiency of the prawn pump and the digger was similar in all areas sampled. Counts were then made of the number of prawns collected in a successive series of 25 pump strokes. This was then converted to the number of prawns per 100 pump strokes.

Results

1. Breeding. Salinity and temperature effects on C.kraussi.

Seasons.

More data are available on the Swartkops and Kleinemonde populations than from other areas. Breeding in the Swartkops estuary occurs mainly in the winter and spring (June-September) with a smaller peak in late spring and summer (November-January) (Fig. 11). The higher numbers of ovigerous females obtained in 1971 reflects the use of the prawn pump alone in sampling. Results from the Kleinemonde estuary were similar to those obtained at Swartkops as regards breeding times although minor differences did appear. In addition each area tended to vary slightly from year to year. Disregarding the results obtained in the Swartkops estuary in 1971, the samples indicated that similar proportions of females in each area carried eggs in each year. It is noticeable that more females produced eggs in the Kleinemonde estuary than in the Swartkops estuary. The reason for this is obscure at present. The histograms tend to fluctuate more rapidly than the absolute numbers of ovigerous females, due to the appearance of newly matured females in the population.

Swartvlei was only visited every second month; the results are shown in Fig. 12. Unfortunately only small numbers of mature females were collected and thus only a tentative interpretation of the results can be offered. There appeared to be differences in breeding period in the three areas sampled as well as differences between this area and those described above. Higher proportions of ovigerous females were recorded in the lake and in the lower estuary than in the channel linking the two. It also appeared that C.kraussi in Swartvlei tends to begin breeding slightly later in the year (August-September) than the

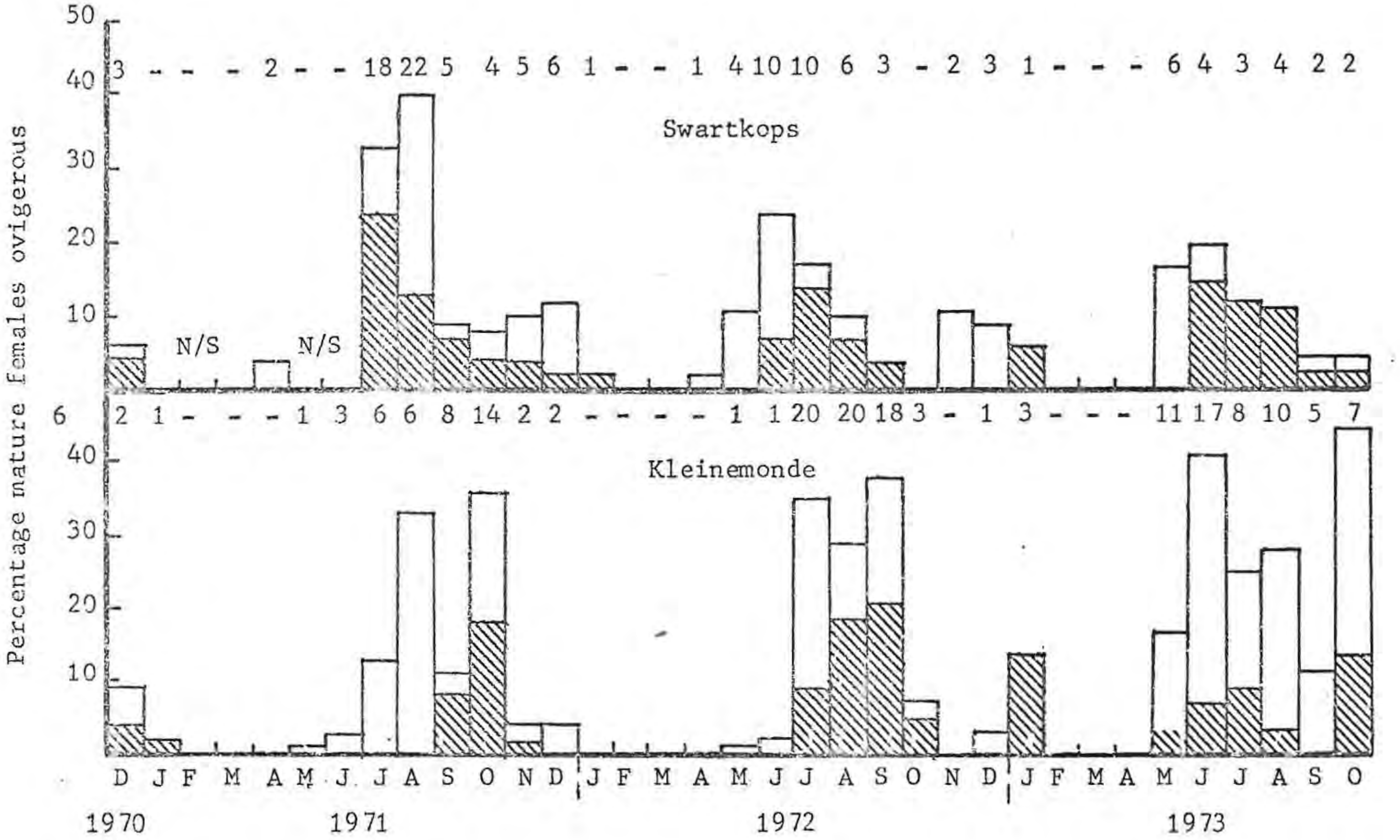


Figure 11. Breeding in the Swartkops and Kleinemonde estuaries. Cross-hatching indicates percentage of mature females carrying eyed eggs. N/S indicates no sampling. Figures indicate actual number of ovigerous females collected.

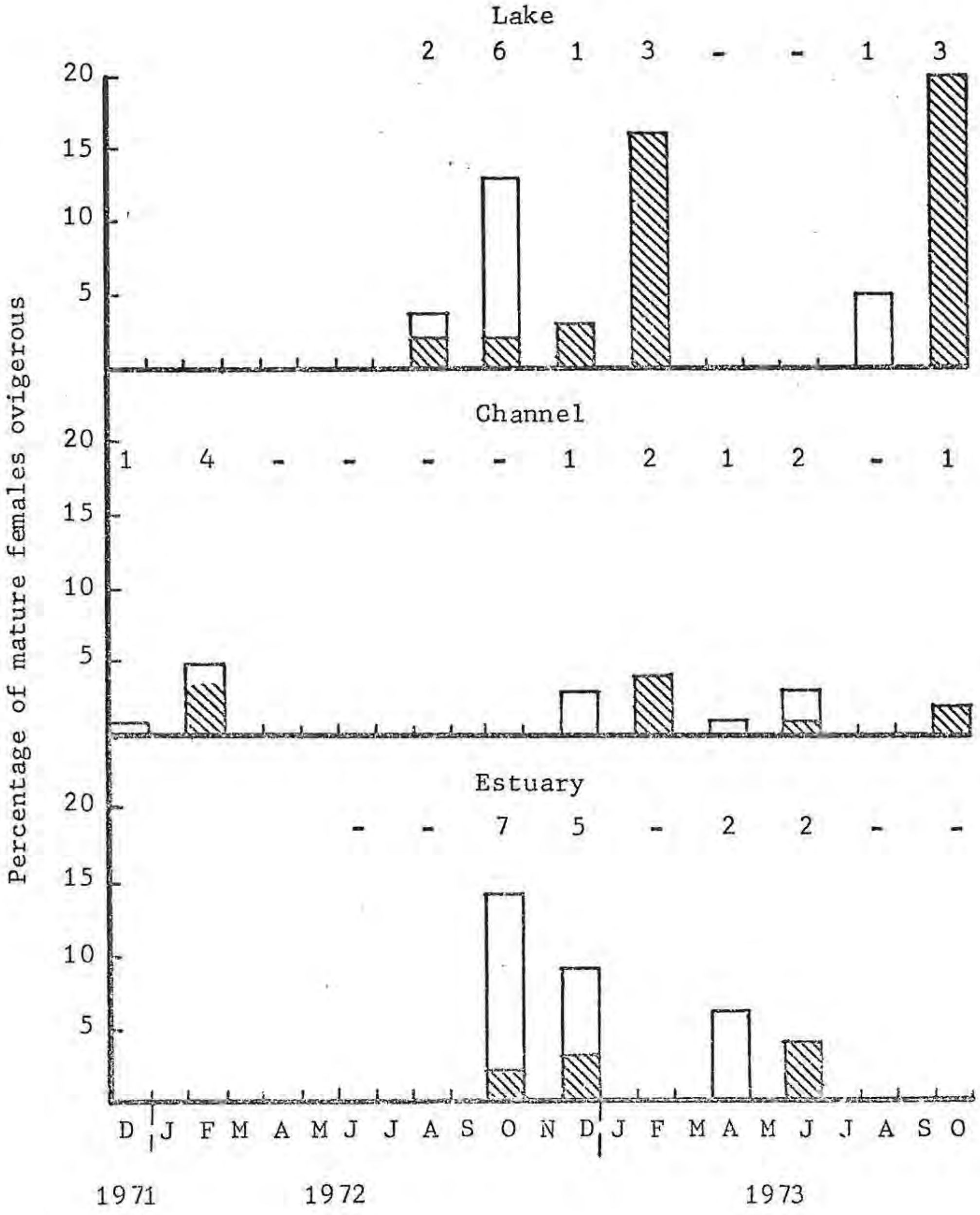


Figure 12. Breeding in the Swartvlei system. Cross-hatching indicates females carrying eyed eggs. Figures indicate actual number of ovigerous females collected.

populations in the Swartkops and Kleinemonde estuaries, and is more of a spring and summer breeder.

A limited number of samples from 32 areas were collected during the general survey. These were generally spot samples and no continuous records are available but it is of interest to compare these areas with those described above. Analyses of these samples are given in Appendix 2.

Samples collected in the western and southern Cape Province in summer (February 1972) were similar to those from the west Kleinemonde and Swartkops estuaries at the same time. Between 33 and 62% of mature females in the 8 areas visited showed signs of early ovary development. Late ovary development was only recorded in the Heuningnes (7%) and Uilenkraal (4%) estuaries (Fig. 1). At Stilbaai 6% of females were ovigerous but 28% had recently shed their eggs indicating the end of the breeding season. Juveniles were generally present but only at Langebaan (48%) and in the Great Brak estuary (42%) in any large numbers. All available evidence suggested similar winter/spring breeding populations with possibly some carry over in to summer as shown by the females at Stilbaai which were ovigerous or had recently shed their eggs.

Nine samples taken in the eastern Cape in 8 areas in the months of April, July, August, November and December also indicated winter/spring breeding populations. Samples taken in July and August 1971 all contained ovigerous females and generally a high proportion of females showing late stage ovarian development.

While populations of C.kraussi in the south-western, southern and south-eastern Cape Province showed basically similar patterns, populations in the Transkei and Natal appeared to vary. Of 12 samples collected in July 1972 in different areas 8 yielded ovigerous females. The proportion of ovigerous females did not exceed 19% and low proportions were usually associated with a high proportion (up to 50%) of females which had recently shed their eggs. In a sample collected at Umgababa on June 1, 1973, 22% of the mature females were ovigerous while 15% had already shed their eggs. The proportion of females with late stage ovaries increased steadily over the period September 1970 to December 1970 (from 11% to 46%) in the Zetani River (Tinley Manor) while similar high proportions were found at Port St.Johns in January 1973 (27%) and at Kosi Bay in January 1971 (65%). These results all suggest breeding earlier in the year than the populations further south. Further information would be required to confirm this trend and to attempt to explain it.

Temperatures in the study areas.

No continuous temperature records are available but monthly records were taken in the west Kleinemonde and Swartkops estuaries. There was an annual range of 14 to 26°C at a depth of about 50 cm in the substrate in the closed Kleinemonde and of 15 to 25°C in the open Swartkops estuary (Fig. 13). Fewer results are available from Swartvlei (Fig. 14) but it appears that the range is similar throughout the system. Available records indicate that the temperature did not rise as high in the Swartvlei system as in the Kleinemonde and Swartkops estuaries and the annual range appears to be 15 to 24°C.

Temperature tolerances of the adults.

Survival at 30°C, 10°C and in the controls at 20°C was similar (Fig. 15). After 500 hours at 30°C 76% of the sample survived as compared with 72% in the control. Observations during the experiment

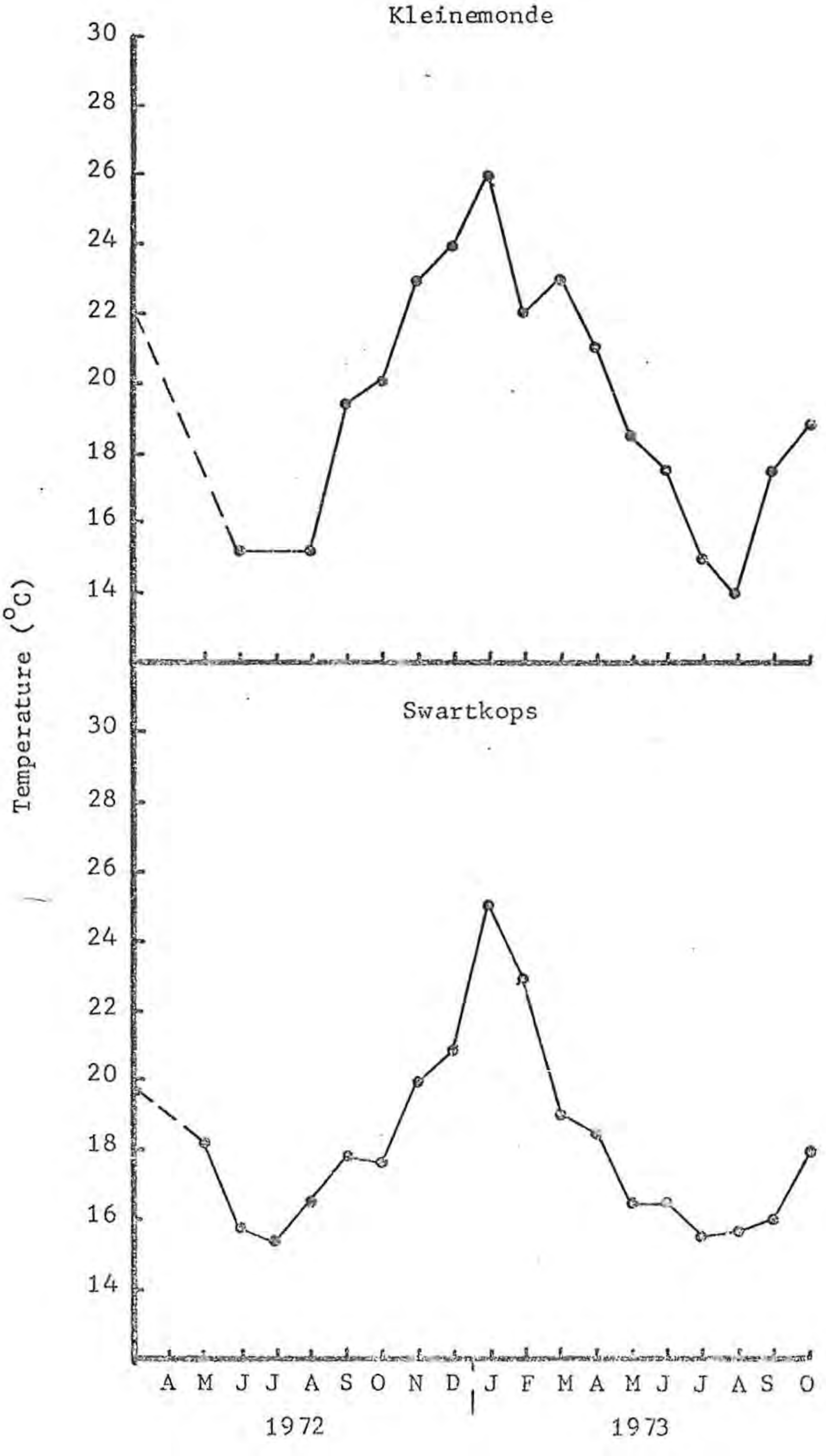


Figure 13. Substrate temperatures at c. 50 cm below the surface of the sand in the Kleinemonde and Swartkops estuaries.

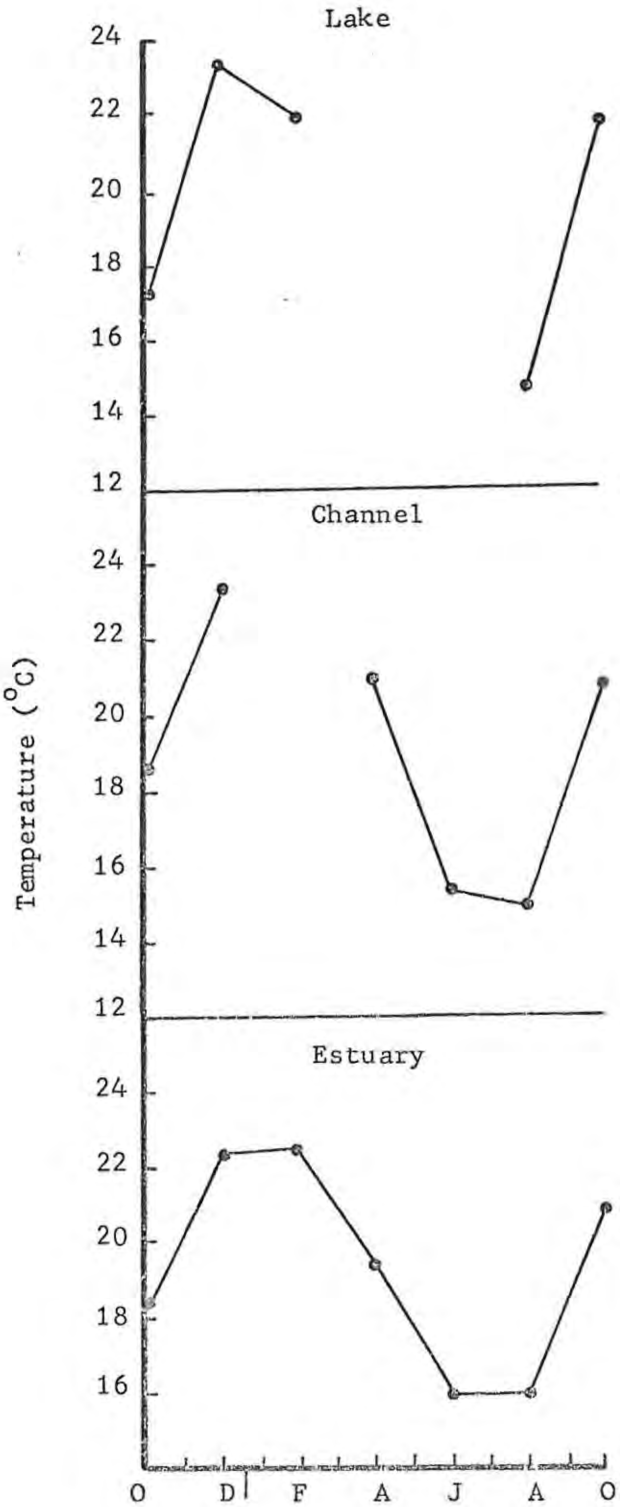


Figure 14. Substrate temperatures at a depth of c.50 cm below the surface of the sand in the Swartvlei system.

showed that C.kraussi remained active and responsive to mechanical stimuli at this temperature. The temperatures of 35 and 33°C were well above the upper lethal limit since all prawns died within 2¼ and 11½ hours respectively. At 10°C survival was comparable to that of the control. 80% survived for 500 hours but all prawns remained almost totally inactive over the duration of the experiment.

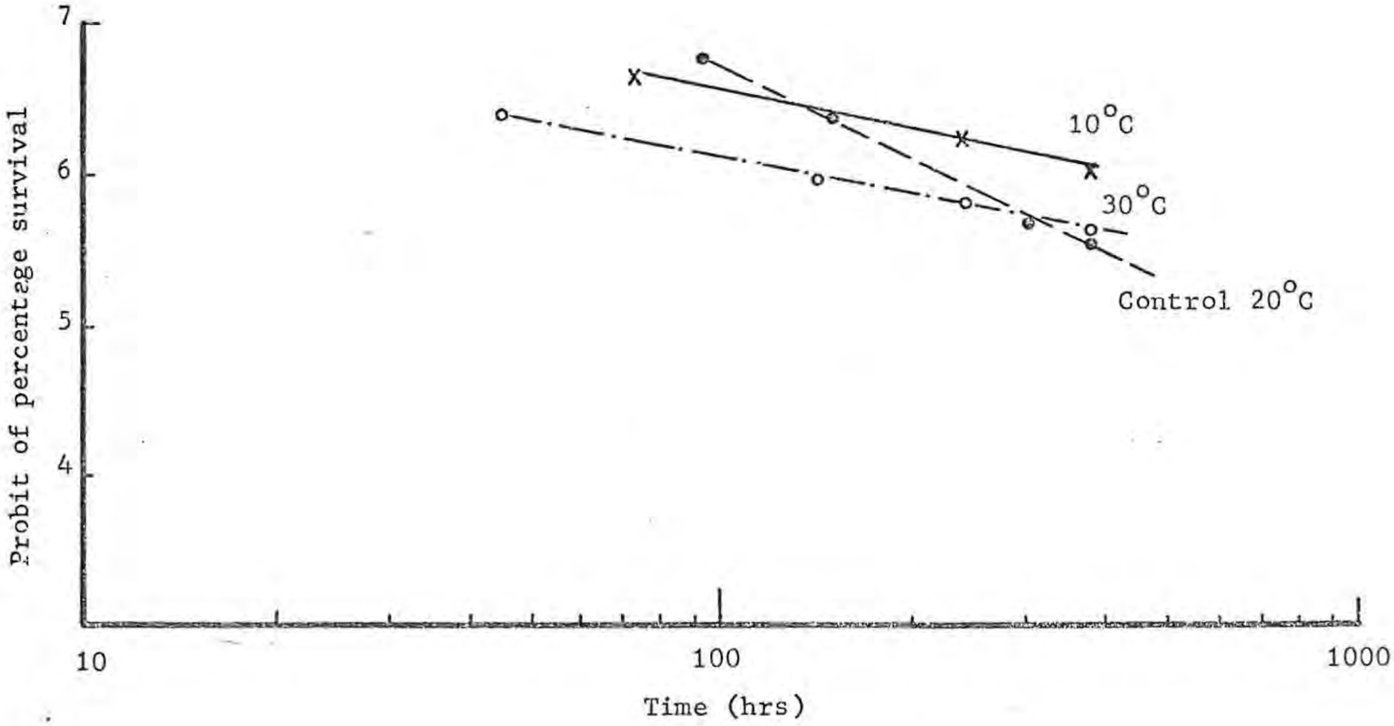


Figure 15. Survival of C.kraussi in sea water (35°/oo) at different temperatures.

Salinities in the study areas.

The Swartkops estuary study area lay at the mouth of an open estuary and was exposed only to full sea water salinities (35°/oo) during the study period. Incomplete records from the west Kleinemonde estuary suggest that the salinity in the lower part of the estuary only dropped below about 20°/oo during floods as in August 1970 and 1971. Salinities fluctuated in the Swartvlei system (Table 6) depending on whether the mouth was open or closed and on the inflow of fresh or sea water. High salinities prevailed when the mouth closed in April 1972 but dropped steadily as the level of the lake rose due to inflow of fresh water until August when the mouth was artificially opened. Little change occurred while the lake level was dropping but the salinity levels rose throughout the system following the equinoctial tides of September. Salinities fluctuated until April 1973 when the mouth closed again. A general equilibration was followed by a drop in salinities although they did not reach the low levels of 1972.

Table 6: Bottom salinities (^{o}/oo) recorded in Swartvlei collecting areas. A range represents samples taken on a low and a high tide.

	Areas			
Date	Lake	Channel	Estuary	State of mouth
April '72	24	24,2	30,6	Closed
June '72	12,6	13,8	19,3	Closed
Aug. '72	9	9	16,2	Just opened
Sept '72	10,6	12,4-15	32,5-34,5	Open
Oct '72	15-28,4	27,6-32,9	34,8	Open
Dec '72	15-21,6	18,1-23,4	30,8-32	Open
Feb '73	15,6-17,8	19-30	31,6-33,9	Open
April '73	13,3-14	14,4-15	24,4-25,9	Open
June '73	23	24	27	Closed
Aug '73	14,5	25	23	Closed
Oct '73	15	21	24	Closed

Size at maturity and number of eggs per female.

Females mature at a carapace length of 6 mm although some ovary development is frequently discernible before this size is attained.

Females with a carapace length of less than 6 mm were only very rarely found to be ovigerous.

The numbers of eggs on all preserved ovigerous females were counted, but since some of these females were damaged during collection and from the very low numbers of eggs present at times it appeared that some might have been lost. Consequently in calculating the mean numbers of eggs carried by females of different sizes, numbers below 20 were disregarded. The numbers of such females are recorded in Table 7.

Table 7: Mean and range of numbers of eggs carried by females of different sizes.

	Carapace length of female (mm)					
	6-6,9	7-7,9	8-8,9	9-9,9	10-10,9	11-11,9
Mean no. of eggs	41,9	86,4	138,7	282,6	177,1	76,5
Range	21-78	20-285	32-500	28-500	36-628	63-90
No. of females examined	12	60	45	32	8	2
No. of females with fewer than 20 eggs	4	13	4	0	0	0

There did not appear to be any variation in different areas in the numbers of eggs produced by females of any one size. With increase in size over the carapace length range 6-9 mm there was a very marked rise in the numbers of eggs produced. The decline in the number of eggs found in the very large prawns may be an artefact due to a combination of damage during collection and the very low numbers of these prawns which could be found.

Egg development. No females produced eggs in the laboratory and consequently the appearance of the eggs on extrusion and the exact hatching periods are unknown. It was possible however to identify the stages of the eggs from their appearance. Recently extruded eggs are orange-red in colour. At this stage they are spherical with a diameter of 0,94-1,24 mm ($\bar{x}$ = 1,12 mm; n = 80 eggs from 8 females). During development the colour fades initially to a dull yellow and eyes appear after about 10 to 12 days. At about 14 days, red pigment spots develop. In the newly hatched larva these spots lie along the ventral edge of the branchiostegite and in the mouth region. The yolk begins to recede noticeably at about 20 days. By this time the eggs have swollen and become more elliptical with measurements of 1,3-1,8 mm x 1,1-1,5 mm ($\bar{x}$ = 1,52 mm x 1,23 mm; n = 30 eggs from 10 females). The yolk continues to recede and just before hatching the egg is almost transparent, although some yolk may still be visible in the hind gut. Maximum hatching periods in the laboratory were 32-33 days (n = 3) in a salinity of 34-35^{o}/oo and at a temperature of 20^{o}C.

Factors affecting egg and larval development.

i) Temperature. All ovigerous females suffered loss of eggs in the laboratory due to handling during inspection of the eggs and probably also due to existence out of the burrow. Development at 20^{o}C in 35^{o}/oo required 30-33 days while the larval stage lasted 3-5 days. The effects of low and high temperatures are summarised in Table 8.

Table 8: Development of eggs and larvae at low and high temperatures.

	Low temperatures 14 ± 1°C	High temperatures 25 ± 3°C
No. of ovigerous females	25	22
No. of egg batches hatched	5	4
No. of larvae	2, 6, 9, 10, 20	2, 3, 4, 4
Development time (days)	102, 68, 110, 36, 83	20, 22, 23, 27
Larval development time (days)	10-14	5-6

At the low temperatures development of both eggs and larvae was markedly retarded. Twenty batches of eggs at 14°C were lost; of these the female died in three, while six developed to a late stage over periods ranging from 75-97 days; others showed negligible development.

Of 18 batches of eggs at high temperatures which did not hatch, nine developed to a late stage in which eyes were present and the yolk had almost disappeared. The other nine showed no development at all or were lost within a few days of their arrival in the laboratory. At 25°C eggs developed in 20-27 days; this is more rapid than the development at 20°C (30-33 days). Larval development times at 20 and 25°C were similar.

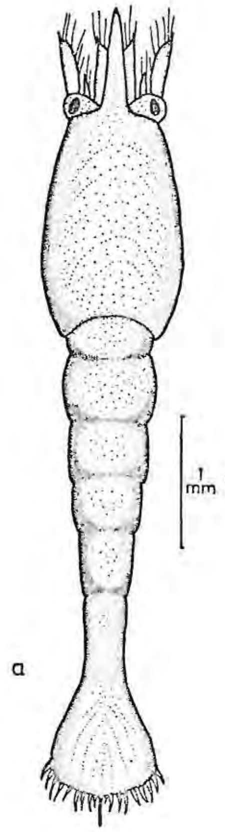
ii) Salinity. The effects of different salinities on egg and larval development are summarised in Table 9.

Table 9: Hatching and larval development of C.kraussi at different salinities.

Dilution (^{o}/oo salinity)	n	Hatched	Development time of larvae (days)
35	18	13	3-5
25-28	3	2	6
17-21	4	1	6
14-16	8	5	5-11
10-13	7	2	9-14
Less than 10	1	0	-

The lowest salinity at which a batch of eggs hatched was 10,4^{o}/oo but these were already at an eyed stage of development when exposed to this dilution and all larvae died on hatching. In all salinities below 17,5^{o}/oo development was only successfully maintained in eggs which had already reached at least the eyed stage of development. Exposure to salinities below 17^{o}/oo, even at late stages of development, always resulted in egg damage. Eggs either swelled and turned opaque or else development proceeded for a short period and then ceased and the eggs dropped off. Low salinities also extended the period of larval development (Table 9). It was concluded that 17^{o}/oo is about the lowest salinity at which the eggs and larvae of C.kraussi can undergo their full development in the laboratory.

Comparison of survival of larval and immediate post-larval stages following direct transfer from 35 to 9^{o}/oo sea water after 24 hours showed that 92% of the post-larvae survived but only 18% of the larvae. This indicated that the post-larval stages are markedly more tolerant of low salinities than the larvae.



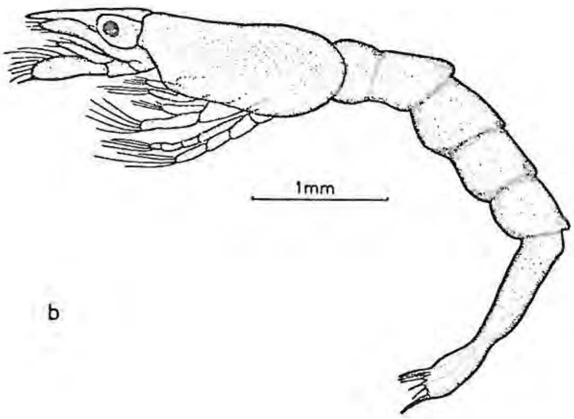
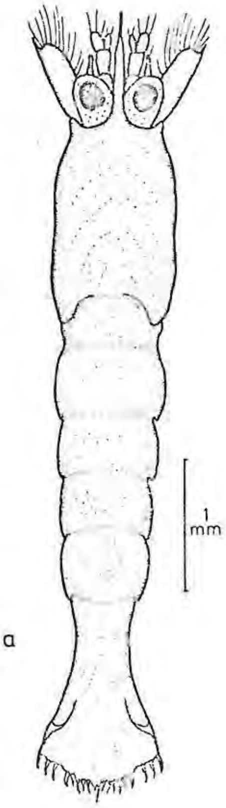


Figure 16. First stage larvae of Callianassa kraussi. a. Dorsal view. b. Lateral view.



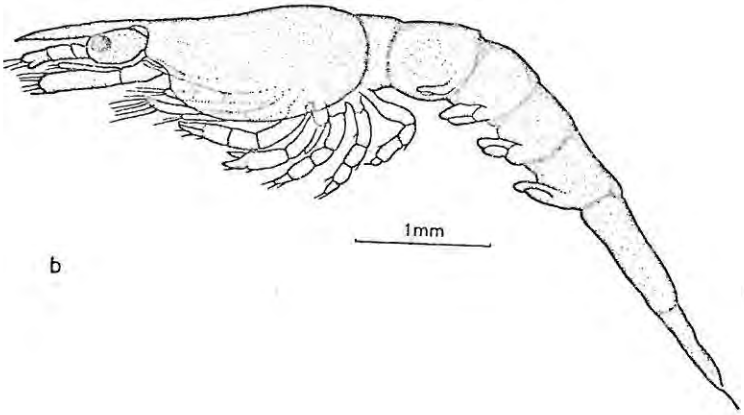


Figure 17. Second stage larvae of Callianassa kraussi.
a. Dorsal view.
b. Lateral view.

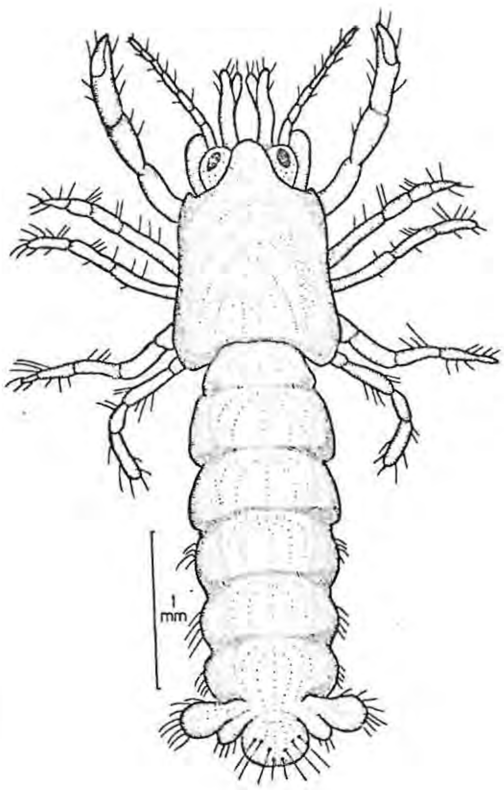


Figure 18. First post-larval stage of Callianassa kraussi.

2. Larval Biology and Dispersal.

Larvae.

Newly hatched larvae as well as the first post-larval phase are 5-6 mm long (Figs 16-18). They are almost transparent except for the red pigment spots and the remains of yolk in the mid-gut and hind-gut retained in some individuals. Feeding does not appear to be necessary for the transition to the young prawn stage to be completed. Once the remains of the yolk disappeared from the gut it remained transparent and apparently empty for the duration of the larval stage. No growth was recorded during this period.

During the larval period the animals do not swim and may be observed lying upside down in the parent burrow. The cephalothoracic appendages beat almost continuously but do not appear to be used for locomotion. Any movement which does occur is accomplished by a rapid flicking of the body. This lasts for only a few seconds before the larva sinks back to the bottom. Laboratory observations indicated that the larvae are incapable of leaving the parent burrow unless forced out, for example by the water currents produced by the parent prawn. In the Kleinemonde estuary plankton samplings were timed to coincide with a period immediately following a decrease in the number of ovigerous females. A preliminary 10 minute night plankton haul, followed by 17 hours continuous sampling over 3 nights using the water pump method yielded a variety of planktonic organisms but no larvae of C.kraussi. No larval stages of C.kraussi were found during an extensive estuarine plankton sampling program run by the Port Elizabeth museum (Wooldridge, personal communication). In view of the inability of the larvae to swim this result is not surprising. It thus appears that this species has both a markedly abbreviated larval life, and has lost its planktonic phase.

Immediately the larval stages have been completed, the young post-larva is capable of burrowing. In the laboratory the post-larvae excavated their own burrows in the wall of the parent burrow. A photograph of a polyester resin cast obtained from the Swartkops estuary is shown in Plate 5. The burrows of the young prawns leading off from the parent burrow can clearly be seen.

Initially the connection with the parent burrow would be the only access to the surface and thus would not be visible on the surface of the sand. As the prawns increase in size their burrows may become

Plate 5: Polyester resin cast of Callianassa kraussi burrow from the Swartkops estuary. Note small burrows of young prawns emerging from larger parent burrow in lower left corner.

separated from the parent burrow and acquire an independent opening to the surface. Observations in the Kleinemonde estuary showed that surface openings to the burrows of juvenile prawns became apparent 2 to 3 months after a large hatching of young.

Dispersal.

Evidence for the migration of post-larval stages was obtained in the east and west Kleinemonde estuaries and in the Swartvlei system.

Three post-larvae - one of 2 mm carapace length and one of 1 mm carapace length were obtained from the continuous water pump method of plankton sampling.

The boxes put down in the east Kleinemonde estuary yielded a total of 47 prawns (Table 10).

Table 10: Numbers and sizes of prawns (mm carapace length) recovered from boxes in the east Kleinemonde estuary at different times.

Date	April 1972	June '73	Aug '72	Oct '72	Dec '72
Numbers and sizes (mm carapace)	2 of 3 2 of 4	4 of 4 1 of 3 1 lost	2 of 3	3 of 5 4 of 4 3 of 3 1 of 2	4 of 4 2 of 3 1 of 2
Totals	4	6	2	11	7

Date	Feb '73	April '73	June '73	Aug '73	Oct '73
Numbers and sizes (mm carapace)	2 of 5 3 of 4 1 of 3	zero	zero	zero	9 of 2 1 of 1 1 damaged
Totals	6	0	0	0	11

Three quarters of the recoveries occurred in spring and summer (October-February) with the period of maximum migration in October. This corresponds to the periods when the maximum numbers of juveniles were found in the population.

During October 1972 at Swartvlei there was an increase in the numbers of 4 and 5 mm carapace length prawns in the channel and in the lake (Fig. 19). Prawns in these size classes had not been present in large numbers in August in either area nor were there any juveniles present which could have grown to 4 or 5 mm carapace length over the space of two months. Thus it appears that the increase must have been

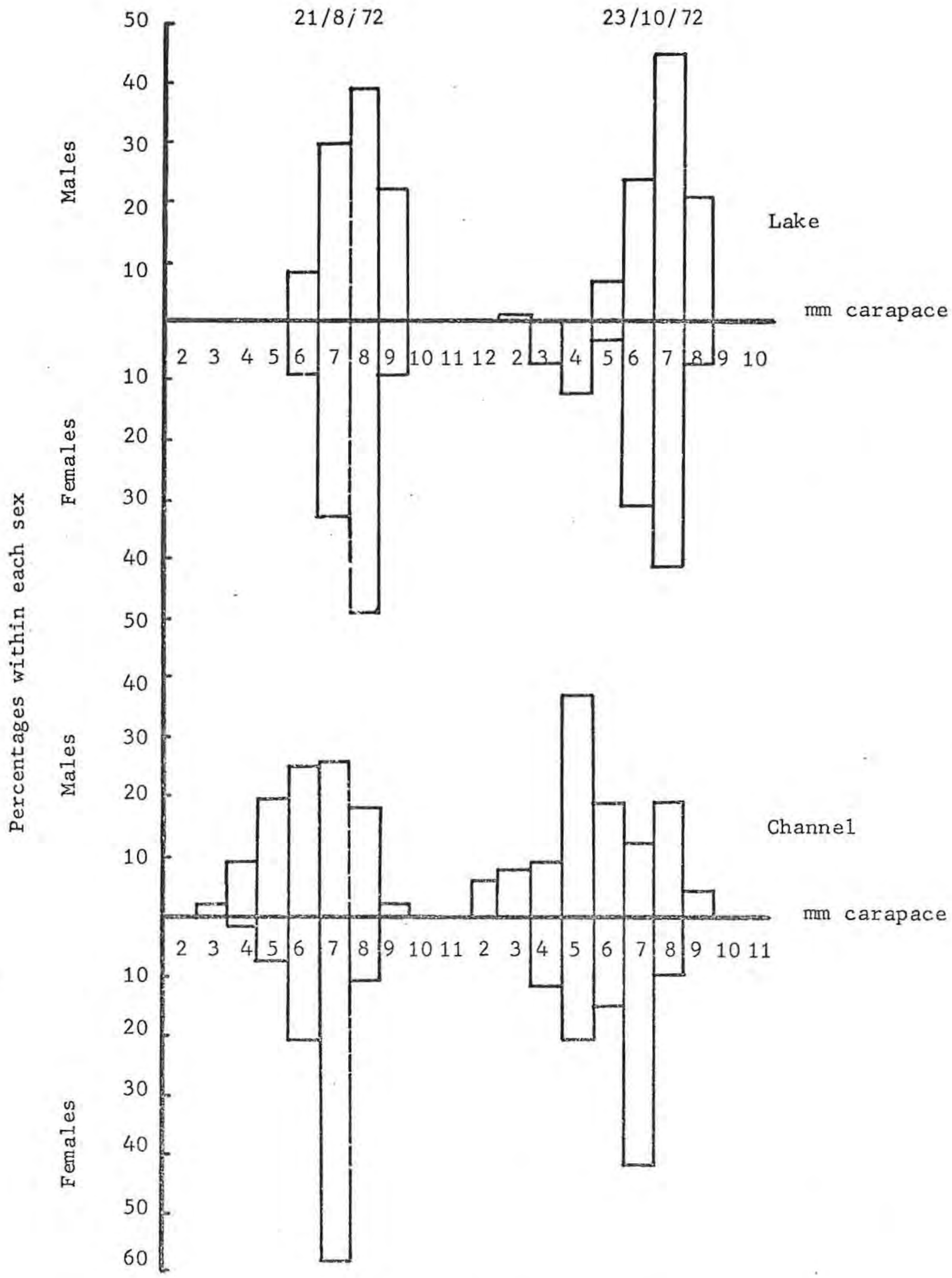


Figure 19. Changes in population structure between August 1972 and October 1972 in the lake and channel in the Swartvlei system.

due to immigration from other areas. In August 1972 there was a large proportion (40% of the population) of 3 and 4 mm carapace prawns in the lower estuary and presumably many of these migrated up the channel and into the lake over the period August to October. This movement would possibly have been assisted by the equinoctial tides of September which resulted in strong tidal currents as well as a rise in salinity in the channel and the main lake.

The period of migration in Swartvlei corresponds to the period when maximum migration was recorded in the east Kleinemonde estuary. Similar size groups were involved in migration in both areas, viz. 2-5 mm carapace length. There was no recorded migration of sexually mature individuals. This extra-burrow activity by the young stages corresponds to suggestions by Hailstone & Stephenson (1961) that in C.australiensis migrations of small post-larval stages also occur. General observations on C.kraussi in the laboratory indicate that the younger stages (2-5 mm carapace length) are stronger, faster swimmers than mature prawns. Experiments on burrowing ability (Part 1) also showed that prawns of these sizes are more efficient at burrow construction and this would be of importance in the distribution of the species. Hailstone & Stephenson (1961) also point out that in the case of adults, migration would probably be restricted to the females as the large males are hindered in swimming by the large cheliped. At Swartvlei equal numbers of males and females moved up from the lower estuary into the channel but only females managed to move as far up as the lake (Fig. 19). In the east Kleinemonde, of the 21 post-juveniles recorded, 12 were male and 9 female. The overall impression is thus one of movement in both sexes although females may be able to migrate further.

3. Recruitment, growth and population densities in different areas.

Recruitment.

Breeding seasons in C.kraussi in the Swartkops and Kleinemonde estuaries were sufficiently discrete to allow very marked increases in the proportions of juveniles in the populations at certain times of year. In the Swartkops estuary a very marked increase in the percentage of juveniles occurred in October/November 1972 (Fig. 20). This increase followed about 4 months after the June-July peak of ovigerous females. A similar increase was found in October 1973 following a June-July peak in ovigerous females. Additional peaks of juveniles occurred in May 1972 and June 1973. The June 1973 peak followed the small summer breeding effort of November 1972-January 1973; the May 1972 peak followed a similar summer breeding effort in November 1971-January 1972 (Fig. 11). It is noticeable that the delay between winter (June-July) production of eggs and spring (October-November) appearance of juveniles is about 4 months while the delay between summer production of eggs (November-January) and autumn-winter (May-June) appearance of young is 5-6 months. The reason(s) for this are obscure at present.

A similar pattern appeared in the Kleinemonde estuary. There were marked increases in the percentage of juveniles in November and December 1972 and again in September and October 1973. As in the Swartkops estuary these increases followed 3-4 months after the large winter peak of ovigerous females. Smaller peaks of juveniles occurred in June 1972 and June 1973 again presumably following the smaller summer breeding effort. As in the Swartkops estuary the delay between the January 1973 peak in ovigerous females and the subsequent appearance of young was 5 months as opposed to 3-4 months in spring and early summer.

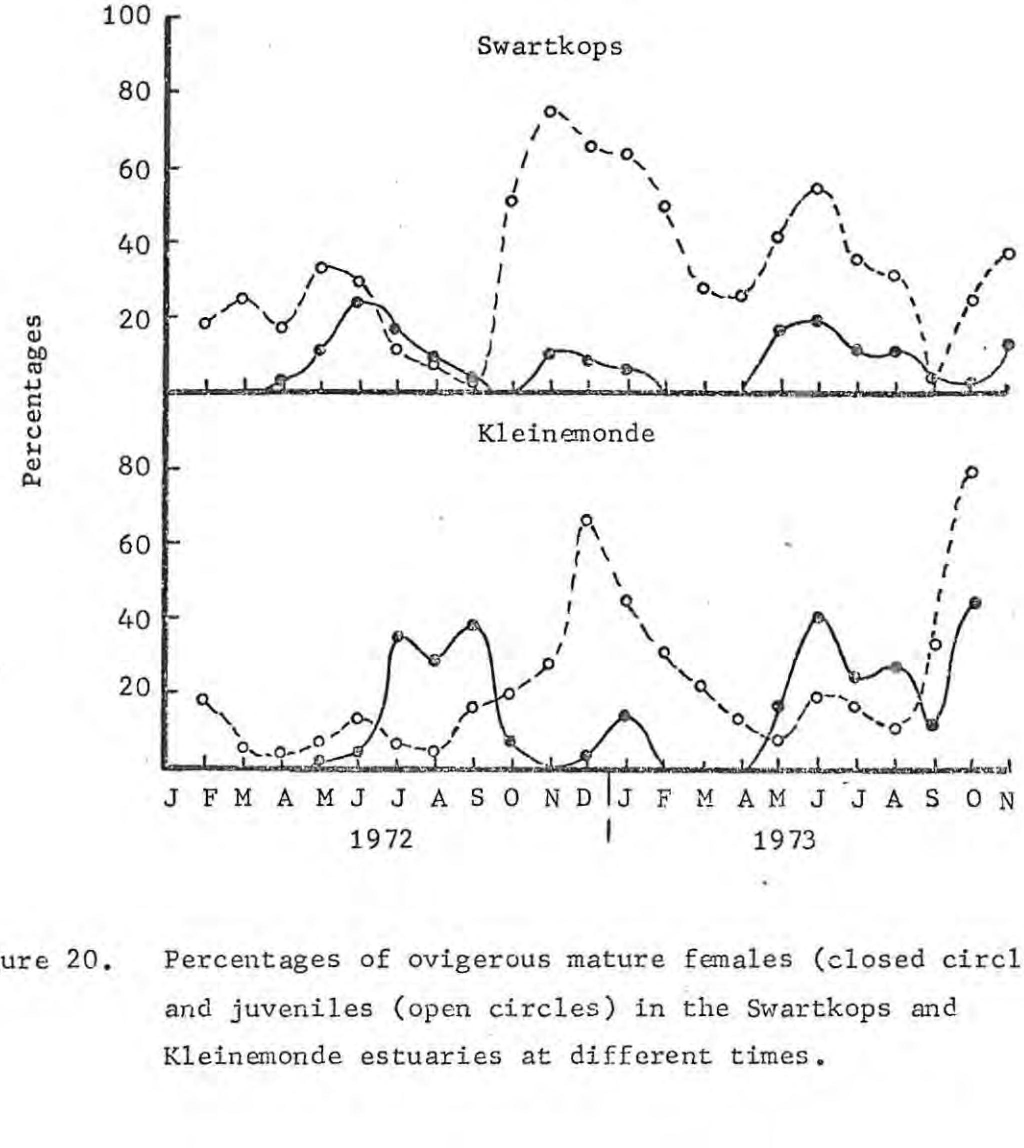


Figure 20. Percentages of ovigerous mature females (closed circles) and juveniles (open circles) in the Swartkops and Kleinemonde estuaries at different times.

In Swartvlei peaks in ovigerous females in the lake and lower estuary in October 1972 were followed 4 months later by marked increases in the percentages of juveniles (Fig. 21). In the channel egg production in February 1972 was only followed by an increase in the percentage of juveniles in October. This increase was not due to

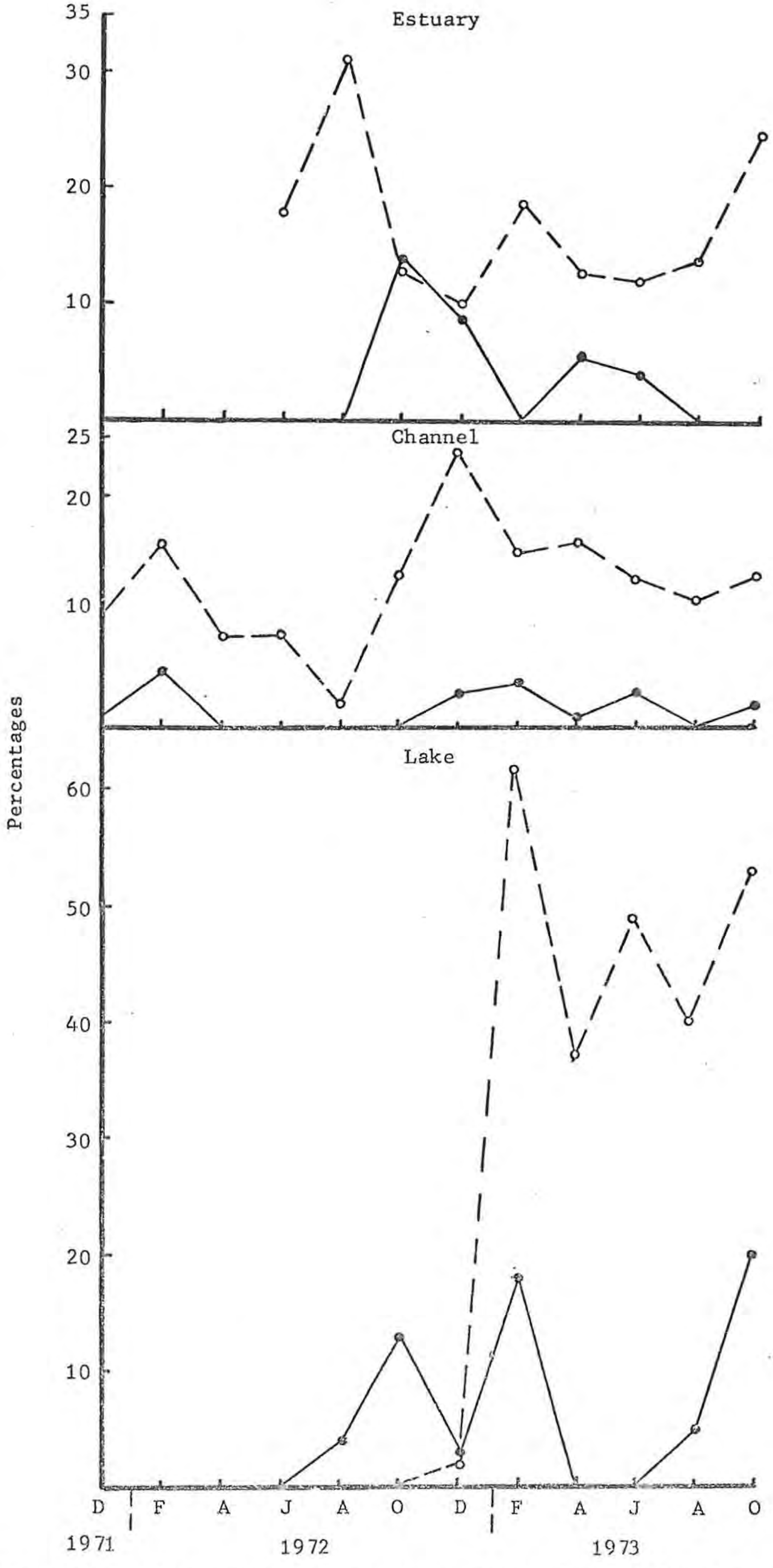


Figure 21. Percentages of ovigerous mature females (closed circles) and juveniles (open circles) in the three sampling areas in the Swartvlei system at different times.

migration from any other part of the system since increases did not occur anywhere else at this time. Similarities to the Kleinemonde and the Swartkops estuaries thus did exist but within the Swartvlei system breeding activity varied in different areas and this resulted in differences in the percentages of juveniles in the three sampling areas at different times.

The magnitude of recruitment is large in all areas. In November and December 1972 and again in October 1973 the populations in the Kleinemonde and Swartkops estuaries consisted of 60-80% juveniles. Results from Swartvlei were generally not as high although the population in the lake consisted of more than 60% juveniles in February 1973. This does not take into account mortality which might have occurred between the hatching stage and the age at which this new generation was first collected.

Growth.

The sampling period in the Swartkops estuary when both sieve and pump were used was not sufficiently long to allow one generation to be followed from hatching to death. Histograms 1-5 in Fig. 22 illustrate the changes occurring in the population structure following the major winter/spring breeding period. Histograms 5 and 6 show that the population structure was similar in March 1973 and March 1972 and thus histograms 6-9 and 1-5 may be used to follow subsequent movement of the modes. Histograms 6 and 7 show the changes occurring following the smaller summer breeding effort when a second generation of juveniles appears. Histograms 1 and 2 show how the growth of the females lags behind when the larger sizes are reached.

Although no juveniles were obtained during 1971 due to the use of

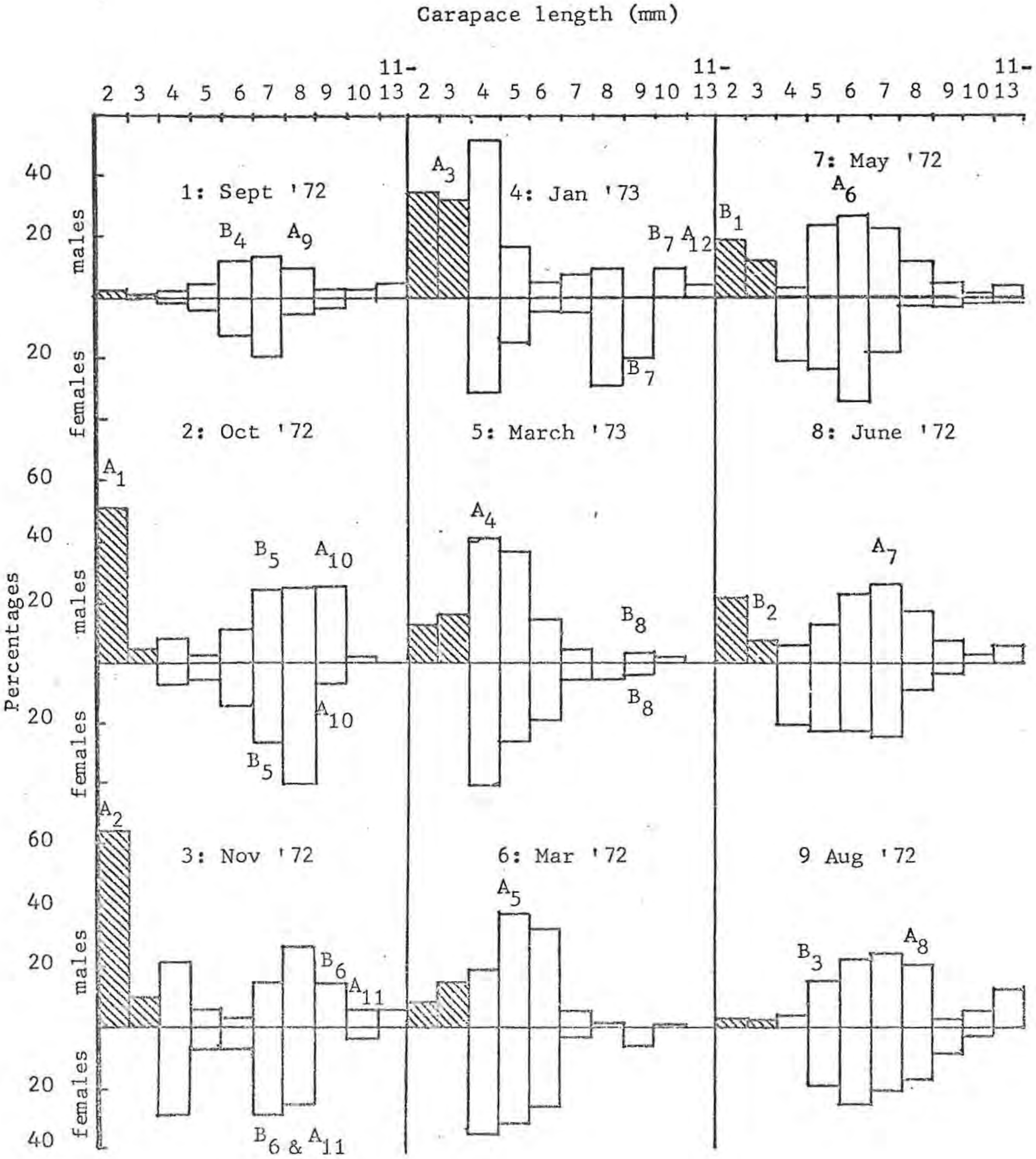


Figure 22. Examples of histograms illustrating the progression of the modes in the population of C.kraussi in the Swartkops estuary. Cross hatching indicates unsexed juveniles. Percentages calculated separately within each sex. For further explanation see text.

the pump alone in collecting, Fig. 11 shows that hatching of larvae occurred in August-September 1971 and in December 1971-January 1972. Subsequent development of these two generations (designated A and B respectively) as well as the changes associated with breeding occurring in the females, are summarised in Fig. 23.

In generation A growth of males and females was similar from the time of hatching in August-September 1971 until they reached a carapace length of 6-7 mm in May-June 1972. Growth of the females then slowed until September and this was associated with a period of ovary development. A little growth then occurred and a carapace length of 8 mm was attained in October. Males of generation A continued growing over winter and by October 1972 had a carapace length of 9 mm. In generation B which had hatched in December 1971-January 1972 both sexes grew at a similar rate and by October 1972 the females had caught up to those of generation A. No ovary development appeared to occur in generation B and summer breeding (November 1971-January 1972) only involved females of generation A. The males of generations A and B then merged (November 1972) and reached their maximum sizes of 11-13 mm carapace in about February 1973. The females of generations A and B had also merged and general ovary development occurred, again associated with a slowing of growth, from about October 1972 until January-February 1973. Growth then resumed and the females reached their maximum size of about 9 mm carapace before the winter-spring breeding period. In October-December 1972 further ovary development occurred in 9 and 10 mm carapace females indicating that they contributed to summer breeding in November 1972-January 1973. Decreases in the numbers of large females (8-10 mm carapace) were noted in November-December 1972 and again in February-March 1973. Similar decreases in the large females occurred in October 1972 to April-May 1973. This indicates that some females

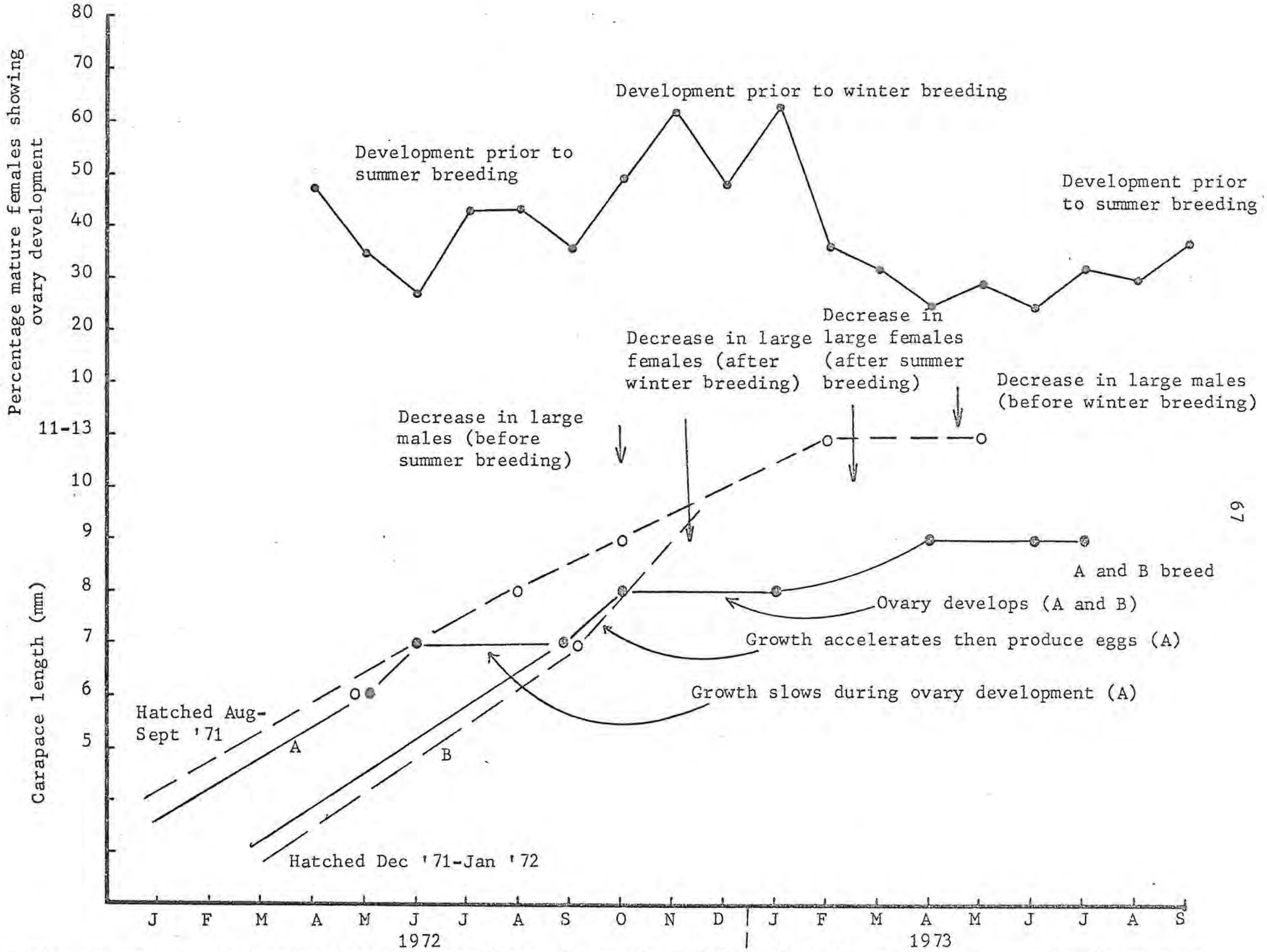


Figure 23: Growth of generations hatched in Aug/Sept '71 and Dec '71/Jan '72 with associated ovary development in females. Open circles: males and closed circles: females. For further explanation, see text.

were dying after the winter-spring breeding season and some after the summer breeding season while males died before the respective seasons. The life cycle of the two generations of C.kraussi can be summarised as follows:

a) Prawns hatching during winter/spring (August-September). Males grow continuously reaching a carapace length of 8-9 mm at the age of one year. Growth continues into the following summer and the maximum length of 11-13 mm carapace is attained in January-February. This is followed by death in the following winter at an age of nearly two years. Females reach a carapace length of about 7 mm in their first year. Ovary development follows over winter with accompanying lack of growth. They reach a length of about 8 mm carapace before breeding in early summer at an age of about 16 months. The ovary then re-develops over the rest of summer and a carapace length of 9 mm is attained before they breed for the second time in the following winter at age of about 2 years. A subsequent decrease in numbers of large females in spring indicates that this is the probable life-span.

b) Prawns hatching during summer (December-January). Males grow continuously and at the age of one year have caught up the males hatched in the previous winter/spring. The maximum size of 11-13 mm carapace is attained after about 15 months and this generation then survives through the following winter before dying in about October at an age, as in the other males, of nearly two years. Females grow at a similar rate to the males for the first year reaching 8 mm carapace before ovary development starts and growth slows. These females breed in winter for the first time at an age of about 18 months. After winter further growth may occur to 10 or occasionally 11 mm carapace length and these can contribute to the summer breeding effort before dying in February-March at the end of summer. Hailstone & Stephenson (1961) also found spring and summer generations in C.australiensis and suggested a similar life span of 2 years. In contrast, MacGinitie (1934) suggests a life span of "several" years in C.californiensis.

It thus appears that females breed twice and, depending on the time of hatching, this may occur in summer followed by a winter breeding or vice versa. The increase in size in the females immediately before egg production indicates that moulting occurs at this time and that this may be the time of fertilization. This period also coincides with decreases in the number of large males. Possibly some of these large old males die following mating.

In the west Kleinemonde estuary a similar pattern prevailed, although fluctuations in the breeding seasons and the attainment of a smaller maximum size than in the Swartkops estuary made interpretation of the results more difficult. Fig. 24 shows how the population structure did change at times due to the appearance of new generations of juveniles and how progression of the modes could be followed to a certain degree. Fig. 25 illustrates the progression of the modes and the growth of the different generations. Prawns hatching in July-October 1971 (generation B) appeared in the samples in November-December 1971 and reached a carapace length of 6 mm by March 1972. Growth in the females slowed during ovary development and whilst they were ovigerous. Meanwhile males grew to a carapace length of 6-7 mm by May. After the breeding season in November 1972 further growth ensued and females attained a carapace length of 7 mm by December 1972. The small generation C hatched in December 1971-January 1972 and the juveniles appeared in the samples in September 1972. They rapidly merged with the generation B and growth was difficult to follow.

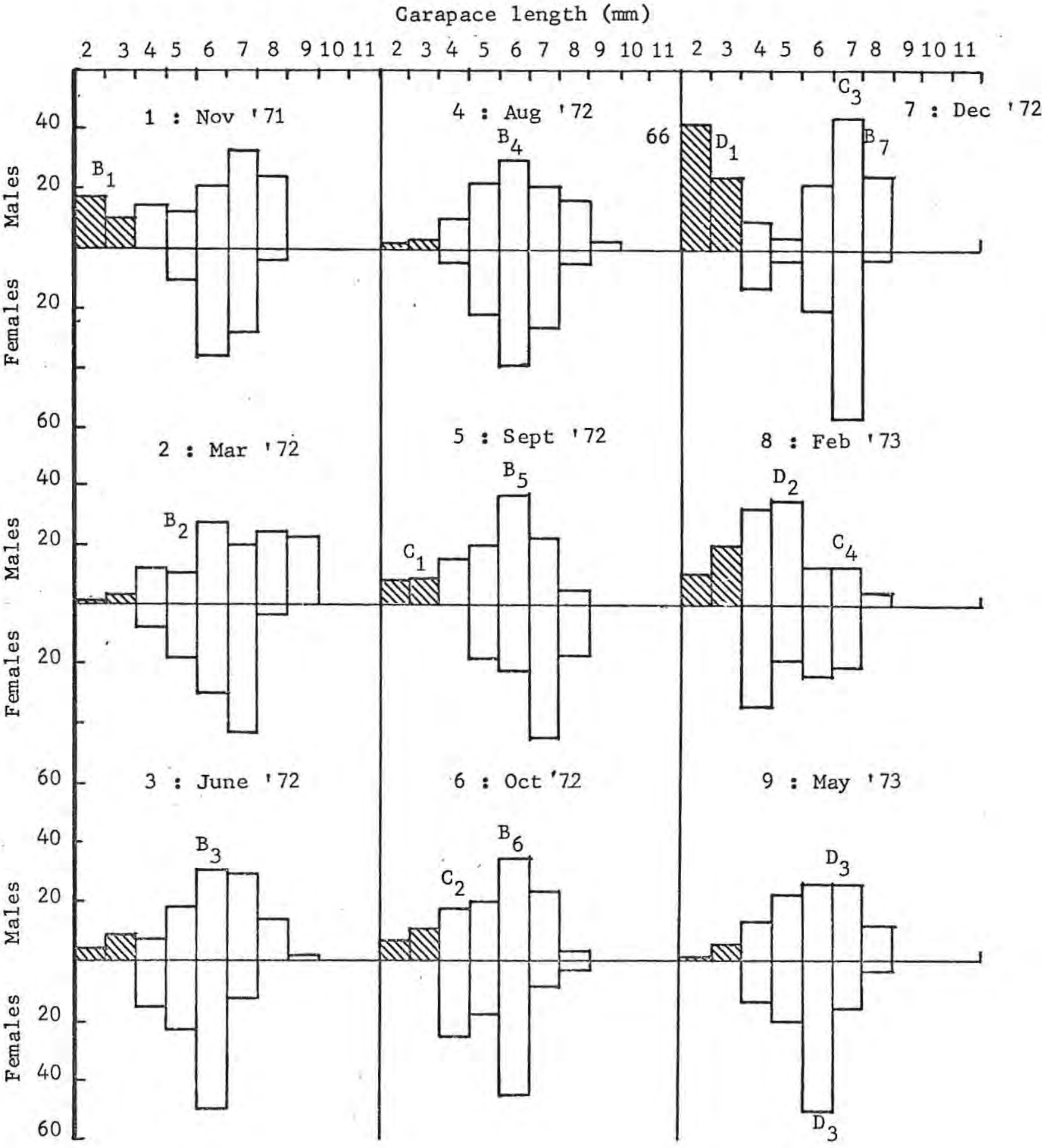


Figure 24. Examples of histograms illustrating the progression of the modes in the population of <u>C.kraussi</u> in the Kleinemonde estuary. Cross-hatching indicates unsexed juveniles. Percentages calculated separately within each sex. For further explanation, see text.

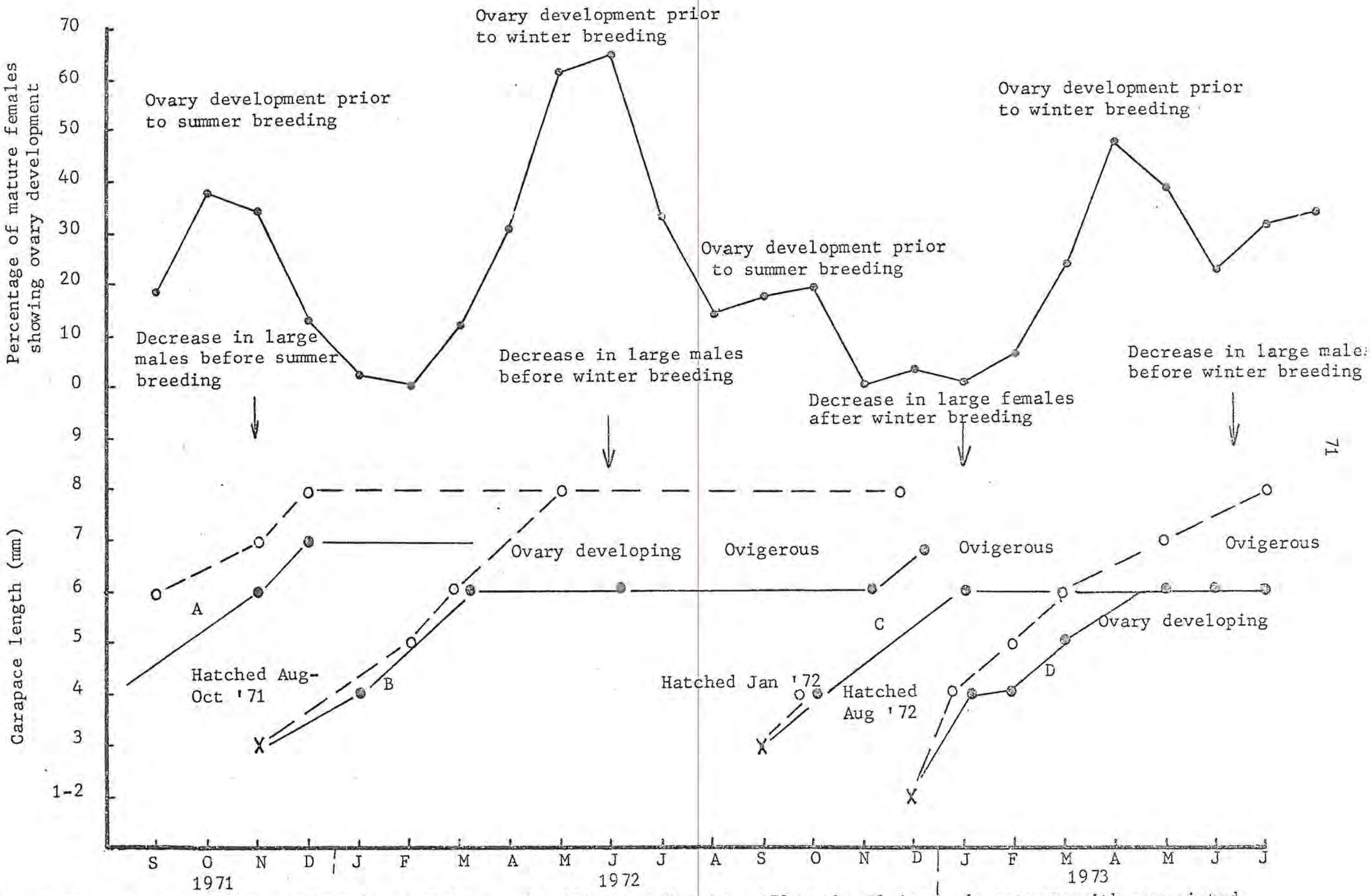


Figure 25. Growth of generations hatched in Aug-Oct '71, Jan '72 and Aug '72 in the Kleinemonde estuary with associated ovary development in the females. Males open circles, females closed circles, juveniles crosses. For further explanation, see text.

Generation D appeared in the samples in November-December 1972 after hatching in August 1972. Males attained a carapace length of 8 mm by June 1973 while the females reached 6 mm in June 1973 and merged with the females of generation C. The females of generations C and D contributed to the winter/spring breeding of 1973.

Kleinemonde is thus similar to the Swartkops estuary in having a major breeding season in winter and spring and a smaller one in summer. As in the Swartkops estuary this is associated with the maturing of two groups at different times of the year, and results in females breeding for the first time either in winter/spring followed by summer or vice versa. Although not as clear as in the Swartkops estuary there were indications of a decrease in the number of large males before the winter/spring breeding season and of a decrease in large females in November and December following the winter/spring breeding season.

In the Swartkops estuary there is very nearly a 50:50 ratio of the sexes in each size class up to a carapace length of 9 mm (Fig. 26). Few females attained greater sizes with the result that the sex ratio changes and the males predominate until at 11 and 12 mm carapace length only males occur. In the Kleinemonde estuary the picture is essentially similar although the sizes are different. Most females attain a carapace length of 6 mm after which growth slows or ceases and they therefore predominate in this class. Males predominate in the larger size classes and the sex ratio changes markedly.

The length/weight relationship of the different size classes and sexes, both of juveniles and adults was similar in the Swartkops and Kleinemonde estuaries (Fig. 27). At a carapace length of 6 mm, however, females from the Kleinemonde estuary do not increase in weight

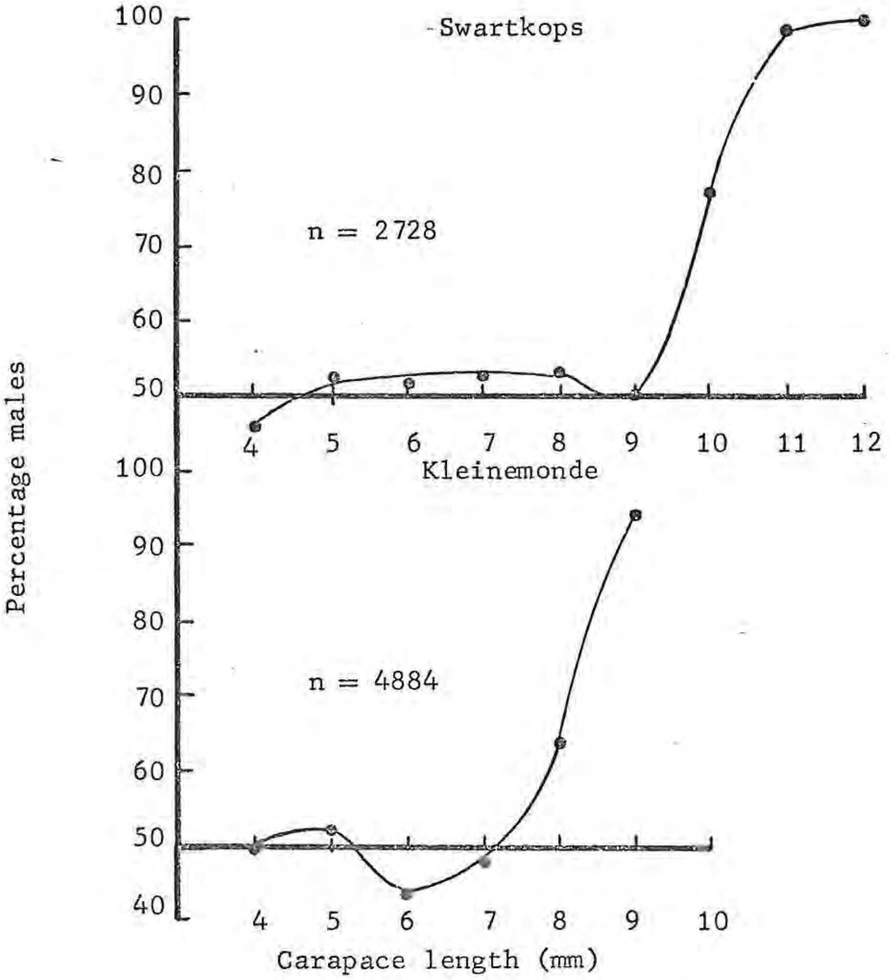


Figure 26. Percentage males in the different size classes in the Swartkops and Kleinemonde estuaries.

as much as those from the Swartkops estuary. Males from the Kleinemonde and females from Swartkops follow similar curves but no Kleinemonde males larger than 9 mm carapace were recorded. The greater weight of Swartkops males than Swartkops females would have been associated with the greater development of the cheliped in the male.

Comparison of the weights of the different size classes in the

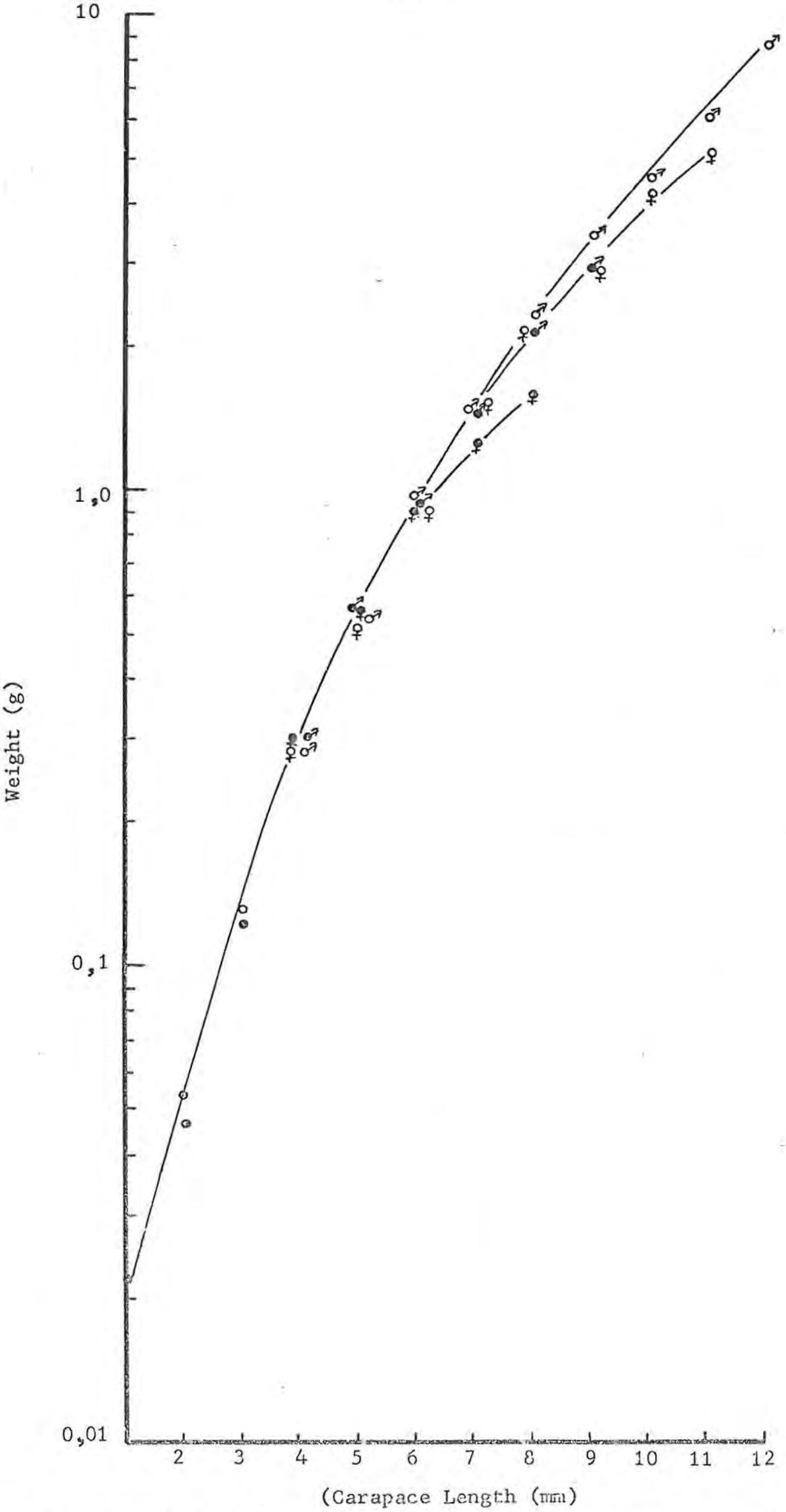


Figure 27. Length/weight relationship of C.kraussi from the Swartkops (open circles) and Kleinemonde (closed circles) estuaries. Carapace lengths of 3 mm or less unsexed; otherwise sexes indicated.

Kleinemonde and Swartkops estuaries by means of a t-test indicated that none of the differences was significant. The most significant difference was obtained when 8 mm carapace females from the Swartkops and Kleinemonde were compared but the value obtained for t, 1,8096 (df 90) was only significant at the 90% level.

Although prawns from the Kleinemonde and Swartkops estuaries attain different maxumum sizes they require the same amount of time to do so. This indicates that growth in the Swartkops estuary is more rapid than in the closed Kleinemonde estuary. The results of an experimental comparison of growth rates in an open and a closed estuary over a period of seven months are given in Table 11.

Table 11: Comparison of growth rates in the Kowie estuary (open) and the east Kleinemonde estuary (closed).

Mean numbers and weights of	12 x 3 mm Mean wt. 0,128g
prawns at start:	16 x 4 mm Mean wt. 0,295g.

	Kowie				East Kleinemonde					
	Males		Females		Juveniles		Males		Females	
Sizes	Nos.	Mean wt	Nos.	Mean wt	Nos.	Mean wt	Nos.	Mean wt	Nos.	Mean wt
3 mm	-	-	-	-	1	0,063	-	-	-	-
4 mm	-	-	-	-	-	-	1	0,306	3	0,217
5 mm	1	0,482	6	0,512	-	-	-	-	4	0,447
6 mm	4	1,02	3	0,819	-	-	-	-	-	-
	Total 14		50% recovery		Total 9		32% recovery			

Recovery from the open Kowie estuary was better than from the closed east Kleinemonde estuary. The single 3 mm carapace juvenile in the east Kleinemonde estuary could possibly have moved into the box from outside.

The amount of growth that occurred in the Kowie estuary was far higher than in the east Kleinemonde estuary. No prawns attained carapace lengths of 6 mm in the east Kleinemonde although 50% of those in the Kowie river did so. Assuming that 3 and 4 mm carapace individuals grew to 5 and 6 mm respectively in the Kowie estuary this represents a 2,8-4 fold increases in weight while comparative figures from the east Kleinemonde estuary are 1,5-1,7 . In addition three ovigerous females as well as seven very young juveniles were recovered from the Kowie estuary box showing that conditions were favourable and growth had proceeded far enough for breeding to occur.

No data on temperature in the substrate in the Kowie and east Kleinemonde estuaries are available but results from the Swartkops and west Kleinemonde estuaries indicate that temperatures are unlikely to have been sufficiently different to have had any effect. The main differences between the two areas was that the east Kleinemonde was permanently closed off from the sea by a sand bar across the mouth while the Kowie was permanently open and the prawns were in a tidal area. It thus appears that the greater size and faster growth of C.kraussi in the Swartkops and Kowie estuaries than in the east and west Kleinemonde estuaries is in some way associated with access to the sea.

Population densities.

The yield per 100 pump strokes, in terms of both numbers and weight of prawns, was recorded in both the west Kleinemonde and Swartkops estuaries over the period March 1972-September 1973 (Fig. 28) and compared (Table 12) by means of a t-test.

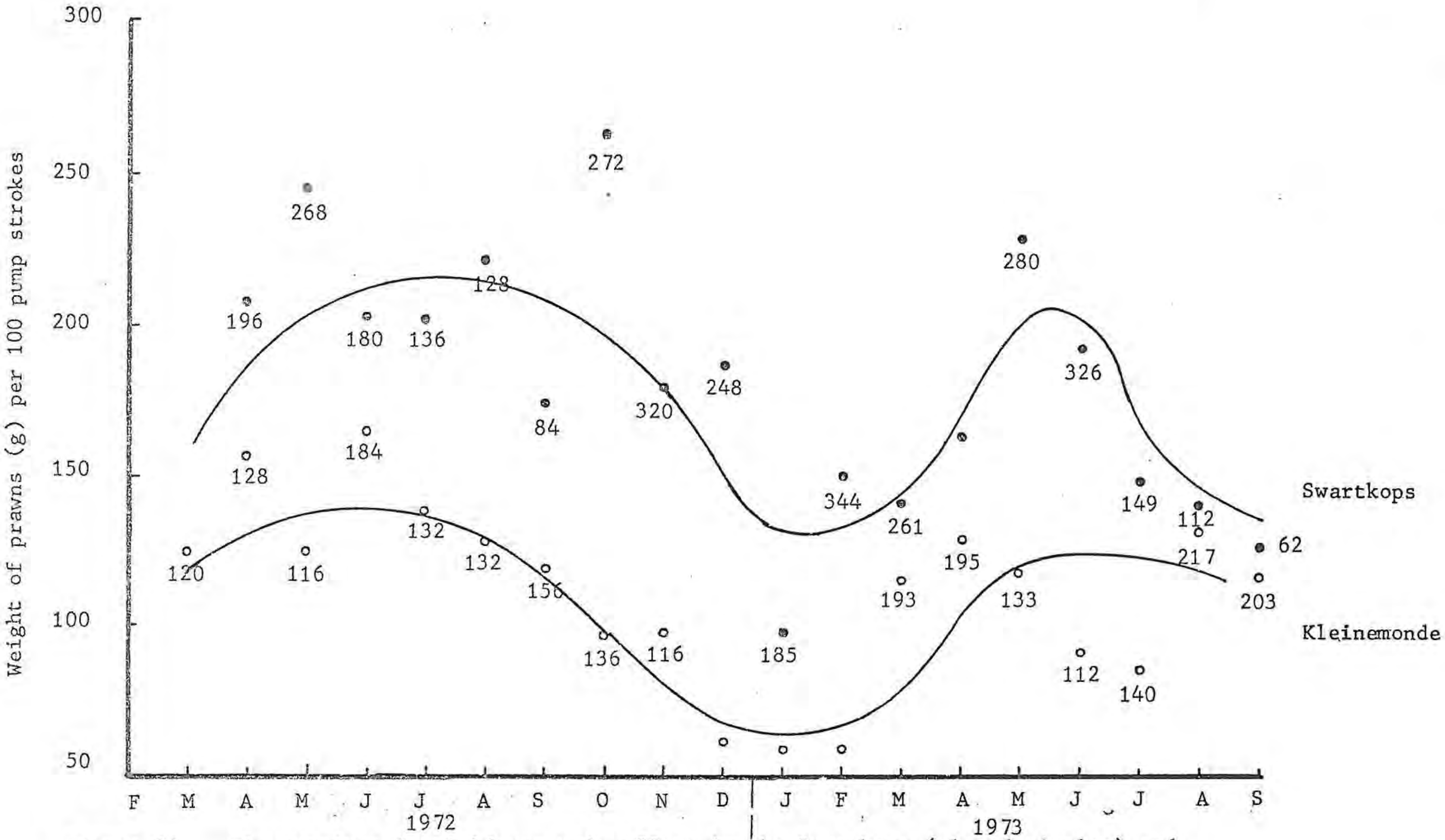


Figure 28. Fluctuations in yield per unit effort in the Swartkops (closed circles) and Kleinemonde (open circles) estuaries. The figures indicate the actual number of prawns obtained.

Table 12: A comparison of the yields of *C.kraussi* from the Swartkops and west Kleinemonde estuaries over the period March 1972-September 1973.

	Mean yield (nos.)	Range	Mean yield (g)	Range
Kleinemonde	146	102-217	111,5	49-164
Swartkops	210	62-344	192,2	98-263
	$t = 3{,}083$ (df 36) $,005 < P < ,001$		$t = 4{,}385$ (df 37) $,001 < P$	
	Significant at 99,95% level		Significant at 99,95% level.	

There is thus a significant difference between these two areas.

On subsequent general surveys of a number of estuaries attempts were made to ascertain whether there was a constant difference between open and closed estuaries. The results were extremely variable (Table 13). Although open estuaries yielded a greater mean number and weight the variation is so large that the differences were not statistically significant.

Table 13: Comparisons of yields of *C.kraussi* in open and closed estuaries.

	Mean yield (Nos.)	Range	Mean yield (g)	Range
Open (9 estuaries)	167	70-306	146,4	71,5-286,6
Closed (13 estuaries)	86	33-272	119,1	70,8-210,2

During the complete isolation from the sea of the west Kleinemonde estuary over the last two years there has been a gradual decrease in the number of large *C.kraussi* in the population (Table 14).

Table 14: Changes in numbers of large prawns in the west Kleinemonde over the period March 1971-September 1973. Numbers calculated as percentages within each sex.

Carapace length and sex	Mar '71-Dec '71	Jan '72-Dec '72	Jan '73-Sept '73
Male 9 mm	2,3	1,9	Less than 0,1
Male 8 mm	27,1	16,4	5
Female 9 mm	0,1	Nil	Nil
Female 8 mm	18,2	4,9	0,2
Female 7 mm	31,6	28,9	13,2

The results showed that while the maximum size reached in 1971 was smaller than in the Swartkops estuary, this maximum size decreased even further over the following two years with successively fewer prawns reaching carapace lengths of 7 mm and more.

Comparison of the maximum sizes reached by prawns in open and closed estuaries showed that access to the sea was invariably associated with a large maximum size (carapace length of greater than 9 mm in both sexes). Prawns of this size were however recorded in a few closed estuaries, e.g. the Bot River in the western Cape and the Izotsha River at Shelly Beach in Natal. Both of these estuaries open to the sea every year and it is possible that the size reducing effects found in the west Kleinemonde which is frequently isolated for long periods, therefore do not appear.

The difference in maximum sizes in the Swartkops and west Kleinemonde estuaries as well as the decrease in maximum size in the Kleinemonde was reflected in the numbers of females of different sizes contributing to the total breeding effort (Fig. 29).

Six mm carapace females contributed a maximum of 1% to the breeding effort at Swartkops in 1971, 1972 and 1973. In the west Kleinemonde, the contribution of this size, already 15% in 1971, increased in 1972 and 1973 to between 30 and 40%. In addition ovigerous females of less than 6 mm carapace length began to appear in late 1973. No ovigerous females of less than 6 mm carapace length had previously been recorded.

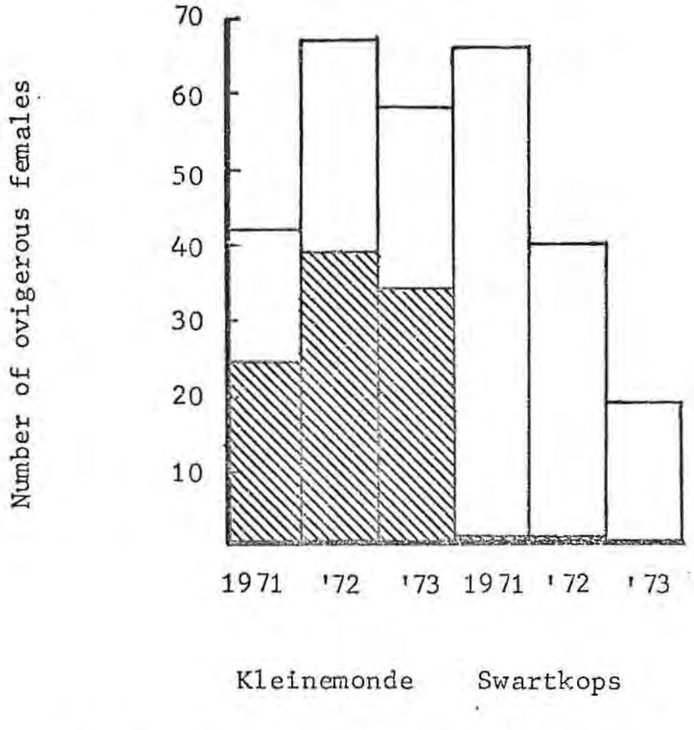


Figure 29. The numbers of ovigerous females with a carapace length of 6 mm or less (cross-hatching) out of the total number of ovigerous females in the Kleinemonde and Swartkops estuaries in 1971, 1972 and 1973.

Discussion

Comparison of the above results with those obtained for related species indicated a number of unique features in C.kraussi. The number of eggs carried by C.kraussi is remarkably low. Pohl (1946) recorded 8,170 eggs on a specimen of C.major and Devine (1966) found 660-1500 in C.filholi of New Zealand. Siegfried (1962) gives a range of two to four thousand on the other common South African thalassinid Upogebia africana. Pohl measured eggs of C.major and found dimensions of 0,88 mm x 0,74 mm (n = 45 from one female). In South Africa an ovigerous female of C.gilchristi from False Bay had eggs 0,6 mm in diameter. It thus appears that C.kraussi may have relatively larger eggs (diameter 1,2 mm) than other species of Callianassa.

The second peculiar feature of C.kraussi is the abbreviated larval life. MacGinitie (1934) reported that C.californiensis hatches as a zoea and passes through a "cypris" stage before settling. Hailstone & Stephenson (1961) found 6 larval stages in C.australiensis, a pre-zoea followed by 5 larval stages which spent 4-5 months in the plankton. Devine (1966) recorded a similar series in C.filholi in New Zealand. In his review of decapod larvae Gurney (1942) stated that there are two types of larval development in the Callianassidae. Type 1 has 5 larval stages. Gurney gave C.subterranea as an example but this group would also include C.australiensis and C.filholi. These species would be expected to have a very small zoea I. Devine (1966) gave a total length of 3 mm for first stage zoeae of C.filholi. Sandifer (1973) recorded a length of 2,79 mm (2,60-3,03 mm for 10 specimens) for a first stage zoea from Chesapeake Bay which he attributed to C.biformis. In Type 2 the number of larval stages is reduced. There are 3 in C.laticauda (=stebbingi) (Gurney, 1942) while in certain Red Sea and Indian Ocean forms there are only two. These forms are also characterized by having undeveloped mouthparts. Unfortunately they were not identified by Gurney. Sandifer (1973) described a further series of two zoeae which he attributed to C.atlantica and places in Gurney's Type 2. The first zoeal stage of this species measured 5,24 mm (4,79-5,56 mm for 10 specimens).

C.kraussi has characters which it shares with both types. The length at hatching (5-6 mm) would place it in Type 2 when compared with the results of Sandifer (1973). The telson in *C.kraussi* larvae is broad and convex, as in Gurney's (1942) Type 2 but the low number of small spines (9) on either side of the median spine of the telson is more similar to Type 1. Gurney (1942) and Sandifer (1973) give figures of 7-8 on either side in Type 1 and 14-18 in Type 2. Gurney (1942) states that "three forms from the Red Sea" have four pairs of pleopods. Four pairs of pleopods are present in the second stage larva of *C.kraussi*. Gurney (1942) also claims that the mouth parts in these forms were "undeveloped". Dissection of the mouthparts of *C.kraussi* larvae showed that a full complement was present and there was no indication that they were "undeveloped".

It thus appears that there is a general tendency for certain species of *Callianassa* to show a reduced number of larval stages. The duration of these larval stages in other species is unknown. *C.kraussi* does not appear to fit into either classification and this leads to questions of the validity of this separation. It would appear more likely that reduction of the larval stages has occurred independently in different groups of callianassids but further work would be required to clarify this problem. There remains, however, one feature in which *C.kraussi* may be unique and that is the loss of the planktonic phase since no mention of this was found in descriptions of other *Callianassa* larvae.

Breeding periods in the different species of *Callianassa* cover virtually every season of the year. The northern hemisphere species

C.californiensis in California (MacGinitie, 1934) and C.jamaicense louisianensis in the Gulf of Mexico (Phillips, 1971) are both summer breeders. In the southern hemisphere, C.filholi in New Zealand (Devine, 1966) breeds in spring and summer and C.australiensis in Australia (Hailstone & Stephenson, 1961) mainly in autumn and spring. Assuming the cycle in the Swartkops and Kleinemonde estuaries to be typical, C.kraussi is similar to the other two known southern hemisphere species.

Although C.kraussi is apparently normally a winter/spring and summer breeder, the results from the west Kleinemonde estuary usually differed slightly from the Swartkops estuary (Fig. 11). There were also marked fluctuations on the Transkei and Natal coasts and within the Swartvlei system. These all suggest that several factors may affect and modify the breeding season and the appearance of juveniles. Insufficient information is available on conditions in Transkei and Natal estuaries to permit interpretation of the results obtained there, and nothing is known of temperature effects on breeding times. Appearance of young in different areas of Swartvlei at different times can be related largely to salinity levels.

The percentage of ovigerous females in Swartvlei varied erratically and the best indication of successful breeding in any area is the presence of juveniles (Fig. 30). The peak in the numbers of juveniles in the lower estuary in August 1972 would have followed breeding activity 3-5 months previously when conditions must have been suitable. As no comparable increase in the percentage of juveniles occurred in the channel and lake, conditions were apparently unsuitable for breeding in these areas in December 1971-February 1972 but no data are available. After the mouth was opened in August 1972, salinities in the lake rose

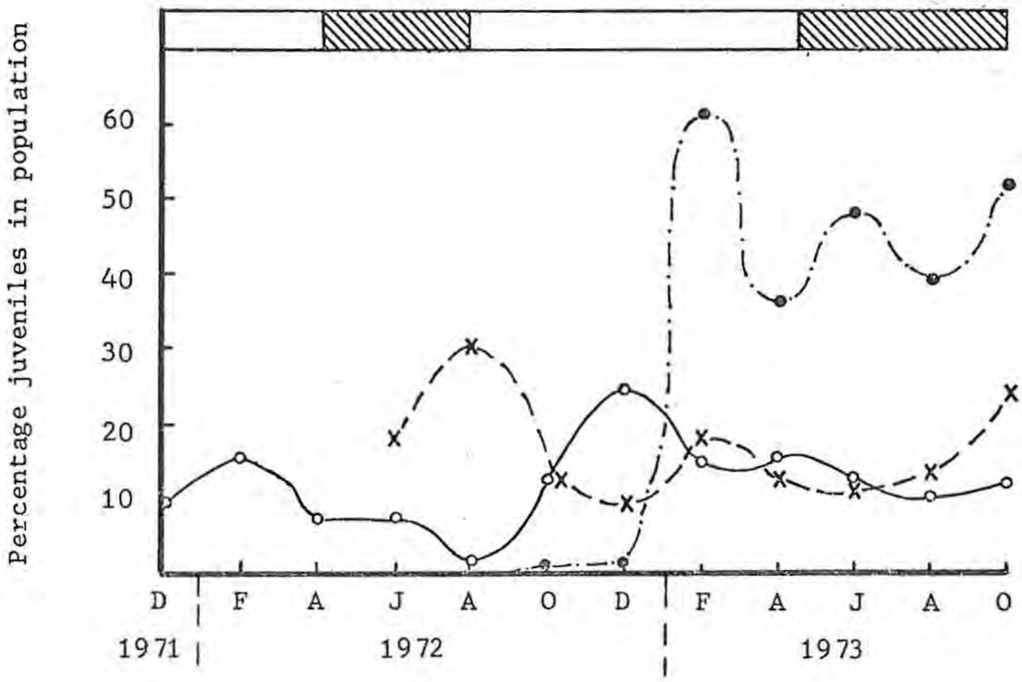


Figure 30. Percentage juveniles in the populations of C.kraussi in the estuary (crosses), the channel (open circles) and the lake (closed circles) of the Swartvlei system. Cross-hatching above indicates periods when the mouth was closed.

rapidly (Table 6) to over 20°/oo in October and December 1972. This permitted breeding and the population consisted of 60% juveniles in February 1973. Eggs of C.kraussi are generally unable to develop at salinities much below 17,5°/oo although this species is frequently found at salinities below this level. Is extrusion of eggs by females at these low salinities inhibited or are they damaged and lost after extrusion? Samples from Swartvlei lake in August and October 1972 both contained 45% of mature females with advanced ovary development. Over this period the number of females showing indications of having shed their eggs rose from 28 to 38% while the proportion of ovigerous females rose only from 4 to 13%. These figures indicate that eggs were being extruded despite the generally unfavourable salinity conditions and were then being lost. Although this would lead to considerable egg mortality it would probably also result in a selection of individuals tolerant of low salinities.

One of the important roles of planktonic larvae is that of dispersal. Although C.kraussi has lost its planktonic phase, dispersion still occurs and has been taken over by the post-larval but sub-adult stages. This probably accounts for the presence of C.kraussi in areas where low salinities preclude breeding and in addition has meant that the spread into low salinity areas has been more pronounced than would otherwise have been possible since the post-larval stages are less sensitive to low salinities than the larval stages.

While low salinities would limit the distribution of C.kraussi in the restricted environment of an estuary, temperature variations would have a much broader effect and could control the geographical distribution of the species.

Surface temperatures recorded in the three study areas ranged from 12 to 30°C but at a depth of about 50 cm in the sand this range was reduced to 14 to 26°C. No comparable data are available from the limits of the range of C.kraussi on the west and east coasts but it may be assumed that the substrate will have an insulating effect, moderating both winter low temperatures on the west and summer high temperatures on the east. The tolerance of the adults has been shown to cover the range from 10 to 30°C but the more significant feature would be the tolerance of the developing eggs. It has been shown experimentally that a development period of 30-33 days at 20°C is more than tripled at 13-15°C and would probably cease altogether at lower temperatures. At 24-25°C development is possibly slightly accelerated but the percentage of successful hatchings is reduced. Temperature extremes on the west coast could be avoided by summer breeding but a sample from Langebaan on the west coast in February 1972 contained no ovigerous females and 48% juveniles indicating that breeding had already occurred. On the east coast high temperature effects could be circumvented by winter breeding but in a sample from Kosi Bay in January 1971 36% of the mature females were ovigerous. This suggests some shift in temperature tolerance in these two areas but could also explain the absence of C.kraussi from the warmer regions of the east coast and the cooler parts of the west coast.

Populations of C.kraussi in the west Kleinemonde and Swartkops estuaries differed in the maximum sizes reached and in the rate of growth while the further reduction in the maximum size reached over the duration of the sampling period indicated that there is an additional long term effect associated with a loss of access to the sea.

Despite the reduction in the maximum size reached by prawns in the west Kleinemonde there did not appear to be any change in the return per unit effort as determined by the weight of prawns per 100 pump strokes (Fig. 28). This suggests that although conditions are in some way changing and affecting the population structure they have not yet affected the total mass of prawns present in the estuary. With progressive reduction in maximum size there will be an effect on the breeding effort as smaller females carry fewer eggs and consequently recruitment will be reduced. An increased number of females breeding could compensate for this, but, as can be seen from Fig. 20 there is no evidence for this and the system would have to be monitored for a number of years to obtain any definite indication.

The increasing number of newly matured females breeding and the precocious production of eggs by females previously considered immature has parallels in other animals although no information on any crustacea could be found. Martin (1966) has shown that the lake trout Salvelinus namaycush is affected by the diet. Poor feeding resulted in reductions in growth rates and longevity as well as in age and size at maturity. Although no changes in longevity and age at maturity have been found in C.kraussi in the west Kleinemonde, it is notable that while reduced growth rates and size at maturity have been found to be responses to poor diet in fish, similar responses in C.kraussi have been found to be associated with a loss of access to the sea. This suggests that the sea may be an important source of nutrient for C.kraussi.

PART III

OSMOTIC, IONIC AND VOLUME REGULATION IN *CALLIANASSA KRAUSSI*

Introduction

Despite the occurrence of thalassinid burrowing prawns in a variety of habitats throughout the world, including estuaries and bays subject to salinity fluctuations, very little is known of their osmoregulatory capacity. In an early review Gross (1957) gave no data but concluded that members of the genus *Callianassa* are osmo-conformers. Lockwood (1962) and Kinne (1963) both considered this genus to be capable of ionic and volume regulation but incapable of osmotic regulation. Subsequent investigations by Thompson & Pritchard (1969) in California supported this assumption. They showed that although *Callianassa californiensis* could survive in salinities of 9-10,5^{o}/oo and the New Zealand *C.filholi* in 12-14^{o}/oo both species showed only slight ionic and no osmotic regulation.

In South Africa *C.kraussi* is found in sheltered bays and open estuaries under marine or virtually marine salinity regimes but it also occurs in the small closed estuaries which are a feature of the south-eastern coast of Africa. In these latter habitats *C.kraussi* frequently has to cope with long periods of low salinity conditions. In addition, rainfall is erratic and floods may fill the estuary with fresh water causing sudden reductions in salinities, even in large open estuaries. During the course of this study *C.kraussi* was recorded at salinities as low as 1^{o}/oo in the upper Keurbooms River. Day (1951) gives a known salinity range of 1,25-59,5^{o}/oo. *C.kraussi* is thus capable of living at these salinities for long periods and is able to cope with sudden fluctuations within this range. This indicated a marked degree of euryhalinity and it seemed unlikely that this wide degree of tolerance was not associated with some osmo-regulatory ability.

Hyper-regulation in low salinities involves the ability to maintain the blood hyper-osmotic to the external medium. In crustacea this is usually done by maintaining the blood salt content at a high level although the ratio of the different ions in the blood will frequently differ from that of the medium. Hyper-regulation also involves the ability to cope with the osmotic inflow of water which results from the differing concentrations of blood and medium.

This osmotic inflow of water in marine animals transferred from sea water to dilutions is accompanied by an increase in weight. This phenomenon has been known for many years and has been most extensively studied in brachyurans. Hukuda (1932) followed weight changes in the crabs Portunus puber, P.depurator, Carcinus maenas, Maia squinado, and Cancer pagurus and speculated on the means by which a new equilibrium was attained. In general, weight changes of crabs in dilutions were found to be relatively small (Gross 1957). This is to be expected since crabs usually have a rigid body wall and any swelling would result in either damage to the gills or expansion of the joints with a resulting hindrance of locomotion. Not all decapods have a body wall as rigid as the average crab and recent work by Davenport (1972a) on volume changes in some British anomura has shown that significant weight changes do occur in species such as Porcellana platycheles, P.longicornis and Pagurus bernhardus. Since C.kraussi is also an anomuran and is also a comparatively soft-bodied decapod it was thought possible that significant weight changes could occur in this species.

Davenport (1972a and 1972b) also demonstrated a unique method of coping with osmotic inflow of water in P. bernhardus. In this species water entering through the gills is directed into the abdomen which acts as a "swelling reservoir" and protects the rest of the animal against the mechanical effects of water inflow. This mechanism worked adequately as P. bernhardus is either sub-tidal or inter-tidal on marine shores and would never have to cope with low salinity conditions for longer than a few hours during low tide.

Thompson & Pritchard (1969) pointed out that contact between Callianassa californiensis and the surface water was minimised by its burrowing habit and that this may protect it from transient low salinities. This study was thus begun with an investigation of the importance of the substrate in protecting C. kraussi against sudden drops in surface salinities. Since the substrate cannot provide an indefinite insulation against these low salinities, the response of C. kraussi to the osmotic inflow of water and the efficiency of the volume regulating organs was investigated by following weight changes of prawns in dilutions of sea water. In addition the possibility that C. kraussi may use the abdomen as a swelling reservoir when exposed to low salinities in a similar fashion to the hermit crab Pagurus bernhardus was investigated. In view of the marked degree of euryhalinity displayed by C. kraussi it was decided to determine the normal blood osmotic pressure, sodium and chloride levels of prawns in sea water ($35^{o}/oo$) and to follow any changes that occurred in these parameters during acclimation to dilutions of sea water. Additional determinations were done after equilibrium was attained. Since acclimation to dilutions of sea water involves both uptake of water and loss of salts this was followed by an investigation of the areas of the body through which water uptake occurred, and also of the routes of salt loss and their relative importance.

Methods

a) Salinity changes in the substrate.

The significance of the substrate in shielding C.kraussi against sudden drops in salinity levels as well as the effect of C.kraussi on salinity changes in the substrate were investigated in the following manner. A perspex tank 60 cm x 9 cm x 60 cm deep was constructed with a vertical series of taps 10 cm apart at one end. The tank was filled (to a depth of 35 cm) with clean beach sand collected in the intertidal zone. The surface sea water was then siphoned off and replaced with 20 cm depth of tap water which was run in onto a plastic bag so that minimal disturbance of the sand was caused. Vigorous aeration was provided so that no salinity layering in the surface water occurred. Salinity changes in the substrate were monitored by analysis of samples of water taken from each tap and from the surface over a period of 20 days. This experiment was then repeated but 30 C.kraussi were allowed to construct burrows in the tank before introduction of the tap water. A record was kept of the number of open burrows in the tank during the experiment.

b) Volume Regulation.

Development of the various problems associated with volume regulation required initial clarification of the organs involved in this function. The green gland or antennary gland is generally assumed to be the main organ involved in volume regulation in decapod crustacea. This was checked in the case of C.kraussi in the following manner. Three batches each of 5 prawns previously kept in sea water (35^{o}/oo) for one week at 20^{o}C were used. Each animal was dried on a towel and then with tissue paper and weighed. In the first batch both anus and urinary pores were painted over with nail varnish; in the second only the anus was painted over while in the third only the urinary pores were painted over. All three batches were then transferred directly to a salinity of 9°/oo. At hourly intervals the prawns were removed, dried and weighed. The weights were combined and the means determined. The mean increase in weight was then expressed as a percentage so as to simplify comparison of the three batches. Possible side effects of the nail varnish were checked in a sham experiment. Two batches of eight and nine prawns respectively were used. The first batch was untreated but those in the second each received a spot of nail varnish on the thorax. After weighing, each batch was transferred directly from 35°/oo to 9°/oo and subsequently dried as above and weighed at hourly intervals.

The significance of urine production in volume regulation was investigated by comparing the increase in weight of untreated prawns with prawns having blocked urinary pores after direct transfer from 35°/oo to 9°/oo. Weight increases in 9°/oo after blocking the urinary pores were also compared in prawns previously acclimated to this dilution for a week and in prawns transferred directly to this salinity from 35°/oo. Finally weight increases in prawns acclimated to salinities of 35, 26, 17,5, 9, and 3,5°/oo were compared after blocking the urinary pores.

A longer term investigation of weight changes in untreated prawns after direct transfer from 35 to 9°/oo was also made. Prawns were removed, dried and weighed at increasing intervals for a period of eight days.

Finally the possible use of the abdomen by C.kraussi as a "swelling reservoir" to cope with osmotic inflow of water in low salinities in a manner similar to that found by Davenport (1972b) in Pagurus bernhardus was investigated. Ten C.kraussi from sea water (35°/oo) were ligatured between thorax and abdomen. They were then dried and weighed and transferred directly to a salinity of $9^{\circ}/oo$. The increase in weight was then compared with weight increases in untreated animals in the same dilution. In the second experiment four batches each of ten prawns were exposed to salinities of 35, 26, 17,5 and $9^{\circ}/oo$ for 12 hours. They were then removed, dried, weighed and the abdomen ligatured. The thorax was cut away and the isolated abdomen weighed. The contribution of the abdomen to the total weight was then calculated.

c) Osmotic and ionic regulation.

Prawns used for blood analyses were collected in the Swartkops and Kleinemonde estuaries except for one occasion when a batch was collected at a salinity of less than $1^{\circ}/oo$ in the upper Keurbooms River estuary. Prawns used for monitoring changes in blood osmotic pressure, sodium and chloride following direct transfer from sea water to salinities of 26, 17,5, or $9^{\circ}/oo$ were first kept at $35^{\circ}/oo$ and 20°C for at least one week. Similarly prawns collected at different salinities in the field or acclimated in the laboratory were kept in the final dilution at 20°C for at least one week before blood analyses were performed.

Dilutions of sea water were made up using sea water ($35^{\circ}/oo$) and glass distilled water. In early experiments prawns were placed in containers with sufficient sand for burrow construction in view of MacGinitie's statement (1934) that <u>C.californiensis</u> soon dies if they are kept where the sides of the body are not in contact with some object. This was subsequently found not to hold in the case of <u>C.kraussi</u> and thus prawns were kept in glass dishes with no substrate.

Blood samples were taken after prawns had been rinsed with distilled water and then dried, first on a towel and then with tissue paper. Blood was collected using 4,5 mm diameter glass tubes 4-5 cm long with a sharply tapered point at one end. The other end was inserted into a rubber tube provided with a glass mouthpiece. Actual collection of a sample was done by inserting the sharp end of the tube into the pericardium immediately behind the carapace. Care was required to prevent puncturing of the gut and any discoloured samples were discarded. In most cases blood immediately welled up into the tube but at times gentle suction was required. Large prawns - those with a carapace length of 8 mm or more - usually provided sufficient blood for a complete analysis of osmotic pressure, sodium and chloride but in the case of smaller prawns, two or three of the same size and sex were used and the blood pooled. Blood was discharged from the collecting tube into small glass tubes sealed with parafilm. The blood did not clot and was not treated in any way before analysis. All analyses were done on the day of collection. Five blood samples were taken from different animals in each dilution.

Determinations of osmotic pressure were done using a Hewlett-Packard Model 301-B Vapour Pressure Osmometer. Chloride and sodium were determined after suitable dilution using an American Instruments Co. Inc. Automatic Chloride Titrator and an Evans Electro-selenium Ltd., Flame Photometer respectively.

d) Water and salt exchange.

When prawns were kept in shallow water a marked inverted meniscus was noticeable where the water surface touched the sides of the animal. This was taken as an indication that the general body surface had hydrophobic properties and was more or less impermeable to water. An attempt was made to define the areas through which passive inflow of water occurred in salinity stressed animals.

It was assumed that the general body surface, apart from the gills, is similar. Two batches of 10 prawns, previously kept in sea water (35^{o}/oo) at 20^{o}C were used. The first batch was dried in a towel and then on tissue paper, weighed and the urinary pores blocked with nail varnish. Each prawn in the second batch was tightly ligatured between abdomen and thorax and the thorax cut away. The isolated abdomens were dried and weighed. Whole animals as well as the isolated abdomens were transferred directly into a salinity of 9^{o}/oo and removed, dried and weighed at hourly intervals.

Uptake of water by drinking or via the anus was investigated by leaving live prawns in sea water (35^{o}/oo and 9^{o}/oo) containing methylene blue. Prawns were removed and dissected at intervals to check on the penetration of the dye into the gut. Previous experiments showed that isolated fore-guts took up the dye very strongly.

It was assumed that salt loss to the medium on transfer to dilutions of sea water would occur via both the urine and the gills, and experiments were carried out to assess the relative importance of these two routes.

Analysis of urine was carried out on prawns in salinities of 35 , 26, 17,5, 9 and 3,5^{o}/oo. Transfer to 26, 17,5 and 9^{o}/oo was direct. Prawns to be transferred to 3,5^{o}/oo were initially transferred to 9^{o}/oo for 24 hours. All were exposed to the final dilution for one week, at 20^{o}C. Prawns used for urine analysis were rinsed briefly with distilled water and the area round the urinary pore dried carefully with tissue paper. Urine production could at times be stimulated by touching the raised pore area with a warm probe as described by Thompson & Pritchard (1969). The apparatus used for blood collection was used except that the tapered end of the glass tube was placed over the pore and gentle suction exerted. At no time was the tube inserted into pore. This precluded the possibility of contaminating the urine with blood. After collection the urine was blown out under liquid paraffin in a wax-lined watch glass. The wax prevented the urine from sticking to the glass. The quantities of urine obtained were very small and the only analyses done were of the freezing point depression following the method of Ramsay & Brown (1955). Blood samples from the same prawns were also collected and the freezing point depressions of blood and urine in different dilutions of sea water compared. In the case of very low urine yields, urine from two or more prawns was pooled; in this case the blood samples were also pooled.

Comparative losses of sodium via the urine and the body surface on transfer to dilutions of sea water were then investigated. The theory behind the method was basically similar to that outlined by Davenport (1972a) in his work on Porcellana platycheles and Pagurus bernhardus. However while he determined the salt lost from the animals to the medium with a conductivity meter, in the present study salt loss was investigated by following the increase in activity in a dilute washing out medium after the prawns had been loaded with ^{22}Na in sea water (35°/oo).

Two dilutions of sea water were used, the first consisting of 9°/oo and the second of 9°/oo but in which the osmolarity was raised to that of 35°/oo by addition of sucrose. In the first medium - which had a salinity of 9°/oo - an animal transferred directly from 35°/oo would be exposed to both an ionic and an osmotic gradient. The ionic gradient should result in a loss of salts, including sodium, via the general body surface while the osmotic gradient would result in an inflow of water which would have to be removed. It was assumed that this removal of excess water would also result in some sodium loss. In the second dilution the prawn would be exposed only to an ionic gradient since the osmolarity of the medium and the body fluids would be similar. This would result in a salt loss only via the body surface without the additional urinary loss. It was hoped that comparison of the respective loss rates in the two media would give an indication of the significance of both the urine and the general body surface in sodium loss.

Similar sized prawns of 6 and 7 mm carapace length were used. After collection in the Swartkops estuary they were kept in 35°/oo in the laboratory at 20°C. ^{22}NaCl from the Radiochemical Centre Ltd., Amersham was then added to a litre of sea water in a pneumatic trough so as to produce a total activity of about 45 microcuries. The amount of sodium chloride added was too small to have any effect on the osmotic pressure of the loading solution. Twenty-five prawns were then placed in this loading medium for 4 days and the dish covered over to reduce evaporation. No aeration was provided but the loading solution was only 3-4 cm deep and thus oxygen levels should have been adequate. No deaths were recorded during the loading period. After the loading period the prawns were removed, rinsed rapidly with sea water, dried as in previous experiments, weighed and transferred to the experimental dishes each containing 50 ml of medium. Five of these dishes contained 9°/oo and five contained 9°/oo plus sucrose. Two or three prawns making up a total weight of 1,3-2 g were placed in each dish. Immediately after introduction of the prawns a 200 μl sample was taken from each dish using an Eppendorf pipette with disposable tips. These samples were used for background counts. Counting was done in glass scintillation vials containing 10 ml of a fluor consisting of 8 g PPO, 0,2 g POPOP, 2 li toluene and 1 li Triton. Each vial was counted over three periods each of ten minutes using a Beckman Model LS-133 liquid scintillation system and the mean count recorded. The activity of the washing out media was monitored by taking 200 µl samples at 3 hour intervals and relating it to the weight of prawns used. The increasing activity in the washing out media was plotted arithmetically and the gradients of the bases of the two curves compared. This was then expressed as increases in activity of the wash out medium per unit weight of prawns in the two batches and used to compare the importance of the body surface and the urine in salt loss. No attempt was made to quantify the fluxes precisely as all that was of interest was the relative rate of loss of sodium in the two media.

Results

a) Salinity changes in the substrate.

In a substrate containing no C.kraussi, salinity changes at depths greater than 10 cm were negligible after a period of 20 days (Fig. 31). When prawns were present salinities dropped rapidly throughout the substrate (Fig. 32). After 2 days salinities had equilibrated to a depth of about 25 cm. After a further 6 days equilibration had occurred throughout the tank. The number of open burrows over the whole period of the experiment, including the period before the tap water was introduced, varied from 3-5. It appeared that the normal activities of the prawns prevent the substrate from acting as a shield against low surface salinities. Similar numbers of burrows were open at all times and there was no apparent effort to reduce contact with the surface water. Although C.kraussi may not actively pump low salinity water through the burrow, movement of prawns through the burrow system would cause a gradual exchange of water.

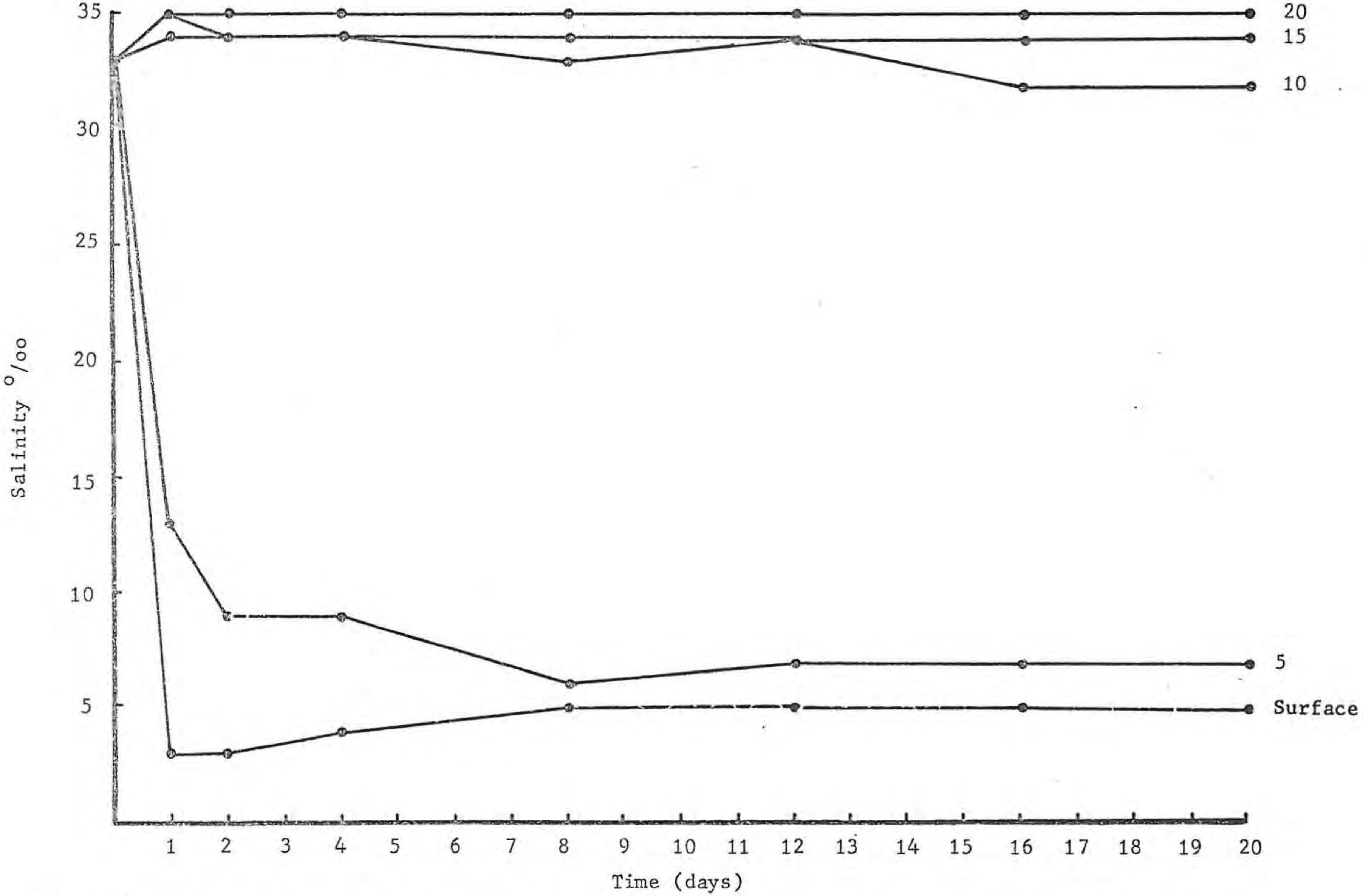


Figure 31. Changes in salinity at different depths in a tank after surface flooded with tap water. Figures indicate depth in cm beneath surface of sand.

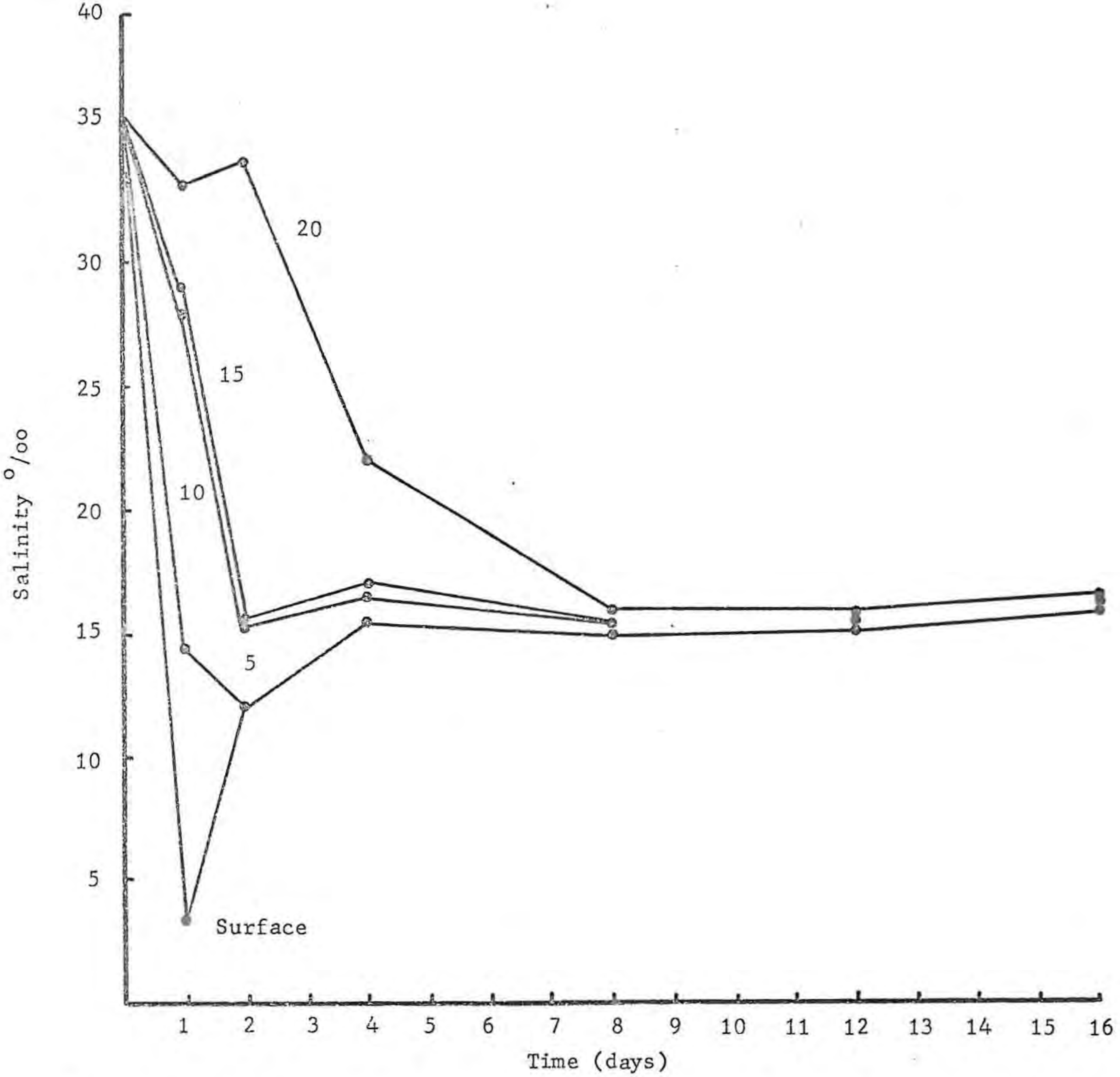


Figure 32. Changes in salinity at different depths in a tank containing C.kraussi after surface flooded with tap water. Figures indicate depth in cm beneath the surface of the sand.

b) Volume regulation.

Preliminary experiments showed that when the urinary pores were blocked there were marked sustained increases in weight over the duration of the experiment (Fig.33). Where only the anus was blocked there was a slight increase over the first hour but no further increase. These results suggested that the green gland is the main organ involved in volume regulation. Comparison of weight increases of untreated prawns and prawns with a spot of nail varnish on the thorax (Fig. 34) showed that the nail varnish did not affect the rate of water uptake and it was considered safe to use in subsequent experiments where the urinary pores were blocked.

When prawns are transferred directly from a salinity of 35°/oo to 9°/oo there is an uptake of water as shown by an increase in weight (Fig. 35), which is more sustained than in prawns in which the anus was blocked off. If the urinary pores are blocked the increase is more than double that of untreated animals. This suggests that urine production is an important factor in volume control. If the prawns were previously acclimated to a salinity of 9°/oo before blocking the urinary pores there is still an increase in weight indicating inflow of water (Fig. 36), but the weight increase is less rapid than in non-acclimated prawns indicating that some change has occurred resulting in a reduced rate of osmotic inflow of water. Further investigations of the rate of increase in weight in acclimated prawns in media between 35°/oo and 3,5°/oo after blocking the urinary pores showed that, although the rate of increase was always less than the figure of 6% of the body weight per hour found in non-acclimated prawns in a salinity of 9°/oo, there was a steadily larger uptake of water in the lower salinities (Fig. 37). This shows that although acclimation does affect the rate of water inflow into the prawn, increasing dilutions

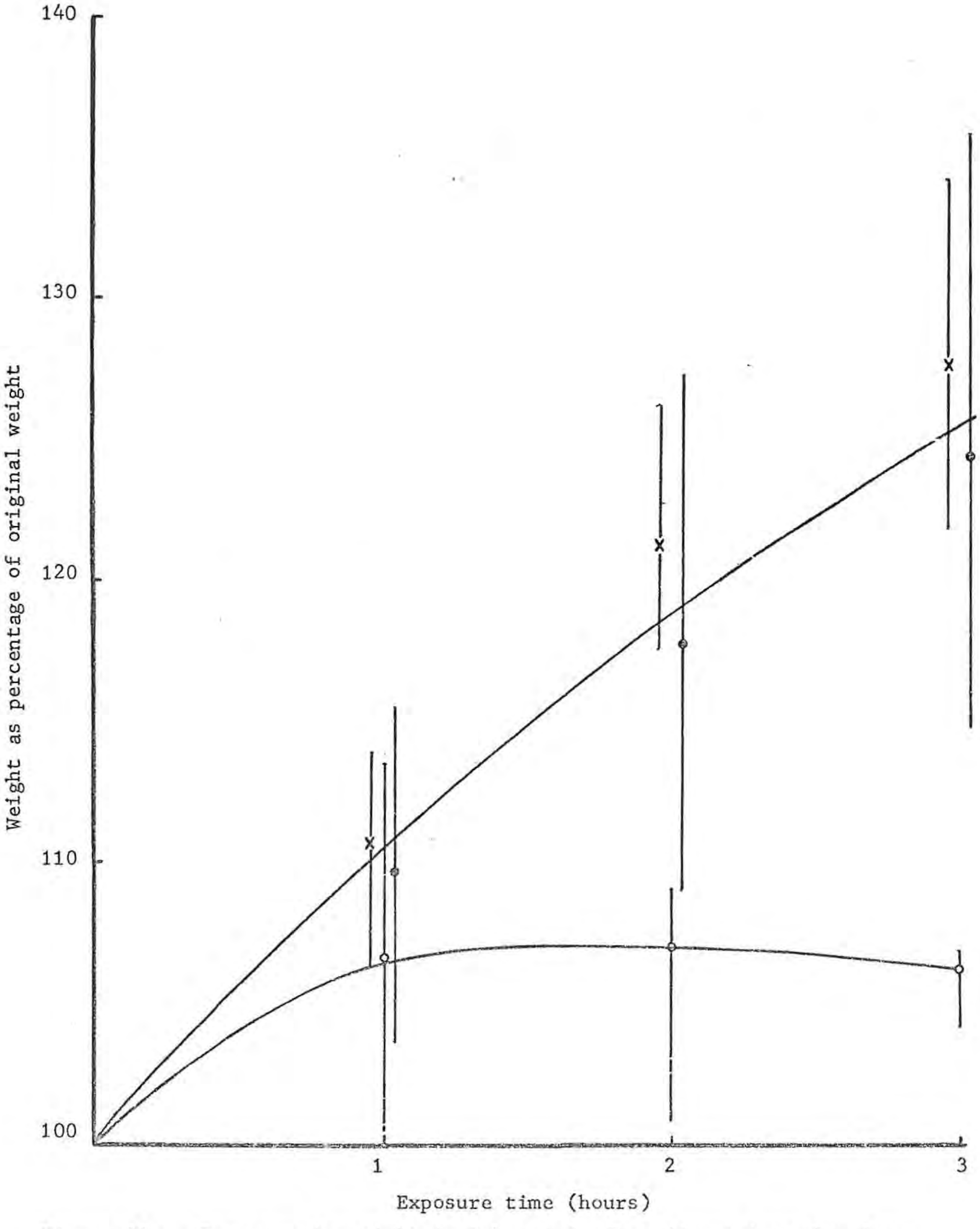


Figure 33. Increase in weight in C.kraussi after direct transfer from 35°/oo to 9°/oo: a) with anus and urinary pores blocked (closed circles); b) with urinary pores blocked (crosses) and c) with anus blocked (open circles). Each point is mean of 5 determinations. Vertical lines indicate range.

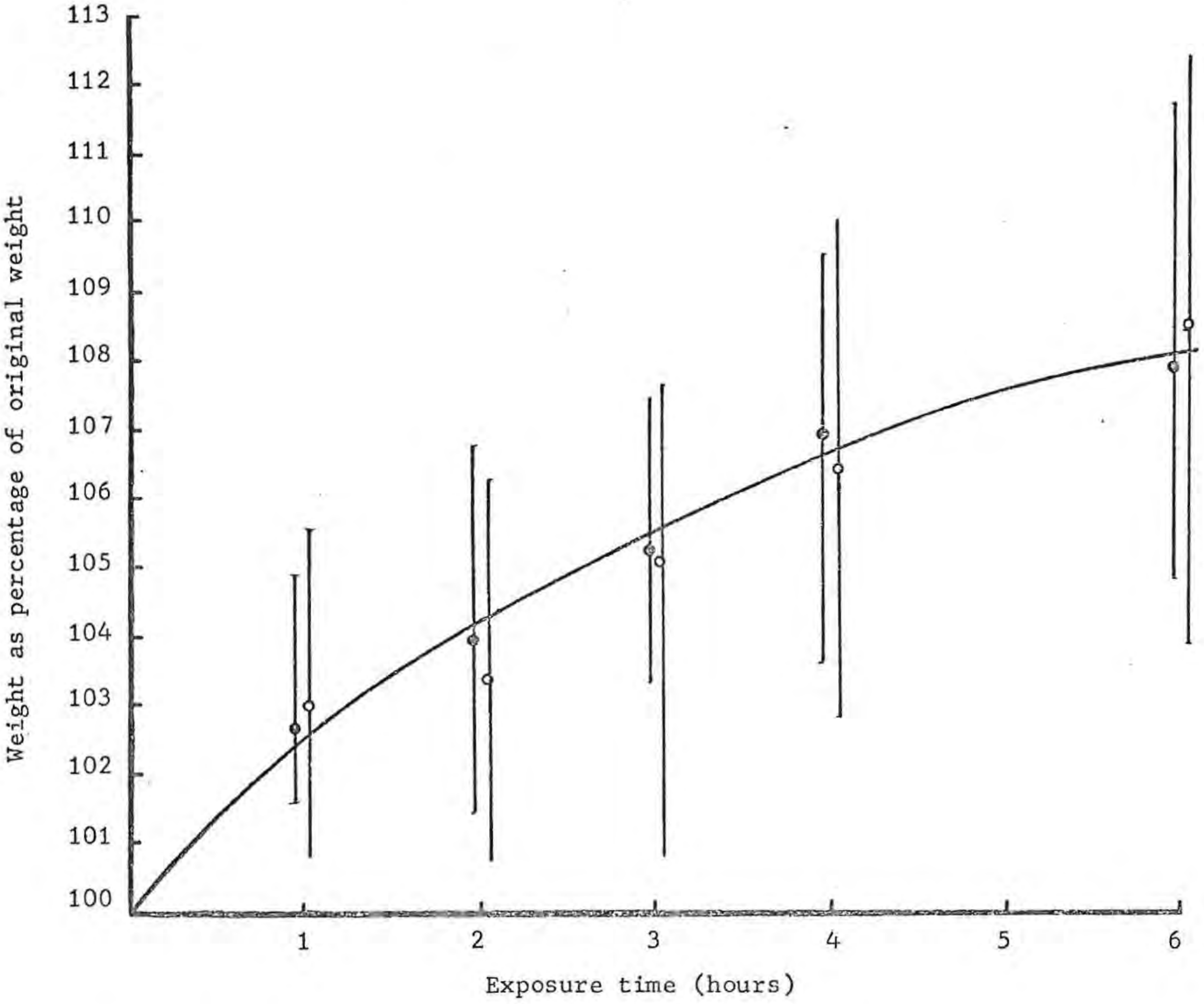


Figure 34. Increase in weight in C.kraussi after direct transfer from 35°/oo to 9°/oo: a) in untreated prawns (n = 9, closed circles) and b) in prawns with a spot of nail varnish on the thorax (n = 9, open circles). Vertical lines indicate range.

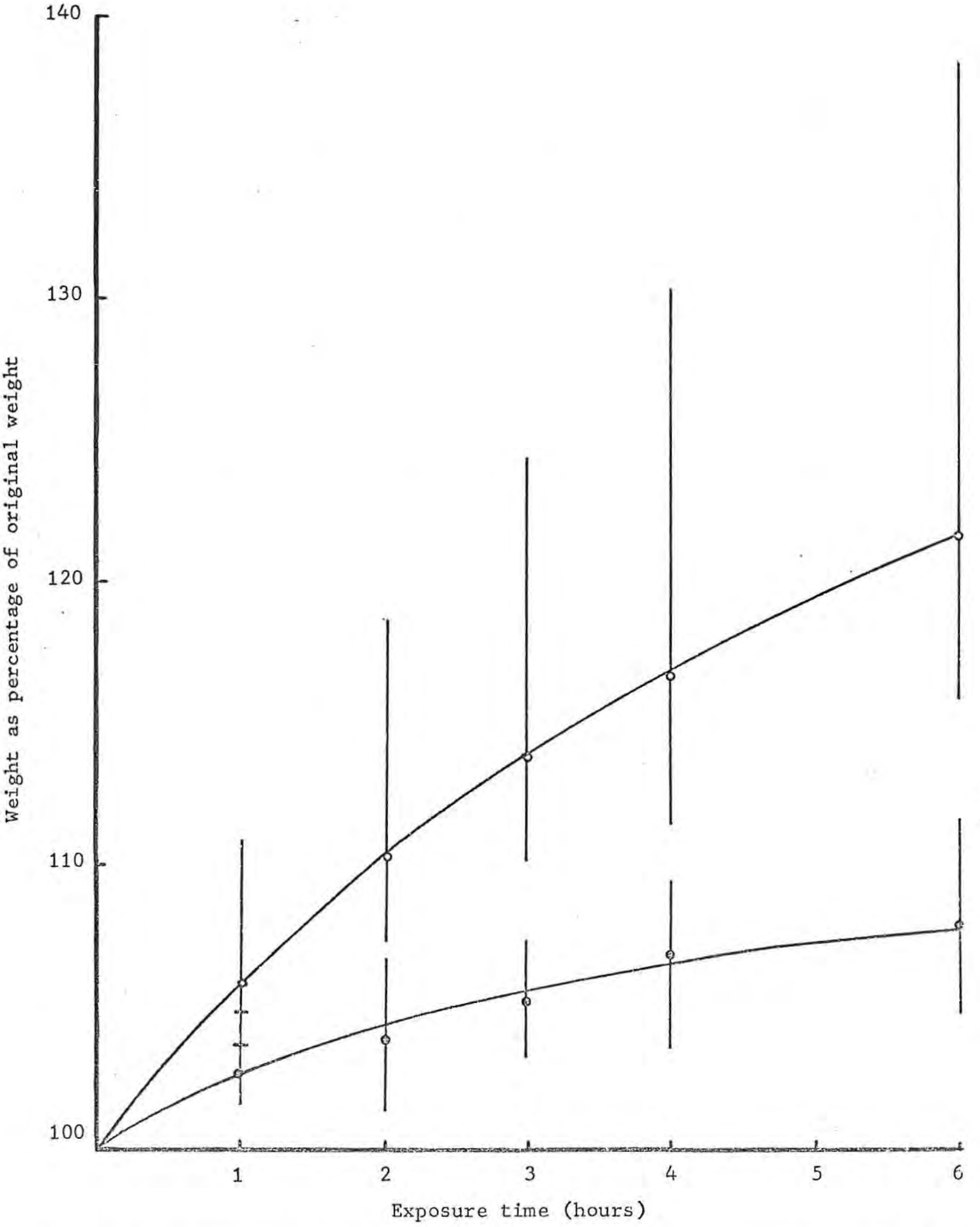


Figure 35. Increase in weight in C.kraussi after direct transfer from 35°/oo to 9°/oo: a) in untreated prawns (closed circles, n = 9) and b) in prawns with blocked urinary pores (open circles, n = 11). Vertical lines indicate range.

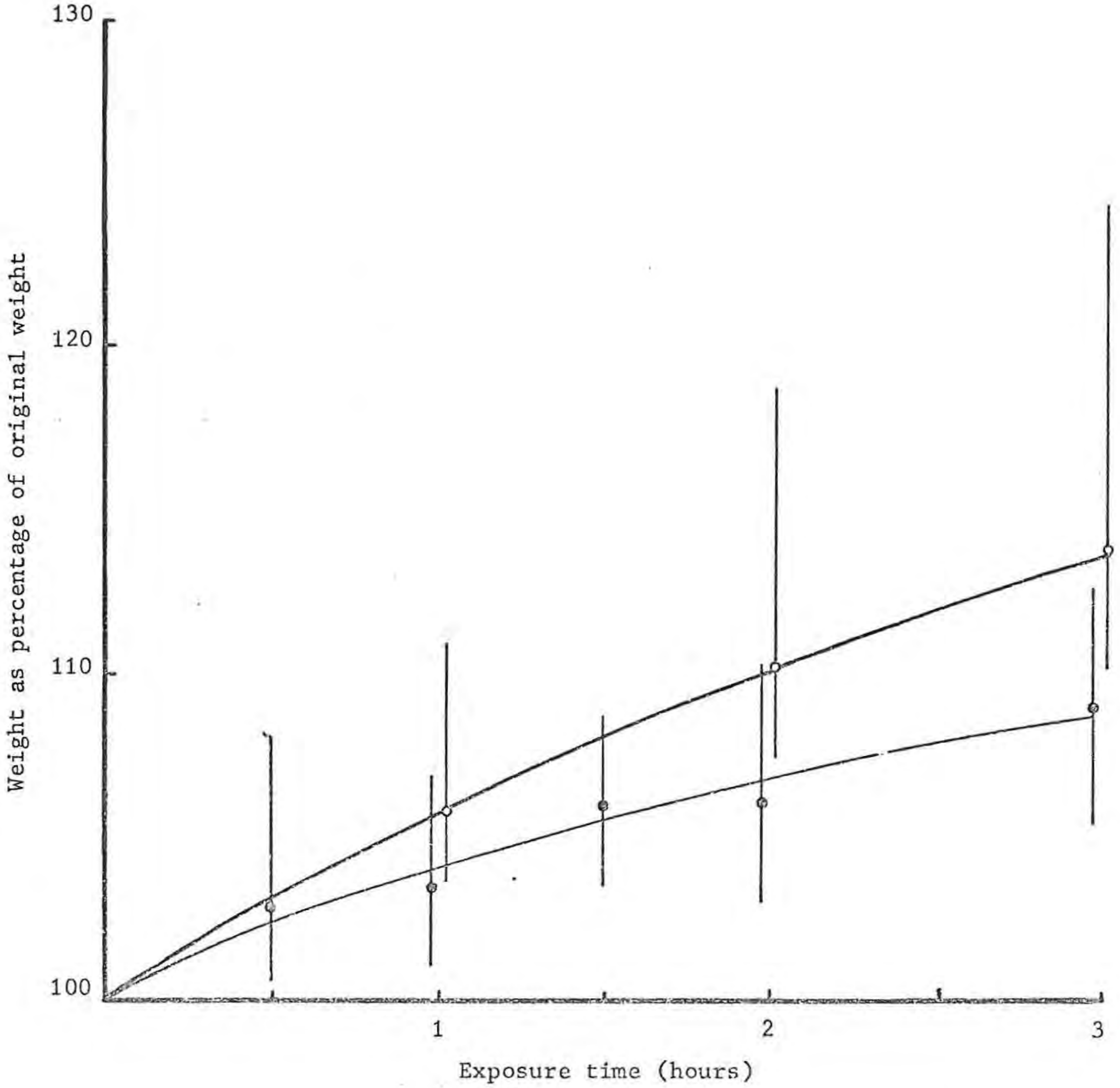


Figure 36. Increase in weight in C.kraussi with blocked urinary pores in 9°/oo: 1) after direct transfer from 35°/oo (open circles, n = 11); 2) after acclimation for one week (closed circles, n = 8). Vertical lines indicate range.

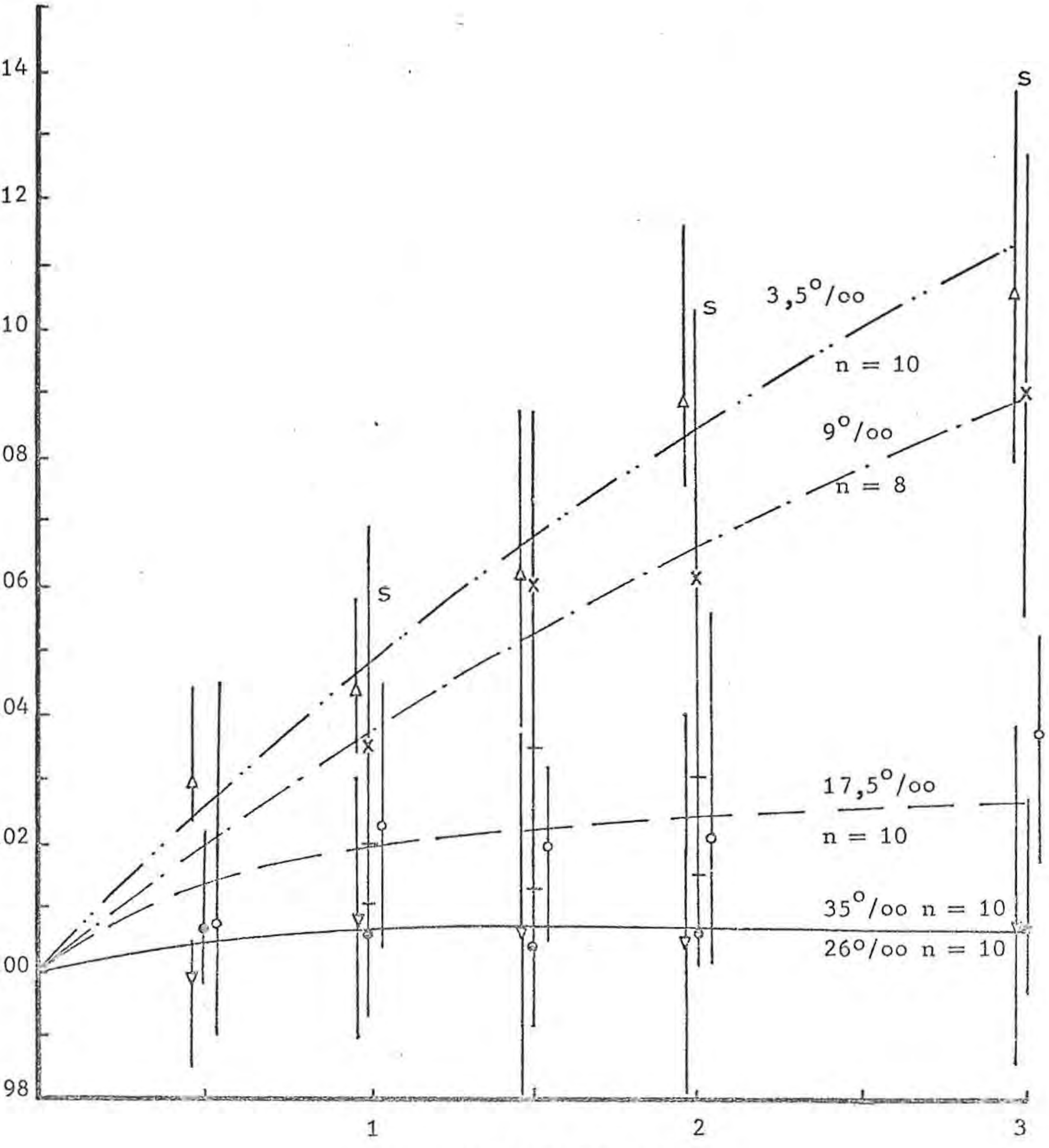


Figure 37. Increase in weight in C.kraussi acclimated to the salinities shown, after blockage of the urinary pores. For comparison, weight increases in 9°/oo after direct transfer from 35°/oo (S) are shown. Vertical lines indicate range.

still result in a greater rate of osmotic inflow of water and a consequent greater rate of urine production.

Long term adaptation by untreated prawns to a salinity of 9°/oo after direct transfer from 35°/oo involves an initial rapid rate of increase in weight over the first 8 hours (Fig. 38) due to osmotic inflow of water. Urine production apparently accelerates and eventually exceeds the rate of water inflow. The increase in weight is followed by a steady decline in weight over the next five days until the original level is attained. However the decline in weight continues and the final steady level appears to fall below the original level.

Davenport (1972b) found that a ligature between the thorax and abdomen in Pagurus bernhardus markedly reduced the weight increase when animals were transferred directly from 35°/oo to 21°/oo because the ligature prevented water entering through the gills from being diverted into the abdomen. A similar experiment on C.kraussi using ligatured and untreated prawns showed that the ligature, if anything, tended to increase the rate of water uptake (Fig. 39). Although the means of the two batches were similar the greatest increases were all recorded in ligatured prawns. Davenport found that the abdomens of P.bernhardus, after batches of animals had been exposed to media ranging from distilled water to twice sea water, contributed a greater amount to the total weight of the animal in increasing dilutions. This was due to the greater amount of water entering the animal and being diverted into the abdomen in the lower salinities. The results of a similar experiment on C.kraussi (Fig. 40) showed that there was no clear trend with decreasing salinities. It thus appears that no mechanism comparable to that in P. bernhardus exists in C.kraussi and volume regulation is accomplished by the gearing of urine production to the rate of water inflow.

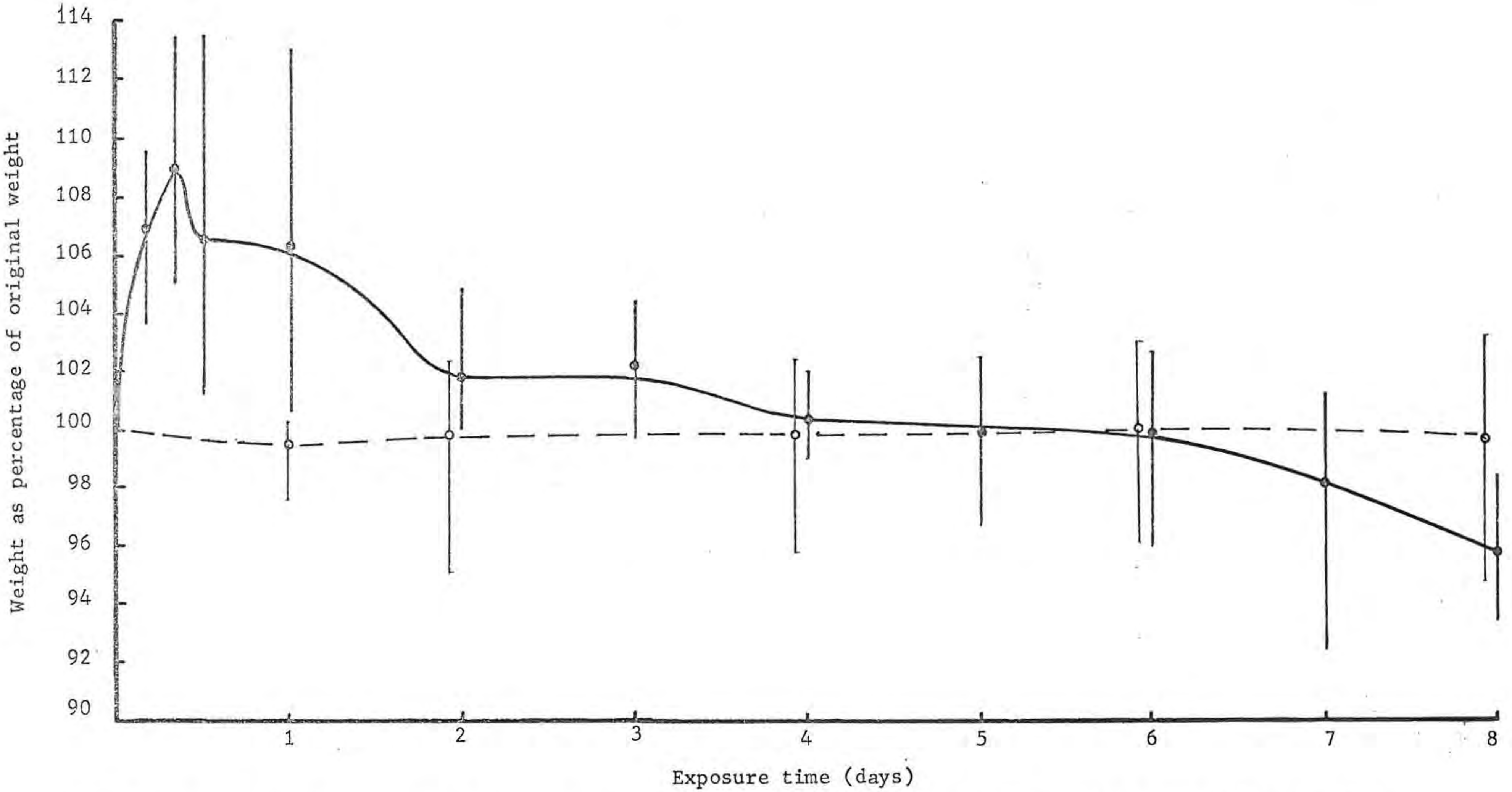


Figure 38. Weight changes in C.kraussi (n = 11, closed circles) after direct transfer from 35°/oo to 9°/oo over a period of 8 days. Control (n = 6, open circles) in 35°/oo. Vertical lines indicate range.

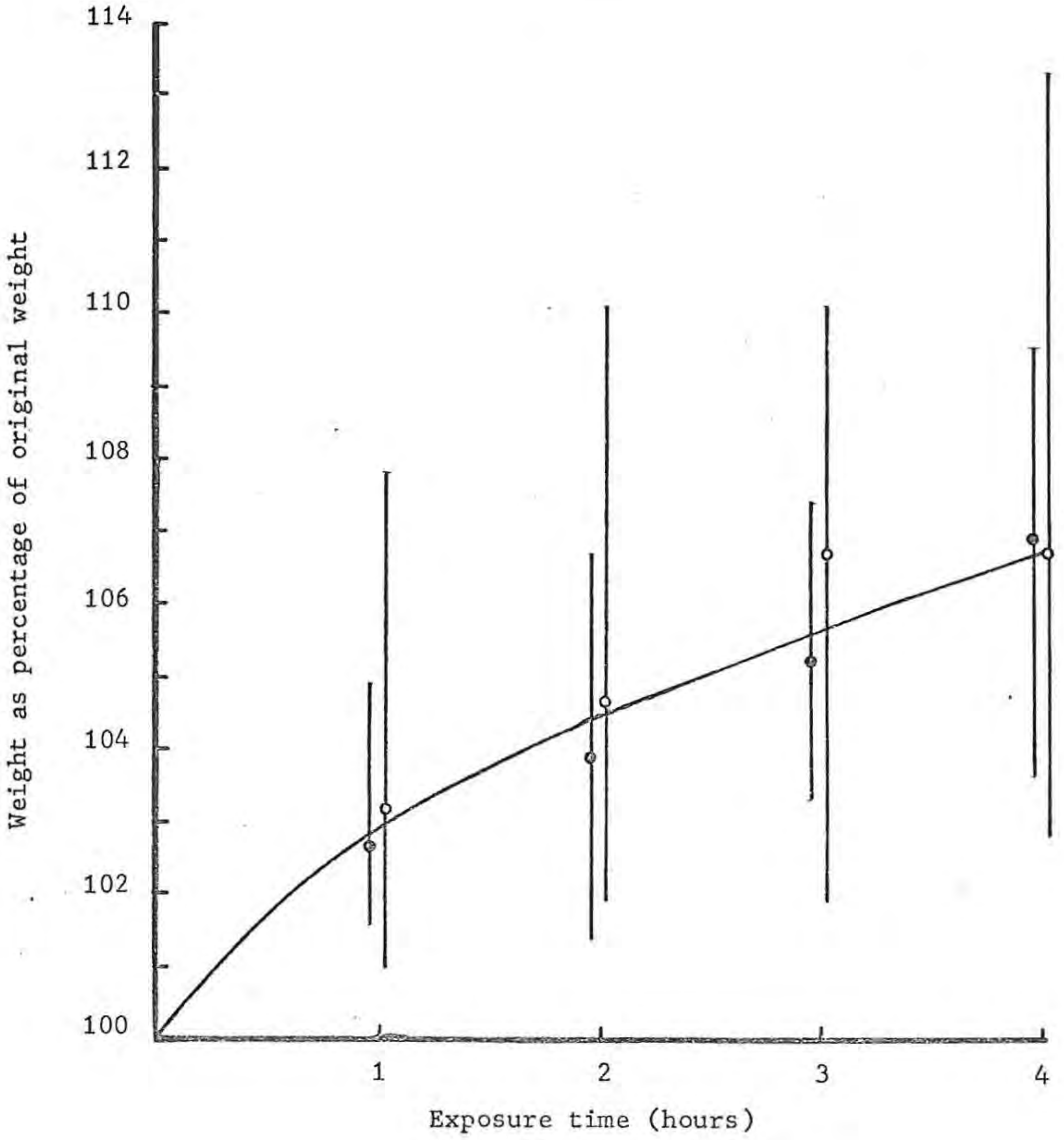


Figure 39. Weight increases in C.kraussi after direct transfer from 35°/oo to 9°/oo: 1) with ligature between thorax and abdomen (n = 9, open circles) 2) untreated (n = 8, closed circles). Vertical lines indicate range.

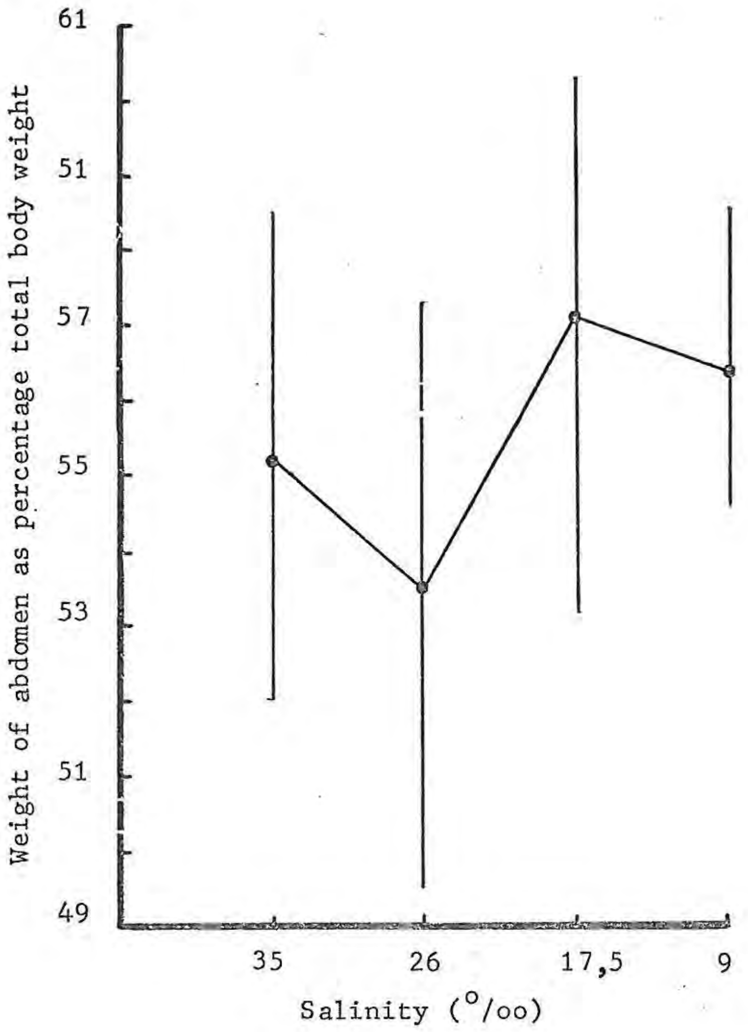


Figure 40. Contribution of abdomen to total weight of C.*kraussi* after 12 hours exposure to different salinities. Points are means of 10 determinations. Vertical lines indicate range.

c) Osmotic and ionic regulation.

After determining the blood osmotic pressure and sodium and chloride concentrations in sea water the changes occurring on direct transfer to salinities of 26, 17,5 and 9°/oo were each followed. In 26°/oo (Fig. 41) the osmotic pressure, sodium and chloride in the blood all dropped to levels similar to the medium in the first 24 hours and subsequent changes were negligible. In 17,5°/oo (Fig. 42) ionic stabilization was virtually complete after the first 24 hours and there was only a slight subsequent decrease up to 8 days. The sodium and chloride levels did not drop to the level of the medium. The osmotic pressure of the blood in 17,5°/oo dropped rapidly over the first 24 hours and then more gradually, only stabilizing after about 8 days. In 9°/oo (Fig. 43) there was a very marked initial undershoot in osmotic pressure, sodium and chloride levels after the first 24 hours although, as in 17,5°/oo, these parameters did not drop to the level of the medium. Following this undershoot there was a rapid recovery and the osmotic pressure had reached a new stable level after 2 days. Blood sodium and chloride also recovered rapidly, and apparently more quickly in the case of sodium. This possibly indicates a better control of this ion than of chloride.

The results obtained above after stabilization had occurred in 26, 17,5 and 9°/oo were then combined with results obtained from natural populations in the Kleinemonde and Keurbooms estuaries so as to give an indication of blood osmotic pressure, sodium and chloride levels at a variety of external concentrations.

Over the range 35°/oo to 21°/oo *C.kraussi* is isosmotic (Fig. 44). Hypo-regulation was not investigated in any detail but the single set

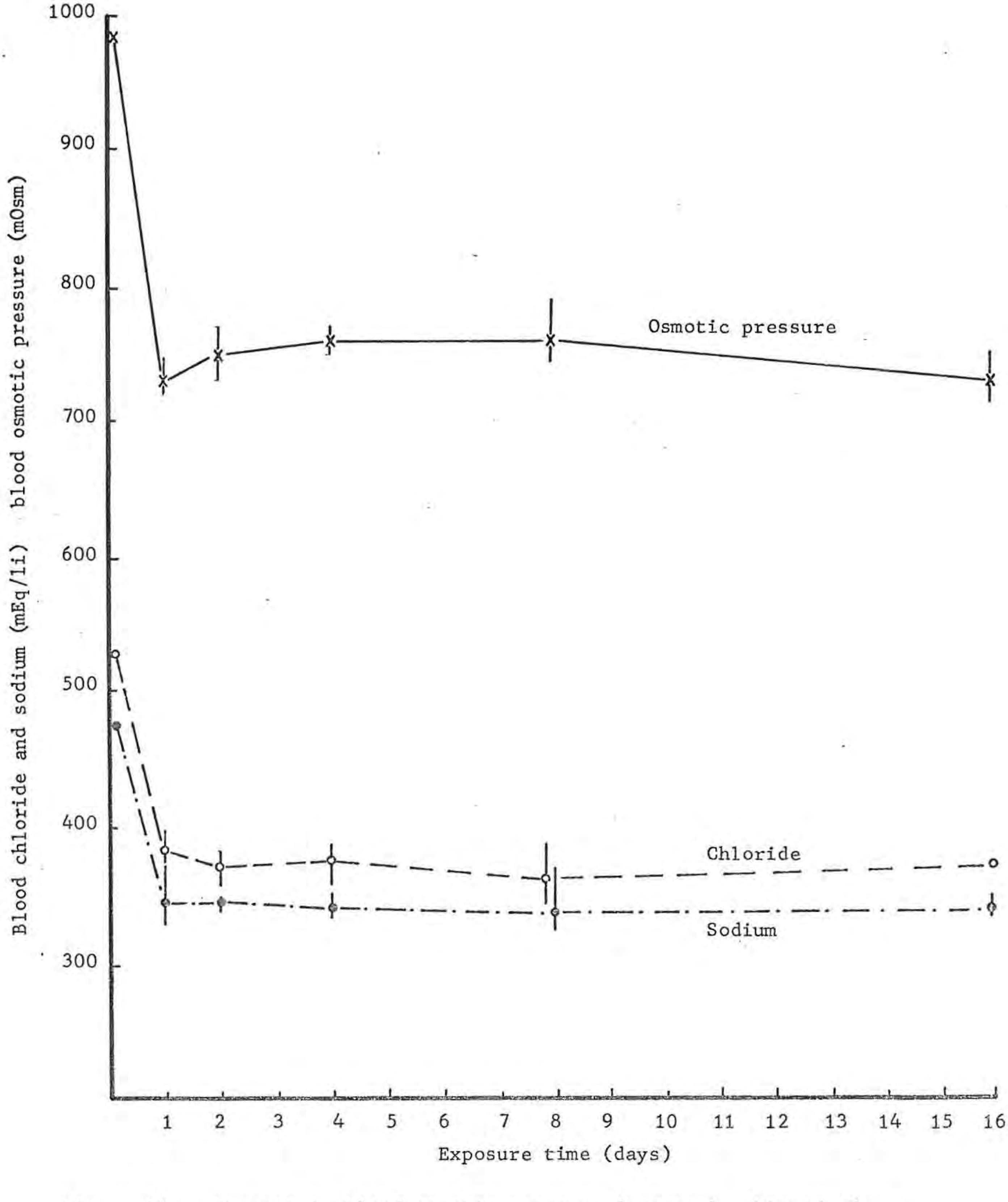


Figure 41. Changes in blood osmotic pressure (crosses), chloride (open circles) and sodium (closed circles) in <u>C.kraussi</u> following direct transfer from 35°/oo to 26°/oo. Initial results indicate values in prawns in 35°/oo. Each point is the mean of 5 determinations. Vertical lines indicate range.

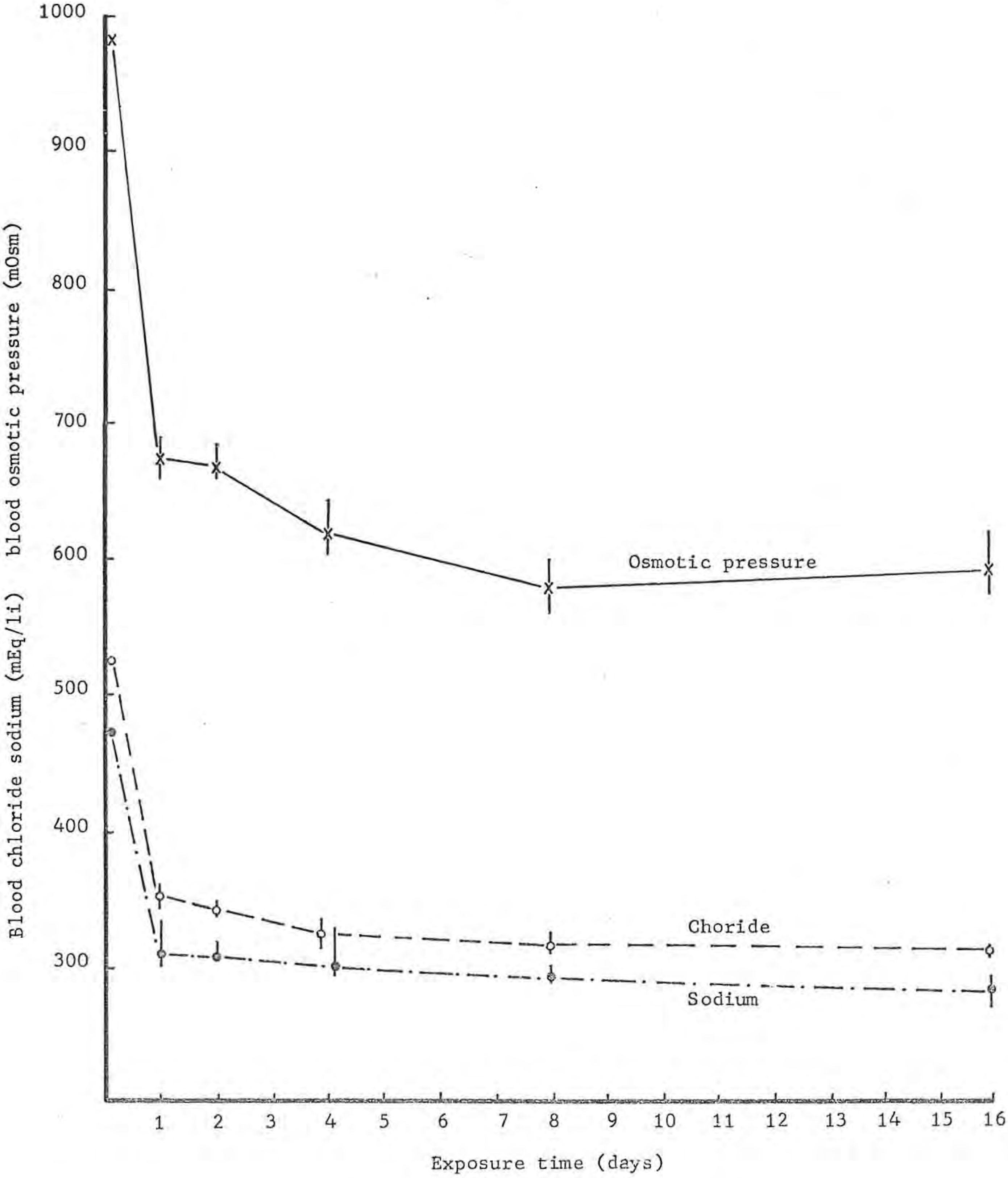


Figure 42. Changes in blood osmotic pressure (crosses), chloride (open circles) and sodium (closed circles) in C.kraussi following direct transfer from 35°/oo to 17,5°/oo. Initial results indicate values in prawns in 35°/oo. Each point is the mean of 5 determinations. Vertical lines indicate range.

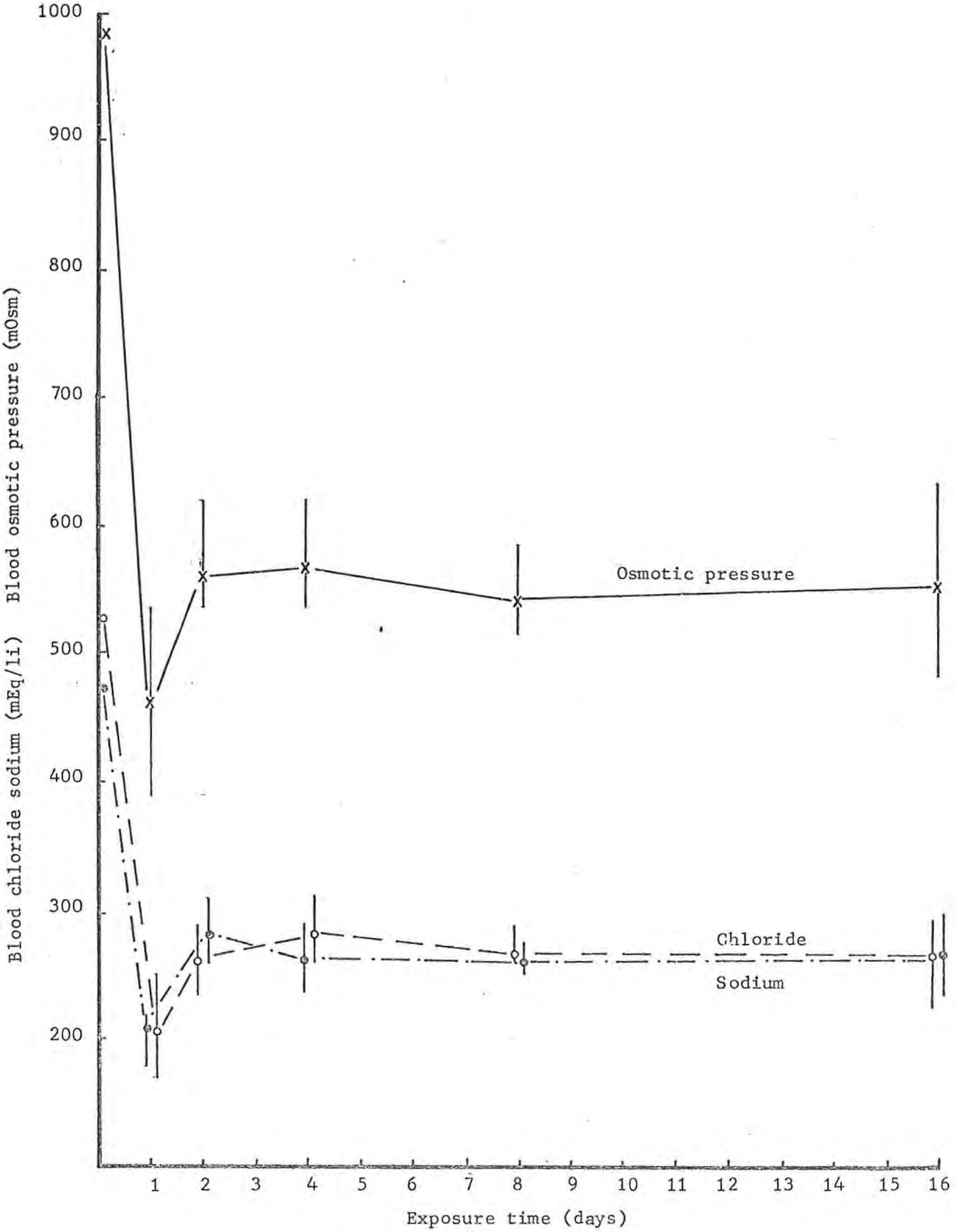


Figure 43. Changes in blood osmotic pressure (crosses), chloride (open circles) and sodium (closed circles) in C.kraussi following direct transfer from 35°/oo to 9°/oo. Initial results indicate values in prawns in 35°/oo. Each point is the mean of 5 determinations. Vertical lines indicate range.

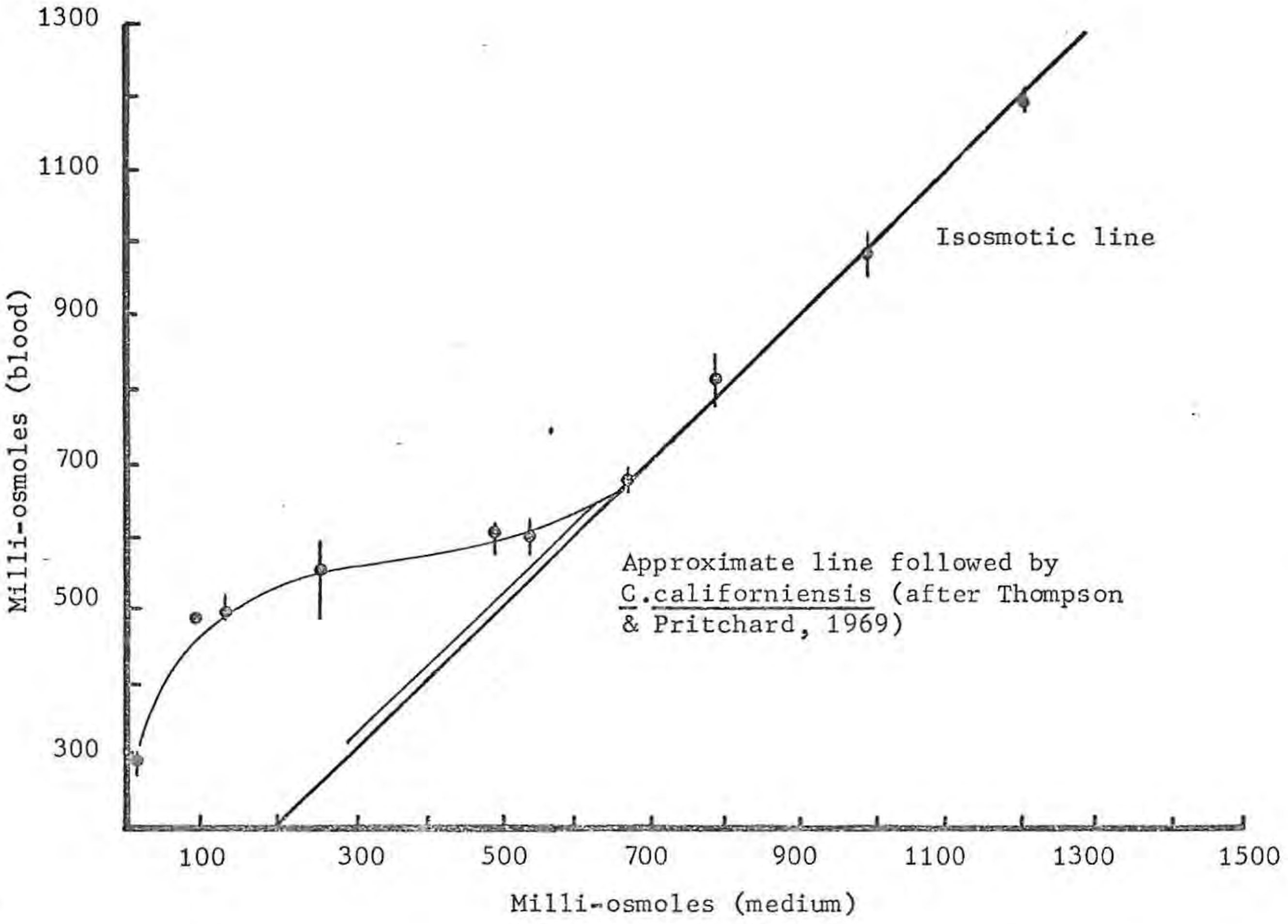


Figure 44. Blood osmotic pressure as a function of medium osmotic pressure. Each point is the mean of 5 determinations. Vertical lines indicate range.

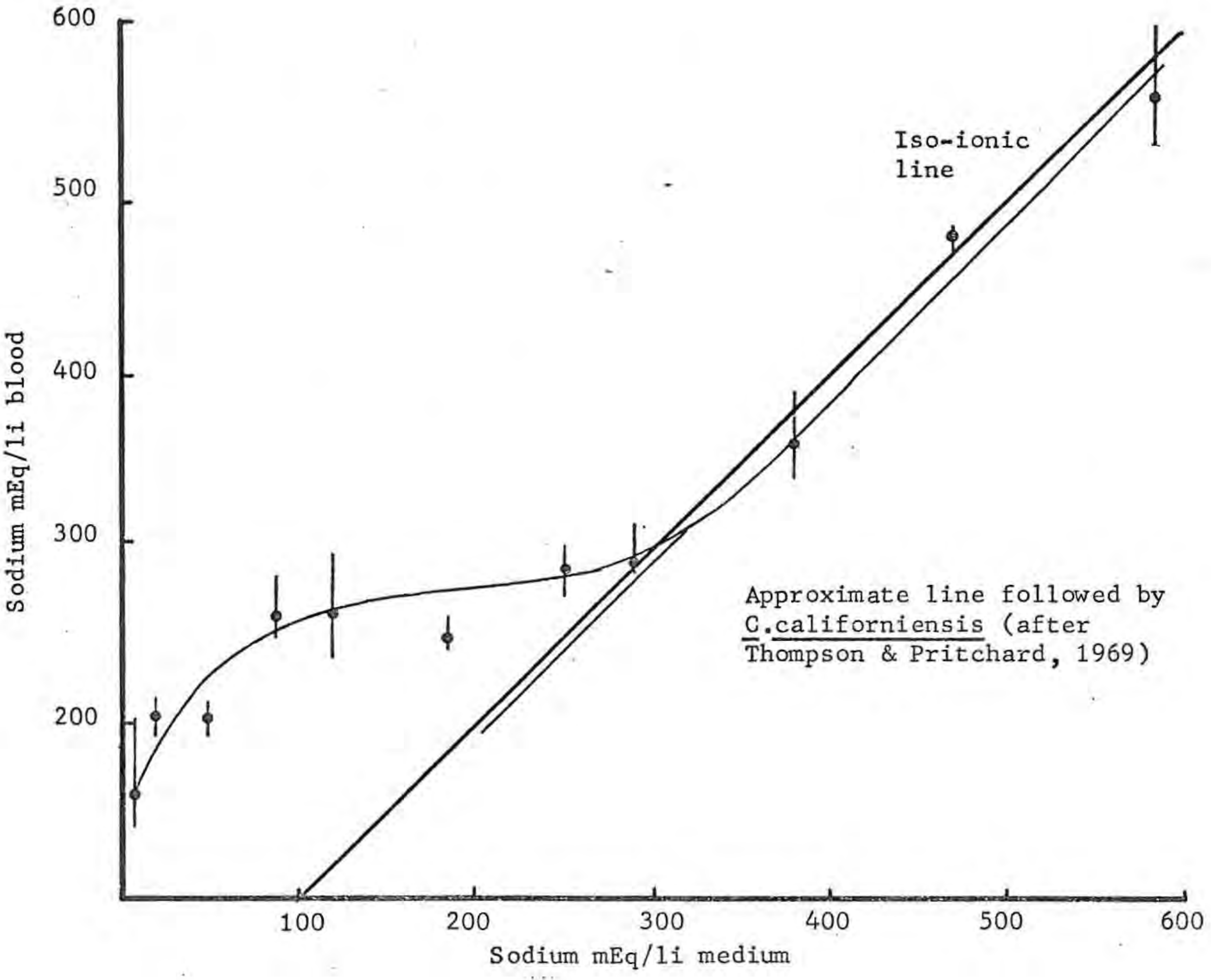


Figure 45. Blood sodium as a function of medium sodium. Each point is the mean of 5 determinations. Vertical lines indicate range.

of results obtained at a salinity greater than normal sea water indicated a lack of any hypo-regulatory ability. In salinities less than 21°/oo <u>C.kraussi</u> regulates hyper-osmotically, maintaining the blood osmotic pressure at a level equivalent to a salinity of 17-21°/oo in external salinities down to 3,5°/oo. The blood osmotic pressure then drops rapidly. Comparative results for <u>C.californiensis</u> (Thompson & Pritchard, 1969) indicate a lack of any hyper-regulatory ability but it is interesting that the lowest blood osmotic pressures measured (300 m Osm.) were similar despite the large difference in osmoregulatory capacity.

At salinities greater than sea water and down to about $21^{\circ}/oo$, sodium (Fig. 45) appears to be regulated slightly hypo-ionically. Below $21^{\circ}/oo$ regulation is hyper-ionic but, as in the case of the blood osmotic pressure, regulatory ability deteriorates rapidly once sodium has dropped to 10% of its sea water concentration. C.californiensis again shows no regulatory ability and in this case the lowest blood sodium levels recorded in the two species differed slightly.

Chloride regulation (Fig. 46) differs from osmotic pressure and sodium regulation in that regulation at external salinities above $21^{\circ}/oo$ is markedly hypo-ionic. There is again marked hyper-regulation in salinities below $21^{\circ}/oo$ which decreases once chloride in the external medium has dropped to 10% of its sea water concentration. Hypo-ionic chloride regulation in C.californiensis is more marked than in C.kraussi. No hyper-regulatory ability was found by Thompson & Pritchard (1969) in C.californiensis but as in the case of the blood osmotic pressure, the lowest blood levels recorded in the two species are similar.

These results show conclusively that C.kraussi is a strong hyper-regulator. Thompson & Pritchard (1969) recorded that while C.californiensis can tolerate dilutions down to $9-10,5^{\circ}/oo$ it lacks any regulatory ability. They also showed that the New Zealand C.filholi can tolerate salinities only down to $12-14^{\circ}/oo$ and suggest that it cannot osmoregulate. C.kraussi is thus distinct from other known species in the genus.

Sodium chloride makes a very similar contribution to the total osmotic pressure of sea water (86%) and to the total osmotic pressure of the blood of C.kraussi (85,7%; n = 10) in sea water ($35^{\circ}/oo$). Acclimation by C.kraussi to dilutions of sea water is characterised by initial fluctuations in the contribution of sodium chloride to the blood osmotic

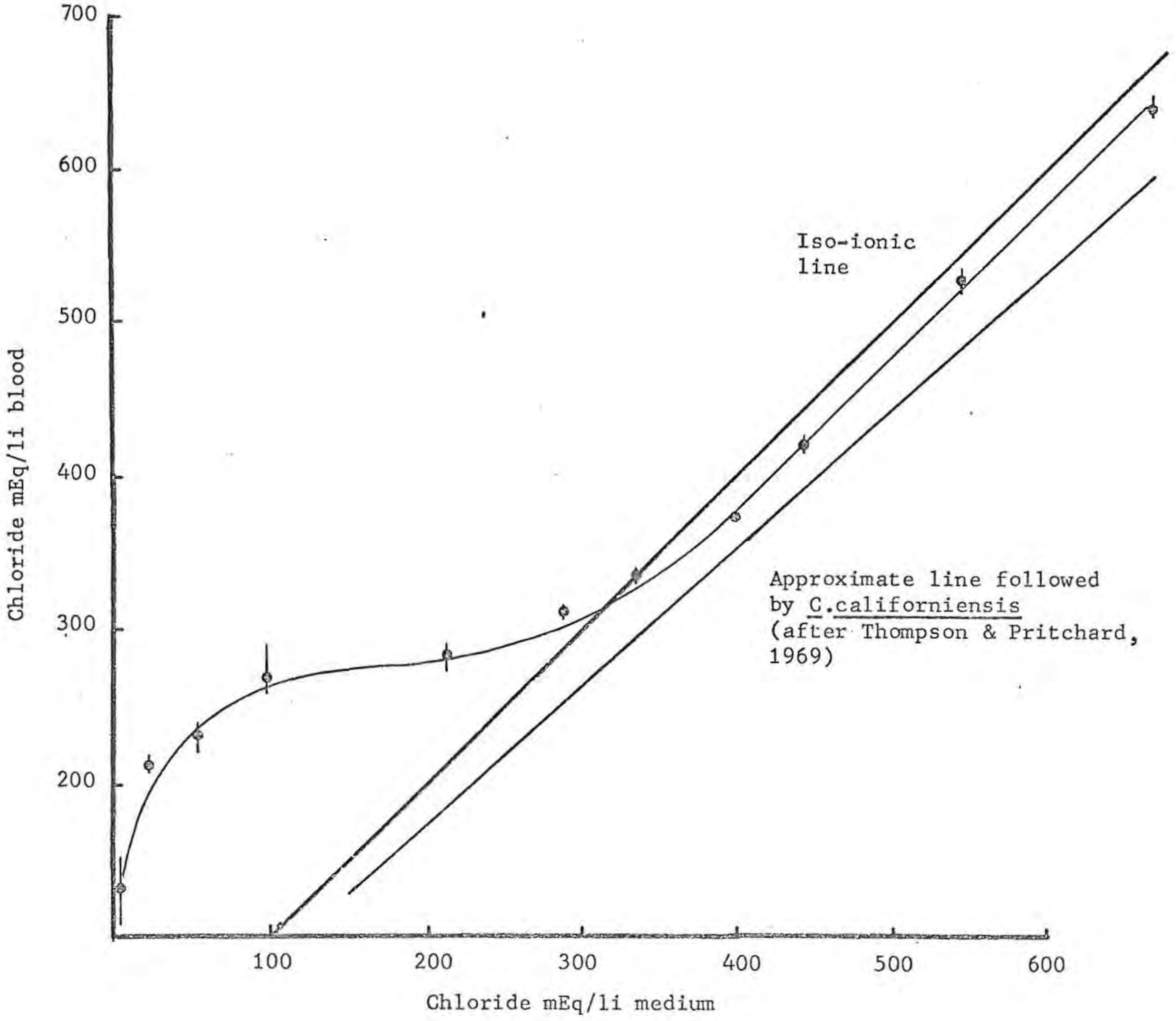


Figure 46. Blood chloride as a function of medium chloride. Each point is the mean of 5 determinations. Vertical lines indicate range.

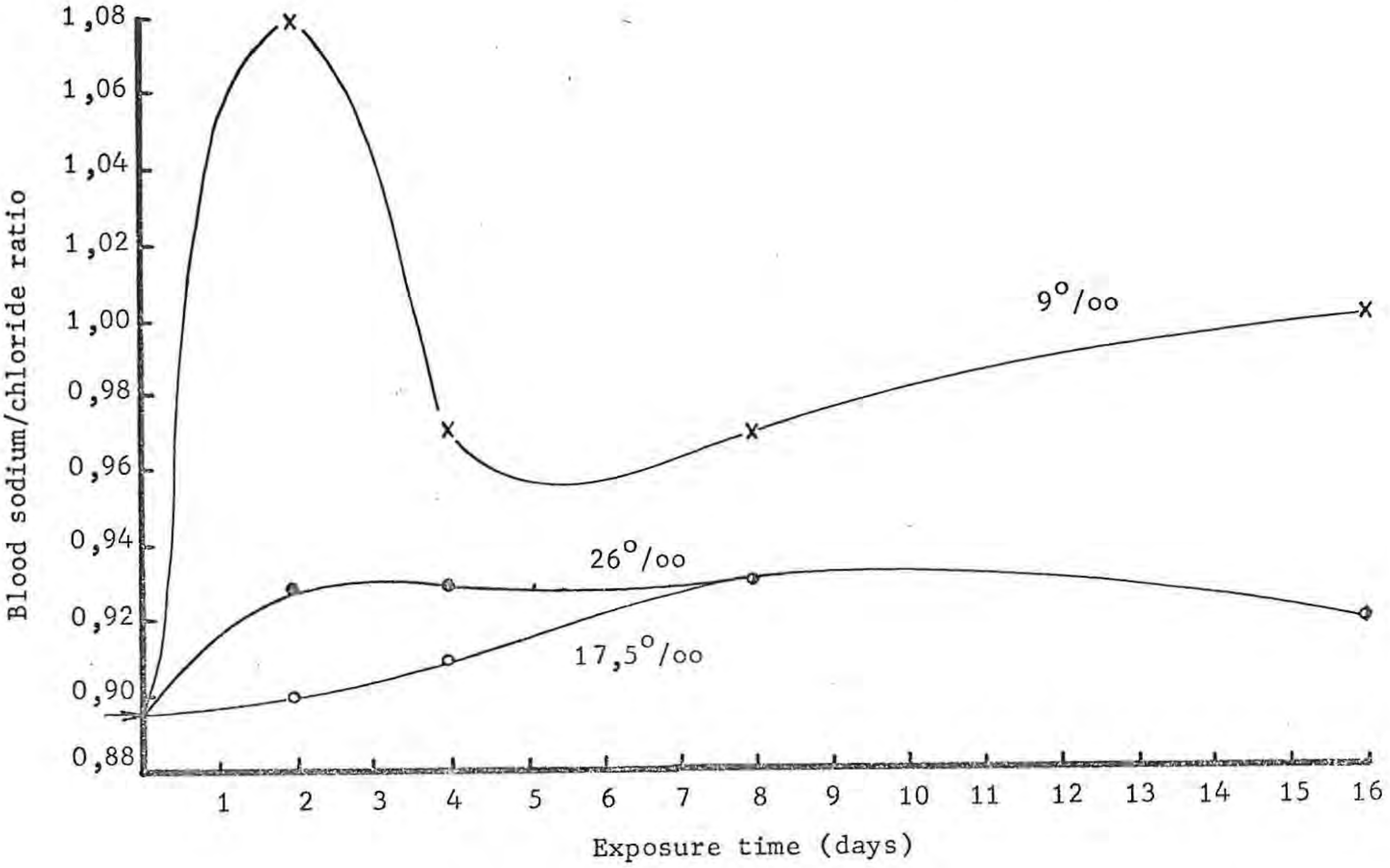


Figure 47. Changes in blood sodium/chloride ratio after direct transfer from sea water (35°/oo) to dilutions. Arrow on y-axis indicates blood sodium/chloride ratio in sea water.

pressure. There did not, however, appear to be any clear pattern in these fluctuations and the means of the eventual contributions of sodium chloride to the total blood osmotic pressure in 26, 17,5 and 9°/oo were between 86,5 and 88,5%. Thus in lowered salinities sodium chloride contributes only very slightly more to the total blood osmotic pressure than it does in sea water.

In addition to changes occurring in the contribution of sodium chloride to total blood osmotic pressure, marked changes occur in the blood sodium/chloride ratio following direct transfer from sea water to dilutions (Fig. 47). Changes in the sodium/chloride ratio in 26^{o}/oo and 17,5^{o}/oo are relatively slight although they both suggest an increase in the proportion of sodium. In 9^{o}/oo where C.kraussi hyper-regulates strongly at equilibrium, the increase in the proportion of sodium was far more marked and in addition did not return to the original level.

In sea water the ratio of sodium to chloride is 0,86:1. In the blood of prawns in sea water (35^{o}/oo) this ratio is slightly different (0,89:1). Fig. 48 shows that, in C.kraussi acclimated to dilutions of sea water, the ratio rises as the osmotic pressure of the medium falls, indicating that the proportion of sodium to chloride increases. These

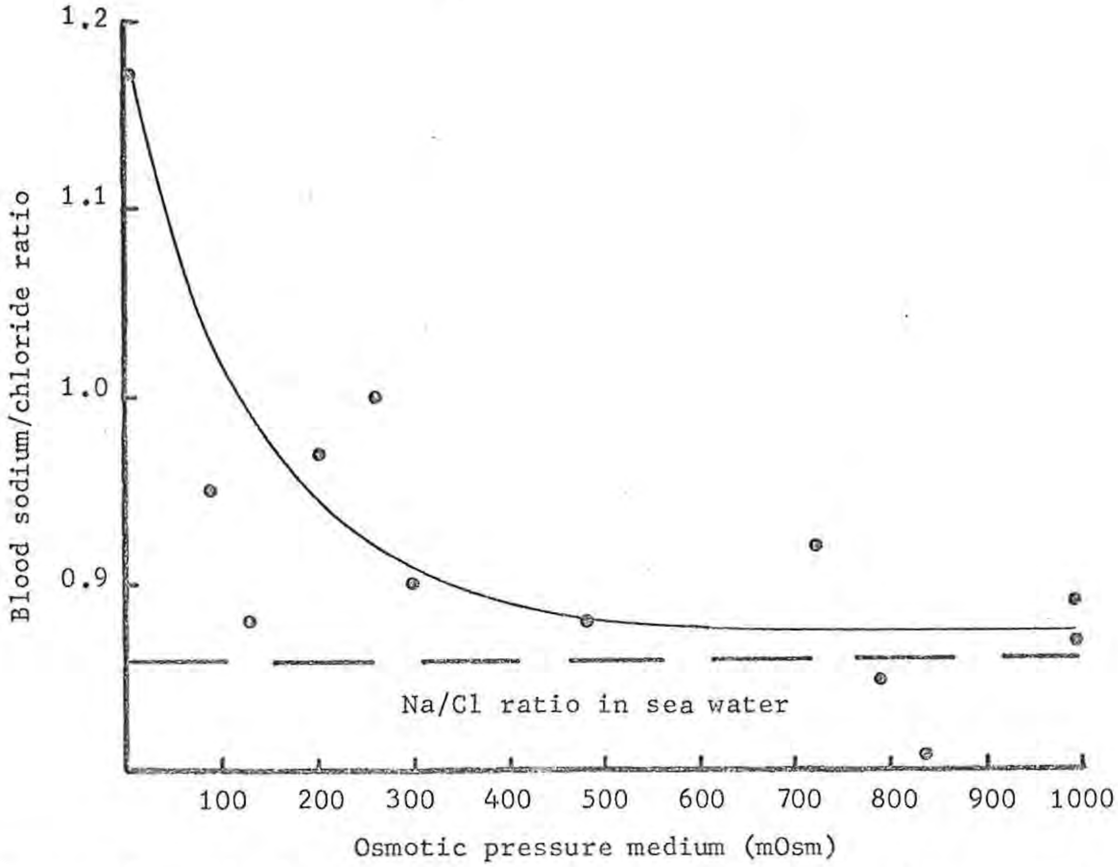


Figure 48. Blood sodium/chloride ratio at different medium osmotic pressures after acclimation to each dilution for at least 1-week.

results suggest that in dilutions of sea water C.kraussi is better able to regulate sodium than chloride although why this should be so is unknown at present.

d) Water and salt exchange.

Weight increases in prawns with blocked urinary pores were much greater than in isolated abdomens in $9^{o}/oo$ (Fig. 49). This showed that more water moved into the cephalothorax than into the abdomen. The body wall of the abdomen is thinner than that of the cephalothorax since the ventral surface of the cephalothorax is heavily calcified to support the limbs while the dorsal surface of the cephalothorax is a single solid continuous structure. The proximal part of the abdomen is thin walled to permit ventral flexing of the body, while the dorsal surface consists of a series of tergites connected by arthrodial membranes. There are more arthrodial membranes associated with the appendages of the cephalothorax than with the pleopods, but the pleopods themselves represent a large surface area. Although the abdomen thus has a generally thinner surface than the cephalothorax, the finding that more water moved into the thorax indicates that the most permeable area of the body lies in the gills. These structures have to be thin walled and have a large surface to fulfil their roles as respiratory organs and they are therefore ideal areas for water uptake and salt loss in dilutions.

Although the gills are highly significant in water uptake, the possibility still existed that drinking of the medium contributed to this uptake. Dissections of live prawns previously placed in sea water and dilutions of sea water containing methylene blue showed that traces of the dye appear in the fore-gut and hind-gut only after 24 hours.

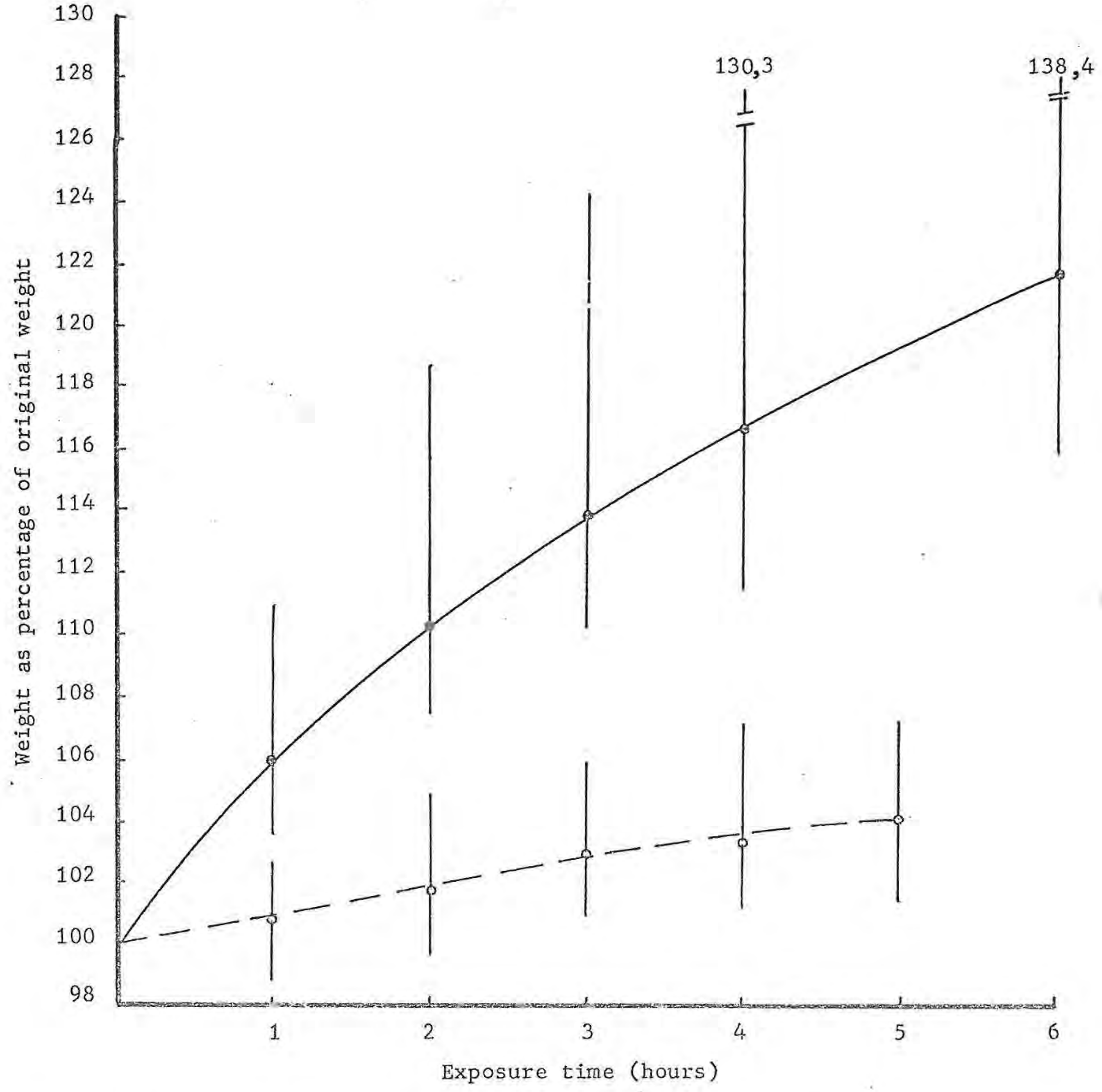


Figure 49. Weight increases in C.kraussi after direct transfer from 35°/oo to 9°/oo: a) intact prawns with blocked urinary pores (closed circles, n = 11); b) ligatured isolated abdomens (open circles, n = 10). Vertical lines indicate range.

This showed that drinking of the medium was negligible and consequently that uptake of water by this route could be disregarded. Similarly, anal uptake of water was negligible. This suggests that blocking of the anus did not reduce the uptake of water on direct transfer from 35°/oo to 9°/oo and the reason for the difference between untreated prawns and prawns in which the anus was blocked is unknown at present.

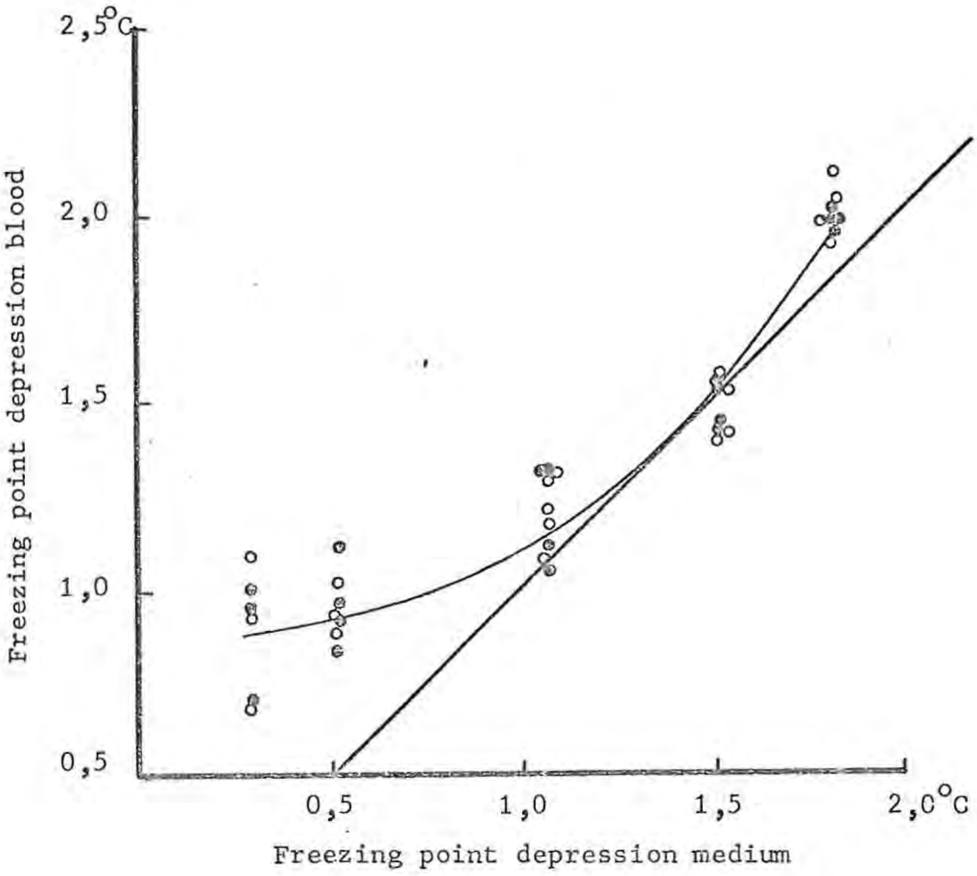


Figure 50. Freezing point depressions of blood (closed circles) and urine (open circles) at different external salinities.

Investigations of the routes of salt loss in C.kraussi were begun with measurements of the freezing point depressions of blood and urine in different salinities. The results (Fig. 50) showed that blood and urine were isosmotic at all external salinities. As urine production rates of up to 6% of the body weight per hour were recorded this implied a large loss of salts via the urine. Attempts were thus made to partition salt loss via the urine and the general body surface where the gills would be the most important area.

A comparison of the loss of sodium via both urine and body surface and body surface alone, based on rates of loss of ^{22}Na from loaded prawns into two different washing out media is given in Fig. 51. In 9°/oo where sodium loss would have occurred via both the body surface and in the urine the increase in activity of the medium was far more marked than in 9°/oo plus sucrose where sodium loss was only via the body surface since there was no osmotic gradient. Comparison of the slopes of the basal parts of the curves showed that increase in activity in 9°/oo was about 60 counts per minute/gram wet weight of prawn/hour, while the corresponding figure in 9°/oo plus sucrose was 34 cpm/g/hr. This indicated that the sodium loss rate in 9°/oo was roughly double that in 9°/oo plus sucrose and consequently that sodium loss in the urine and via the gills was similar.

Discussion

The initial finding that salinity changes in the substrate were negligible at depths greater than 10 cm when no prawns were present (Fig. 1) agrees with results obtained by Alexander (1932) and Reid (1932) on the rivers Tay and Tees. They found that fresh water flowing over mud and sand banks at low tide had little or no effect on salinity levels at depths of about 30 cm. The results obtained in the present experiment indicated that no changes occurred at even shallower depths but this was not a flowing water system. Equilibration between interstitial and

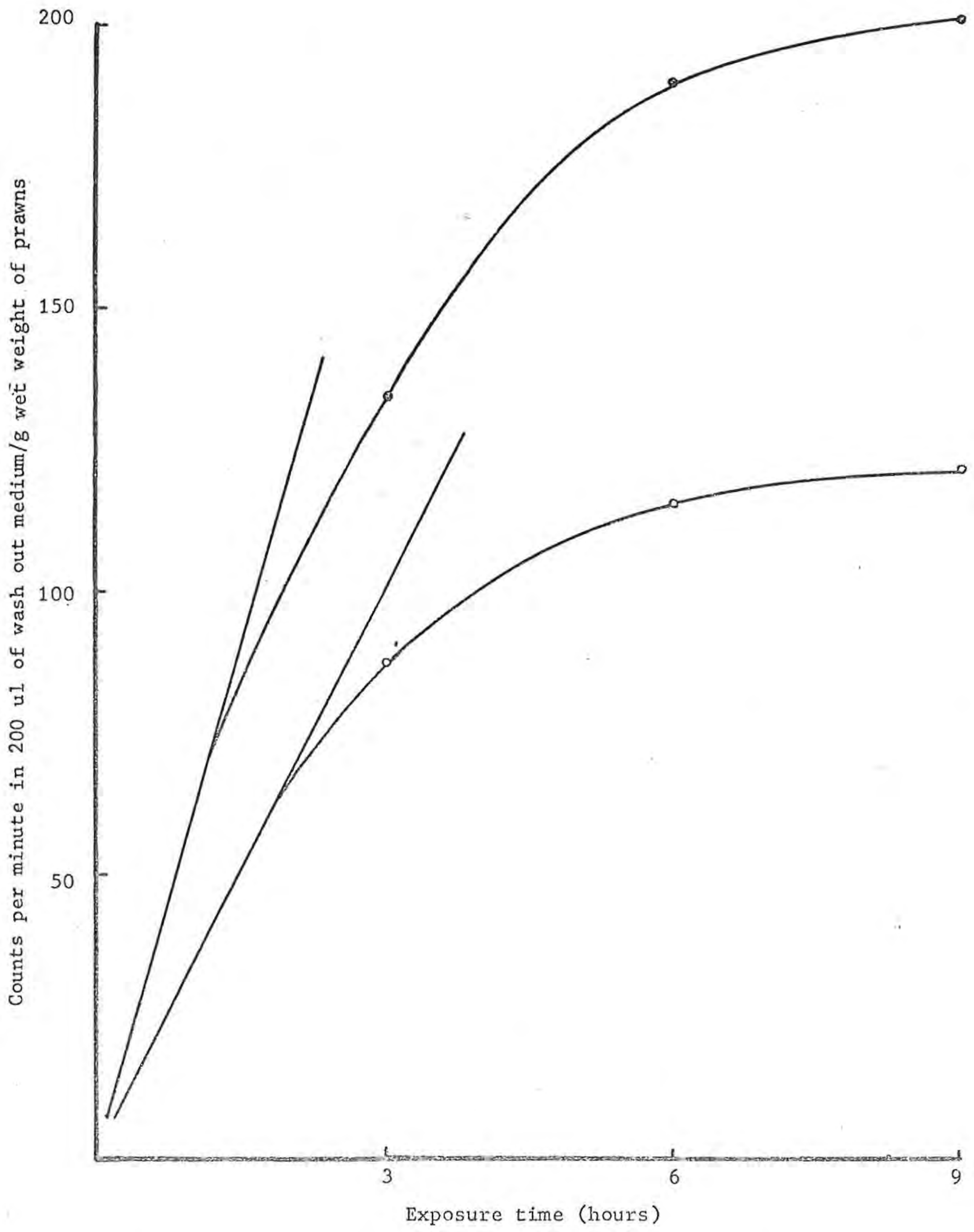


Figure 51. Increases in activity of wash out media: 1) sea water diluted to $9^{o}/oo$ (closed circles); 2) $9^{o}/oo$ plus sucrose to give osmolarity equivalent to $35^{o}/oo$ (open circles). Each point is the mean of 5 determinations.

overlying water occurred rapidly when prawns were present (Fig. 32) implying that the burrowing habit in this species does not necessarily provide protection against sudden changes in surface water salinities. Thompson & Pritchard (1969) suggest that the absence of a well formed burrow system in C. californiensis provides a shield against low surface salinities, although Upogebia pugettensis which has open burrows is not insulated in this way. Hill (1971) found that U.africana will pump water of a lethal salinity through the burrow. It appears that the more tolerant euryhaline species C.kruassi, Upogebia africana and U.pugettensis will pump low salinity water through their burrows but not C.californiensis which has no regulatory powers.

Exposure to low salinity conditions has two immediate effects: 1) there is an osmotic inflow of water and 2) there is a loss of salts to the medium. The osmotic inflow of water occurs primarily via the gills and results in a measurable increase in weight. On direct transfer from 35°/oo to a 9°/oo dilution the weight of C.kraussi with blocked urinary pores increased at a rate of about 6% of the body weight per hour (Fig. 35). Untreated prawns transferred directly from 35°/oo to 9°/oo increased in weight at a rate of about 3% of the body weight per hour. This suggested a urine production rate of 3% of the body weight per hour. This rate of water uptake is similar to that found by Davenport (1972a) in Porcellana platycheles on transfer from 35°/oo to 21°/oo. In both P.platycheles and C.kraussi, the response to entry of water was rapid, and at no time did weight increases in untreated animals compare with those in animals with blocked urinary pores. This implies a rapid rise in the rate of urine production in response to some stimulus which could possibly be a reduction in blood concentration or an increase in volume due to entry of water.

Weight increases in C.kraussi on direct transfer from 35°/oo to 9°/oo reached a maximum after about 8 hours (Fig. 38) but blood osmotic pressures and associated sodium and chloride levels reach their minimum levels only after 24 hours (Fig. 43). This suggests either that salt loss continues after the volume regulatory mechanisms have begun to overcome the osmotic inflow of water or that blood osmotic pressure, sodium and chloride have already begun to recover after 24 hours and the levels measured do not represent the minimum values. This would require further investigation.

The marked undershoot in 9°/oo did not occur in 26°/oo and 17,5°/oo (Figs. 41, 42 and 43). The minimum blood osmotic pressure, sodium and chloride levels recorded in 9°/oo represent a drop to less than half of their values in 35°/oo, although not to the level of the surrounding medium. The extent of the changes which occurred in the blood in 9°/oo when compared with the practically negligible fluctuations in weight indicated that the reductions in blood osmotic pressure, sodium and chloride were not due to a flooding effect but to salt loss.

Salt loss occurred via both the gills and the urine. Loss via the gills is simply down a concentration gradient but loss via the urine would be more complex. The urine in C.kraussi and in C.californiensis (Thompson & Pritchard, 1969) is isosmotic with the blood in all external salinities and in the case of C.californiensis is iso-ionic with respect to chloride. Reduced salt levels in the urine of crustacea are only known in fresh water species including crayfish, atyid shrimps and some gammarids. It is therefore probably safe to assume that blood and urine sodium and chloride are iso-ionic in C.kraussi. Salt loss via the urine is thus due to an inability to produce a hypotonic urine; thus when an increased amount of urine is voided to cope with the osmotic inflow of water in low salinities there is a considerable accompanying salt loss.

As shown by the tracer studies sodium loss through the gills is about equal to the loss via the urine. Comparative figures in other crustacea are few; in most species so far studied the urinary loss of ions constitutes only about 10% of the total loss (Eriocheir sinensis 14%, Krogh 1938; Astacus pallipes 10%, Shaw 1959a; Potamon niloticus less than 5%, Shaw 1959b). More recent work by Lockwood (1965) has shown that when the urine and blood are isosmotic, urinary sodium loss in Gammarus duebeni may account for 80% of the total loss. The only work on anomura is that of Davenport (1972a) who found that urinary salt loss accounted for almost 75% of the total salt loss in Procellana platycheles and Pagurus bernhardus. It seems significant that most of the species showing a low rate of sodium loss in the urine spend either all, in the case of Astacus pallipes (Shaw 1959a) and Potamon niloticus (Shaw 1959b) or part, in Eriocheir sinensis (Krogh 1938), of their lives in fresh water. Gammarus duebeni is exceptional in being able to produce both an isosmotic or an hypotonic urine but both Davenport's work and the present study were done on species more typical of higher salinities. The ability to reduce salt loss in the urine is characteristic of brackish or fresh water crustacea which have shown some ability to cope with excess water inflow either by reduced permeability (Potamon niloticus, Shaw 1959b) or by production of hypotonic urine as in the fresh water crayfish.

The increased urine flow combined with salt loss via the gills in dilutions results both in the removal of excess water and also in a reduction in the concentration of salts in the blood. This reduces the osmotic gradient between medium and blood and consequently also the rate at which water will flow into the prawn and thus ultimately the rate of urine production. Prawns acclimated to dilutions down to 3,5^{o}/oo produce less urine than prawns immediately after transfer from 35^{o}/oo into 9^{o}/oo (Fig. 7). Nevertheless Fig. 46 shows that the lower the salinity to which the prawns are exposed the greater the amount of urine produced. Prawns in 35^{o}/oo and 26^{o}/oo are isosmotic with the medium and urine production amounts to less than 1% of the body weight per hour, a figure which agrees with results given by Parry (1960). Acclimated prawns in salinities lower than 20-21^{o}/oo regulate hyperosmotically and consequently there is still an osmotic gradient along which water will tend to flow into the prawn. Urine production in 9^{o}/oo and 3,5^{o}/oo thus increases to c. 3,5% and 5% of the body weight per hour respectively.

Are animals acclimated to dilutions able in some way to reduce their permeability to water, or are the differences in the rate of urine production simply due to a reduction in the osmotic gradient between blood and medium with a consequent reduced rate of water inflow? Prawns acclimated to 3,5^{o}/oo maintained the blood concentration at a level equivalent to a salinity of about 21^{o}/oo which involves a concentration difference between blood and medium equivalent to about 400 m Osm. Prawns transferred directly from 35^{o}/oo where they are isosmotic, to 9^{o}/oo have to cope with an immediate concentration difference between blood and medium equivalent to about 750 m Osm. This explains to a large extent the difference between the respective rates of increase in urine output. Data concerning a reduction in water permeability are generally sparse and contradictory. Smith (1967, 1970) claimed that *Rhithropanopeus harrissi* and *Carcinus maenas* were able to reduce their permeability to water in low salinities but Rudy (1967) found no evidence of reduced permeability in *Palaemonetes varians* nor in *Carcinus maenas*. Hannan & Evans (1973) found an ability to reduce permeability in Limulus polyphemus but not in Penaeus duorarum nor in three species of Uca. It would appear that the whole problem of water permeability requires further investigation.

The response to transfer to low salinities involves more than simply a reduction in blood osmotic pressure, sodium and chloride levels. Before a new stable level is attained, marked changes have occurred in the contribution of sodium chloride to the total blood osmotic pressure and the sodium/chloride ratio (Fig.17) while acclimation to new low salinities results in new sodium/chloride ratios. Ionic stabilization occurs fairly rapidly being virtually complete within two days (Figs 41, 42 and 43) but total osmotic stabilization may require up to a week. This suggests that whereas ionic regulatory mechanisms can be mobilized rapidly there is some longer term adaptation occurring which is associated with smaller, slower changes in blood osmotic pressure than occur over the first 48 hours. This could be associated with changes in some non-ionic osmotically active particles in the blood, such as amino-acids.

The loss of the salts in the urine and through the gills must be compensated by an active uptake mechanism. In the absence of any evidence of drinking or anal uptake it must be assumed that this salt uptake occurs through the body wall, probably through the gills. Acclimation to low salinities would thus be associated with an increased rate of salt uptake, a phenomenon previously unknown in the genus Callianassa although common in many brackish and fresh water crustaceans.

It can be concluded therefore that the southern African species of Callianassa, C.kraussi is a euryhaline species capable of hyperosmotic regulation although apparently not of hyporegulation.

PART IV

CONSERVATION MEASURES

Introduction

Conservation implies the rational use of any particular resource. The need for conservation measures in the case of *C.kraussi* has only really come about during the last four or five years because of changing methods in collection of this species. Prior to the advent of the prawn pump this animal was collected by digging. Digging is not only an inefficient method of collecting this animal but is also extremely tedious due to the effort required to excavate near the water table and to examine large quantities of sand. No comparative figures are available on the amount of prawns taken in the various areas before and since the development of the prawn pump, but discussions with fishermen and general observations suggest that the use of *C.kraussi* as a bait organism has expanded tremendously in areas where once it was barely known. This has necessitated a consideration of available stocks of *C.kraussi* and the formulation of conservation measures based on a knowledge of the general biology of this species.

Present Bait Regulations

Present regulations as drawn up by the Department of Nature Conservation of the Cape Province forbid the use of spades in estuaries. *C.kraussi* may only be collected by using a prawn pump. The number of prawns which may be collected is limited to 70 per person per day. There is no limit on size or sex. Areas in which collecting of prawns is prohibited do exist in a few estuaries and *C.kraussi* collected in one estuary may not be used for bait in another estuary nor in the sea.

These regulations suffer from two obvious shortcomings. Firstly there is no restriction on the number of bait diggers and secondly the figure of 70 does not appear to be based on availability of prawns but simply on the number that one angler might find sufficient for a day's fishing.

Aspects of the biology of C.kraussi of significance in conservation.

The present study revealed several facts which are relevant to conservation. The first important aspect relates to distribution, since the restriction of this species to areas of sheltered water means that along the southern African coast it is predominantly estuarine. Offshore populations are known to occur in False Bay and Algoa Bay but the extent and density of these populations are unknown. They do suggest, however, that offshore populations could be expected in other areas. The significance of these populations in providing reserve stocks is uncertain at present. The burrowing habit and lack of any planktonic larval stage, despite the degree of mobility of the juvenile stages, suggests that there would probably be little contact between adjacent populations. It would, however, be of importance to establish whether exchange does occur between estuarine and offshore populations. If this exchange were very small, this would imply that recovery of a heavily exploited area would have to come from within that population and not from outside. It would thus probably be very slow. This compares with the situation in the blood worm Arenicola where the larval stage is only planktonic for a few hours and consequently dispersal is limited. This species, which is also exploited for bait, has been completely eliminated from some southern African estuaries.

A second important factor is the distribution within any particular estuary or bay. C.kraussi is largely restricted to areas sheltered from wave action and strong tidal currents. Consequently, although it can occur throughout a closed estuary it cannot do so in an open one. The nature of the substrate can also exert a limiting effect.

The distribution of C.kraussi in an estuary does not appear to be depth limited; thus it can extend below the low tide mark and be shielded against the activities of bait diggers. This of course will only be applicable in the few areas which are deep, are not subject to tidal currents and do not have a muddy substrate occupied by Upogebia africana.

Apart from physical features of estuaries, the nature of the population itself must also be considered. This refers particularly to aspects such as breeding potential, recruitment of juveniles to the population and the times of year when most collecting is done in relation to the breeding seasons. The sampling program has shown that the number of eggs produced by females of this species is comparatively low, and also that the proportion of mature females carrying eggs seldom exceeds 40%. Nevertheless, the recruitment of juveniles to the population is large and may constitute 60-70% of the population at certain times of the year. This implies that populations could probably stand a large amount of exploitation. The relation between breeding season and maximum collecting effort by anglers is also relevant. The amount of collecting varies from area to area; for example in the Swartkops estuary near Port Elizabeth collecting is more or less continuous over the whole year. However in areas like the Kleinemonde estuary which is more isolated, exploitation tends to be limited to summer holiday periods. Since the main breeding effort occurs during late winter and early spring with a very much smaller peak during late spring and summer this means that in many areas absence of collectors will afford a degree of protection to the stocks during the main breeding season.

C.kraussi must attain a minimum carapace length of 6-7 mm before they are of use to anglers. In the west Kleinemonde estuary prawns reach this size in their first year and a maximum of 7-9 mm at an age of about 2 years. In the Swartkops estuary a carapace length of 7-8 mm is attained after one year and a maximum of 8-10 mm in females and 11-13 mm in males after about 2 years. It was shown in a previous section that C.kraussi can breed at the age of one year but that the maximum contribution to the breeding effort occurs after the first year at a size which is exploited by anglers.

The results of the sampling program and the visits to other estuaries showed that the numbers of C.kraussi varied greatly during the year in the Swartkops and Kleinemonde estuaries as based on the number of prawns obtained per unit effort. Despite this, the weight of prawns per unit effort remained more constant. Yields from the Swartkops estuary were consistently heavier than those from the Kleinemonde estuary. Collections from other areas likewise showed that there were marked variations between different areas. Thus a limit of 70 prawns per person per day might have a negligible effect in one area but a very marked effect on another, and when this is combined with differences in collecting pressure it becomes obvious that blanket restrictions of the type presently applied are inadequate.

Conservation measures thus have to be drawn up with due regard to the distribution of C.kraussi both along the coast and within estuaries, to the variations between different areas, to the breeding seasons and finally to the demand by anglers for the largest available specimens of C.kraussi.

Suggested conservation measures

It is obvious that conservation measures are of little use unless it is possible to enforce them. A number of suggestions will thus be made, beginning with what could be considered the optimum situation and progressing through less satisfactory but more practical solutions.

The obvious optimal situation is to have complete control of all bait removal activities with no independant collecting allowed. This would allow exact records of removals to be maintained and determinations of the flux in catch per unit effort to be followed. This would probably be the most effective method in conservation of stocks and, in view of the ease with which the larval stages are reared in the laboratory could ultimately be combined with a restocking program in heavily fished areas.

Whether collecting was completely controlled or not, an accompanying measure would be the use of a rotation system of collecting with alternate open and closed areas.

A rotation of closed areas would be based on the fact that C.kraussi has an initial growth period of one year followed by maximum breeding during the second year. Only two closed areas would be required so that a prawn bed could be divided into two. These two areas would be closed alternately for one year periods. The rationale behind this system is that in any one closed area in a particular year breeding would occur uninterrupted and would be followed by the appearance of a generation of juveniles. When this area is opened to collectors during the following year the juveniles would be maturing but would still be too small to be of interest to anglers. On the other hand the generation that had bred during the previous year would be available for collection. In the following closed year the juveniles would now have reached an age of about 12-15 months and would breed during that winter and be available during the following open year. Such a system would ensure that there was always one undisturbed portion of the breeding stock. Catch limits should be retained and possible reductions could be applied in areas with small populations.

Areas permanently closed to bait collection exist in some estuaries. This can be used as an alternate method of conservation since it involves easier control. Migrations from these closed areas would re-populate depleted areas, but would have to be chosen to ensure that accessibility exists between the two areas. It is obvious that closed areas have to be selected with care and also with due regard to other species that might exist in the same area and also be of use as bait. The alternative of rotating closed areas for one year periods however is probably a more effective method of control.

It is apparent that with the present information, the measures suggested above relate simply to the conservation and maintenance of stocks of C.kraussi. The long term effects of collecting and the effects of pumping on the juveniles are unknown.

DISCUSSION

One of the aims of this investigation was to clarify some of the factors affecting the distribution of C.kraussi in southern Africa, and it has been shown that this is controlled in a number of ways. The geographical range is probably largely temperature controlled. In this regard the eggs and larvae would be the critical stages as they are more sensitive to low and high temperatures than the adults. This would limit further expansion on the west and east coasts of southern Africa. Within estuaries and bays distribution may be limited by increasing coarseness of the substrate or by sand and water movement or both. Low salinities at the heads of estuaries do not necessarily limit the spread of C.kraussi despite the inability of this species to breed at salinities below c.17°/oo, if the populations can be maintained by immigration from elsewhere.

An aspect which has not been investigated in the present study is the nature of the interaction that exists between this species and the other common southern African burrowing thalassinid prawn Upogebia africana. Wooldridge (1968) showed that C.kraussi was able to burrow in a wide range of substrate types including that inhabited by U.africana, and the presence of C.kraussi in muddy areas when U.africana is absent has been commented on by other workers. Millard & Scott (1953) noted that "at Milnerton and Hermanus (where U.africana does not occur) C.kraussi abounds in muddy sand, whereas at Knysna it occurs in sand being replaced in muddy sand by the mud-prawn U.africana". Macnae (1957) working on the Swartkops estuary discussed the distribution of C.kraussi which occurred near the mouth and near the tidal limit but only sporadically in between. He suggested that the occurrence of U.africana precluded colonization by C.kraussi.

The factor which results in the mutual exclusion of *C.kraussi* and *U.africana* is possibly related to their respective habits. It is generally accepted that *U.africana* is a filter feeder (Hill, 1968) constructing relatively simple U- or Y-shaped burrows with very little subsequent burrowing activity. On the other hand *Callianassa* species are generally assumed to be "sand sifters" (Day, 1951) picking up their food from the sand during their burrowing activities (MacGinitie, 1934; Devine, 1966). Workers such as MacGinitie (1934) have also commented on the extent to which the substrate is turned over by the burrowing activities of *Callianassa* species. A densely populated *C.kraussi* area with its numerous cones of sand has an entirely different appearance to an *U.africana* area where each burrow has only a small lip. The continual burrowing activities of *C.kraussi* would interfere with the more sedentary habits of *U.africana*. Hill (1968) has shown that *U.africana* is an energetic defender of its burrow. In *C.kraussi* this reaction is absent, apparently due to its constant likelihood of intruding into some other burrow. The habits of *C.kraussi* are such that interconnected burrows would not interfere with its way of life but an interconnected system would possibly not suit a filter feeder such as *U.africana*. We can thus see a possible rationale for the exclusion of *C.kraussi* from *U.africana* areas but the actual mechanism of this exclusion would require detailed long term investigation.

One aspect of the life cycle of *C.kraussi* which deserves further discussion is the reduced larval life and the loss of a planktonic phase. Thorson (1950) reviewed the different larval types and larval development in marine benthic invertebrates and pointed out that large numbers of small eggs are generally associated with a long planktonic larval life. Conversely, production of a small number of large eggs as found in *C.kraussi* is associated with a reduced planktonic phase and the hatching of the eggs at a later stage in the development of the young. It is generally accepted that planktonic stages and the period of settlement are vulnerable phases in the life cycle and the production of large numbers of eggs is required to offset the mortality that occurs at these periods. The extent of the mortality in some species is indicated by Ayers (1956) finding that in the lamellibranch Mya arenaria survival of only .0013% of the larvae is required to maintain the population. Thus reductions in the planktonic phase would be expected to confer some advantage on the individual. Thorson (1950) reviewed the conditions under which reduction or loss of the planktonic stages in the life cycle occurred and the whole subject has been more recently discussed by Mileikovsky (1971). Their conclusions were very general although they concluded that there was a tendency towards a decrease in the number of species having pelagic development from the equator to the Poles and from shallow water to greater depths. Reduction of the larval stage is fairly common in freshwater species, for example in the crab Potamon niloticus (Gurney, 1942). In congeneric estuarine and freshwater species, the estuarine form may retain the full series of zoeal stages while these may be absent or reduced in the freshwater form. This is well illustrated in Australian crabs of the genus Hymenosoma, in which the estuarine H.paralacustris has indirect development with three zoeal stages while the freshwater H.lacustris has direct development (Lucas, 1969). Reduction of the larval stages does not, however, necessarily occur in fresh water and some species of Atyidae, for example, have long series of larvae (Gurney, 1942).

The genus Callianassa as a whole does not fall into any one of these categories. Gurney (1942) states that reduction in the number of larval stages is found in Callianassids from the Red Sea but does not specify the species. Fishelson (1971) lists three species from this area, all from shallow water. Reduction has thus occurred in a tropical area and probably in shallow water. This trend is opposite to that described by Thorson (1950) and Mileikovsky (1971). We are thus left with Gurney's (1942) statement that while abbreviated larval lives are found in most decapod groups there is no clear connection between habitat and duration of larval life.

How does C.kraussi fit into this picture? Hailstone & Stephenson (1961) recorded up to 90% of mature females ovigerous at any one time in C.australiensis and Devine (1966) up to 80% in C.filholi both of which have long planktonic phases. The maximum proportion of ovigerous mature females recorded at one time in C.kraussi was only 40%. Despite this comparatively low figure the populations of C.kraussi in the west Kleinemonde and Swartkops estuaries at times consisted of 60-80% juveniles as opposed to a maximum of 40-50% on C.australiensis. It thus appears that the loss of the planktonic phase in C.kraussi and the fact that they do not emerge at all from the parent burrow during the larval period has conferred a marked advantage on the species. It has also allowed the production of a comparatively small number of eggs.

The nature of the stimulus which initiated a trend towards reduction of the larval phase in C.kraussi is uncertain, especially since other species in the genus have retained it. If the reduction originally occurred in the sea, it would have acted as a pre-adaptation to an estuarine environment where the marked difference in sensitivity to low salinities between larval and post-larval stages would presumably be a factor tending to favour the further reduction in duration of the larval stage. Any factor which would lessen vulnerability to sudden decreases in salinities would be of advantage to species living in estuaries.

One of the results of the loss of the planktonic phase is an increased stability of the population. This was first shown by Thorson (1950) on some benthic invertebrates in Danish waters in comparisons of the fluctuations in weight per square metre of species with pelagic and non-pelagic development. This was subsequently also demonstrated in the thalassinid *Calocaris macandreae* off the Northumberland coast of England by Buchanan (1963). Although females of this species produce an average of only 38 eggs the population density remained virtually constant at 18-20 animals per square metre over a period of 2 years. As recorded above, although the population density of *C.kraussi* does fluctuate widely the yield in weight per unit effort fluctuated by only about 50% of the mean value which compares well with Thorson's (1950) figures for stable populations with non-pelagic development.

The results from the present study emphasize the importance of the burrow in the life of *C.kraussi*. MacGinitie (1934) has listed the anatomical features of *C.californiensis* associated with its burrowing existence and these features appear to be common to all species of *Callianassa*. The life cycle and habits of *C.kraussi* indicate a far stronger association with the substrate and the burrow than is the case in *U.africana*. This association starts in the early stages when the newly hatched larvae remain in the parent burrow, unlike the planktonic larvae of *U.africana*. Although this would reduce the mortality associated with a planktonic stage as already discussed, it does not appear to provide significant protection against low surface salinities as shown in Part III. The post-larval stage is capable of burrowing and it is apparent that a dispersal phase is still important in the life cycle since this function is taken over by these post-larval phases. These stages are more tolerant of low salinities than are the larvae and thus are able to migrate into lower salinities than would be possible if the larvae were the dispersal phase. In addition these stages are also more efficient swimmers and burrowers than the adults and thus better able to fulfil the function of dispersion. Once established in a burrow, C.kraussi is far more dependent on the substrate than U.africana which uses the burrow primarily as a shelter, depending for its food supply on what it can filter out of the water which it pumps through the burrow. On the other hand C.kraussi obtains its food from the substrate although Devine (1966) maintains that some food is carried into the burrow of C.filholi in New Zealand by respiratory currents.

The route by which C.kraussi has invaded estuaries is not precisely known at present. Hill (1968) has shown that in the genus Upogebia, there is a succession from U.capensis which burrows in the open sea and which occurs in the intertidal zone on rocky shores where it burrows in sand-filled crevices, to U.africana which burrows in mud banks in open estuaries. It is probably safe to assume that Callianassa evolved as a burrower in sheltered waters in the sea from where it invaded the sheltered waters of estuaries. Offshore populations of C.kraussi exist and populations are known to occur in very sheltered rock pools but no sequence similar to that in Upogebia has been found. In addition it is unknown wheter differences in larval development or low salinity tolerance exist between offshore and estuarine populations.

The invasion of estuaries by C.kraussi has undoubtedly been greatly assisted by its hyper-osmotic regulatory ability. As shown in Part III this ability is well-developed in C.kraussi, although it appears that tissue tolerance to low blood osmotic pressures and low ionic levels is not greater than other species since the minimum blood osmotic pressures, sodium and chloride levels are similar in C.kraussi and

C.californiensis which is unable to hyper-regulate (Thompson & Pritchard, 1969). It is interesting to note that *C.californiensis* is typical of the Yaquina Bay area of Oregon and not of the Yaquina River which opens into the bay. From the brief review of the habitats of the different species given by Thompson & Pritchard (1969) it appears that, although some may be subjected to reductions in salinities at times, this is only a temporary situation and, apart from the little known *C.turnerana* of the Cameroons, which apparently migrates into fresh water, (Monod, 1927 in Thompson & Pritchard 1969), *C.kraussi* is the only species in the genus which is known to exist permanently in salinities below 35^{o}/oo.

It appears significant that the two thalassinids (*Callianassa kraussi* and *Upogebia africana*) with the best known hyper-regulatory ability should both occur in the estuaries of southern and south-eastern Africa. This is probably related to the peculiar nature of the majority of southern African estuaries. During most of the year salinity gradients are slight; much of the tidal section of an estuary, in the case of open estuaries, will be exposed to a marine salinity regime. Floods, however, are a feature of the rivers of the eastern Cape Province. Macnae (1957) discussed the nature of the rainfall in the Swartkops river catchment and pointed out that "in most years between one third and a half of the annual total fell over periods of a few days". These floods result in sudden very marked decreases in salinities for a few days. Species which live permanently in the river thus require some mechanism which would enable them to cope with these conditions which occur in both open and closed estuaries. A situation thus prevails which would favour the development of regulatory ability, more so than in estuaries in other parts of the world where a classical type of salinity regime is the norm.

Kinne (1967) roughly separated the methods of coping with reduced salinities into escape, reduction of contact, regulation and acclimation while stressing that combinations of these were also very likely. Anomurans rely on a number of different methods. Escape would usually be difficult since they are not as mobile as fish. Reduction of contact would be of greater importance in burrowing forms like *Callianassa*. Thompson & Pritchard (1969) maintain that the substrate shields *C.californiensis* against transient low surface salinities. Davenport (1972a and 1972b) has shown that the hermit crab *Pagurus bernhardus*, although apparently incapable of osmotic regulation, copes with the osmotic inflow of water in low salinities by using the abdomen as a "swelling reservoir". *C.kraussi* and *U.africana* (Hill, 1971) are the only known thalassinids which cope with low salinities by both regulation and acclimation.

C.kraussi provides an abundant food supply for common estuarine fish such as *Lithognathus lithognathus* and *Pomadasys operculare* which are able to extract these prawns from their burrows. It is possibly of far greater significance in an estuary because of its burrowing activity. The maze of burrows that is constructed ensures that the substrate is oxygenated to depths of over a metre and this presumably makes the habitat suitable for other burrowing animals. They use detritus buried in the sand and subsequently produce faeces which are discharged from the burrow. These are then utilised by surface feeders such as crabs, hermit crabs and amphipods, as was found by Frankenberg et al (1967) in the case of *C.major*. Thus they are of significance in making what would be otherwise inaccessible nutrient, available to other species. It is important in this regard to bear in mind that the conservation regulations suggested are at present based only on the need to ensure continued existence of the populations of

C.kraussi. It must be realized that extensive collecting could significantly reduce the population density as was found by Hailstone & Stephenson (1961) in C.australiensis in Moreton Bay in Queensland. The long term effects on an estuary of such a reduction are at present completely unknown and this would require studies on a far broader scale than the present investigation.

This study has shown that C.kraussi has been a very successful invader of the estuarine environment and is able to cope with many of the stresses normally associated with this habitat. This invasion has even extended into the specialized environment of the closed estuary where the number of species is invariably lower than in an open estuary. However, one of the main features to emerge from this study was the differences that exist between populations of C.kraussi in open and closed estuaries, or more accurately between populations in areas with or without access to the sea.

The discovery that the maximum size of C.kraussi in the west Kleinemonde estuary, while originally less than that of the Swartkops estuary, was declining further, led to the question whether or not C.kraussi could survive indefinitely in a closed estuary. It is apparent that some sort of deterioration occurs although no records have been kept of populations of C.kraussi in estuaries isolated from the sea for long periods. The problem of the length of time an estuary is isolated from the sea arises again with regard to the sizes reached by prawns in closed estuaries. Carapace lengths of 10 and 11 mm were recorded in the Klein and Bot river estuaries in the south-western Cape when these estuaries were closed. Both estuaries, however, open every year suggesting that periodic connection with the sea is sufficient to obviate the size reducing effects associated with isolation.

The effects of isolation from the sea on the faunal diversity of an estuary are very marked. Day, Millard & Harrison (1952) recorded 319 species from Knysna, a clear open estuary, while Scott, Harrison & Macnae (1952) list only 134 species from the Klein river estuary near Hermanus which is closed for about half the year. In addition many marine species die after the bar at the mouth has closed so that the permanent fauna is poorer than this.

Precise investigations of the reasons for the absence of particular species from closed estuaries are virtually non-existent. Similarly little is known of the less obvious changes occurring in closed estuaries following isolation from the sea. Rapid changes such as the loss of tidal movements and the salinity stabilizing influence of the sea are immediately apparent and will doubtless affect some species, but other long term factors may be more important. The abundance of species such as the thalassinid mud prawn Upogebia africana, the crab Cleistostoma edwardsii and the hermit crab Diogenes brevirostris in open estuaries and their rarity in closed systems indicates that these restrictions are not only acting on C.kraussi. The portunid crab Scylla serrata and the sparid fish Rhabdosargus holubi both enter estuaries as juveniles and mature there before migrating back to the sea to breed. In both species growth continued in the west Kleinemonde estuary after the mouth was closed off from the sea by a sand bar although the condition factor of R.holubi was inferior to that of fish from the open Kowie river estuary (Blaber, 1973). No sexually mature R.holubi were recorded in the Kleinemonde estuary and although ovigerous S.serrata were found in the Kleinemonde the larvae did not survive in the estuary and no recruitment occurred (Hill pers.comm.). This suggests that breeding is a critical period in the maintenance of many species in closed estuaries. It is possibly significant that U.africana, C.edwardsii and D.brevirostris all possess planktonic larvae while *C.kraussi* does not. This may confer some advantage in a closed estuary although it does not apply to all species. The polychaet *Mercierella enigmatica*, the bivalve *Musculus virgiliae*, the barnacle *Balanus amphitrite* and the oyster *Crassostreamargaritacea*, all of which have planktonic larvae were able to maintain themselves in the east and west Kleinemonde estuaries after they were isolated from the sea.

Although *C.kraussi* can apparently survive long isolation from the sea, it is nevertheless affected and the species appears thus to be ultimately dependent on at least some access to the sea. In this regard it is interesting that Korringa (1956) is of the opinion that "the source of all fertility in ... estuaries is to be found in the ocean itself". He discusses a variety of means by which the fertility of an estuary can be built up, all depending on the influence of the sea. This is supported by figures for primary productivity in Langebaan Lagoon given by Mostert & Henry (1973). They found that nutrient concentrations inside the lagoon were higher than in the sea while primary productivity in the upper part of the lagoon was only 10% of that in parts of the lagoon exposed to the sea. The upper parts of the lagoon approach the conditions in a closed estuary while the lower parts exposed to the sea would compare with an area such as the mouth of the Swartkops river. In this study maximum growth and size in *C.kraussi* was invariably found in areas which correspond to the areas of maximum productivity found by Mostert & Henry in Langebaan Lagoon. Future work on *C.kraussi* could profitably explore the relationship between sea and estuary dwelling populations as well as the long term effects of complete isolation from the sea.

SUMMARY

1. The distribution of *Callianassa kraussi* in southern Africa extends from Lamberts Bay on the west coast to San Martinho in Mocambique. This represents a northerly extension of the range from the previous known limit of Inhaca Island. In this area 59 localities were visited and records obtained for an additional 16. Three areas were selected for detailed study. These were the west Kleinemonde estuary, which is normally closed off from the sea by a sand bar and the open Swartkops estuary both on the south-eastern Cape coast, and the Swartvlei system, which consists of a lake connected to the sea by a channel which closes intermittently, on the southern Cape coast.

2. The nature of the burrows constructed by *C.kraussi* was investigated in these areas. Burrow complexes may have up to nine entrances but more commonly two to four. Laboratory studies suggest that the number of entrances does not exceed the number of prawns present and consequently burrow opening counts will give an estimate of population density. Water movement can result in the closing off of burrows while strong water and sand movement will exclude *C.kraussi* from an area. *C.kraussi* is also excluded from areas which have very coarse substrates.

3. A three year regular sampling program showed that *C.kraussi* breeds mainly in winter/spring with a smaller breeding peak in summer. Egg development time at 20°C in a salinity of 35°/oo is 30-33 days. There are two larval stages which last 3-5 days. Development time of the eggs is tripled at temperatures of 13-15°C while larval development time is extended to 9-14 days. Development

is possibly slightly accelerated at 25 ± 3°C but the number of eggs hatching is markedly reduced. Larval development times were similar to those at 20°C and 35°/oo. There are no planktonic larval stages. Growth was more rapid and greater size was attained in the open Swartkops estuary than in the closed Kleinemonde estuary. Prawns hatching in winter/spring breed for the first time in the following summer at an age of about 16 months and then again in the following winter/spring at an age of about 2 years. Prawns hatching in summer breed in the following winter at an age of about 18 months and then again in the immediately following summer. Longevity in both sexes is about 2 years.

Dispersal is accomplished by migration of the post-larval juvenile phases at an age of 3-5 months. Non-selfmaintaining populations exist in areas where salinities are too low to permit breeding. Population densities were found to vary markedly in different areas.

4. Investigations of osmotic and ionic regulation showed that *C.kraussi* is a strong hyper-regulator and thus distinct from any other known species in the genus. Volume regulatory ability is well developed and depends on variable rates of urine production. Salt loss in dilutions occurs almost equally via the gills and the urine. The general responses of *C.kraussi* to dilutions of sea water are discussed.

5. Various suggestions for conservation measures based on the distribution and life cycle of *C.kraussi* were made.

6. The factors affecting the distribution of *C.kraussi* are discussed. The problem of the larval development in *C.kraussi* was discussed in relation to reviews of larval types of benthic invertebrates. The importance of the burrow, the possible route by which *C.kraussi* has invaded estuaries and the differences between open and closed estuaries as shown by the effects on *C.kraussi* were discussed.

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APPENDIX I

LOCALITY RECORDS FOR C.KRAUSSI IN SOUTHERN AFRICA.

U.C.T. represents University of Cape Town Zoology Department.

1) Lamberts Bay. Estuarine and offshore record. Unpublished U.C.T. survey record.
2) Langebaan Lagoon. A large, shallow, sheltered bay.
3) Milnerton estuary. Closed estuary, open in winter.
4) Kommetjie. Small sheltered bay. Unpublished U.C.T. survey records.
5) Klaasjagers Lagoon. West coast Cape Peninsula (Barnard, 1950).
6) False Bay. Offshore. Unpublished U.C.T. survey record.
7) Other areas in False Bay: Muizemberg (U.C.T.), Kalk Bay, St. James, Strand (Barnard, 1950), Gordon's Bay (Hill, pers.comm.).
8) Bot River. Closed estuary, opens in winter.
9) Klein River, Hermanus. Closed estuary.
10) Uilenkraal. Open estuary.
11) Heuningnes. Open estuary, rarely closed.
12) Breede River. Large open estuary. No C.kraussi found.
13) Stilbaai. Sheltered lagoon off an open estuary.
14) Gouritz River. Sheltered open estuary.
15) Great Brak River. Open estuary.
16) Kaaiman's River. Open estuary.
17) Wilderness lagoon. Opens intermittently.
18) Swartvlei estuary. Sampled regularly. May close at any time.
19) Knysna lagoon. A very large, clear, open estuary.
20) Keurbooms River. Open sheltered estuary.
21) Groot River. Opens intermittently, very sheltered.
22) Kromme River. Large open estuary.
23) Kabeljous River. Large shallow estuary, usually closed.

24) Algoa Bay. Offshore record.

25) Swartkops River. Sampled regularly, open estuary.

26) Sundays River. Large open estuary.

27) Boknes River. Small closed estuary.

28) Bushmans River. Open estuary. U.C.T. survey record. Not found during present study.

29) Kasuka. Small closed lagoon.

30) Kowie River, Port Alfred. In lagoons off the main estuary.

31) Riet River. Small closed estuary.

32) West Kleinemonde River. Sampled regularly; small closed estuary.

33) East Kleinemonde River. Small closed estuary.

34) Fish River. Open estuary.

35) Tatchana. Very small closed stream.

36) Mpekweni. Small closed estuary

37) Begha River. Open estuary, sometimes closes.

38) Keiskama River. Large open estuary.

39) Gulu River. Closed estuary.

40) Bonza Bay. Closed estuary.

41) Nahoon River. Barnard, 1950.

42) Gonubie River. Open very sheltered estuary.

43) Bulugha River. Open very sheltered estuary.

44) Bashee River. Open estuary.

45) Mendu Point. Very small, closed stream.

46) Nenga River, Coffee Bay. Closed sheltered estuary.

47) Umngazana River. Large open estuary.

48) Umgazi River. Open sheltered estuary.

49) Port St. Johns. Two small closed streams.

50) Mbotyi. Closed estuary.

51) Msikaba River. Open estuary. No *C.kraussi* found.

52) Mtamvuna River, Port Edward. Open estuary. No *C.kraussi* found.

53) Southbroom. Unnamed closed estuary.

54) Mbizane River, Ramsgate. Small open estuary.

55) Izotsha River, Shelly Beach. Small closed estuary.

56) Umtentweni River, Port Shepstone. Open estuary; no *C.kraussi* found.

57) Umzumbe River. Open estuary; no *C.kraussi* found.

58) Umzimai River. Small open estuary.

59) Umzimbuzi River, Karridene. Small closed estuary.

60) Umkomaas River. Open estuary. No *C.kraussi* found.

61) Umgababa River. Closed estuary.

62) Durban Bay. A large very sheltered bay. U.C.T. survey record.

63) Umgeni River. Open estuary. U.C.T. survey record.

64) Zetani River, Tinley Manor. Open sheltered estuary.

65) Mtunzini River. Pers.comm. B.J. Hill.

66) Richards Bay. A large sheltered very shallow bay. Millard & Harrison (1954).

67) St.Lucia estuary and lake. An extremely large shallow lake. Never recorded.

68) Kosi Bay. A series of inter-connected lakes finally opening to the sea.

69) Inhaca Island. Recorded by Macnae & Kalk (1958) from a sheltered bay.

70) San Martinho. A coastal lake joined to the sea by a narrow channel.

APPENDIX 2

Results of spot samples in localities other than the main study areas. Juveniles are expressed as percentage in the sample; other categories as percentages of mature females. c = closed; o = open.

Date	Percentage ovigerous	Percentage Eyed	Early ovary development	Late ovary development	Dropped eggs	Juveniles (Percentage)	Place
				Western Cape Province			
Feb '72	-	-	50	-	4	Nothing <5 mm	Bot River (c)
Feb '72	-	-	46	-	3	42	Great Brak (o)
Feb '72	-	-	53	7	-	11	Heuningnes (o)
Feb '72	-	-	33	-	-	11	Klein River, Hermanus (c)
Feb '72	-	-	62	-	-	48	Langebaan
Feb '72	-	-	45	-	2	12	Milnerton (c)
Feb '72	6	-	61		28	14	Stilbaai (o)
Feb '72	-	-	52	4	8	24	Uilenkraal (o)
				Southern and Eastern Cape			
Aug '71	10	10	50	-	-	2	Begha (o)
Aug '71	20	20	40	40	-	-	Fish (o)
April '72	-	-	18	5	-	10	Kabeljous
Aug '71	21	14	70	21		?	Keiskama (o)
Nov '70	-	-	20	-	-	?	Knysna
Dec '70	-	-	19	-	-	10	Kowie - East lagoon
July '71	66	-	66			?	Kromme (o)
April '72	-	-	50	28	-	-	Kromme (o)
Aug '71	10	5	30	35	-	4	Mpekweni and Tetshana
				Transkei			
Oct '72	8	3	33	30	-	13	Mbotyi
July '72	11	9	36	11	2	4	Port St Johns 2nd Beach small stream
Oct '72	-	-	11	-	6	9	Port St Johns 2nd Beach small stream
Jan '73	-	-	46	-	8	59	Port St Johns 2nd Beach small stream
Oct '72	-	-	15	6	-	30	Port St Johns 2nd Beach main stream
Jan '73	-	-	50	27		23	Port St Johns 2nd Beach main stream
July '72	6		33	14	50	20	Umgazi
July '72	4	3	61	27	40	4	Coffee Bay
July '72	-	-	20	6	22	-	Mendu Point
July '72	6	3	42	6	45	14	Bulugha
July '72	19	3	19	62	8	32	Bonza Bay
July '72	6	6	48	20	4	2	Kidds Beach
				Natal			
Jan '71	36	22	19	65	-	?	Kosi Bay (o)
Sept '70	-	-	61	11	-	-	Tinley Manor
Oct '70	-	-	65	19	-	-	Tinley Manor
Nov '70	-	-	45	21	-	-	Tinley Manor
Dec '70	-	-	25	46	-	-	Tinley Manor
July '72	19	13	35	15	31	-	Tinley Manor
July '72	-	-	11	11	22	-	Umgababa (c)
May '73	22	11	19	30	15	-	Umgababa (c)
July '72	3	-	16	5	30	4	Umzimai (o)
July '72	-	-	43	21	14	81	Shelly Beach (c)
July '72	-	-	-	-	50	84	Ramsgate (o)