CONTRIBUTIONS TO THE ECOLOGY OF THE ANOMURAN MUD PRAWN *UPOGEBIA AFRICANA* (ORTMANN)

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CONTENTS

	Page
INTRODUCTION	2
SECTION A: DISTRIBUTION	4
Influence of temperature	7
Influence of salinity	12
Conclusions	13
SECTION B: BIOLOGY OF A POPULATION IN THE KOWIE ESTUARY	14
Introduction	14
Temperatures in the Kowie Estuary	17
Salinities in the Kowie Estuary	27
Distribution of Upogebia on the shore	29
Burrows	31
Feeding	36
Size composition and growth	40
Breeding cycle	52
SECTION C: EXPERIMENTAL STUDIES	
Temperature	58
Salinity	90
Moulting at low salinity	110
Interaction between temperature and salinity	117
Respiration	126
Effect of temperature on respiration	142
Effect of salinity on respiration	146
Respiration at low tide	152
Respiration at low oxygen tensions	159
SECTION D:	
PARASITES OF UPOGEBIA AFRICANA	164
UPOGEBIA CAPENSIS AND THE VALIDITY OF UPOGEBIA AFRICANA	175
DISCUSSION	183
ACKNOWLEDGEMENTS	193
REFERENCES	194

INTRODUCTION

Estuarine ecology in South Africa has progressed in two distinct stages. The first of these was a necessary descriptive phase which documented the general distribution of estuarine animals and recorded the physical conditions within estuaries. This phase has been carried out by the Zoology Department of the University of Cape Town which has made a series of ecological surveys of southern African estuaries. These surveys have provided a vast amount of valuable information which was utilised by Day (1964) to state some general conclusions about estuarine faunas. The most important of these conclusions is that most of the estuarine fauna is really a quiet water fauna which also occurs in sheltered non-estuarine water.

The information gained in this first stage is necessarily general and it can only indicate overall trends or reveal major features of distribution. Further estuary surveys are not justified unless they deal with unique conditions. It is at this point that the second phase of estuarine ecology becomes necessary. This phase involves a detailed investigation of individual species or particular problems.

The present investigation falls into this second stage of estuarine ecology and was designed to extend our knowledge of the anomuran mud prawn Upogebia africana (Ortmann). The general estuarine surveys have shown that U. africana is a common inhabitant of many estuaries and sheltered bays along the southern African coast from Langebaan on the West coast to Inhambane on the East coast. However these surveys only revealed and could not explain anomalies in its distribution such as its apparent absence

from closed estuaries and from estuaries in the tropics. In addition it was not even certain whether this abundant and widespread animal should really be considered a valid species distinct from a common West Coast prawn Upogebia capensis (Krauss).

It was felt that a study of an estuarine species should be based upon a sound knowledge of its distribution, population structure and habitat. Knowledge of the habitat must be gained by studies in the field to establish which facets of the environment are of importance to the species. It was decided on the basis of field observations that temperature and salinity are of prime importance in limiting the distribution of U. africana and a detailed laboratory study was therefore made of the tolerance of U. africana to these two physical factors. The results of laboratory experiments together with field observations were finally used to interpret the ecology of the species.

Most of present day knowledge of crustacean ecology has been gained from a study of European and North American animals and information about southern hemisphere species has lagged behind. It is hoped that the present study will contribute to a wider understanding of Crustacea and that it will lead to further more advanced research on South African marine and estuarine animals.

SECTION A: DISTRIBUTION

The geographical distribution of *U. africana* around the southern African coast has been determined by a study of the published records as well as by visits to numerous estuaries and bays. *U. africana* has been found at the following places: (See also map figure 1)

Locality	Nature of Locality and Authority
Langebaan Lagoon	Sheltered arm of the sea. Barnard (1955), Day (1958), Hill (present investigation).
Gordon's Bay	Sheltered area of coast. Barnard (1950), Hill (present).
Uilenkraal's estuary	Open estuary. Siegfried (1962).
Breede River estuary	Open estuary. Barnard (1950), Hill (present).
Gouritz River estuary	Open estuary. Hill (present).
Groot Brak River estuary	Open estuary. Hill (present).
Knysna estuary	Open estuary. Barnard (1950), Day et al (1952), Korringa (1956), Hill (present).
Keurbooms Lagoon	Open estuary. Barnard (1950), Hill (present).
Zwartkops River estuary	Open estuary. Barnard (1950), Macnae (1957), Hill (present).

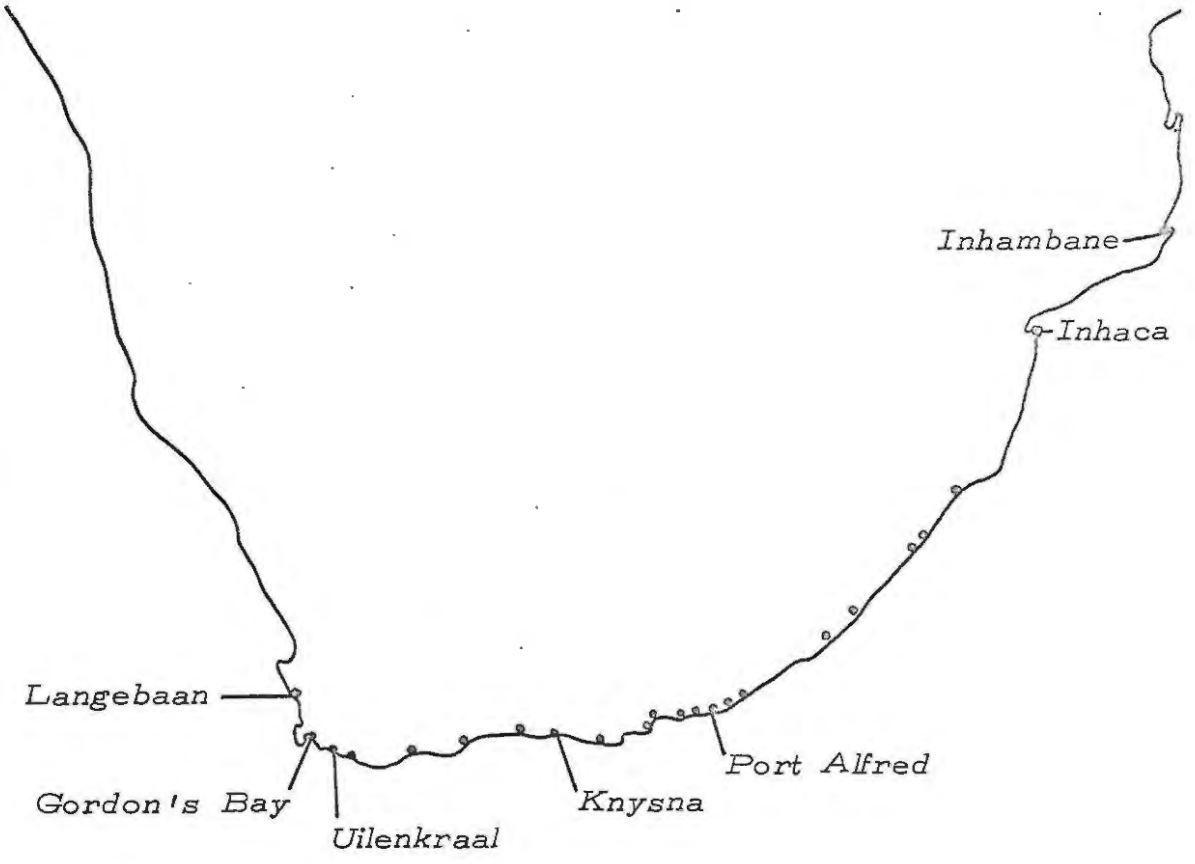


Fig 1. Sketch map of southern Africa showing places (•) where U.africana has been found. Names refer to places mentioned in the text.

Sundays River estuary	*Open estuary. Barnard (1955).*
Bushman's River estuary	*Open estuary. Hill (present).*
Kariega River estuary	*Open estuary. Hill (present).*
Kowie river estuary	*Open estuary. Hill (present).*
Keiskama River estuary	*Open estuary. Barnard (1955).*
Bashee River estuary	*Open estuary. Macnae (1963).*
Umngazana estuary	*Open estuary. Macnae (1963).*
Umtata estuary	*Open estuary. Macnae (1963).*
Umkomaas estuary	*Open estuary. Day (1964).*
Durban Bay	*Sheltered bay. Day and Morgans (1956), Macnae (1963).*
Umlalazi estuary	*Open estuary. Macnae (1963), Hill (1966).*
Richard's Bay	*Open estuary. Macnae (1963).*
Inhaca Island	*Mangrove swamps on sheltered shore. Macnae & Kalk (1958).*
Inhambane, Morrumbene estuary	*Mangrove swamps. Barnard (1955).*

All the above records are from only two habitats, either open estuaries or sheltered bays or inlets. Day (1964) has pointed out that many so called estuarine species are also found in sheltered bays. He concluded that many animals found in estuaries are actually quiet water species. U. africana appears to fall into this category, since apart from estuaries it occurs in sheltered bays such as Langebaan Lagoon and

even protected parts of the sea coast, such as at Gordon's Bay.

Brown (1953) recorded U. africana from the Kleinmond estuary in the eastern Cape, this is a blind estuary. However Brown pointed out that U. africana was never found in burrows, only wandering over the surface of the bottom and he therefore suggested that Upogebia does not normally occur in the estuary but is put in by anglers discarding bait.

Examination of the published records listed above as well as observations made personally on visits to most of the areas inhabited by U. africana indicate that it is only found in areas of either fine mud (most estuaries), fine mud mixed with coarse gravel (part of Keurboom's estuary), fine sand (Langebaan Lagoon), or even in crevices filled with mud and shelly grit (Gordon's Bay). Nowhere was it found in coarse sand. Similarly Day et al (1952) recorded that in Knysna estuary, Upogebia was abundant wherever sandy mud occurred, but that where the bottom changed to clean sand it was absent.

Prawns kept in the laboratory in aquaria failed to construct burrows in clean beach sand. They managed to excavate a shallow depression but the sides continually collapsed. After a few hours the prawns abandoned attempts at burrowing and swam or walked around. Thus it appears that U. africana requires fine sediments in order to construct

a burrow. This probably explains its occurrence in quiet waters since in areas exposed to wave action, the substratum is either rocky or composed of clean loose sand.

The influence of temperature on the coastwise distribution of U. africana.

The only locality on the West coast where U. africana has been recorded is Langebaan Lagoon. Day (1958) recorded winter temperatures of 13.8°C and summer temperatures of 14.7 - 18°C in the seaward parts of the lagoon which is much warmer than in the sea.

On the south east coast U. africana occurs in the Knysna lagoon where temperatures have been recorded for five years by the Oyster Research Unit. They show a summer average of 22 - 24 °C and a winter average of 14 - 16 °C. Hill (1966) recorded U. africana from the Umlalazi estuary on the east coast. He reported a summer average of 25 - 26°C and winter average of 17 - 20 °C. Unfortunately no records are available for temperatures from Inhaca or Inhambane, the most northerly recorded limits of U. africana. However on 27th January 1967 a series of temperatures were taken in the Kosi estuary which is 100 km south of Inhaca. The lower reaches of the Kosi estuary where the temperatures were taken, is

characterised by large expanses of open sandbanks which are only covered at high tide. Dense mangrove swamps border the lower reaches. U. africana does not occur in the estuary.

Temperatures were taken in three areas. Firstly in water over sandbanks, secondly in channels in mangrove swamps and thirdly in shallow water which was heavily shaded by mangroves. The day on which the temperatures were recorded was hot and cloudless with a light breeze. The sea temperature in the breaker zone was 28.5°C.

Time	Open shallows	Swamp channels	Shade of mangroves
1100	34.5	38.5	-
1130	36.3	40.9; 39.0; 43.0	28.0
1200	38.1; 39.2	39.9; 40.2	31.2; 29.2

Water in the open shallows did not heat up to the same extent as water in the channels in the swamps. This was probably a result of the breeze blowing over the open shallows. The dense mangroves effectively cut off the breeze from the water in the swamps. However in the dense shade of the mangroves temperatures were lower than elsewhere.

Professor J.H. Day has informed me that Upogebia from Inhambane were found in the mud amongst dense mangroves. Thus Upogebia at Inhambane inhabits an area which was shown at Kosi to be the coolest part of the estuary.

The highest temperatures in which U. africana has been found to live in the field, are in a heated pond at

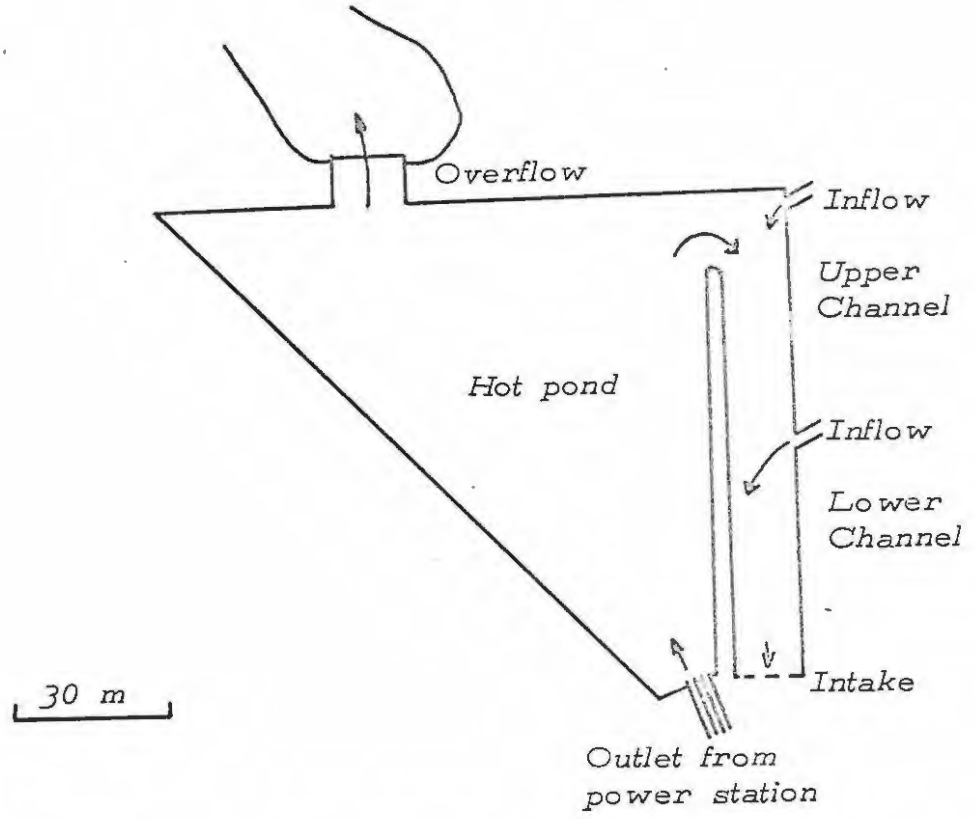


Fig 2: Sketch map of the Knysna Power station cooling pond. Arrows show direction of water currents.

Knysna. The Knysna power station on Thesen's island uses sea water in its heat exchangers. This heated sea water is circulated in a cooling pond shown diagrammatically in figure 2. The average depth of the pond is 0.5 metre and the bottom is muddy sand. Along one side of the pond a mixing channel leads to the power station intakes. Sea water from Knysna estuary is pumped through an adjoining pond containing commercial oysters and then enters the mixing channel halfway along its length. There is also a slow leakage of water from the oyster pond into the end

of the mixing channel furtherst from the power station intake. Heated water from the power station is returned to the main pond. Although the inflow of water from the oyster pond is strong, it is less than the amount of water used by the power station, the result is that much of the water in the pond is continually being recirculated.

The water temperature in the pond is affected by two main factors. Firstly the temperature of the sea water entering from the oyster pond, and secondly the temperature of the power station effluent. Temperatures have been recorded for the past five years in the oyster pond. Normal summer temperatures are in the region of 22 - 24 °C whilst winter temperatures are 14 - 16 °C. The output of heated water from the power station varies according to electricity demand. During the day the effluent is as much as 15 ° above intake water temperature. At night and over weekends the temperature rise is only about 8 °. The result is that the ponds have eight hours of high temperatures each day during the working week. The rest of the time the temperatures are moderate although always higher than those in the estuary.

Because of the design of the pond and the addition of cool sea water at two points, there are three distinct temperature zones. Firstly the major part of the pond which only receives water from the power station, this area will be referred to as the Hot Pond (see figure 2). Secondly that part of the mixing channel which receives Hot Pond

water together with a little cool sea water leaking from the oyster pond, this will be referred to as the Upper Channel. Thirdly that part of the mixing channel between the point where oyster pond water enters the mixing channel and the power station intakes, this will be termed the Lower Channel.

Despite the temperature fluctuations it is possible to give a reasonable picture of the temperature regime in each of the three areas. This picture is based upon a series of readings taken in March, April and June 1967. Night temperatures were only taken in April and the magnitude of the changes recorded have been used to estimate night temperatures in March. Because of the occasional occurrence of temperature layering, especially in the Upper Channel all temperatures are from readings taken on the bottom. The temperatures in degrees centigrade are shown in the following table:

Area	March		April		June
	day	night	day	night	day
Sea water	23	23	18	17	14
Heated effluent	35	28	32	25	30
Hot Pond	35	28	30	24	30
Up. Channel	34	27	27	19	24
Low. Channel	27	25	24	18	19

It was decided to utilise counts of the number of holes in the bottom as an indication of the population density of Upogebia. Other animals which make holes similar to Upogebia for example Callianassa or Cleistostoma do not occur in the pond and so at least the overwhelming majority

of holes are made by Upogebia. A square frame with 0.5 metre sides was thrown into the pond and the number of holes enclosed by the square were counted. This was repeated 12 times in each of the three areas mentioned above as well as in the transition zone between the Upper Channel and the Hot Pond. The arithmetic mean and standard deviation of the number of holes in each area is shown below:

Area	Mean	Std. Dev.
Hot Pond	0	0
Transition zone	1.5	1.5
Upper channel	18	1.0
Lower channel	62	1.5

Apparently the temperatures in the Hot Pond are too high for Upogebia, however the slightly lower temperature regime in the Upper channel is associated with a fairly dense population. The cooler waters of the Lower channel have the highest population. The results indicate that U.africana is tolerant of fairly high temperatures but that it cannot survive frequent exposure to temperatures between 28 and 35°C.

The influence of salinity upon the distribution of U.africana

There are few published records of U.africana living in low salinity. Day et al (1952) recorded Upogebia at Westford Bridge in the Knysna estuary. Salinities at Westford bridge drop to 4.4 - 5.4°/oo after rain but generally average 14 - 16°/oo. In Durban Bay, Day

and Morgans (1956) found Upogebia living in the Sanctuary where salinities varied from 26 to 34 °/oo.

Most South African estuaries are subjected to periods of flooding during which salinities drop to extremely low values. For example Korringa (1956) reported salinities down to 3 °/oo in the lower reaches of the Knysna estuary after heavy rain.

Clearly U. africana is able to live in dilutions of sea water but the lower limits are not clear from the available field data. The data do not indicate to what extent low salinity may limit the distribution of Upogebia in estuaries, if at all.

Conclusions on Distribution

U. africana appears to be a quiet water species which is limited to areas protected from wave action. These areas can be either sheltered bays or open estuaries. It does not normally inhabit closed estuaries.

Temperature seems to be a major factor in determining the distribution around southern Africa. On the east coast high temperatures appear to limit prawns to the coolest part of the estuary. However further north even these parts are possibly too warm and thus U. africana is not found in the tropics. On the west coast cold water may be a limiting factor although this is not certain. The only locality where U. africana has been found on the

West coast is at Langebaan where temperatures are higher than in the sea. U. africana does not occur at Luderitzbucht despite the presence there of sheltered water and mud flats (Mr C. Berrisford, personal communication).

The role of salinity in limiting the distribution of U. africana is not clear from the published records and further work is obviously required.

The population of U. africana living in the Kowie estuary is at the centre of the geographical distribution of the species. Information gained from a study of this population should therefore assist in an interpretation of the distribution of U. africana on both the West and the East coasts.

SECTION B: BIOLOGY OF A POPULATION IN THE KOWIE RIVER ESTUARY

INTRODUCTION

The Kowie river estuary opens into the sea at Port Alfred (33°36'S, 26°54'E). The lower reaches of the estuary have been canalised but above the town of Port Alfred it broadens out and extensive mud flats and salt marshes occur (Figure 3). U. africana occurs in nearly all the intertidal mud banks (Figure 4). A study was made of prawns obtained from the mud banks at Centenary Park and Bell's Reach, and the temperature and salinity changes of the water in this area were recorded.

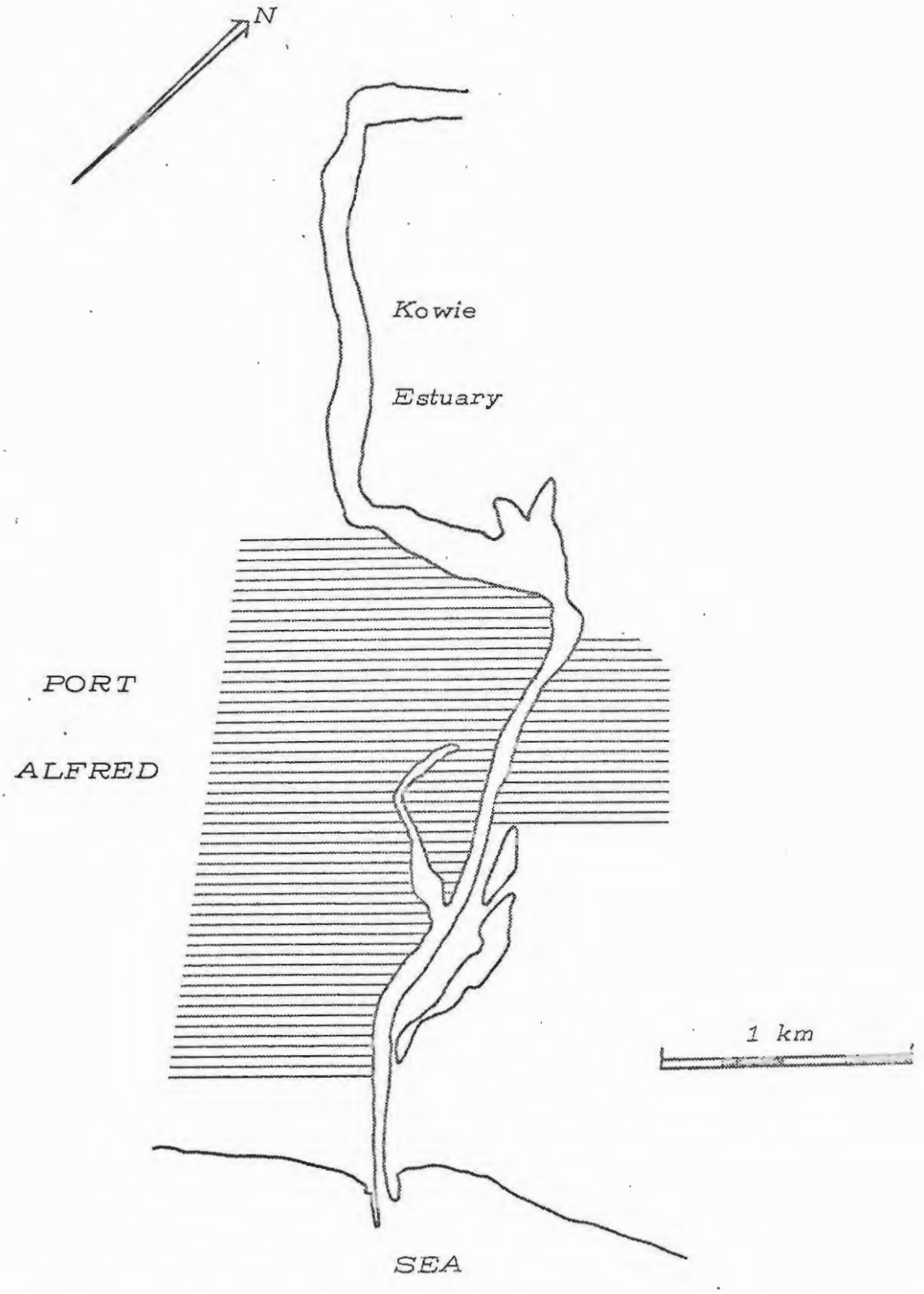


Fig 3: Sketch map of the town of Port Alfred (shaded area) and the lower reaches of the Kowie estuary.

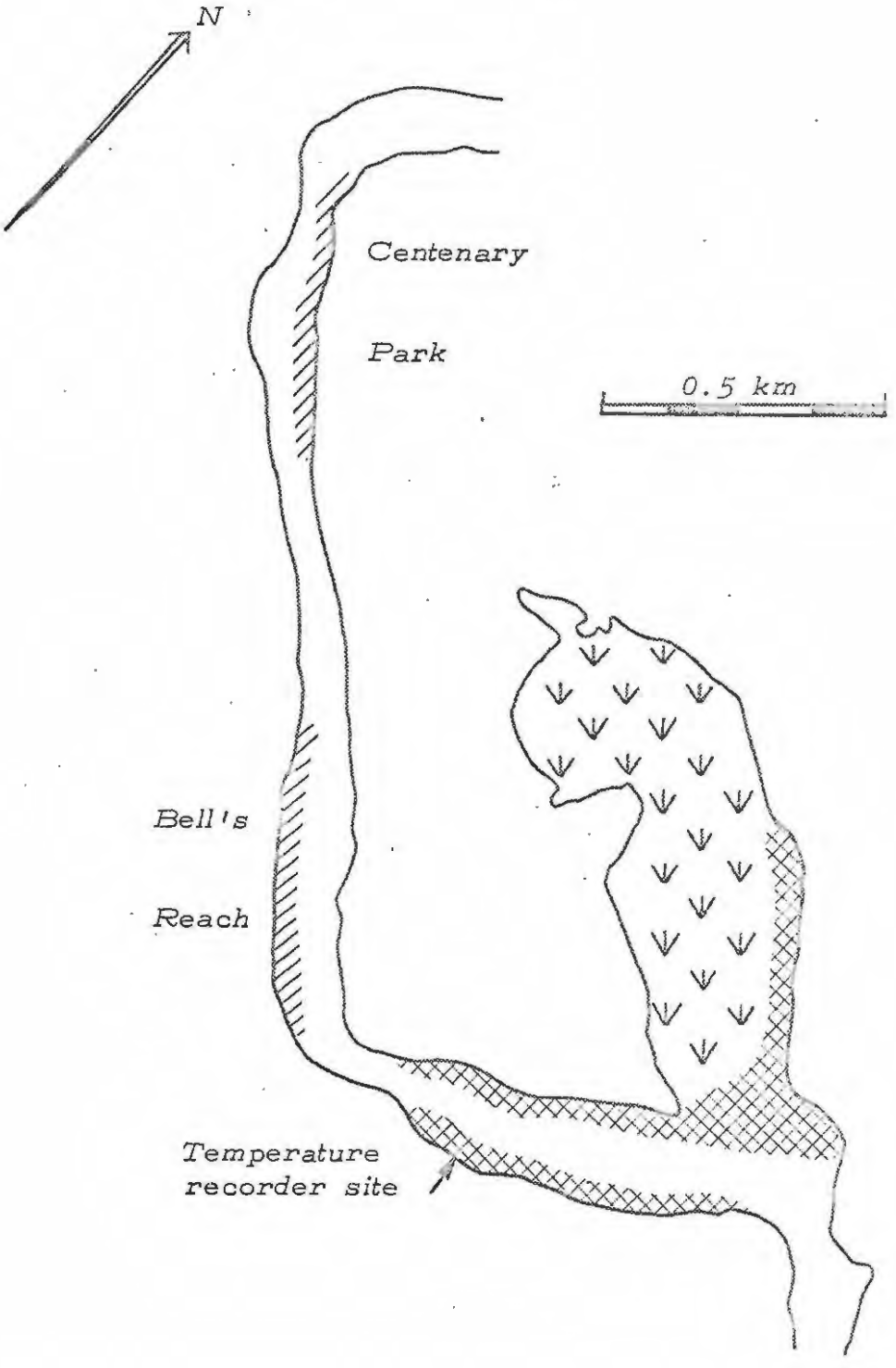


Fig 4: Sketch map of the lower reaches of the Kowie estuary above the town of Port Alfred. Mudbanks inhabited by U. africana are indicated by diagonal lines. Areas in which collecting of U. africana is prohibited are indicated by cross hatching.

Temperatures in the Lower Reaches of the Kowie Estuary

METHODS:

Temperatures in the estuary were recorded continuously during 1967. An Oceanographic Engineering Corporation Hydro Products Model 401 Temperature Monitor was used for this purpose. The thermistor probe was installed on a floating jetty over a bed of prawns 2.5 km from the mouth of the estuary (Figure 4). The thermistor was situated 10 cm below the water surface in order to avoid surface heating or cooling effects. At low tide the depth of water at the thermistor was only 10 - 15 cm; at high tide the depth varied between 1 and 1.5 metres. The temperature monitor was coupled to a Rustrak DC recorder which continuously recorded the temperature on a strip of paper. Although the equipment could run continuously for two months without attention, it was visited every two weeks and a temperature check was made to ensure accuracy.

The equipment was set up in January 1967 and a record was kept for one year. In April the record was interrupted for two weeks following the collapse of the jetty in a storm. During July the probe developed a short circuit and it took several weeks to obtain a replacement.

Temperatures over the mud flats were measured by means of a battery operated thermistor thermometer which

was built in the workshop of the Zoology Department, Rhodes University. The unit had six waterproof probes. The probes were on the ends of leads which enabled temperatures to be measured up to 30 metres from the readout unit.

RESULTS:

The continuous record of temperatures in the Kowie estuary in 1967 showed large daily variations. The variations on a typical summer's day are shown in figure 5. High temperatures clearly coincided with low tide and low temperatures with high tide. The water within the estuary is warmed by the sun and thus temperatures tend to be higher than in the sea. When the tide rises, cool sea water floods in and temperatures drop to values comparable to those in the sea.

The record of a typical winter's day is shown in figure 6. In winter high temperature corresponds to high tide and low temperature to low tide. This indicates that in winter the temperature of the estuary water drops below that of sea water, almost certainly due to cold conditions inland. In this case relatively warm sea water enters the estuary at high tide. Thus temperatures in the lower reaches of the Kowie estuary are clearly related to tides. Sea water only penetrates about 6 km up the Kowie estuary at high tide and thus temperature fluctuations due to sea water entering and leaving the

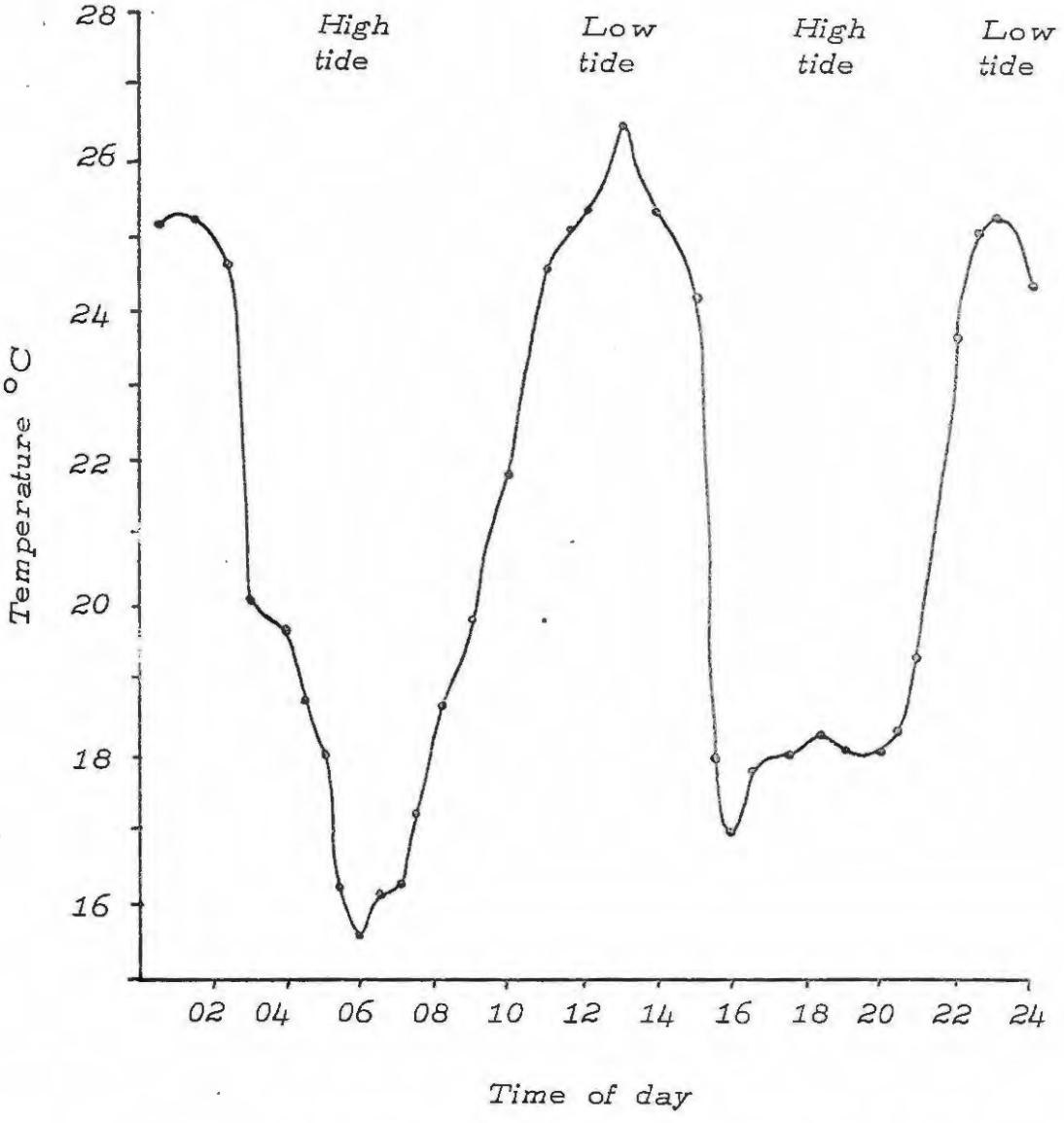


Fig 5: Temperatures recorded in the lower reaches of the Kowie estuary on a day in summer (27th January 1967).

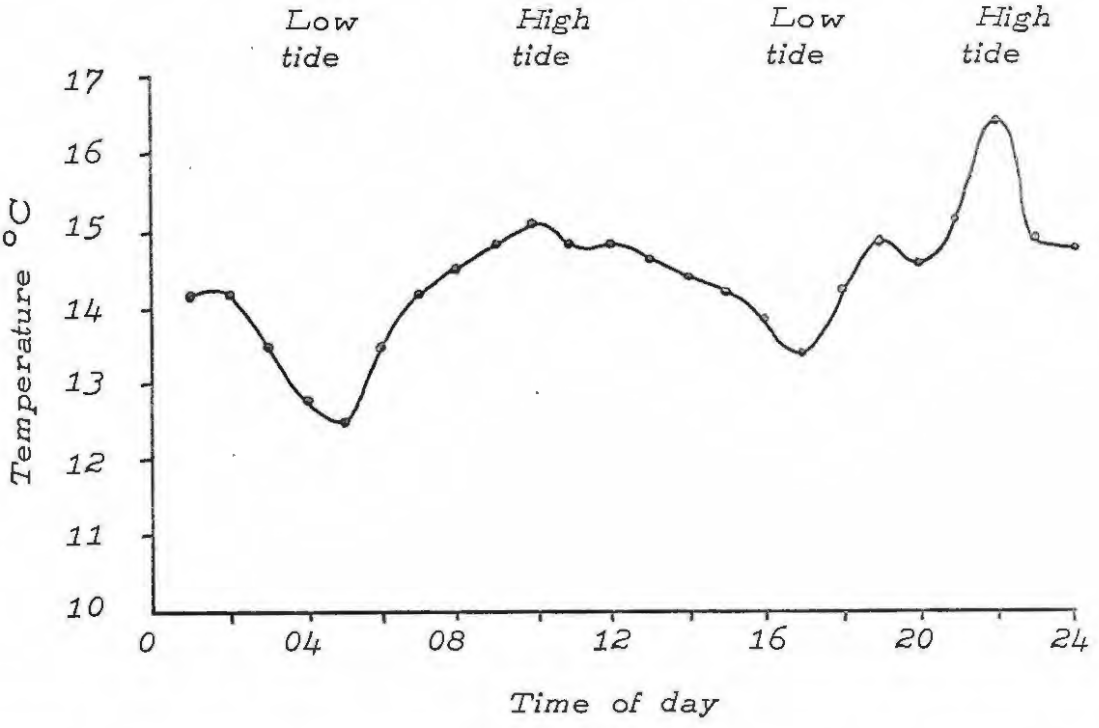


Fig 6: Temperatures recorded in the lower reaches of the Kowie estuary on a day in winter (16th June 1967).

estuary are limited to the lower reaches. In the upper reaches temperatures are probably more uniform on a daily basis although there may be a greater difference between winter and summer means.

The mean daily temperatures based on five readings at approximately five hour intervals for a typical week in summer and another in winter are shown in figures 7 and 8 together with the daily maximum and minimum temperatures. It must be emphasized that these weeks were

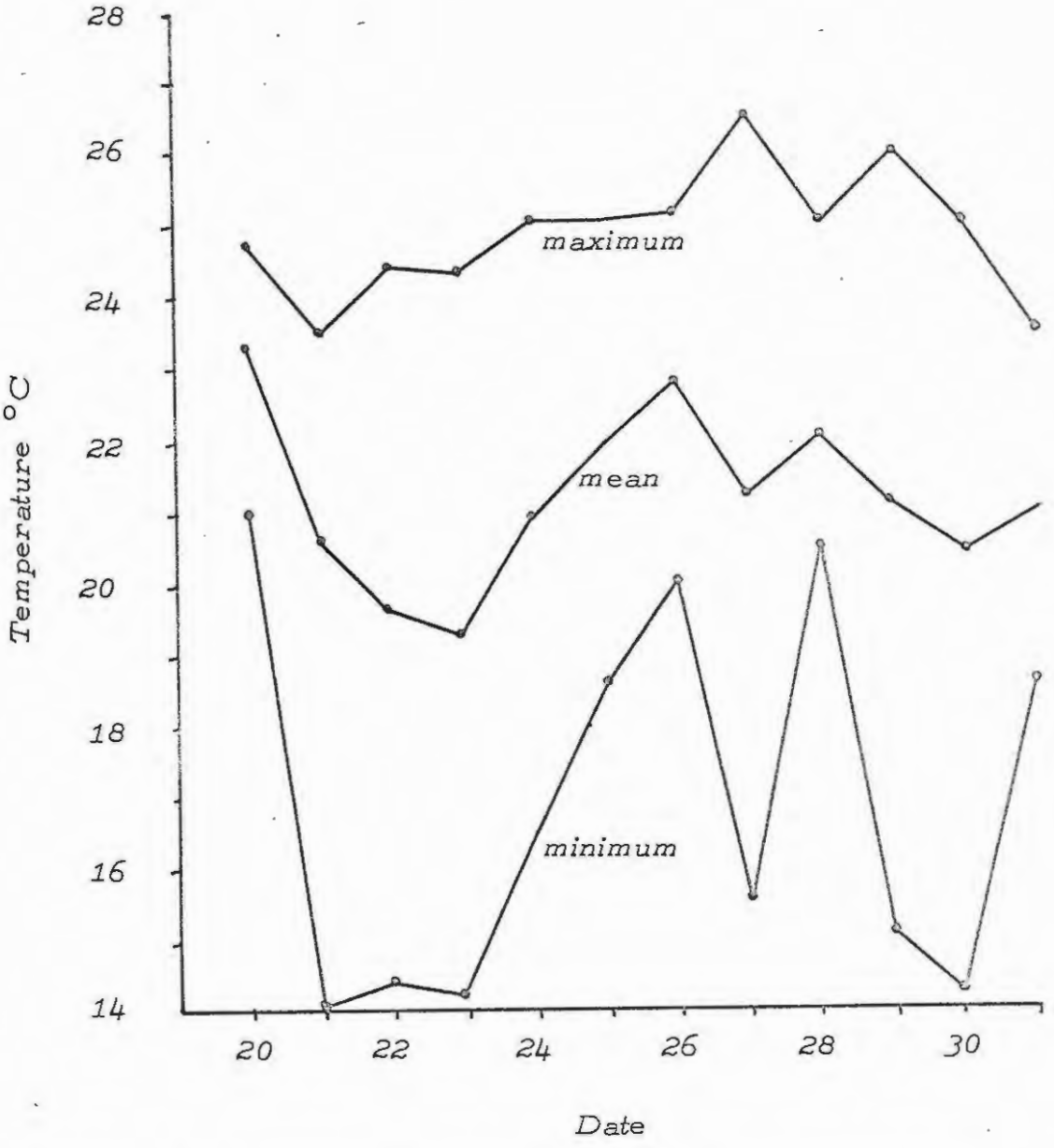


Fig 7: Daily maximum, minimum and mean temperatures recorded in the lower reaches of the Kowie estuary in a week in summer (January 1967).

not exceptional but reflected typical summer and winter conitions. As stated above low tide reflects 'estuary' temperatures whilst high tide reflects sea temperatures. The sea temperature in winter does not change as rapidly as it does in summer. An example of the summer

fluctuation can be seen in figure 7 in which sea temperature as reflected by high tide estuary temperature dropped by 7°C from 20th to 21st January. The fluctuating sea

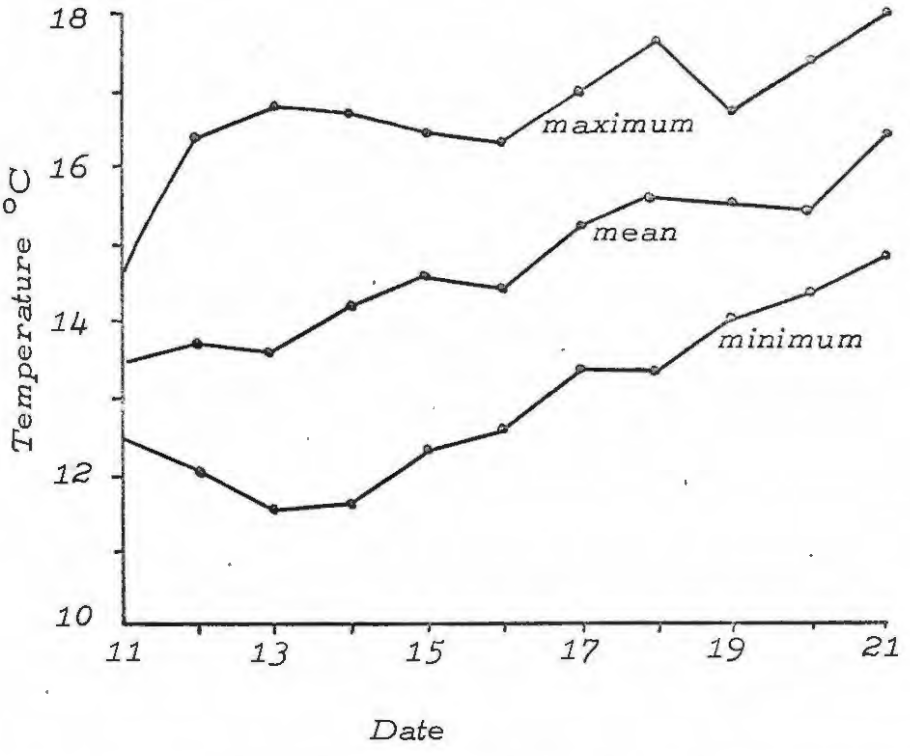


Fig 8: Daily maximum, minimum and mean temperatures recorded in the lower reaches of the Kowie estuary in a week in winter (June 1967).

temperatures reflect the complicated hydrological conditions off the south eastern coast of southern Africa. Unfortunately extremely little hydrological work has been done in this particular area.

Utilising the data given by Orren (1964) it appears that the Agulhas current in the vicinity of Port Alfred is usually 16 - 32 km off the coast. The current temperature in this region is 21 - 23°C. Inshore of the current there is

a strip of cooler water. Shannon (1966) points out that in general on the south east coast the inshore water is thermally stratified with a thermocline at 40 metres. Surface temperatures are in the region of 14 - 18 °C in winter, whilst in summer they are about 18 - 23 °C. Below the thermocline the water temperature drops to 9 - 10 °C. In summer upwelling is common along the south east coast. The cause of this upwelling is complex but a main contributing factor is the strong south easterly wind. This wind induces surface drift and if it blows continuously for several days, causes transport of deeper water. Due to Corioli's force these water movements are not parallel to the wind direction but are deflected to the left (Sverdrup et al 1942). Thus in summer there is an offshore transport of water. This water is replaced by upwelled water which causes the temperatures at the surface to drop rapidly. For example Day (1951) reported a drop in sea temperature at the mouth of the Knysna estuary from 21.8 ° to 11.5 °C in a single day.

This explanation of the fluctuating sea temperatures is possibly an oversimplification since the actual picture is undoubtedly extremely complex. But it does provide an explanation of the sharp decreases in temperature as shown in figure 7.

In order to obtain an overall picture of general temperature conditions in the Kowie estuary in 1967 a weekly

mean was calculated on the basis of the daily means. The highest and lowest daily mean was used as the mean maximum and minimum temperature for the week. The resulting weekly maximum, minimum and mean temperatures in the lower reaches

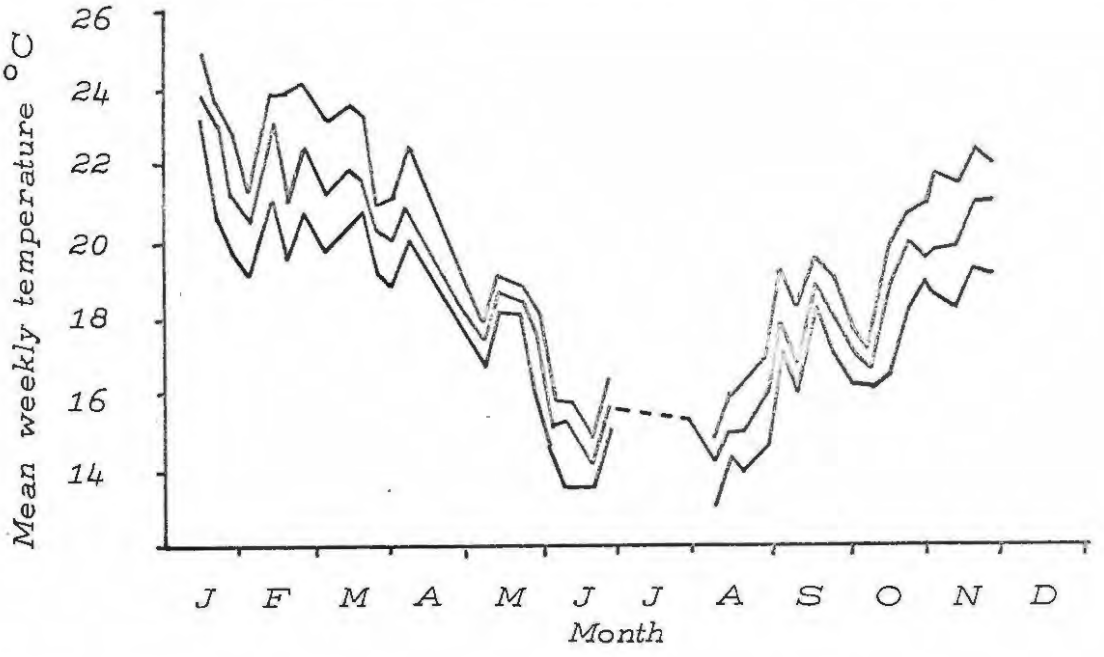


Fig 9: Weekly maximum, minimum and mean temperatures recorded in the lower reaches of the Kowie estuary in 1967.

of the Kowie estuary are shown in figure 9.

There was a clear temperature cycle in the estuary in 1967. Summer temperatures (November - March) are high, 19 - 24 °C. Winter temperatures (June - August) are moderate, 13 - 16 °C. Autumn (April - May) and spring (September - October) are seasons of temperature change.

On a hot summer's day there is a noticeable warming of shallow water in the estuary. The most striking

case of this warming was recorded in the water over a mudflat in February 1966. The surface temperature in the shallows a few centimetres from the shore was 34.5 °C. Two metres from the shore the surface temperature was 32.0°C. The surface temperature 4.5 metres from the shore was 30.2 °C.

The characteristics of this type of heated shallow water were investigated more closely on a rising spring tide on 10th March 1966. Five thermistor probes were placed at intervals over the surface of a mudflat at Centenary Park, (Map figure 4). As the tide rose it succesively covered each probe. The water temperature at each probe was taken at five minute intervals from the time when the probe was first covered by the rising tide. The total observation time was four hours.

The temperatures recorded at each probe are indicated in figure 10 in which the horizontal distances of the probes from the top of the intertidal zone are shown next to each temperature curve. The figure shows that there is a narrow band of heated water which moves up the mudflat as the tide rises. This band of water gradually cools down near the top of the shore. Immediately behind the band the water is several degrees cooler, and as the tide rises this causes a sudden drop in temperature.

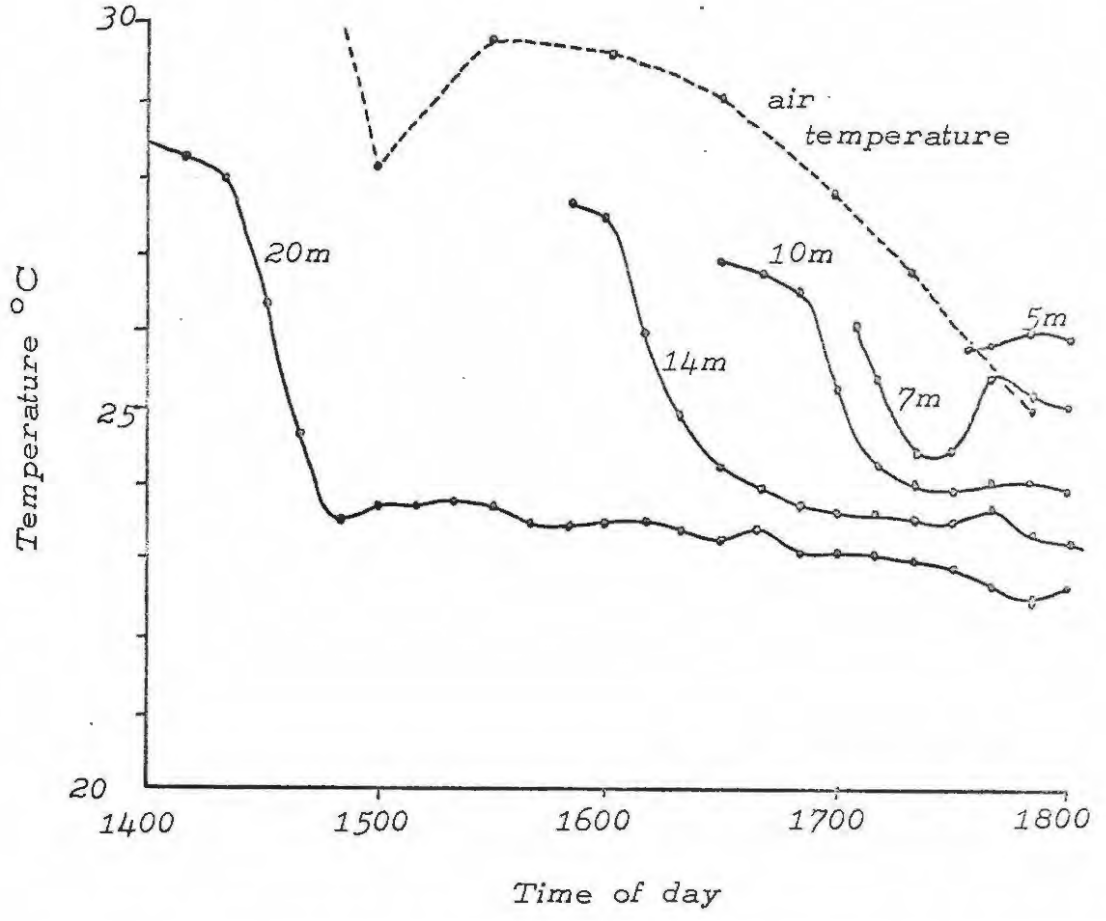


Fig 10: Water temperatures recorded at a series of thermistor probes on a mudflat at Centenary Park on 10th March 1966. The horizontal distance of each probe from the top of the intertidal zone (HWOS) is shown next to each temperature record. The air temperature is indicated by a dotted line.

Salinities in the lower reaches of the Kowie river estuary.

METHODS:

Salinity samples were taken at irregular intervals in the Kowie estuary by means of a Friedinger water sampling bottle operated from a boat. The samples were titrated using Harvey's modification of the standard Mohr method as described by Barnes (1959). The technique is not as accurate as the standard Mohr titration but the latter method is itself not completely accurate in dilutions of sea water. The Harvey modification gives results accurate to 0.1 °/oo which is adequate for estuarine water. The silver nitrate solution used for titrations was standardised against standard sea water obtained from the Hydrographic Laboratories in Copenhagen.

RESULTS:

The rainfall and flow of the rivers of the Eastern Cape is extremely irregular. Most of the year the rivers have a small flow which is slightly augmented by the autumn and spring rains (March - April and October). The result is that the majority of Eastern Cape estuaries have salinities approaching that of sea water throughout their length. The Kowie river estuary is a typical example of this condition. Except after heavy rain the salinity in the lower reaches is always above 33 °/oo.

Macnae (1957) gave figures to show that in many

years the total annual rain in the Eastern Cape may fall in a few days. Much of this rain is lost to the land as run-off into the rivers which come down in flood for a short period. A large volume of silt laden fresh water enters the estuary and may flush out the system resulting in extremely low salinities. An example of this flooding was recorded in June 1967 in the Kowie river estuary.

On 27th June, 99 mm of rain fell at Grahamstown in the Kowie river catchment. On the following day a further 26 mm was recorded. On the afternoon of the 27th June the level of the estuary rose to high spring tide level and remained there for two days. During this period there was no apparent tidal effect in the estuary and water ran out to sea continuously. On the third day the level dropped and normal tides resumed. Water samples for salinity determination were collected on the surface and at a depth of 2.5 metres at points in the estuary on 29th June and again on 4th July, that is 2 days and 8 days after the commencement of flooding. The salinities recorded are shown in table 1.

Although two days after the start of the flood the salinities were still extremely low, after eight days they had risen considerably. The rise was especially marked at high tide in deeper water and extensive salinity layering was evident. Animals living in the lower 7.5 km of the estuary were thus not exposed to low salinities for long. Animals in the higher sections of the estuary would have to contend

with reduced salinities for at least two weeks.

Table 1: Salinities (in parts per thousand) in the Kowie river estuary after heavy rain in the catchment.

Distance from mouth	Depth in metres	29th June (no tides)	4th July low tide	4th July high tide
2.5km	0	1.1	7.0	12.8
	2.5	2.4	10.6	31.1
3.5km	0	-	5.9	8.7
	2.5	-	13.0	28.3
5.0km	0	0.5	3.5	3.0
	2.5	0.5	4.3	12.7
6.5km	0	-	1.1	3.0
	2.5	-	3.3	8.7
7.5km	0	-	0.7	2.9
	2.5	-	0.9	2.9

Distribution of U.africana on the shore

In the Kowie estuary U.africana is found in the subtidal as well in the intertidal mud flats. Macnae (1957) has shown that in the Zwartkops estuary the vertical distribution of U.africana is determined by the depth of the water table and that the numbers fall off where the water table is more than 15 cm below the surface. The same is true of animals in the Kowie estuary but an interesting additional factor controlling their subtidal distribution was shown to be substrate composition. In figure 11 the distribution of Upogebia holes along a traverse perpendicular to the shore is shown. These counts were obtained by Mr R.E. Boltt and myself using underwater breathing apparatus.

A rope was laid from the bottom of the intertidal zone into the centre of the estuary at the site of the temperature recorder (figure 4). A counting frame with 0.5 metre sides

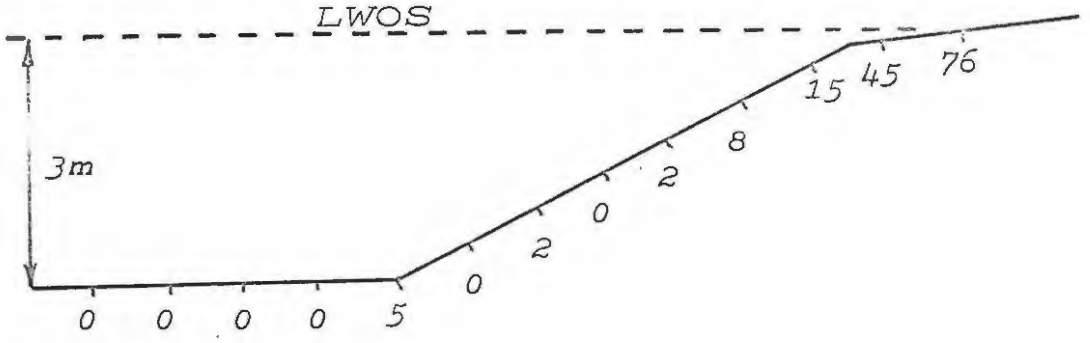


Fig 11: Diagrammatic cross section of part of the Kowie estuary at the site of the temperature recorder (see figure 4) showing the number of Upogebia holes per 0.25 sq metres. The depth of water in the channel was 3 metres. The counts were started at the level of low water of ordinary spring tides (LWOS).

and divided into four equal squares was placed on the bottom alongside the rope and the number of holes in each square was counted. This was repeated at 1 metre intervals.

Although prawns do live below low water mark, the number is reduced and apparently no prawns live on the bottom of the channel. This bottom is composed of muddy sand. A sample of the substrate was collected and put into an aquarium in the laboratory. The substrate was covered with sea water and three prawns were put into the aquarium. The prawns began to burrow but when the burrows reached a depth of 5 to 6 cm the sides tended to collapse. Overnight all the prawns abandoned attempts at burrowing and the holes

filled up. Prawns put into aquaria containing mud rapidly constructed burrows and did not abandon them.

The bottom of the channels of the Kowie estuary are exposed to continual strong tidal currents, so rapid that even at neap tides a diver has to hold onto a rope to maintain position. These currents stir up the bottom and carry away fine particles resulting in a sandy substrate which is apparently not suitable for the construction of burrows. Any prawns that did manage to start a burrow at slack tide would probably have it filled in when the tide began to flow. Clearly U. africana is limited by the substrate. Since the nature of the substrate is largely determined by currents it can only inhabit sheltered areas such as the intertidal zone or backwaters and creeks.

Burrows

Macginitie (1930) described the method of constructing burrows by U. pugettensis. His description applies equally well to U. africana. The chela are used for loosening the mud which is collected by the 'basket' formed by the long setae on the base of the chela and on the first walking legs (Figure 12). The mud is then carried up to the entrance of the burrow and pushed out. Alternatively mud may be used for patching the walls or closing up a disused tunnel. In these cases the mud is kneaded into place using the distal segments of the first

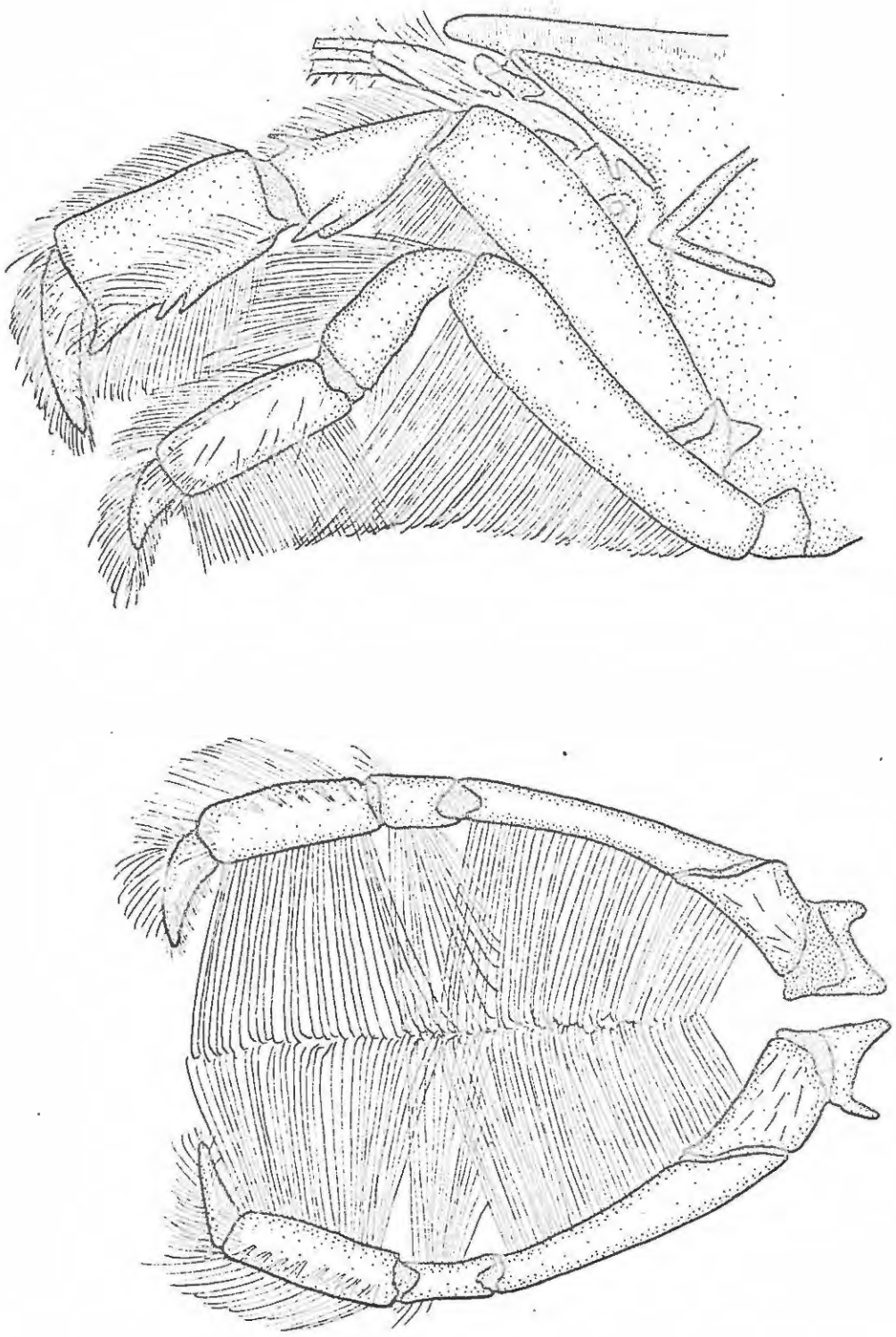


Fig 12: The anterior end of U. africana showing the 'basket' formed by the setae on the chela and the first walking legs. The upper sketch is a lateral view showing the chela and first walking legs. The lower sketch is a ventral view of the first walking legs.

and second walking legs.

U. africana burrows in the Kowie estuary have a vertical or near vertical shaft which goes down into the mud for about 45 cm. This depth is extremely variable, some burrows only going down for about 20 cm whilst others have been found to extend to at least 60 cm depth. At the bottom of the vertical shaft there is a short horizontal passage which varies in length from a few cenitmetres to 20 cm and possibly even more. At the end of the horizontal passage a second vertical shaft communicates with the surface. Rarely there may be three shafts to the surface. At one or two points in the burrow there is an enlargement which is used by the prawn for turning around. Elsewhere the burrow is only slightly larger than the prawn. Observations in the laboratory coupled with impressions gained in the field indicate that the burrow is not a static structure, it is continually being altered or extended.

Extensions to the burrow are often abandoned or filled in. If the burrow is being extended there is an extra blind passage - the extension, which usually opens from the horizontal part of the burrow.

The total length of the burrow varies from 50 to 150 cm. Prawns with a total carapace length of 15 mm have a burrow about 10 mm in diameter. The volume of the burrow of an average sized prawn (15 mm total carapace) is thus in the region of 80 - 120 ml. Field measurements of

volumes gave results varying from 50 to 140 ml. There was no way of ascertaining whether all the water in the burrow was sucked out and so the results must be treated with considerable reserve, but in general it appears that a range of 80 to 150 ml is a reasonable estimate of burrow volume. If the water table is deep down then the volume of burrow water at low tide will be substantially less than the burrow volume.

Upogebia irrigates its burrows by means of its pleopods. The current produced can be seen in shallow water as a stream of muddy water emerging from the mouth of the burrow. In the laboratory, prawns kept in aquaria containing mud occasionally constructed sections of the burrow against the transparent walls of the aquaria. This made it possible to see the water inside the burrows. If a few drops of sea water containing a little Rhodamine B dye were introduced at the inhalent opening of a burrow, the coloured water could be followed as it was pumped through the burrow. Movements of the coloured water indicated that the entire column of water in the burrow moved when the prawn was pumping. The speed of water movement could be determined by timing the flow of the coloured water over a distance of 10 cm inside the burrow. An average speed was calculated on the basis of at least five and usually about eight observations on a particular burrow.

It was found that the size of the prawn did not affect the current speed although it would obviously determine the volume of water which was pumped. The type of activity did have a considerable effect on current speed. Normal irrigation of the burrow involving a slow pumping of water, usually for filter feeding, resulted in speeds of 1.7 to 2.2 cm per second. When the burrow was being constructed or modified, prawns would occasionally create a powerful rapid current which cleared fine mud from the burrow. This action caused speeds of up to 7 cm per second. In the case of an average sized animal of 15 mm total carapace length, these current speeds would result in a flow of 5.4 and 18 litres per hour respectively.

However pumping is not continuous and in the case of rapid pumping the duration is usually only for 20 to 30 seconds. Slow pumping usually lasts for 20 to 30 minutes after which the prawn may clean itself or begin repairs or extensions to the burrow. When prawns are constructing burrows very little time is spent in irrigation. The following times were recorded in the case of a prawn which was extending its burrow:

Work Periods (No irrigation): 2 min 7 sec;
6 min 22 sec; 2 min 52 sec; 1 min 50 sec.

Irrigation periods (Between working):
21 - 23 seconds.

Thus over a period of more than 13 minutes, only one and half minutes was spent in irrigation.

Feeding

Upogebia africana feeds by filtering water which is pumped through the burrow. The feeding mechanism is the same as described for U. pugettensis by Macginitie (1930) and consists of a filtering basket of setae carried on the chela and the first walking legs (Figure 12). The filter is spread across the burrow and all water pumped through the burrow must pass through it. Particles which are caught by the filter are brushed off by the third maxillipedes which transfer them to the mouthparts. On the basis of the volumes noted above an average Upogebia probably filters at least 15 litres of water at each tidal cycle.

Macginitie (1930) stated that U. pugettensis feeds on detritus which it filters from the water. This detritus is composed of rotting vegetation together with a large amount of bacteria and algae. Diatoms are apparently not of importance.

In burrows built against the glass sides of an aquarium U. africana could be seen to filter out fine particles from the water. If large objects are introduced into the burrow and fall onto the filter, the prawns carry them up to the entrance and push them out. Macginitie (1930) tried feeding U. pugettensis pieces of meat but the prawns rejected them. Attempts to feed U. africana with polychaets, either intact small animals or chopped up into pieces failed. Similarly a variety of small planktonic organisms including Betaeus larvae, amphipods and copepods were all rejected.

The food of U. africana was determined by first starving prawns for two weeks in filtered sea water in glass dishes and then putting six into the estuary in glass tubes. The glass tubes were closed at the ends by plastic mesh and were suspended in the water for two hours. At the end of this period the prawns were removed and dropped into 10% formalin. The gut contents were removed and compared with controls which had merely been starved for two weeks. The guts of the controls were empty. The prawns which had been in the estuary for two hours had a mass of fine material in their guts. This fine material consisted of unrecognisable organic debris mixed with a little mud. Ten species of diatoms were identified in the gut contents by Mr C. Archibald. However all the diatoms were present in small numbers. The diatom sizes varied from a maximum of 150 x 20 mu (Pinnularia virides) to a minimum of 30 x 6 mu (Navicula cryptocephala). The small diatoms may have been taken in together with larger particles of detritus.

Schaeffer (1967) investigated the gastric mill of U. africana. The gastric mill of decapods usually consists of a crushing region and a filtering region. Schaeffer found that in Upogebia the crushing region was modified to function as a filter which functioned with a squeezing action. He concluded that Upogebia was not capable of crushing large particles of food but merely of sorting out digested food from mud particles.

When U. africana is feeding a small pile of faecal pellets collects below the animal. These pellets are extremely friable and appear to consist entirely of fine mud particles. If previously starved prawns are put into a dish containing a thin layer of estuary mud they scrape up the surface mud into the filter basket and apparently swallow it. However this action has not been observed in burrows in aquaria. The organic matter which Upogebia apparently utilises as food is probably derived from detritus and from the rich organic growth which occurs on the fine mud particles.

Korringa (1956) suggested that the richness of open estuaries was principally derived from the sea. Sea water entering the estuary on each high tide, floods over mud banks containing large quantities of marine bacteria. The small particle size of the sediments provides an enormous surface area for these bacteria. The bacteria are able to utilise the dissolved or colloidal organic matter in the sea water. Zobell and Grant (1943) according to Korringa found that marine bacteria can convert about 30% of the organic matter around them into bacterial protoplasm and mineralise the remainder. Recent work by Pomeroy et al (1965) has shown that there is a large build up of phosphates in sediments when estuarine water is allowed to flow over them. They ascribed this to utilisation of available phosphates in the water by micro-organisms on the sediments.

Day (1967) has suggested an additional important

effect of the tides in an estuary. He states the following:

> *"As the water of a falling tide seeps into the porous sand, any plankton or suspended organic matter it contains must be caught on the surface like a precipitate on a filter paper. The wet sand banks at low tide must therefore, be covered by a layer of food, and they provide a rich feeding ground for detritus feeders which form the bulk of the estuarine fauna".*

This food source can be utilised by animals which feed directly on the intertidal sediments such as the crabs Uca or Cleistostoma. In addition at high tide currents churn up the fine sediments and make this food source available to filter feeders. Mr A. Genade (personal communication) has found higher growth rates in the muddy waters high up in the Knysna estuary than in the clearer water at the mouth of the estuary.

This is an important result of an estuary being open to the sea. Firstly the supply of nutrients to the micro-organisms which live on the mud and the deposition of plankton. Secondly the stirring up of the fine sediments makes the micro-organisms and detritus available to filter feeders such as Upogebia. It appears reasonable to suppose that a major cause of the absence of U. africana from closed estuaries is because there are no tides in them and therefore the food supply is inadequate.

Size composition and growth

METHODS:

Samples of Upogebia africana used in the present investigation were collected by digging in the mud banks in which they live. This is the method used by bait collectors. Prawns can also be collected by hydraulic pressure. This is usually done by putting a tin upside down over an entrance to a burrow and then suddenly pressing it down into the mud. Air and water is forced down one arm of the burrow and the prawn shoots out of the other arm. At Knysna digging for prawns is prohibited and samples collected there in the course of the present study were obtained by means of a 'prawn pump'. This is merely a modification of the tin collecting method and utilises a piece of piping about 10 cm in diameter and 30 cm in length. The tubing is put over the top of the burrow and a piston is pushed down the tube forcing air and water into the burrow.

Both collecting methods suffer from the disadvantage that juvenile prawns (carapace less than 8 mm long) tend to be overlooked in the mud and muddy water. Attempts to sieve large quantities of mud in order to obtain juveniles were unsuccesful. Without assistance it was not possible to sieve a reasonable amount of mud in the short time available at low tide.

Samples of prawns were collected at Centenary Park (map figure 4) for two years (1965, 1966). They

were obtained by digging at low spring tide at approximately two week intervals. In 1967 samples were collected from the mudflats in Bell's Reach (map figure 4). The collecting area was changed because of the installation of a temperature recorder near Bell's Reach in January 1967. The collection of prawns from near the temperature recorder made it possible to establish whether breeding was related to temperature.

A minimum of 50 but more commonly about 100 prawns were collected on each occasion. If prawns were required for experimental purposes the samples were larger. In 1965 and 1966 a total of 4,600 prawns were collected and measured. The measurement taken was the distance from the tip of the rostrum to the hind margin of the carapace and will be referred to as total carapace length. After collecting and measurement had been in progress for one year, the work of Siegfried (1962) on a population of U. africana in the Uilenkraal estuary (see map figure 1) came to my attention.

Siegfried measured the distance from the posterior margin of the eye socket to the hind margin of the carapace. He referred to this distance as 'standard carapace length', and compared this with total carapace length. He found that there was a linear relationship between the two measurements and that they were directly comparable so that one measurement can be converted into the other. I have used his graph to

convert standard carapace lengths into total carapace lengths in order to facilitate comparison between his results and the present investigation.

A preliminary experiment to determine the growth rate of Upogebia was started in May 1967. Two asbestos cement boxes each 30 cm deep and with a surface area of 30 x 40 cm were filled with estuary mud. This mud had been put through a sieve with 2 mm square holes and than allowed to dry out for 48 hours to ensure that all prawns had been removed or were dead. Twenty measured prawns were put into each box. One box contained prawns with a total carapace length of 13.0 - 13.9 mm and the second, prawns with a total carapace length of 15.0 - 15.9 mm. The boxes were tightly covered with a galvanized steel mesh with openings 4 - 5 mm square and were then sunk into the mud in the intertidal zone alongside the temperature recording probe (map figure 4). The boxes were put down in May 1967.

The holes in the covering mesh were too small to allow the prawns to escape as prawns of 10 mm total carapace length could only just be forced through the mesh. The openings in the mesh were large enough to allow a free exchange of water and it was regularly checked in order to prevent it from becoming clogged with silt or debris.

At the end of October 1967 the mud in the box containing the larger prawns was removed and washed through a sieve with 2 mm square holes. The prawns which

were removed were measured. It is intended to remove the prawns from the second box in May 1968.

RESULTS

The population studied by Siegfried (1962) was undisturbed and was not exploited for bait collection purposes. Siegfried collected monthly samples for a period of one year (March 1955 - June 1960) and examined 4,500 prawns. He compiled size frequency data for the population at Uilenkraal but could find no indication of size groups. Siegfried also carried out an experiment to determine the rate of growth in U. africana. He put six females in the 19 - 19.9 total carapace length class into a wire mesh cage. The cage was buried in the mud of the Uilenkraal estuary for four months over winter (June - September). At the end of this period he found no significant increase in size.

The results of a similar experiment to determine the amount of growth in U. africana in the Kowie estuary are shown in figure 13. Initially there were 20 prawns of total carapace length 15 - 15.9 mm. At the end of five months there were 10 prawns still in this class and 10 in the 16 - 16.9 mm class, indicating a general growth of less than 1 mm. Siegfried found no growth at all over four months. However he used extremely large prawns (19 - 19.9 mm total carapace) and it is well known that growth in large and therefore probably old crustaceans is slow (Teissier 1960).

All the prawns smaller than 15 mm total carapace shown in figure 13, must have entered the box in the five months during which it was in the estuary. No prawn

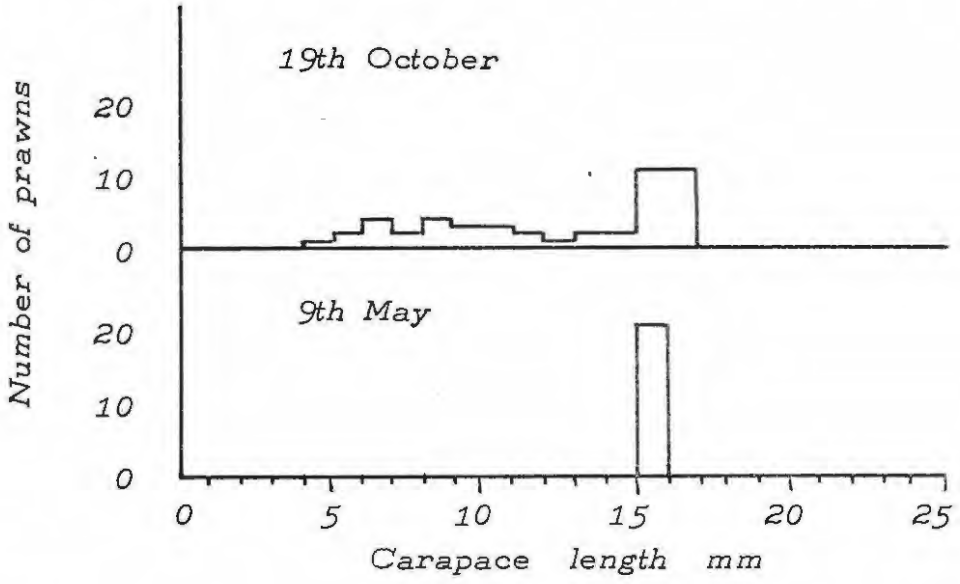


Fig 13: Size frequency analysis of a sample of U.africana put into a screened box in the Kowie estuary on 9th May 1967 compared with a size frequency analysis of the prawns which were removed from the same box on 19th October 1967.

larger than 10 mm total carapace could pass through the mesh and thus the prawns in the 13 - 14.9 mm total carapace lengths must have entered the box at 10 mm or less. If it is assumed that they did so shortly after the boxes were put down, these prawns must have grown by at least 3 to 4 mm in the five months. This is a far more rapid growth rate than was shown by the 15 mm carapace prawns.

The smallest prawns ever found in the mud in the Kowie estuary had a total carapace length of 2 - 2.9 mm.

Thus the prawns in the 6 - 11 mm carapace size range were at least a few months old. These small prawns probably represent a recruitment of juveniles and post larvae to the population in late summer or autumn.

The prawns used in the present investigation were obtained from Centenary Park or Bell's Reach. Both of these areas are exploited by bait collectors. The possible effects of this collection on the population were determined by collecting samples from exploited and unexploited areas. Sixty minutes of digging in an area closed to digging yielded 234 prawns. Seven diggings each lasting 60 minutes in an exploited area gave a mean of 132 prawns per digging with a maximum of 160 and a minimum of 99. It is clear that the exploited area had fewer prawns.

Most of the commercial collecting is done in the intertidal zone in the lower reaches of the estuary. The digging is done in the five or six days over low spring tides by between 10 and 20 diggers. Each digger collects two to four tins of prawns. Counts of prawns in tins gave numbers varying from 50 to 100 with an average of about 80. These figures indicate that between 5,000 and 48,000 prawns are collected from the Kowie estuary every fortnight. The numbers vary enormously and depend upon factors such as weather and demand for bait.

A comparison was made of the size frequency of samples of prawns from exploited and unexploited areas together with samples of bait collected in September - October 1966.

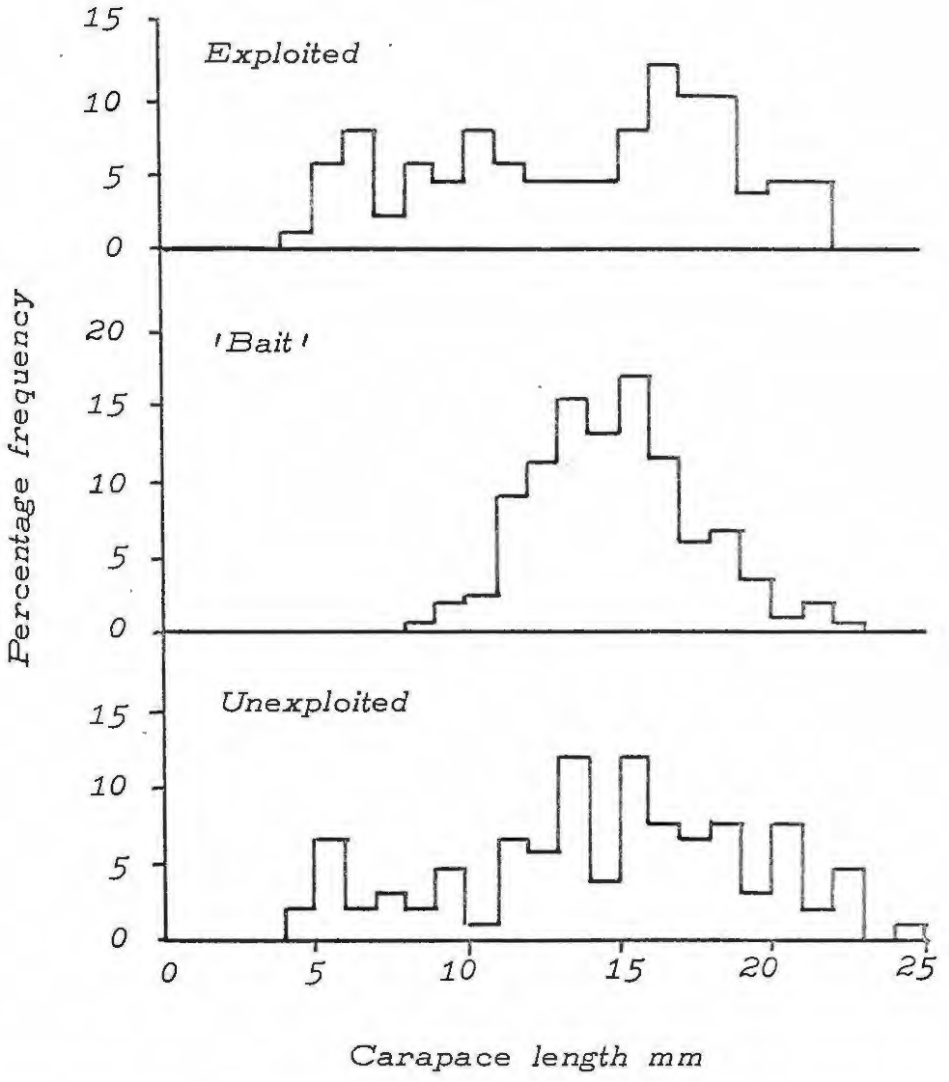


Fig 14: Size frequency analysis of prawns collected from an exploited area compared with a sample of 'bait' and a sample from an unexploited area.

Four tins of prawns (294 animals) were purchased from bait collectors at Centenary Park. A sample of 91 prawns was collected by digging at Centenary Park and a second of 107 by digging in a prohibited area. All the prawns were measured and the results are shown in figure 14.

The bait collectors do not take small prawns and hence the numbers of these in the sample was very low. Although they prefer the larger prawns, in fact they appear to miss many of them. They dig very rapidly taking a few spadesful from one patch, breaking up the mud clods with the back of the spade and picking up any prawns. They then move on a few paces and dig again. The larger prawns usually emerge from the burrows opening into the excavation a few minutes after the diggers have left.

The sample of prawns from the unexploited area had a peak in the region of 13 - 16 mm total carapace length. This peak corresponded with a clear peak in the bait sample. However in the sample from the exploited area there was a definite absence of this peak. Thus it appears that the removal of large numbers of prawns in the 12 - 17 mm carapace length classes by commercial collectors results in a reduction in the numbers of these sizes in the population. This reduction will tend to obscure any size classes which may be present in the population.

The range of prawn sizes was about the same in the exploited and unexploited areas and in addition the numbers of prawns below 10 mm carapace length were apparently not reduced.

Size frequency data obtained from routine fornightly samples of prawns from the mudflats adjoining Centenary Park were grouped into four seasons on the basis of temperature,

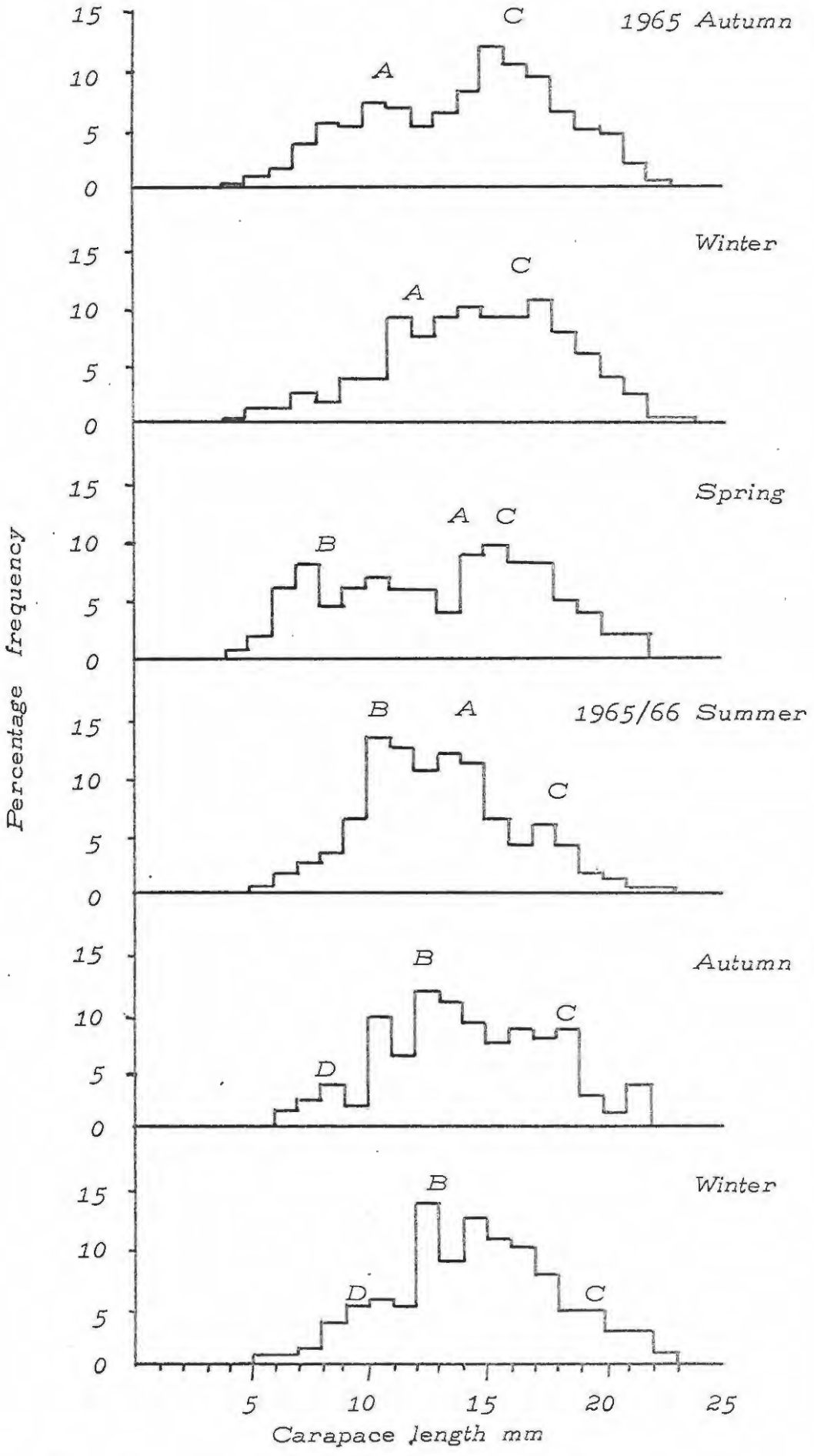


Fig 15: Size frequency analysis of sample of U. africana from the Kowie estuary at different seasons. The possible size groups are labelled A - D.

namely Summer (November - February);

Autumn (March - May);

Winter (June - August);

Spring (September - October).

The results of this grouping are shown in figure 15 which includes data for 1965 and 1966. The numbers of prawns measured in each season are as follows:

Autumn	1965	741
Winter		617
Spring		259
Summer	65/66	216
Autumn		218
Winter		348

The histograms in figure 15 for Autumn and Spring in 1965 both show a bimodal distribution centering around 8 - 12 and 6 - 11 mm carapace length respectively. If the data for autumn 1965 are plotted graphically as probits of cumulative frequency, the split probit shown in figure 16 is obtained. This split probit confirms that the population had a bimodal distribution.

It was suggested above that prawns in the 6 - 11 mm carapace length class found in spring, probably represent a recruitment to the population from the previous autumn. Thus the bimodal of spring 1965 may be a result of the presence of juveniles in the 5 - 11 mm class which were recruited in the previous autumn. This group has been marked B in figure 15.

Similarly the prawns in the 7 - 12 mm carapace length class (A) which made up one peak of the bimodal distribution

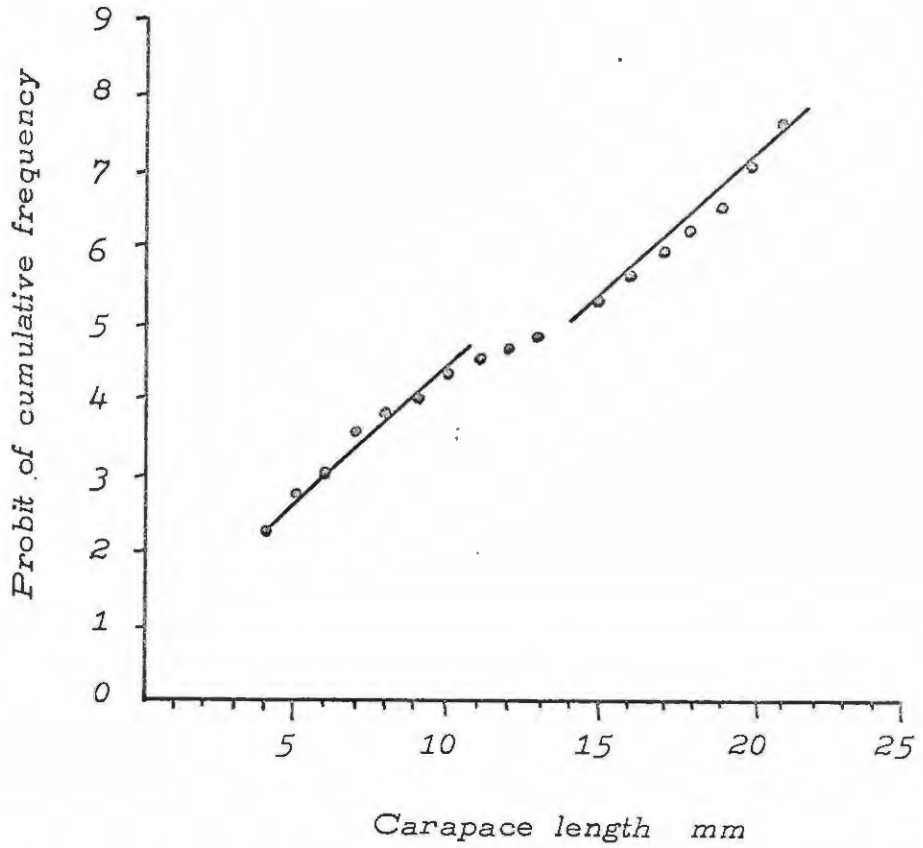


Fig 16: Probit values of cumulative frequency of prawn sizes in Autumn 1965.

in Autumn 1965 may represent juveniles which joined the existing population in the previous spring.

It was shown above (page 44) that prawns of 10 mm carapace length grew to 13 - 14.9 mm carapace length from Autumn to spring 1967. Thus the juveniles marked A in Autumn 1965 (figure 15) would probably have merged into the general population by summer 1965. Similarly juveniles in spring (Group B) probably grew rapidly through summer so that by autumn they had also merged into the general population. This merging of juveniles into the existing population

of adult prawns was probably a result of the different growth rates of small and large prawns.

The merging of different size groups in the region of 15 mm carapace length together with the large scale removal by bait collectors of prawns in this size range make it difficult to draw any conclusions from the size frequency data. However it was shown above that 15 mm carapace prawns grew extremely little from Autumn to Spring. This group has been marked C in autumn, winter and spring 1965 in figure 15. If a more rapid growth rate is assumed to occur in summer due to higher temperatures, this group may increase to 17 or 18 mm by autumn. In summer and autumn 1966 there was an indication of a group (C) in this size range. However the numbers of prawns larger than 18 mm are always low in samples and it appears that they die after reaching this size. Thus group C disappeared from the population in winter 1966, leaving only a few large prawns in the following summer.

If we can accept this interpretation then the life cycle can be tentatively summarised as follows:

Age (years)	Season	Size (mm total carapace)
1	autumn	2 - 4
	spring	6 - 11
2	autumn	15
	spring	16
3	autumn	18 - 19
	spring	19
4	autumn	21 - 22

Breeding Cycle of Upogebia africana in the Kowie Estuary

As stated above fortnightly samples of prawns were collected in 1965, 1966 and 1967 for determination of the size frequency composition of the Kowie population. The breeding cycles of *U. africana* were studied by recording the number of ovigerous females in these samples. In 1967 all the ovigerous females were examined and divided into two groups, those carrying eyed eggs and those with eyeless eggs.

RESULTS

Eleven ovigerous females in which there was no sign of differentiation of the eggs were kept in sea water in the laboratory. Eyes appeared in the eggs after 13 to 14 days, and the eggs hatched 11 to 16 days after the eyes became visible. Thus *U. africana* from the Kowie estuary carried its eggs for a period of 24 to 30 days.

Records of the numbers of females collected and the number carrying eggs were grouped for each month and the percentage of ovigerous females was calculated. As the smallest recorded ovigerous females were in the 10 - 10.9 mm total carapace length class, it was assumed that they only become sexually mature at a total carapace length of 10 mm. The percentage of ovigerous females in each month was therefore based on the number of females larger than 10 mm total carapace. The records for 1965 and 1966 are shown in figure 17.

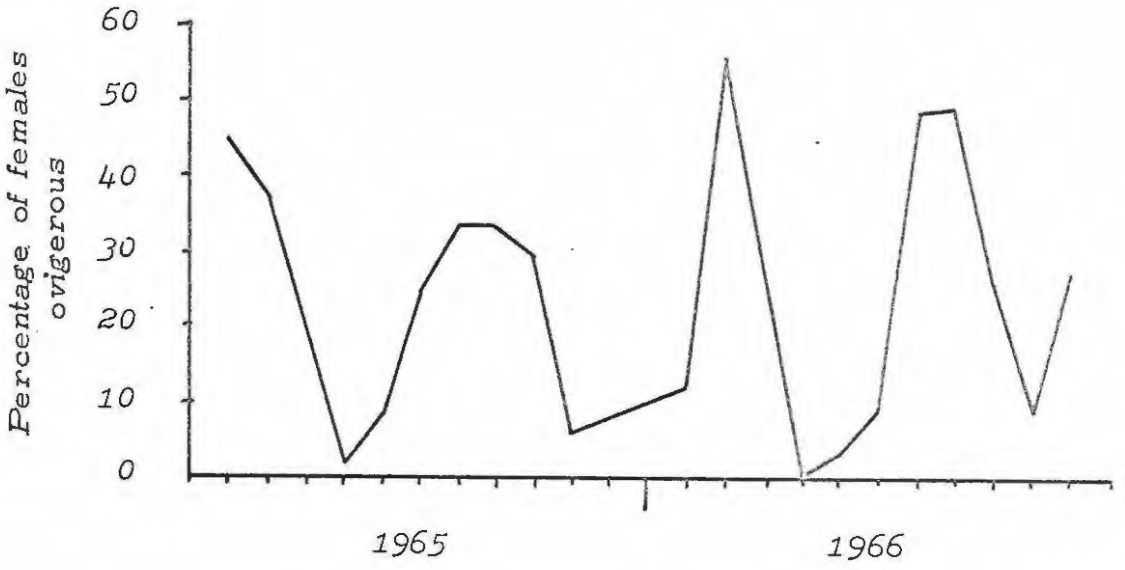


Fig 17: Percentage of females which were ovigerous during 1965 and 1966.

In both years there were two distinct breeding cycles each lasting for six months. One cycle reached a peak in August - September and will be referred to as the spring cycle. The other has a peak in February - March and will be referred to as the summer cycle. The breeding cycles in 1967 are shown in figure 18. Breeding in 1967 followed the same pattern as in 1965 and 1966. There were two cycles a summer one and a spring one. In 1967 over 50% of the females became ovigerous in each cycle. This indicates that the double breeding cycle is not caused by one half of the females breeding in spring and other half in summer.

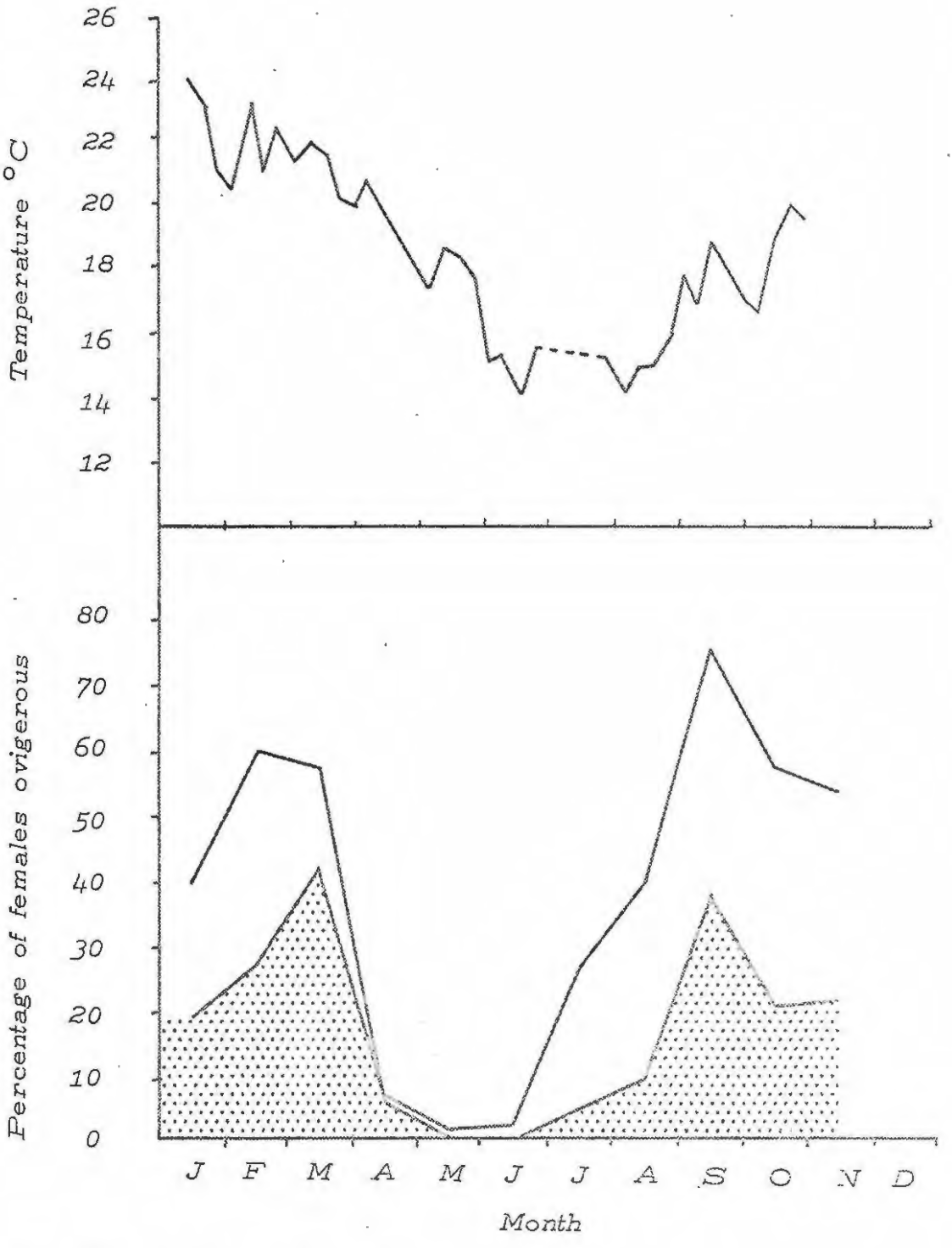


Fig 18: The upper section shows the mean weekly temperatures in the lower reaches of the Kowie estuary during 1967. The lower section shows the percentages of females which were ovigerous in samples collected in 1967. The shaded area in the lower section represents the percentage of females which were carrying eyed eggs.

In March 1967 most of the eggs had eyes, this indicates that few females were becoming ovigerous despite the high temperatures (20 - 22 °C, see figure 18). In April temperatures began to fall and simultaneously the percentage of ovigerous females dropped to 6%. All these females had eyed eggs and thus no females were breeding at this time. In July and August the percentage of ovigerous females increased despite the fact that the temperatures only rose at the end of August. In October the percentage of ovigerous females dropped once more although temperatures in this period were still rising.

It appears that the temperature cycle was similar to the breeding cycle but the two are slightly out of phase. The fall off in the percentage of females carrying uneyed eggs at the end of summer occurred before the drop in temperature. Similarly the increase in breeding at the end of winter occurred before the rise in temperature. It is also apparent that U. africana can breed over the full range of temperatures recorded in the Kowie estuary, namely 14 - 24 °C.

After the eggs hatch the females probably enter a short resting period before becoming ovigerous once more. Thus in November most females were in a resting phase after the spring breeding cycle. This resting phase did not result in a complete absence of ovigerous females in any of the years probably because there was some overlap between those females which were at the end of the spring cycle and those which were at the start of the summer cycle.

At the end of the summer cycle in 1967 temperatures fell and carried on falling till June. The effect of this fall in temperature was to temporarily inhibit breeding. The same result was seen in 1965 and 1966 (figure17) when no ovigerous females were recorded in May of both years. In June and July 1967 temperatures stabilised and in July the prawns began breeding once more.

Thus although temperature was not the cause of the breeding cycle, the fall in temperature in April and May resulted in breeding in the females being brought into phase. If temperatures remained uniformly high throughout the year breeding might occur at the same level and no cycles would be evident.

The two cycles of breeding give rise to two batches of planktonic larvae each year. It was shown earlier (figure 15) that two recruitments of juvenile prawns occurred in 1965 and again in 1966. These are probably the result of these two breeding cycles.

Comparison of the above results with data reported by Siegfried (1962) reveals several differences between U. africana in Uilenkraal estuary and those in Kowie estuary. Siegfried found that U. africana only bred at a total carapace length of 11 - 11.9 mm which is larger than in the Kowie estuary (10 - 10.9 mm). In addition he found that females carried eggs for a much longer time, namely in the vicinity of 40 days, with eyes appearing 15 days before hatching.

However Siegfried established this time by keeping two ovigerous females in an aquarium containing "25% diluted sea water". This reduced salinity could have lengthened the development time of the eggs. According to Allen (1960), Broekema (1941) found that egg development in the shrimp Crangon vulgaris was twice as long at 16 °/oo as at 35 °/oo.

Siegfried only found one cycle of breeding activity in the Uilenkraal estuary. This cycle as in the case of Kowie estuary prawns, lasted for six months. He found no females carrying eggs in the period April to September. This is the rainy season at Uilenkraal estuary and thus there are two possible environmental causes of the absence of breeding, namely low temperature and low salinities.

Unfortunately Siegfried gave no temperature or salinity data for the Uilenkraal estuary. However the rainfall in the region is fairly evenly spread over the whole winter. In addition the mouth of the estuary remains open to the sea so it is unlikely that any marked drop in salinity occurred. Very little information is available on temperatures of water in the region of Uilenkraal estuary. Scott et al (1952) stated that

"observations on landlocked bodies of water along the coastal strip of the Western Cape Province show that annual range of temperatures in such waters does not extend much beyond 12 °C in winter and 28 °C in summer ."

If temperatures do drop to 12 °C for extended periods in the Uilenkraal estuary, it is possible that this may inhibit breeding. At the present stage although temperature is the probable cause, no definite reason can be given for the halt in breeding in winter.

Experimental Studies on Temperature

Temperatures in the Kowie estuary are extremely variable as discussed above, it was also shown that the temperature of water over mud flats can reach at least 34.5 °C for short periods. In addition U. africana appeared to be limited by high temperatures in the heated pond at Knysna. Experiments were therefore carried out to determine the upper lethal temperature of U. africana and to establish whether it was possible to alter this temperature by acclimation.

METHODS

Temperatures in shallow water over mud flats do not necessarily reflect temperatures in the substrate or in burrows. Johnson (1965) investigated the temperatures at different depths in intertidal sands and found that the temperature varied between 9 °C and 30 °C one centimetre below the sand surface. At a depth of 20 cm the temperature only ranged between 12 °C and 18 °C. However as U. africana lives in a relatively large burrow and actively pumps water through the burrow, it is reasonable to expect that temperatures inside the burrow would be similar to those of the overlying water.

In order to determine if this was a valid assumption heated water was run over the mud in an aquarium containing prawns. Temperatures in the burrow were measured by means of a miniature thermistor probe 6 mm long and 3 mm in diameter. This probe could be inserted into a burrow but could not be left

there as the prawns pushed it out. The procedure adopted was to insert the probe, allow it to stabilise, read out the temperature and then remove the probe. As the thermistor reacted rapidly to temperature change there was insufficient time for the prawns to remove the probe.

Experiments were carried out to determine the temperature tolerances of U. africana using the following procedure. Prawns from the Kowie estuary were put into shallow plastic boxes containing sea water immediately after collection. They were then taken to the laboratory and transferred to covered plastic dishes containing aerated sea water.

Experiments were carried out in circular borosilicate glass dishes 25 cm in diameter and containing four litres of clean sea water (salinity 34 - 35 °/oo) collected in the sea at Port Alfred. The water was heated by means of Buhler 750 watt heater stirrers controlled by a 0 - 100 °C Jumo MS D.P.P. contact thermometer operating through a relay. The impellers were enclosed in a PVC coated fibre glass mesh screen to prevent prawns being drawn in and damaged. (Plate I). A plastic box with 9 cm square base was put into the dishes with the prawns. The purpose of this box was to reduce the movement of water in the dishes as otherwise the prawns were carried round and round in the current. A perspex cover over the dishes reduced evaporation and consequent increase in salinity. The heaters maitained water temperature within 0.1 °C of the setting.

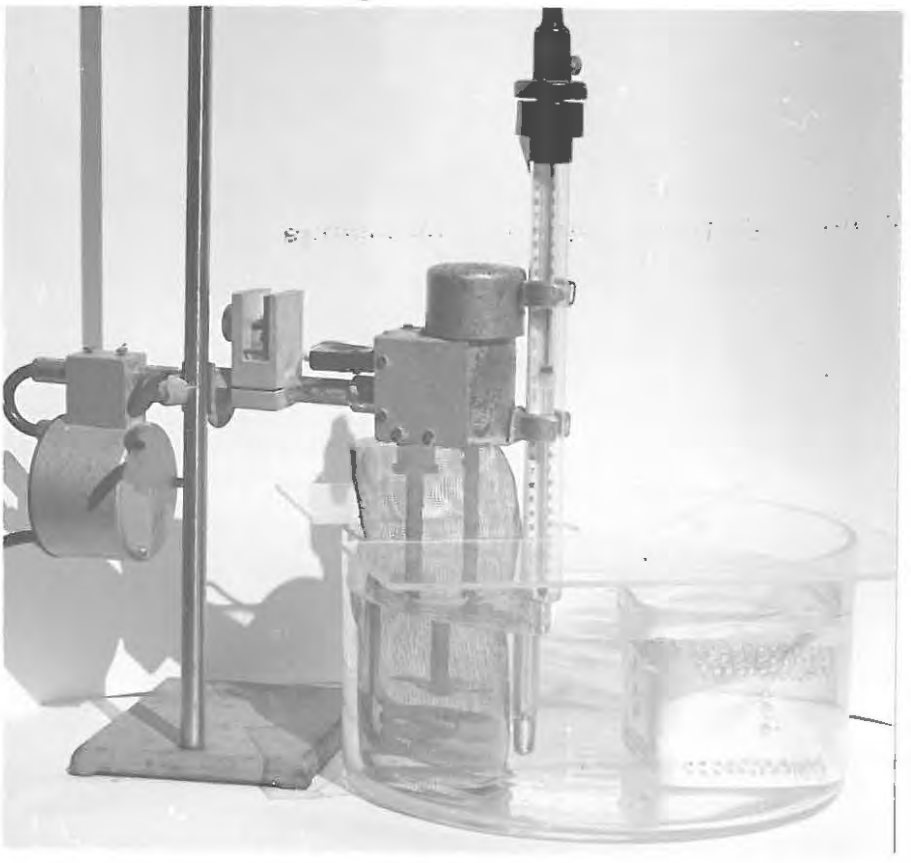
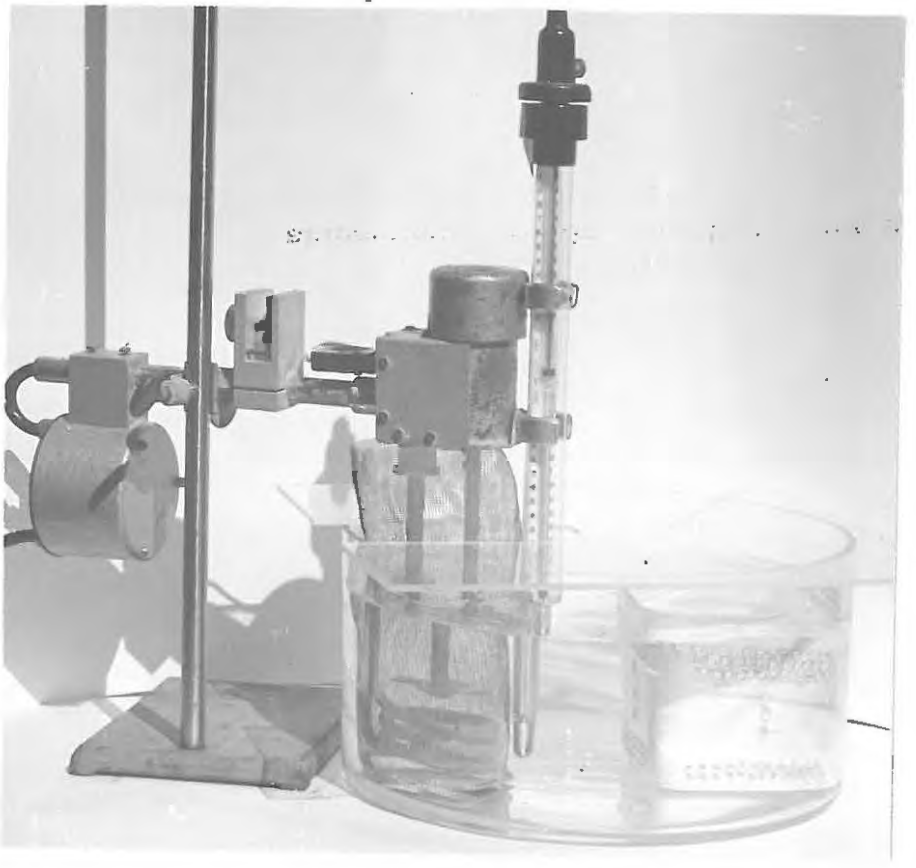


Plate I: Apparatus used in temperature experiments on U. africana.



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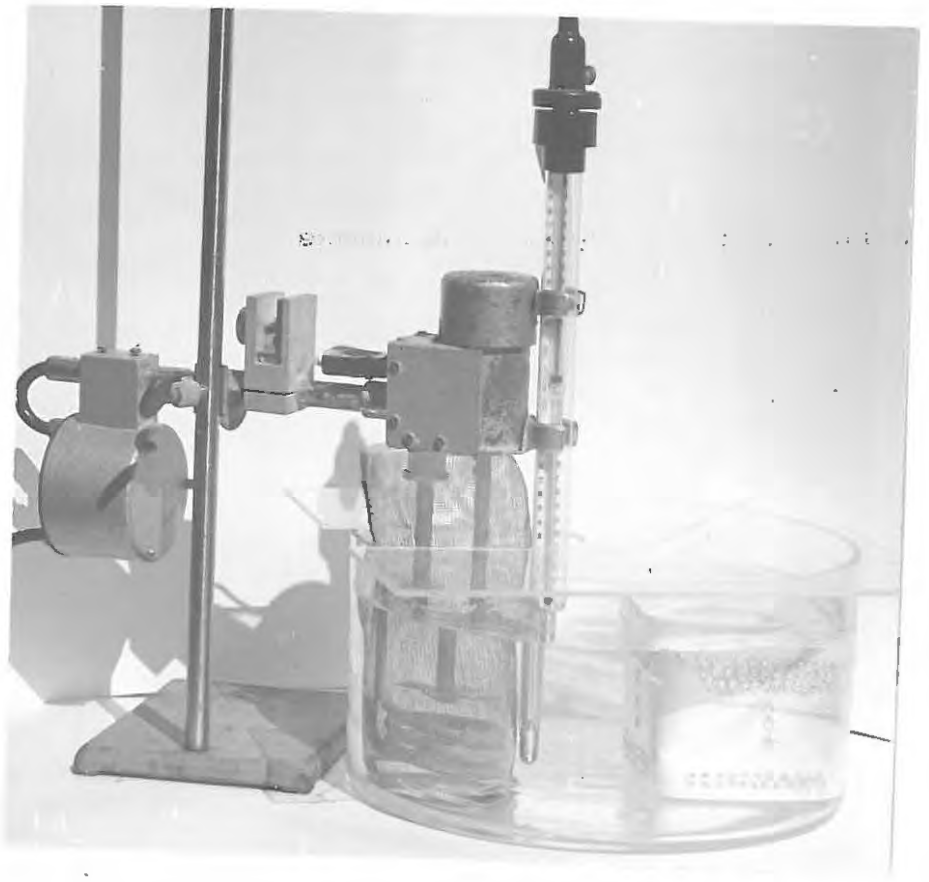

Plate I: Apparatus used in temperature experiments on U.africana.

Temperatures were measured with a -10 to +50 °C mercury in glass thermometer graduated in 0.1 °. This thermometer (No 2E8) had been standardised by the South African Bureau of Standards and had been found to be accurate in the range in which it was used (+4 to 40 °C). Experiments at or below ambient temperatures were carried out in a cold room to prevent temperatures rising above the desired level.

Water in the dishes was changed regularly. At temperatures above 30 °C water was changed every 24 hours as high temperatures and a large number of prawns caused rapid fouling of the water. At lower temperatures the water was changed every 48 hours. In any particular experiment all dishes were treated in the same manner. Thus if a series of dishes were set up with only one above 30 °C, all water was changed every 24 hours. New water was preheated to the correct temperature before replacing old water.

In experiments in which direct transfer was used, the prawns were put into the dishes which were at ambient temperature. The heaters were then switched on and the temperature rose at a rate between 2.6 ° and 2.8 °C per minute. The exact rate of increase depended upon the individual heaters. The starting time of the experiment was taken as the time at which the final experimental temperature was reached.

Low temperature experiments were carried out by putting prawns into sea water in shallow plastic dishes floating in a water bath. The water bath was cooled by metal coils

containing glycol circulated from a refridgeration system.

Prawns were kept overnight before carrying out experiments. Some prawns inevitably suffer damage during collecting, by keeping them for about 18 hours it was possible to discard any that were obviously damaged or did not appear to active and 'healthy'.

The prawns were randomised into batches by drawing numbers from a tin and allocating prawns to numbered dishes. This method has been shown by Allanson and Noble (1964) to give random distribution with no significant bias. The number of prawns in each dish varied slightly in the different experiments. The lowest number was 20 but more commonly 25 to 30 were used.

Death in most animals is usually accompanied by a slowing down of activity. This slowing down makes it difficult to determine the exact time at which death occurs. It is therefore necessary to decide on a criterion for death for each individual species which is tested. U. africana normally beats its scaphognathite continually although the beat may occasionally stop briefly. When approaching death the animals 'collapsed', rolling over onto their sides or backs. Some time (variable according to stress) after collapse the scaphognathite beat ceased. If the prawns were handled at this stage the beat sometimes recommenced, in this case they were regarded as being alive and were returned to the experiment. If the scaphognathite did not recommence beating when the prawn was handled it was discarded and regarded as dead.

Observations were made at approximately two hour intervals for the first 12 hours. Thereafter observations were made on a gradually increasing time scale. After the first 12 hours observations were extended to every three to four hours for a further 12 hours followed by six to eight hour intervals. From 96 hours after the commencement of the experiment, observations were made at 12 hour intervals until the end of the experiment.

RESULTS

The relationship between the temperature of the burrow water and the overlying water was investigated in the laboratory using an aquarium containing mud in which prawns had constructed burrows. Water at various temperatures was circulated over the mud and temperatures in the burrow were measured by means of a miniature thermistor probe. The temperature of the mud at a depth of 5 cm remained fairly constant at 18 °C throughout the experiments.

It was found that if water at temperatures of 24 °C or lower was circulated through the aquarium, the temperature in the burrow corresponded almost exactly to that of the overlying water. When water at 27.5 °C was circulated through the aquarium the prawns only pumped it slowly through their burrows. As the mud of the burrow walls was cooler than the inflowing water the temperature of the inflowing water dropped slightly from 27.5 °C to 25 - 26.5 °C (Figure 19).

When the temperature of the overlying water was above 32 °C the prawns did not pump continuously. Pumping lasted for three to five seconds and then ceased for several minutes, with the result that only a small amount of water entered the burrow.

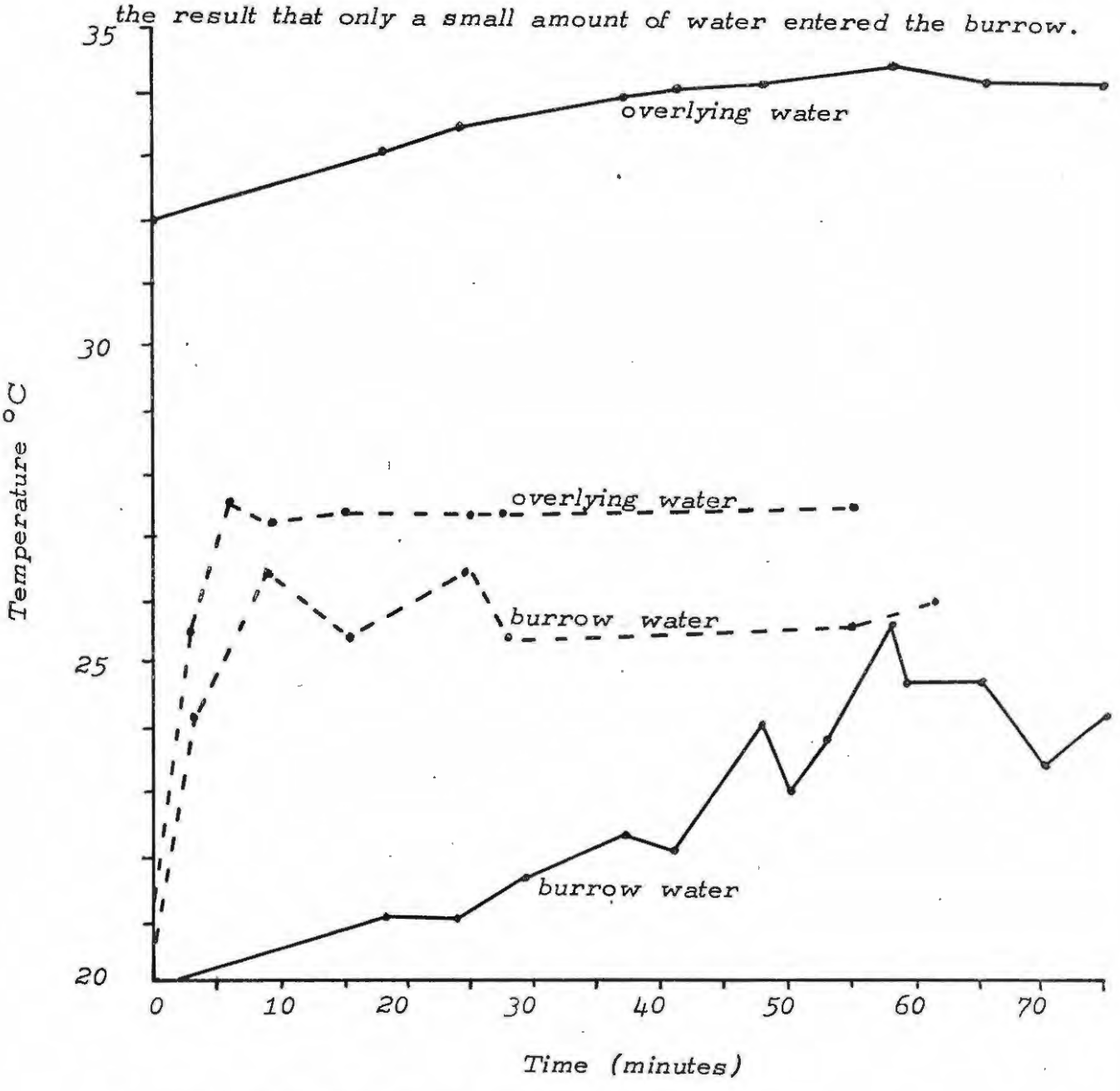

Fig 19: Temperature of burrow water compared with overlying water when warm water (dotted line) or hot water (solid line) is allowed to flow over the mud.

In this case the temperature of the burrow water rose to 20 - 21 °C. After about 30 minutes most of the prawns began to close down one of the entrances of the burrow by plastering mud around the holes. The temperature in the burrow gradually rose to 23 - 25.5 °C probably due to the occasional pumping. The minimum temperature difference between overlying and burrow water was 9° and the maximum 12°. After an hour the highest temperature recorded in the burrows was 25.5 °C.

In contrast when the overlying water temperature was 27.5 °C, the burrow reached a temperature of 26.5 °C after only 10 to 20 minutes and the greatest temperature difference between the burrow and the overlying water was 2°.

Clearly if a band of heated water moves over a mud flat, the temperatures in the burrow will be less than in the overlying water. However if high temperatures were sustained for long periods of time the temperatures will rise.

Orr (1955) has pointed out that there are a whole series of temperatures at which animals will die depending upon the duration of the exposure. He therefore concluded that it is not sufficient to state that an animal dies at a certain temperature with the implication that it will have an indefinite survival at all other temperatures. Thus it is necessary to determine the time to death over a range of temperatures. This approach has been adopted in the present study on U. africana *and was extended by determining the times to death of both summer and winter animals in view of the difference between summer and winter temperatures in the Kowie estuary.*

The method of recording and analysing the results of experiments is best illustrated by means of an example. The example used was that of a preliminary experiment designed to determine whether sex and size had any effect on survival at high temperatures.

A batch of 30 prawns was collected in August (winter) and exposed to 31 °C. When a prawn was found to be dead it was sexed and measured (total carapace length). The results are shown in table 2. The time of death of each individual was assumed to have occurred half way between the time when it was found to be dead and the time of the previous observation. This time is shown as the 'half interval' in table 2. The mean survival time for males and females was calculated using the half interval as individual survival times. The mean survival time of males was 25.5 hours and of females 26.8 hours. Considering the spread of deaths (two hours to 108 hours), this is a remarkable correspondence. It indicates that there is no detectable difference in survival between males and females using the method described.

If the survival time is plotted against size of prawns the points shown in figure 20 are obtained. There is no obvious trend, any line drawn through them would be bioloigically meaningless. It appears that there is no difference in temperature tolerance between large and small prawns.

As a result of the above experiments it was decided not to separate males and females nor to divide prawns into size groups in temperature experiments. All temperature

Table 2: The survival of prawns collected in August when exposed to 31 °C. The experiment was started at 1000 hours and there were 15 male and 15 female prawns in the dish.

Time of observation	Hours elapsed	Sex	Carapace length	Half interval	Percent survival	Probit value
Mon 1400	4	fem	13.2	2	96.7	6.838
1800	8	male	19.6	6	76.7	5.729
		male	20.0			
		fem	14.5			
		fem	15.8			
		male	14.5			
		fem	12.8			
2100	11	male	19.4	9.5	56.7	5.169
		fem	18.3			
		male	19.5			
		fem	15.7			
		male	14.3			
		fem	11.6			
Tue 0200	16	male	17.5	13.5	46.7	4.917
		fem	15.3			
		male	16.5			
0800	22	male	16.3	19.0	36.7	4.660
		male	15.3			
		fem	14.5			
1700	31	fem	16.0	29.0	30.0	4.476
		male	11.0			
2100	35	fem	14.2	33.0	23.3	4.271
		male	11.9			
Wed 0300	41	fem	13.6	38.0	16.7	4.034
		male	10.2			
2400	62	fem	13.7	56.5	10.0	3.718
Fri 0800	94	male	17.1	86.0	3.3	3.162
		male	13.5			
2400	110	fem	17.3	108.0	0.0	-

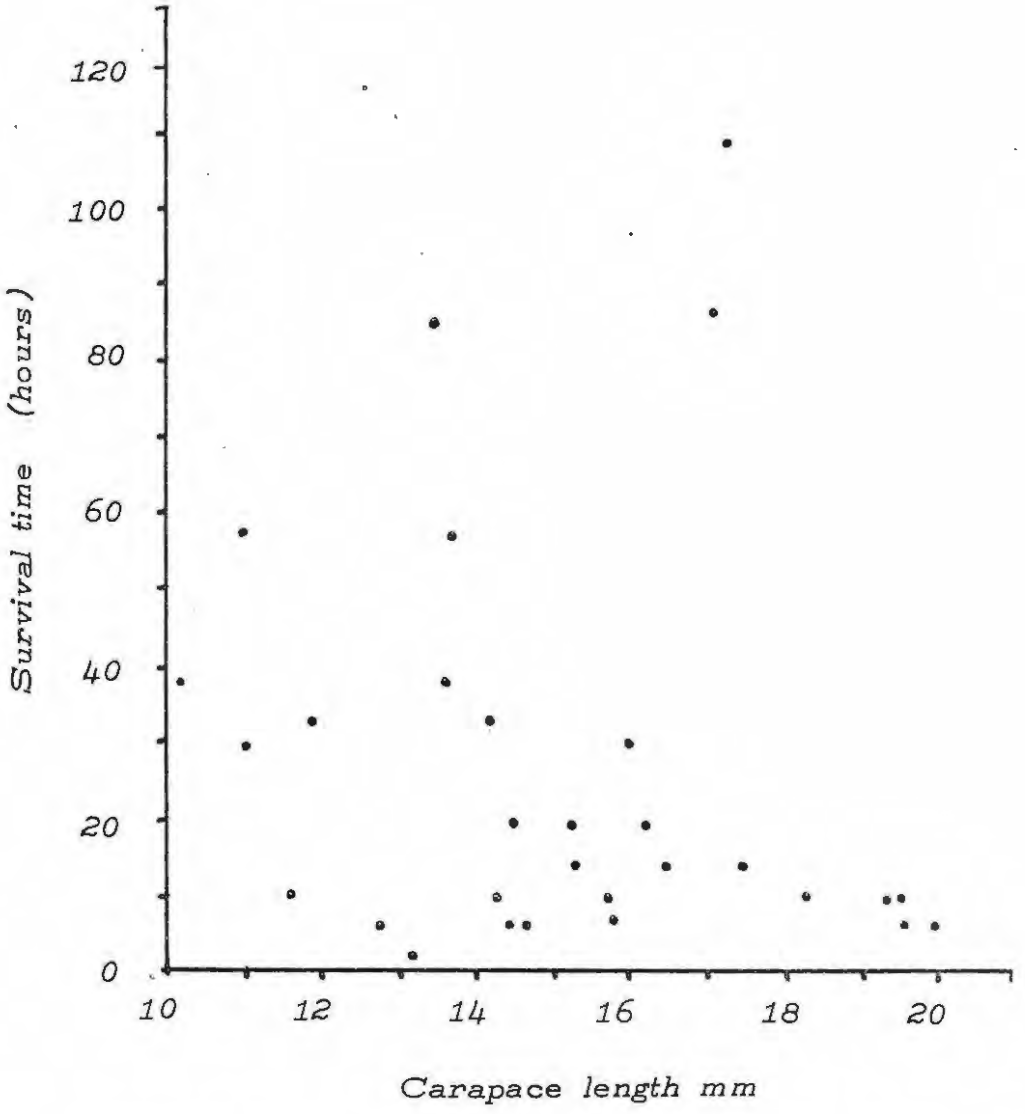

Fig 20: Survival times of various sizes of prawns when exposed to a temperature of 31 °C.

experiments are therefore based on completely mixed samples containing males and females of all sizes.

A mean survival time is liable to be seriously affected by the presence of extremely resistant individuals in the sample. In order to avoid bias from this source it was decided to utilise a parameter which is independant of the survival time of both

the extremely sensitive and the extremely resistant individuals in a sample. The parameter chosen was the period of time for which 50% of the sample survived the experimental conditions. This time will be referred to as the Median Time of Survival or MTS. The MTS was determined using methods described by Finney (1952) and is illustrated by means of an example using the data given in table 2.

The percentage of prawns alive at each half interval was calculated and is shown in the column headed ' Percent survival' (Table 2). The probit value of the percentage survival was obtained from probit tables and is shown in the table. The probit value of percentage survival was then plotted against the logarithm of the half interval on log/normal paper. The logarithmic transformation simplifies the analysis since it normalizes the distribution and reduces bias which may be introduced by a few animals with an exceptionally low or high survival time. A line was fitted to the points by eye and the resulting graph is shown in figure 21.

The MTS (probit 5) can be obtained directly from the graph and in the case of figure 21 was 12.7 hours. This procedure was adopted for analysing the results of all temperature experiments.

Survival at high temperatures in summer was tested by exposing prawns to the following temperatures:

40°; 35°; 34°; 32°; 30°; and 28°C. A control was kept at room temperature (20 - 24°C). All prawns

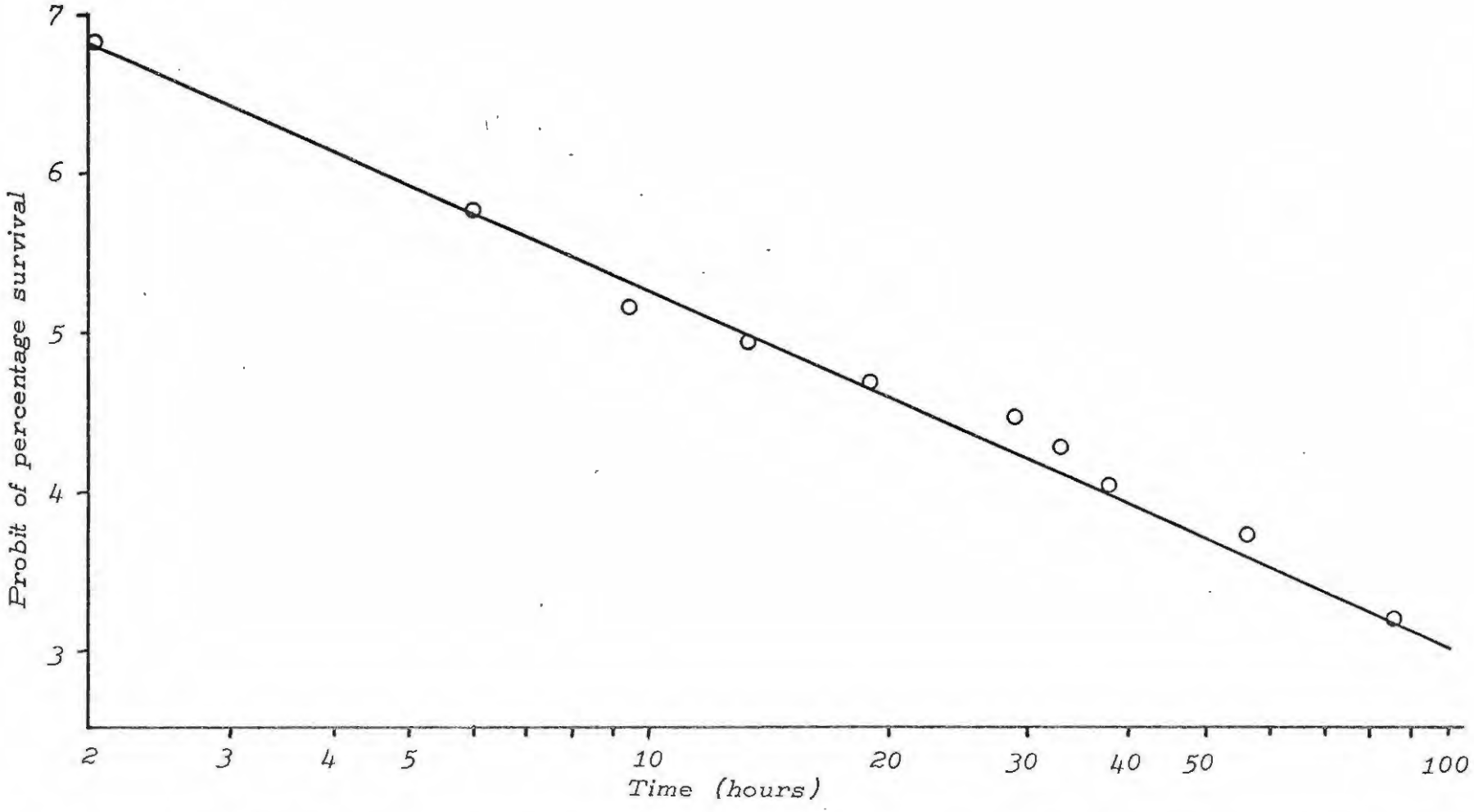

Fig 21: Probit values of percentage survival plotted against survival time of prawns exposed to 31 °C.

exposed to 40 °C collapsed immediately and were dead within three hours. The survival of the remainder was recorded as described above and curves of probit of percentage survival against the logarithm of the time drawn up. These curves are shown in figure 22.

At temperatures of 34 and 32 °C there was a clear split probit. As it has been shown that there is no apparent sex or size difference in the prawns' temperature tolerance the cause of the split is not certain. It must be borne in mind however that the collecting method, namely digging, results in injury to some of the collected prawns. Although obviously damaged prawns are discarded some that may be internally injured are inevitably used in experiments. These injured prawns are probably more sensitive to any stress such as high temperature. At a temperature of 35 ° death is so rapid - 100% in less than 9 hours, that the greater sensitivity of injured prawns is not noticeable. However at temperatures of 34 ° and 32 ° where survival is much longer, these prawns probably die before the majority of normal animals. A temperature of 30 ° or less subjects the animals to a far lower stress and the injured animals do not reveal themselves. It will be noticed that even in the control some deaths occurred. It is suggested therefore that the first part of the split probit reflects deaths of injured animals and that the second part reflects death due to temperature stress.

In order to indicate the spread of deaths about the MTS it is customary to give the survival time for one standard deviation on either side of the MTS. However where a split

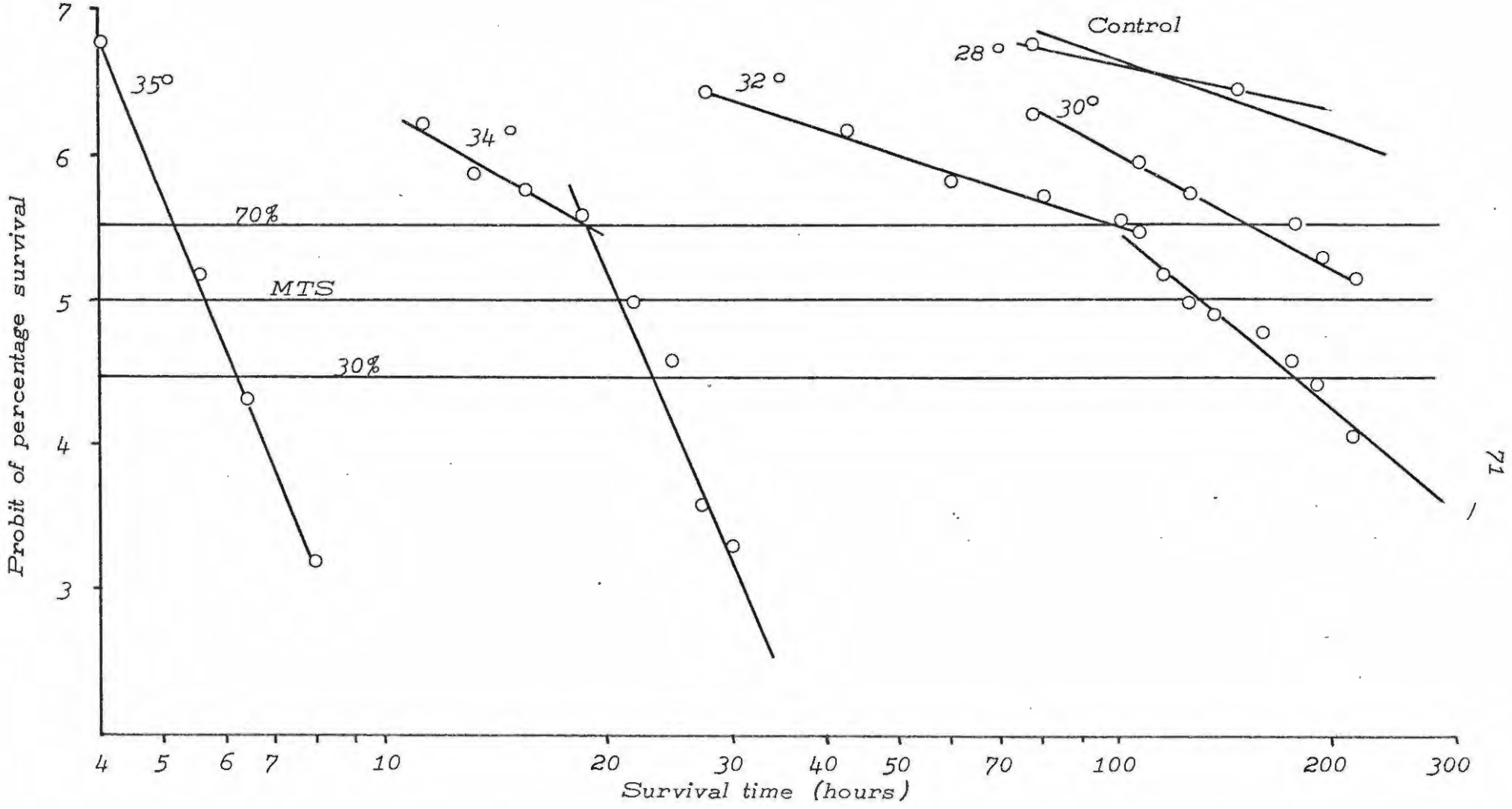

Fig 22: Percentage survival (expressed as probits) of batches of prawns exposed to a series of high temperatures in summer. Horizontal lines indicate 70%, 50% (MTS) and 30% survival.

probit occurs, one standard deviation (34%) from the MTS would have included animals which are presumed to have died from other causes operating together with the temperature stress. Gibson (1954) who worked with fish also obtained split probits at certain temperatures when determining survival times at lethal temperatures. She assumed that if only one cause of death, namely temperature, had been present, the survival times would all have followed the second curve of the split probit. She therefore extended the second half of the probit to obtain theoretical survival times for the first part of the experiment. However this assumption is not necessarily valid and in the present investigation it was decided to utilise survival times of 70% and 30% of the sample instead of a standard deviation. These percentage survivals have been shown in figure 22 and it is seen that they include only those prawns which are presumed to have died solely due to temperature stress. The MTS, 70% and 30% survival times obtained from figure 22 are shown in table 3.

Table 3: Survival of summer prawns (in hours) when exposed to high temperatures.

Temp °C	MTS	70% survival	30% survival
40	<3.0	<3.0	<3.0
35	5.6	5.0	6.2
34	20.5	18.5	23.0
32	130.0	95.0	175.0
30	250.0	150.0	>250.0
28	-	>250.0	-
Control	-	>250.0	-

U. africana is apparently sensitive to temperature above 34 °C and death occurred rapidly. At temperatures below 34 °C there was a striking increase in survival time with an accompanying slower rate of death. Although there was a significant mortality at 30 °C, the survival at 28 °C paralleled the control which had been kept at 20 - 24 °C. This indicates that between 28 ° and 30 °C there was a transition zone below which prawns were not killed by temperature. This temperature zone of 29 ± 1 °C will be referred to as the Upper lethal temperature of *U. africana*.

Fry (1964) divided the total range of temperature with respect to its effect on organisms into an upper and a lower zone of thermal resistance and a central zone of thermal tolerance, bounded above and below by the upper and lower lethal temperatures respectively. Thus in summer *U. africana* is in the zone of resistance if exposed to temperatures higher than 29 °C and in the zone of tolerance below this temperature.

A similar experiment perfomed in winter (August) gave the results in table 4 .

Table 4 : Survival of winter prawns (in hours) when exposed to high temperatures.

Temp °C	MTS	70% survival	30% survival
34	2	2.5	-
32	8.5	13	5.5
31	13	22.5	7.5
30	135	190	60
control	-		250

The median times of survival of winter and summer prawns are expressed graphically in figure 23 in order to facilitate comparison.

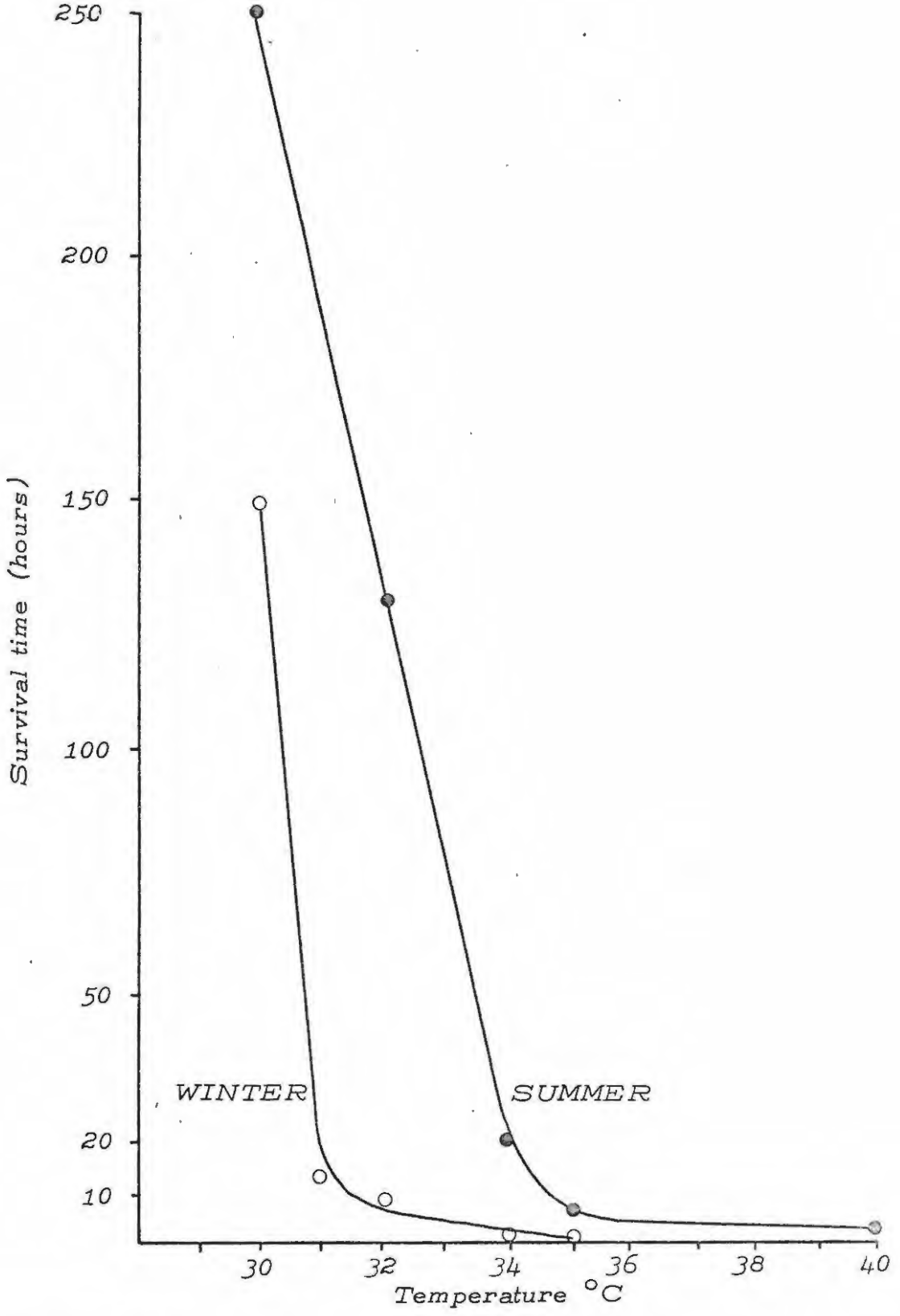

Fig 23: Median times of survival of winter and summer prawns at a series of temperatures.

Winter prawns are obviously far more sensitive to high temperature than are summer prawns since the zone of resistance is smaller in winter than in summer (figure 23). The most striking case is the survival at 32 °C. Winter prawns have a MTS of 8.5 hours whereas summer prawns in the same contiions have a MTS of 130 hours. However at 30 °C winter prawns, although more sensitive than summer prawns, do have a fairly high MTS. The upper part of the curve for winter prawns indicates that the upper lethal temperature of winter prawns is probably the same as for summer prawns, namely 29 ± 1 °C.

The difference in high temperature resistance between summer and winter prawns may be due to the higher thermal regime to which summer prawns are exposed. High temperatures in the Kowie estuary in summer may cause an acclimation effect. The possibility of such an acclimation effect in U. africana was therefore investigated.

Winter prawns were exposed to summer temperatures (24 °C) for varying lengths of time after which the survival time in 34 °C was determined. It was decided to test prawns at 34 °C since from figure 23 it can be seen that at this temperature there is a marked difference between winter and summer animals. Although the difference is greater at 32 °C, initial experiments utilising this temperature failed owing to the development of black areas on the body and gills. This fungus or bacterial infection can be seen on freshly collected prawns as tiny black spots. After long exposure to high temperature the black spots increase in

size eventually causing the gills to become completely black after which the animal dies. Experiments with fungicides and bacteriacides met with some success but complete control could not be attained. It was therefore decided to test at the highest temperature which would give a reasonable difference between summer and winter prawns and yet would kill rapidly enough to prevent the black spot disease from becoming an important factor. The occurrence of this disease also limited the acclimation experiments to relatively short times.

The survival of winter prawns at 34 °C after acclimation at 24 °C is shown in the following table (Table 5). There were at least 20 prawns in each acclimation.

Table 5: Survival of winter prawns tested at 34 °C after acclimation for different periods of time at a temperature of 24 °C. Survival times are in hours.

Acclimation time	MTS	70% survival	30% survival
0	2.2	1.4	3.4
3	4.8	3.0	6.9
12	4.3	3.0	6.5
16	5.5	5.0	6.2
24	5.0	3.5	6.0
36	4.0	3.5	7.5
48	11.0	6.0	19.5
58	11.0	5.0	14.0
63	9.0	5.5	12.0
86	9.5	8.0	heater failed
112	10.0	6.0	20.0

The median time of survival of each group has been used to construct the curve in figure 24. The figure shows that exposure to 24 °C for three hours results in a slightly

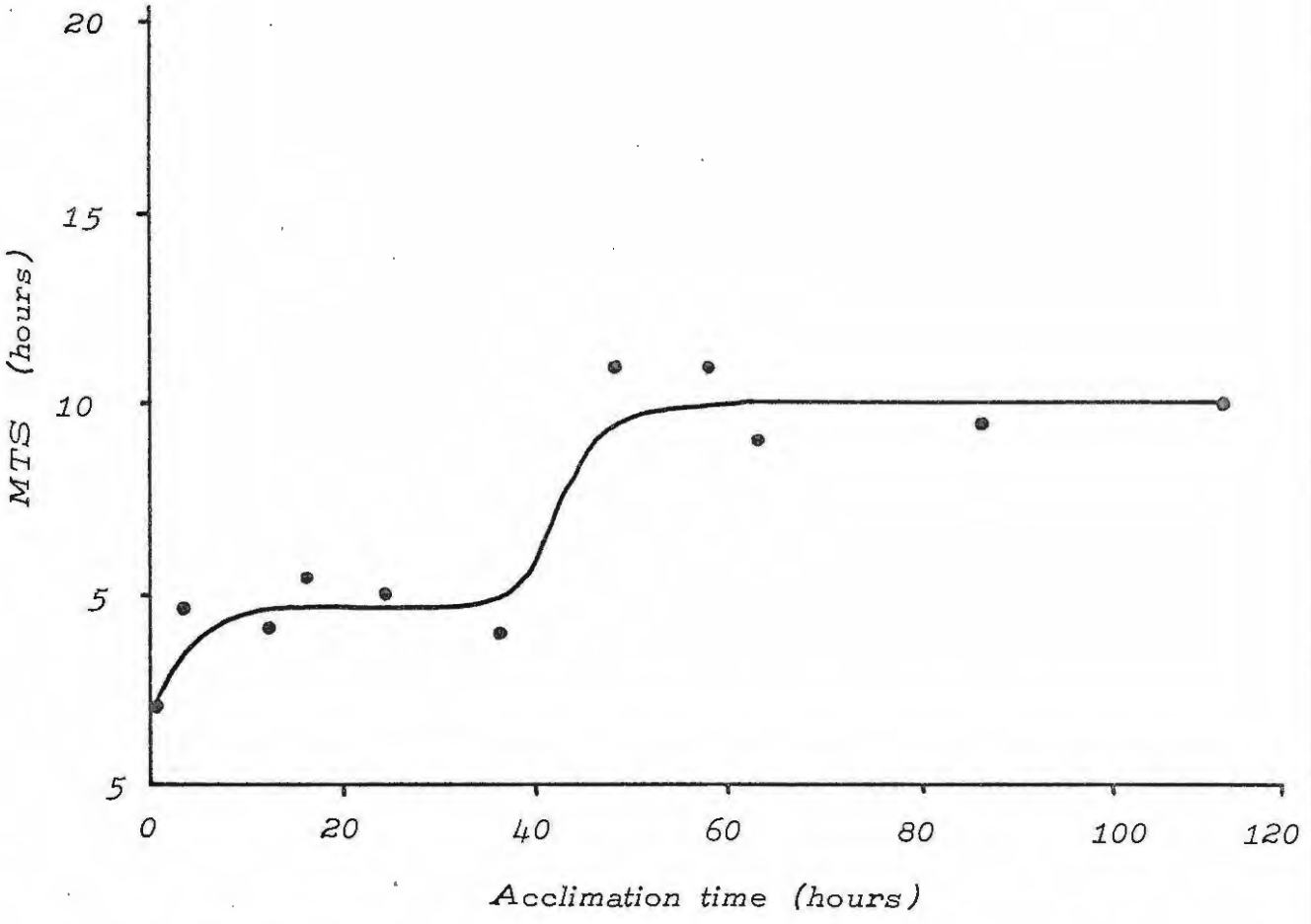

Fig 24: Median times of survival of a series of winter prawns transferred to 34 °C after acclimation at 24 °C for different periods of time.

greater survival time as compared with direct transfer. However this is probably merely due to decreased temperature shock on transfer to 34 °C. Winter prawns living at 15 - 17 °C transferred directly to 34 °C undergo a rapid temperature increase through 17 to 19°. Exposure to 24 °C for three hours breaks this increase into two stages of nine to ten degrees each. The value obtained by direct transfer is thus probably low since in the field changes of this rate and magnitude do not occur.

In figure 24 there appears to be no acclimation effect before about 40 hours exposure. After 40 hours there is a rapid acclimation resulting in a MTS of about 10 hours. Within the limits of the experiment, exposure times greater than 50 hours did not increase survival times at 34 °C. A delay or latent period of 10 days before acclimation effects occurred was found by Mcleese (1954) in the lobster Homarus americanus. The cause of the latent period in the lobster is not known. However in the case of U. africana it has been shown above that the environment is subjected to large daily fluctuations in temperature, both in winter and in summer. Because of the tidal movement of water in the estuary there are usually two daily cycles of high and low temperatures in the lower reaches of the Kowie estuary. The delay or latent period in U. africana is probably an adaptation to the constantly changing temperatures. The prawns only react (in terms of thermal acclimation) if the temperature remains high for a relatively long period of time. When this does occur acclimation is rapid and is apparently complete within a few hours.

The studies of acclimation times were all made at one temperature (24 °C). It was found that the highest MTS at 34 °C obtained after acclimation at 24 °C was 10 hours. This is only half the MTS of summer prawns when exposed to 34 °C. The effect of different acclimation temperatures on survival time at high temperature was therefore determined. Winter prawns were exposed to various temperatures for a fixed acclimation time

and were then exposed to 34 °C. As shown above acclimation times of less than 40 hours appeared to have no effect. On the other hand if acclimation times were extended unduly black spot disease appeared. It was eventually decided to utilise a time of 58 hours. Batches of prawns were kept in covered plastic dishes containing aerated sea water in constant temperature rooms at different temperatures and tested at 34 °C. One group was acclimated at 28.6 °C for 72 hours as an example of extreme conditions. The MTS of the various batches is given graphically

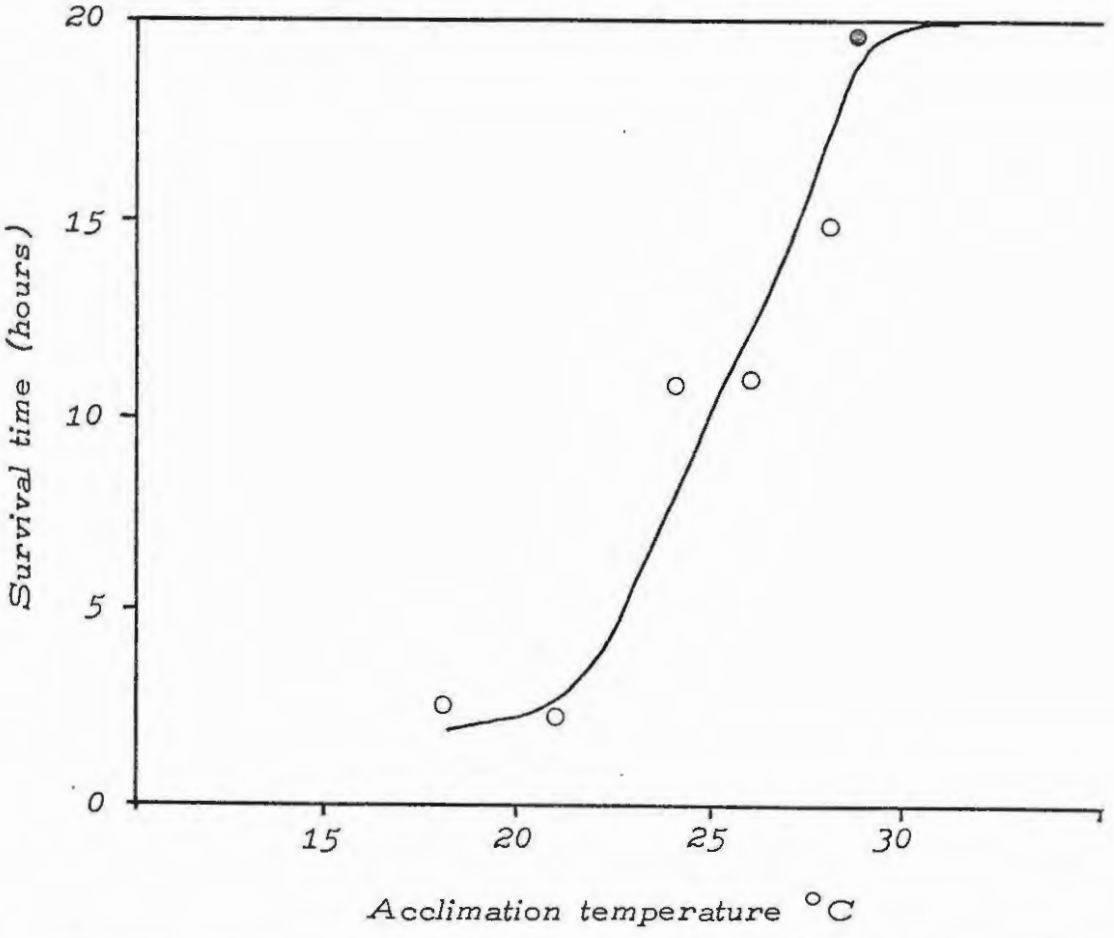

Fig 25: Median times of survival of a series of winter prawns transferred to34 °C after acclimation at different temperatures. Open circles indicate an acclimation time of 58 hours, the solid circle indicates 72 hours acclimation. Horizontal line at 20 hours shows the MTS of summer prawns after direct transfer to 34 °C.

in figure 25.

Figure 25 indicates that temperatures below 21 °C do not result in any acclimation effect. Temperatures above 21 °C cause a marked increase in survival times. The higher the acclimation temperature the greater the acclimation effect. Exposure to 28.6 °C for 72 hours resulted in a MTS of 20 hours (70% survival: 14 hours; 30% survival : 22.5 hours). The summer prawns on direct transfer to 34 °C had a MTS of 20.5 hours (70% survival 18.5 hours; 30% survival 23 hours). These results are extremely close and indicate that it is possible to experimentally increase the temperature resistance of winter prawns to that of summer prawns.

Attempts were made to increase the temperature resistance of summer prawns by exposure to a range of acclimation temperatures for various times but all experiments failed to increase the survival time at 34 °C. In fact survival times at 32 °C and lower were reduced due to the development of black spot disease in acclimated prawns. It does not appear to be possible to increase the resistance of U. africana above the normal summer values using this particular experimental approach.

In the experiment designed to establish survival times of winter prawns at high temperatures, it was found that the MTS at 30 °C was 135 hours (Table 4). However these prawns could be regarded as acclimated since before they died they had been exposed to 30 °C for long periods.

The experiments on acclimation time and temperature

temperature recorded above indicate that after 40 hours exposure to temperatures above 21 °C winter prawns undergo temperature acclimation. It has also been shown that it is possible to obtain the same survival times for winter prawns after acclimation as for summer prawns on direct transfer. Thus it appears that the correspondence between the upper lethal temperatures of winter and summer prawns is actually due to the acclimation of the winter animals during the course of the experiment. Similar effects should operate in the field and thus it is not possible to distinguish between winter and summer prawns on the basis of their upper lethal temperatures. In this respect U. africana differs from the mole crab Emerita in which the upper lethal temperature is 10 °C higher in summer than in winter (Edwards and Irving 1943 in Waterman 1960).

U. africana living in the power station effluent pond at Knysna are subjected to a thermal regime which is higher than that of the Kowie estuary in summer. This regime might act as an acclimatization and result in a greater temperature resistance to high temperatures than is found in summer prawns from the Kowie estuary. In order to test this possibility experiments were carried out on prawns from the ponds.

Unfortunately it was not possible to perform experiments on prawns living in this heated water in summer. However during April 1967 equipment was taken to the Fisheries Development Corporation Oyster Research Laboratory which adjoins the pond. Unfortunately temperatures had dropped from the summer

average (22 - 24 °C) to 17 °C over the previous two weeks. However most organisms acclimate to lowered temperatures extremely slowly and take long periods to lose their acclimation to high temperatures (Mihursky and Kennedy 1967).

Digging for prawns is not permitted in the pond as the mud and sand stirred up might damage or block the pumps and heat exchangers. Prawns were therefore collected using a pump (see page 40). Even this method did not meet with complete approval from the engineers and collecting was limited. Prawns were obtained from the Upper and Lower Channels as well as from the estuary for comparative purposes. One batch of 20 from each area was tested at 34 °C and a further 20 from the Upper Channel were tested at 33 °C. All methods and equipment utilised were exactly as described for temperature experiments on Kowie estuary prawns except that the samples were obviously not randomised. The resultant survival times in hours are shown in table6.

Table 6: Survival times of prawns from the heated pond and the estuary at Knysna when tested at high temperature.

Source of material	Test °C	MTS	70%surv.	30% surv.
Estuary	34	7.6	6.1	9.5
Lower channel	34	9.5	8.3	12.5
Upper channel	34	16.0	13.5	19.0
Upper channel	33	43.0	36.0	52.0

In figure 26 the median times of survival shown in table 6 have been plotted graphically together with part of the curve shown in figure 23 which showed the median time of survival of summer prawns from the Kowie estuary. It is obvious that

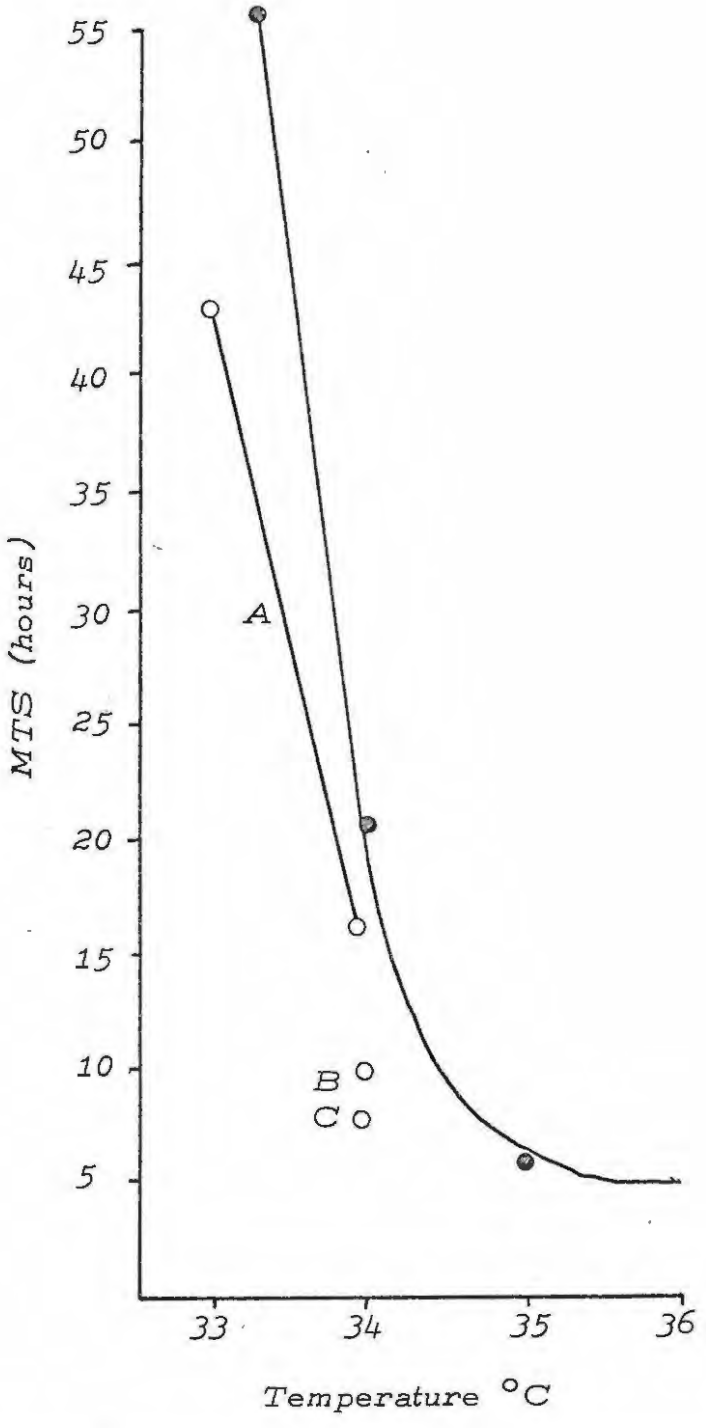

Fig 26: Median times of survival at different temperatures of prawns from the Upper Channel (A) and lower channel (B) of the Power station cooling pond and the estuary (C) at Knysna, compared with summer prawns from the Kowie estuary (solid circles).

no prawns from the power station pond were more resistant to high temperatures that Kowie estuary summer prawns. In fact prawns from the Upper Channel had a far lower MTS at 33 °C than Kowie summer prawns (43 hours compared to 75 hours). This suggests that long term exposure to high temperatures is deleterious to U. africana .

U. africana is limited to certain areas of the pond and it was suggested above that this was possibly due to temperature. The number of U. africana holes per square metre on the bottom together with the maximum temperature regime (summer) for each area of the pond is shown in the following table: (summarised from data given on pages 11 and 12).

Area	Day temp °C	Night temp °C	Holes/sq metre
Hot Pond	35	28	0
Upper channel	34	27	72
Lower channel	27	25	248

The high temperatures in the Hot Pond prevent prawns from surviving in this region since 35 °C results in rapid death (MTS of Kowie summer prawns only 5 hours). Prawns in the Upper Channel are exposed to lethal temperatures (34 °C) during the day. However prawns from this area had a MTS of 16 hours at this temperature (Table 6). Since the Upper Channel is only exposed to 34 °C for about 8 to 10 hours daily, U. africana is capable of surviving in this area. The maximum temperatures in the Lower Channel are below the upper lethal limit of U. africana and so therefore present no problem to survival. Thus it is not necessary to invoke an increased thermal

resistance to explain the presence of U. africana in the heated pond.

The occasional occurrence of cold water (10 °C) in Cape estuaries has been noted above. Macnae (1957) reported a mass mortality of U. africana in the Zwartkops estuary in July / August 1950. He stated that pollution of the estuary was probably the cause of the mortality although local residents claimed that the water in the estuary was unusually cold at the time when the prawns died. In order to establish the lower lethal temperature of U. africana an experiment was carried out in which prawns were exposed to low temperatures. The results are given in table 7.

Table 7: Number of prawns alive at low temperatures after various periods of time. The control prawns were kept at a temperature of 10 - 12 °C.

Temp:	3.9-4.7	4.3-5.6	4.8-5.8	5.4-6.5	control
Time (hours)					
0	10	10	10	10	10
15	8	10	10	10	10
22	6	10	10	10	10
28	6	10	10	10	10
38	4	8	10	10	10
52	2	8	10	10	10
88	1	6	10	10	10
94	1	6	10	10	10

From this table it appears that U. africana is only killed by temperatures below 5 °C. The sensitivity to low temperatures is fairly acute since temperatures of 3.9° - 4.7 °C result in a much greater mortality than temperatures of 4.3° - 5.6 °C. As this lower lethal temperature (5 °C) is well below temperatures ever recorded on the South African coast, it would appear that

low temperature is not a factor in the survival of U. africana adults.

Conclusions on the temperature relations of U. africana

It was shown above (figure 9) that in summer, the mean weekly temperatures in the Kowie estuary fluctuated between 19 °C and 25 °C. The mean weekly temperature fluctuated between 13 °C and 17 °C. Experiments indicated that the upper lethal temperature of U. africana is 29 ± 1 °C and the lower lethal temperature is 5 °C. Thus in terms of average environmental temperature, U. africana in the Kowie estuary is living well within its biokinetic range. However on hot days insolation of shallow water over mud flats can result in temperatures above 30 °C. Above 30 °C U. africana is in its zone of thermal resistance. It was shown that in summer this zone is relatively broad (figure23) , for example the MTS at 32 °C was 130 hours (Table 3). In winter the zone of resistance is narrower (figure 23) and at 32 °C the MTS was only 8.5 hours (Table 4). However, in winter temperatures in the Kowie estuary are lower than in summer. The maximum temperature recorded in the Kowie estuary in 1967 from the beginning of March to the end of September was 22.5 °C. Thus despite the decreased temperature resistance in winter, U. africana has a large safety margin.

The results of temperature measurements in burrows when heated water was circulated over the mud were shown in

figure 19. The experiment revealed that when water near the upper lethal temperature of U. africana was circulated over the mud, the prawns would pump it slowly through their burrows. However if water at a temperature above the prawns' upper lethal limit (32 - 34 °C) was pumped over the mud, the temperatures remained fairly low in the burrow (21 - 25 °C). This was a result of the particular behaviour reaction of the prawns to the heated water. The prawns only pumped infrequently and in addition they closed down the entrance of the burrow. Thus U. africana is not only resistant to temperatures above the upper lethal limit but it also exhibits a behaviour which results in an avoidance of these temperatures.

Prawns in the power station cooling pond at Knysna cannot avoid high temperatures in this manner since they are exposed for extremely long periods and the substrate is also heated. It was found that temperatures measured inside the burrows with a thermistor probe were the same as those of the overlying water. Thus survival in the power station pond depends solely upon thermal resistance. However temperature experiments showed that the zone of resistance of prawns from the heated pond was narrower than in the case of summer prawns from the Kowie estuary (figure 26). It was suggested that this was due to the deleterious effects of frequent exposure to high temperatures.

In April 1967 measurements were made of 37 prawns from the Upper Channel and 45 prawns from the Lower Channel of the Knysna power station pond. The results are shown in figure 27.

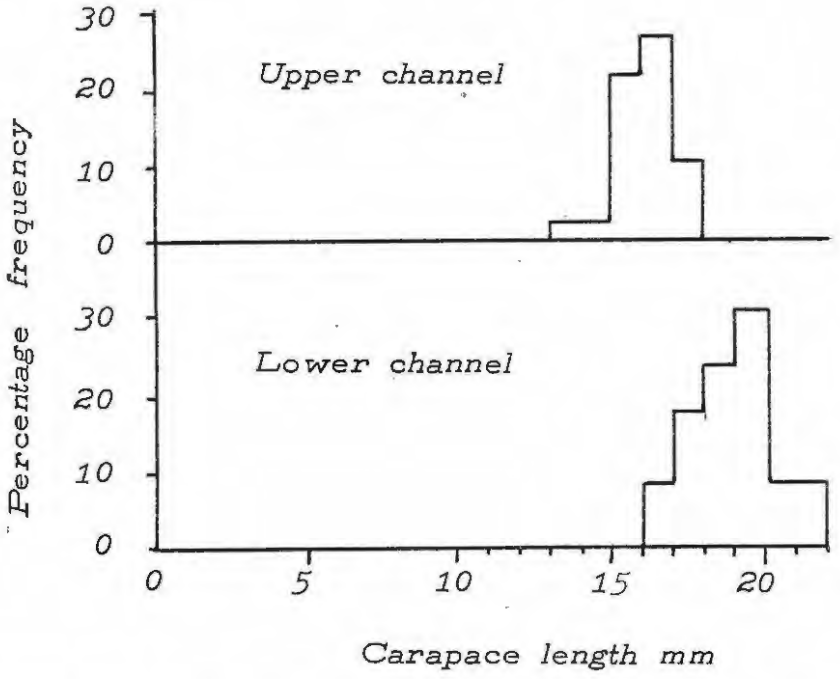

Fig 27: Size frequency composition of prawns from the Upper and lower Channel of the Power Station cooling pond at Knysna.

Although the samples were small there appears to have been a clear size difference, the prawns from the higher thermal regime (Upper Channel) were smaller than prawns from the cooler area (Lower Channel). The deleterious effects of high temperatures on thermal resistance may also be the cause of the smaller size of prawns from the areas of higher temperatures. If high temperature does result in smaller size, this would explain an interesting observation made by Professor J.H. Day on U. africana at Inhambane, namely that "they were only about one third to one half the size of those we have had at Langebaan". Measurements of a sample of 60 prawns collected personally at Langebaan in

September 1965 showed that the size range of prawns was similar to that of prawns from the Kowie estuary. Thus U. africana from a subtropical estuary were considerably smaller than those from temperate regions.

There are two possible causes of the smaller size which is apparently attained at higher temperatures. Firstly that large individuals are less resistant to high temperatures. An experiment has been described above in which the effect of high temperature in relation to size was determined on prawns (see figure 20). Although it was concluded from the experiment that size was not related to temperature tolerance, reference to figure 20 shows that in fact all the largest prawns (greater than 18 mm total carapace) died before 10 hours had elapsed. The MTS for the whole sample was 12.7 hours (see figure 21). It is possible that in a population exposed to high temperatures the prawns die at an earlier age than in a population exposed to a lower temperature regime.

The second possible cause of the smaller size at high temperatures is that the prawns may mature and pass through their life cycle more rapidly. There is some evidence to support this possibility since it was shown above (page 56) that female prawns from the Kowie estuary breed at a slightly smaller carapace length (10 - 10.9 mm) than prawns from the Uilenkraal estuary (11 - 11.9 mm). As already explained it appears that temperatures in the Uilenkraal estuary are lower than in the Kowie estuary. The possibility cannot be excluded that both these causes can operate simultaneously.

It appears from the evidence presented above that U. africana lives well within its thermal limits through most of its geographical distribution. It can survive in areas in which the thermal regime is close to its upper lethal limit but in these cases the high temperatures have deleterious effects. These deleterious effects operate on both the thermal resistance of the prawns and the size which the animals attain.

Experimental Studies on Salinity

Records given above (page 12) indicated that U. africana can live in salinities as low as 15 °/oo. In addition it was shown (page 27) that in times of flooding the prawns would have to withstand salinities of 1 - 3 °/oo for periods of at least a week. The salinity tolerance of U. africana was determined experimentally by exposing prawns to dilutions of sea water and determining the survival. In addition the osmoregulatory ability was studied by means of measurements of the freezing point depression of the blood of prawns which had been kept in various dilutions of sea water. Finally an experiment was carried out to establish whether there is an interaction between salinity and temperature in U. africana.

METHODS

U. africana were collected from the Kowie estuary and transferred to the laboratory using the methods described above (page 58). They were randomised into borosilicate dishes 25 cm in diameter and containing 1.25 litres of medium. The medium was

either sea water (34 - 35 °/oo) collected in the sea at Port Alfred or a mixture of sea water and glass distilled water. The dishes were covered to reduce evaporation and the medium was aerated. Measurements of dissolved oxygen with a Beckman Oxygen Analyzer showed concentrations varying from 7 ppm to 5 ppm. Unless otherwise stated the experiments were carried out in a temperature range of 18 - 20 °C. Experiments involving high temperature utilised the same technique and equipment as described in the temperature section (page 58).

The criterion for determining when death had occurred was the same as in the temperature experiments namely, permanent cessation of scaphognathite beat. Observations were carried out on an increasing time scale as in the temperature experiments.

Freezing point depression (Δ_i) was measured on blood samples withdrawn from prawns which had been kept in various dilutions of sea water. The prawns were carefully dried in a towel and were then held upside down in one hand under a dissecting microscope. The arthrodial membrane at the base of one of the periopods was dried with filter paper and then pierced with a silica capillary containing liquid paraffin. A little paraffin was drawn up to cut off the blood sample from the air. The capillary was put into a larger 'Pyrex' capillary which was closed with sealing wax. Freezing point was measured as soon as possible after collection. However if this was not possible samples were stored in a deep freeze at a temperature of -12 °C. Samples were not stored for longer than 12 hours. Experimental determinations before and after storage for 12 hours showed no significant difference in freezing point.

The freezing point depression of the samples was measured according to the method and using the apparatus described by Ramsay and Brown (1955).

An experiment to determine the effects on the freezing point depression of the blood of prawns after long term exposure to low salinity was also carried out. The apparatus is shown in figure 28. Prawns were kept in an aquarium (30 x 60 cm) containing a 20 cm deep layer of mud collected from the Kowie estuary. Two tides were produced each day in the aquarium by means of an electric pump controlled by a time switch. Considerable difficulty was experienced in obtaining a suitable pump and the one finally used could not be run continuously for longer than one hour. This resulted in a considerably more complex apparatus having to be set up than would have been the case if a better pump had been available.

The electric pump lifted water from the 20 litre reservoir A (figure 28) into a second reservoir B which had a five litre capacity. The pump was self priming as it was positioned below the water level of reservoir A and a one way valve prevented water from siphoning back through the pump when the latter was not running. Water in reservoir B could drain into the aquarium through tap C or via a gooseneck. This gooseneck had an air bleed on the top in order to prevent it from acting as a siphon. All water reaching the aquarium passed through a loose glass wool filter. Water could leave the aquarium via an overflow which drained into reservoir A. A self starting siphon kept water in container D

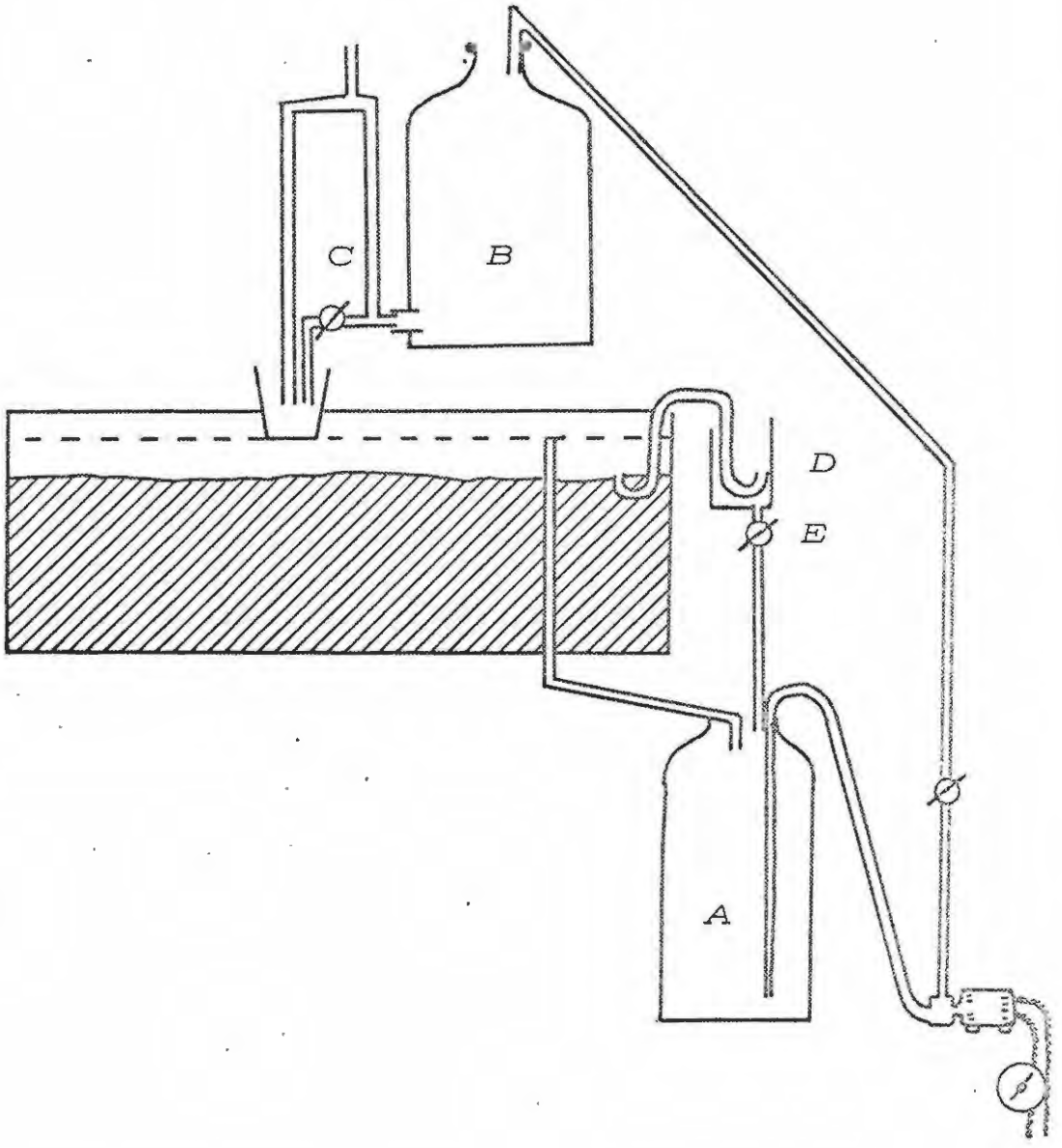

Fig 28: *Tidal aquarium. Explanation in text.*

at the same level as in the aquarium. Water could also drain out of D into reservoir A but it had to pass through tap E in order to do so. The pump body was plastic and all tubing was either glass neoprene or rubber. No metal was allowed to come into contact with the water in the system. A time switch controlled the pump and was set to operate it for one hour every 12 hours.

A typical tidal cycle was as follows: Starting with no water in the aquarium (low tide), the pump was switched on by the time switch. Water was lifted into the upper reservoir (B) at a rate of $\pm$ 1 litre per minute. This flow rate was too high for the tap C to cope with and so the reservoir B filled up and after about 5 minutes overflowed through the gooseneck. The aquarium filled up and overflowed into the bottom reservoir A from where the water was recirculated.

The self starting siphon raised the water in container D to the same level as in the aquarium. Tap E was set so that flow out of D back into reservoir A was extremely slow.

Circulation of water continued for one hour after which the time switch stopped the pump. At this stage reservoir B was full and the aquarium was at the high tide level. Water continued to drain out of reservoir B through tap C but as this was set to run slowly it took about two hours to drain. During this time water left the aquarium via the side container D through tap E. This tap was set to run at about the same speed as tap C, thus water in the aquarium remained high for two hours after the pump switched off. When reservoir B was empty water continued to drain from the

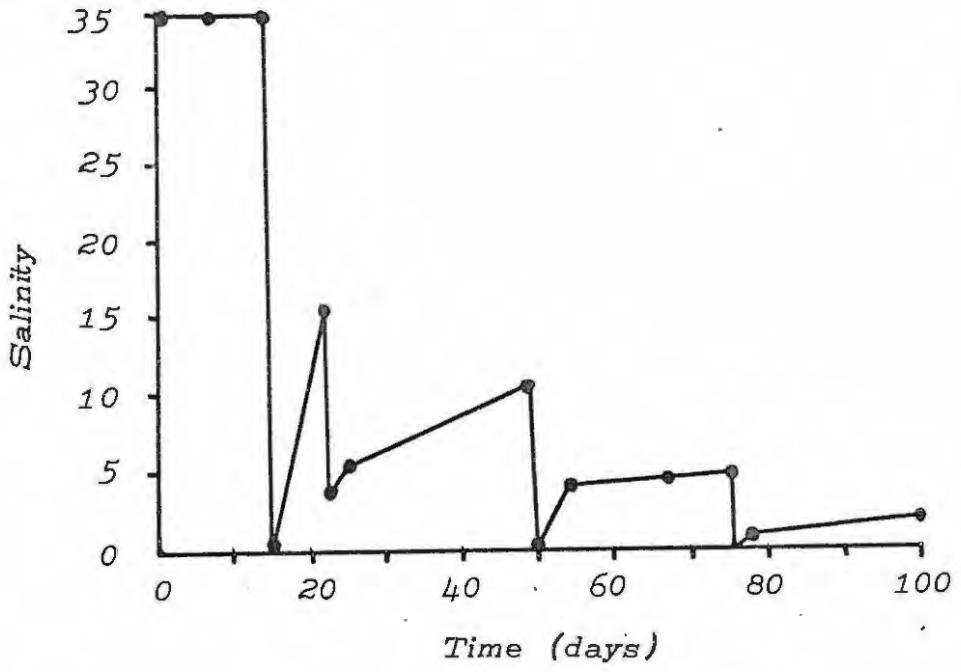

Fig 29: Salinity in parts per thousand in a tidal aquarium over a period of 100 days.

aquarium via the siphon and container D. Because of the slow setting of tap E this took a further two hours. The total effect was a five hour period of high tide followed by seven hours of low tide after which the tide rose once more.

The system was set up in December 1966 and allowed to run for 100 days. Thirty prawns were introduced at the start of this period and they rapidly established burrows. The salinity of the water in the system was reduced by complete replacement with tap water after 15, 23, 50 and 76 days. Samples of water from the aquarium were taken at irregular intervals and the salinity determined by titration. The results are shown in figure 29. Prawns were removed 75 days and 100 days after the commencement of the

experiment and the freezing point depression of the blood was determined.

RESULTS

It was shown above that salinities in the Kowie estuary drop to extremely low values during periods of flooding. Despite this flooding, animals living in the mud are not necessarily exposed to low salinities. Smith (1956) has shown that the salinity of the interstitial water of mud flats may be higher or lower than the water flowing over the mud. In nearly all cases the salinity of interstitial water changes at a much slower rate than the overlying water. The deeper the interstitial water the more constant its salinity.

Animals which live in burrows and pump water through them will be exposed to salinities approaching or equal to that of the overlying water. Thus in cases of flooding U. africana *would be expected to have low salinity water in its burrow. However it is reasonable to expect that if the burrow is in the intertidal zone, salts will diffuse from the interstitial water into the burrow water at low tide.*

In order to obtain some idea of the possible magnitude of this change over the short period of a low tide, a flood was introduced into an aquarium containing mud and prawns in burrows. Tap water was allowed to flow over the mud at a rate of 20 to 30 litres per hour for six hours.

Under normal conditions, as soon as the tide rose in the

aquarium, prawns would retreat to the bottom of the burrows and commence pumping. However when tap water was introduced prawns with burrows next to the transparent walls of the aquarium ceased pumping as soon as the tap water reached them. After a few minutes they pumped for a short period and then stopped again. This intermittent pumping characterised the behaviour of the prawns during the first 30 minutes of the flood. After this period some prawns began to pump and filter feed continuously whilst others repaired or extended the burrows.

At the end of the flood period of six hours the water was turned off and the aquarium was allowed to drain (4 minutes drainage time). A thin plastic tube was then inserted into a burrow and 15 ml of water was siphoned out. This was repeated at irregular intervals for eight hours. The salinity of the samples was determined by titration and the results are shown in figure 30.

As described earlier burrows which are being extended may have an extra passage opening out of them. Water in this passage cannot be pumped out by the prawn as it is a blind tube. Movements of the prawn into and out of the passage will result in some mixing of the water in the passage with that in the burrow. If the passage leads downwards and contains sea water, mixing will be reduced in the event of low salinity water entering the burrow because of the higher specific gravity of the water in the passage. The presence or absence of this passage, which is invisible from the surface will affect the salinity of the burrow. This may account for the one extremely high reading of 24 °/oo obtained in a burrow after six hours (figure 30).

Figure 30 shows that the salinity of the water in the burrows does increase over an artificial low tide. If the salinity increase is due to diffusion of salts from interstitial water into the burrow water, then the area of burrow wall relative to the volume

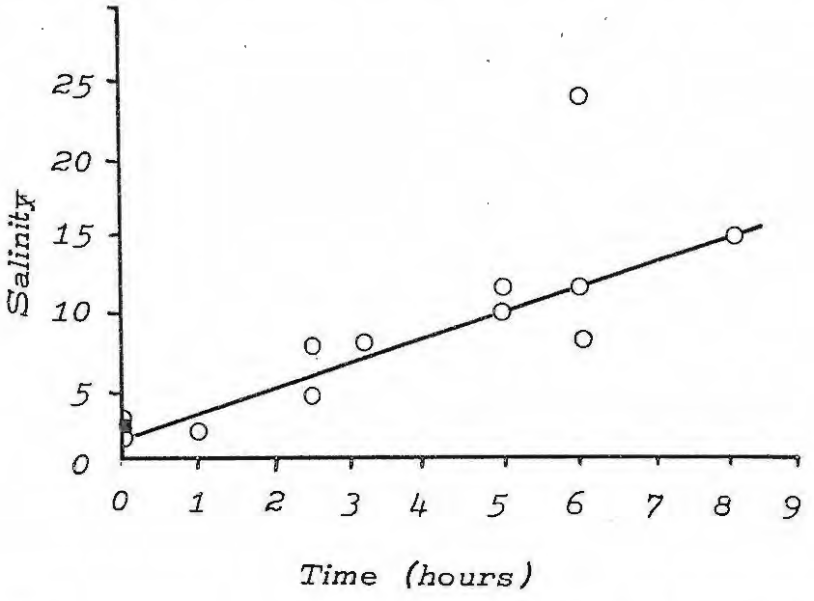

Fig 30: Salinity in parts per thousand of samples of water extracted from burrows in an aquarium after the end of an artificial flood.

of burrow water will be of importance in determining the salinity. The smaller the diameter of the burrow the greater is the surface area of wall relative to the volume of the burrow and therefore the greater the increase in salinity which can be expected.

Figure 30 shows that immediately after the flood had drained away the salinity in the burrows was only 1 - 3 °/oo. This indicates that as long as the flood covers the burrow, salinities inside the burrow will be extremely low. Thus diffusion of salts from the interstitial water into the burrow water is only of importance to prawns living in the intertidal zone at low tide.

As U. africana in the subtidal zone would be exposed to low salinity for about a week in the event of a flood, an experiment

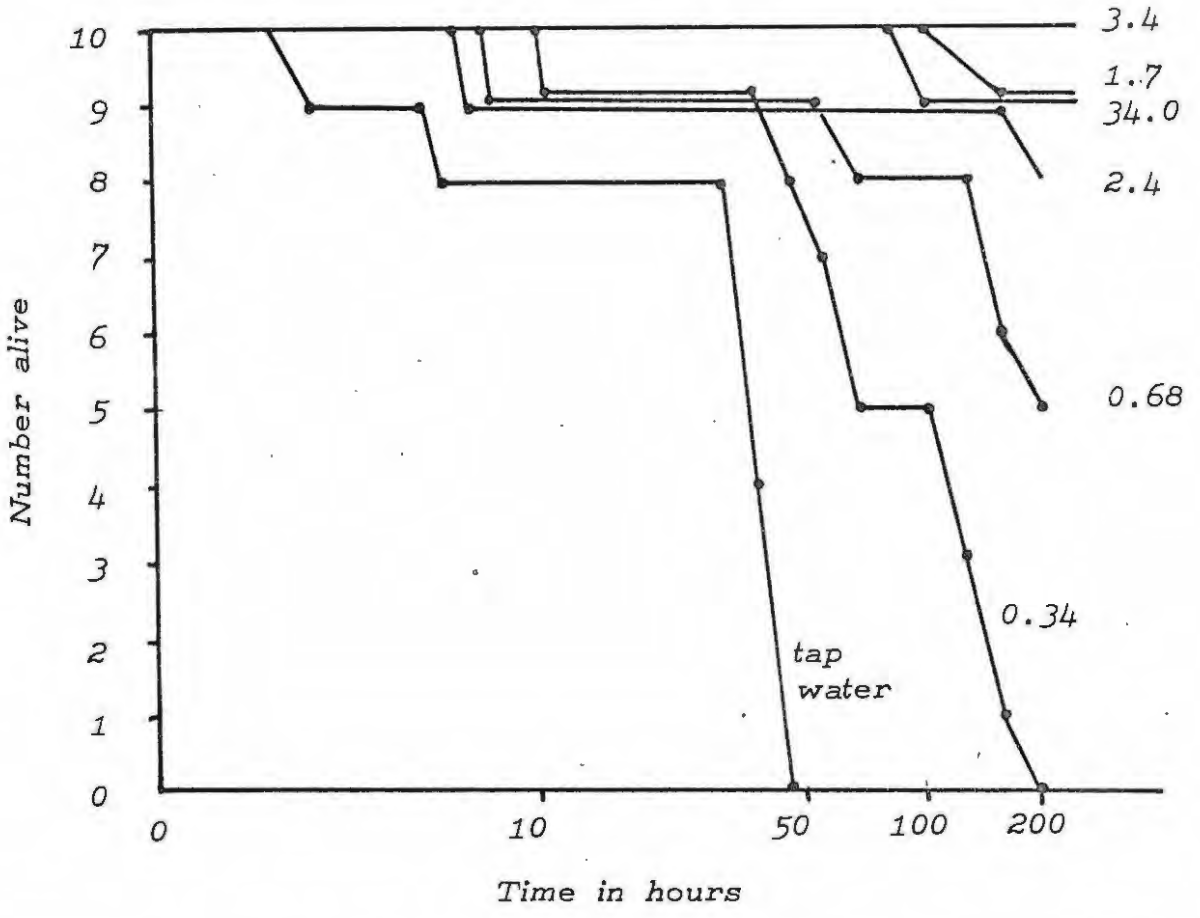

Fig 31: Survival of batches of prawns exposed to a series of salinities. Salinity in parts per thousand is shown next to each survival curve.

was carried out to determine the lowest salinity at which U. africana could survive for eight days (200 hours). The results are shown in figure 31.

Survival in salinities of 34, 3.4, 2.4, and 1.7 °/oo was similar although in 0.68 and 0.34 °/oo and in tap water survival was reduced. A concentration of 1.7 °/oo appeared to be a critical value, below it prawns died fairly rapidly, above it survival occurred

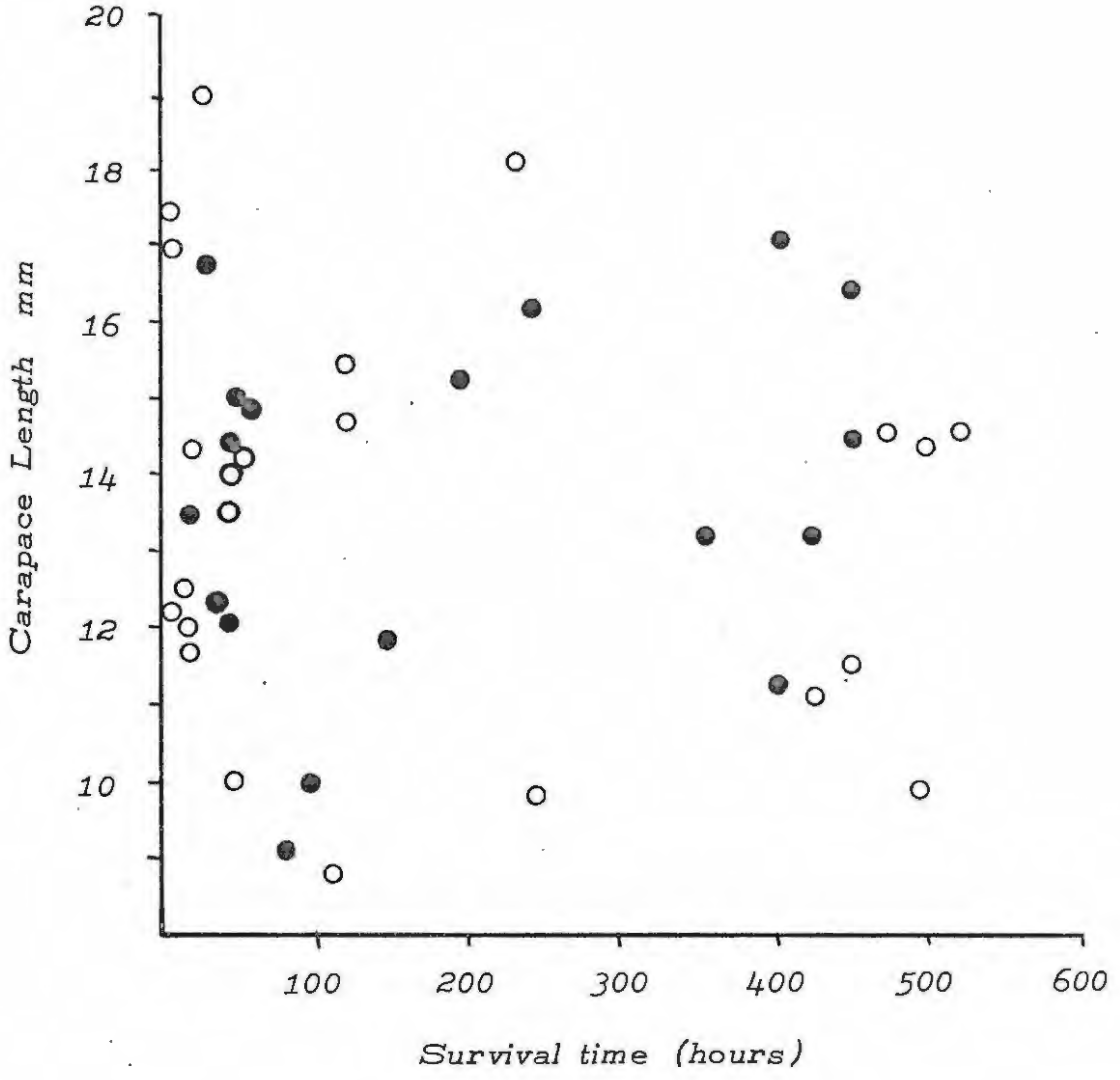

Fig 32: Survival time of males (open circles) and females (solid circles) of various sizes in a salinity of 1.7°/oo.

for at least 200 hours.

In order to establish whether sex and size had any effect on survival at low salinity, a batch of 75 prawns was exposed to this critical dilution of 1.7°/oo. Records were kept of the sex and size of each prawn that died. After 540 hours deaths began to occur in the control group of 37 prawns which had been kept in sea

water and records of sex and size were terminated. The results of this experiment are shown in figure 32 in which the size of each prawn is plotted against its survival time. The sex of each individual is also indicated.

No trend can be observed in the figure and so it was decided that, as in the case of temperature experiments, no attempt would be made to separate males and females or different size groups in the subsequent salinity experiments.

The ability of U. africana to osmoregulate was determined by measuring freezing point depressions of blood samples of prawns collected in August. The prawns were kept in a salinity of 3.4 °/oo for varying periods of time. The temperature during the holding period varied between 15 and 16 °C. The results are shown in figure 33.

Although each point in figure 33 is only derived from a single animal the trend is clear. In sea water Upogebia africana has a Δ_i of 1.65 °C. When the prawns were put into 3.4 °/oo there was a rapid reduction in the osmotic concentration of the blood. After about 20 hours the freezing point depression of the blood reached a stable level of 1.0 °C which was maintained for at least 90 hours. Since the freezing point depression of the medium (Δ_e) was only 0.19 °C, the prawns were maintaining a large osmotic difference between the blood and the medium. They are therefore effective osmoregulators.

The relationship between the concentration of the blood and medium was established by determining the freezing point

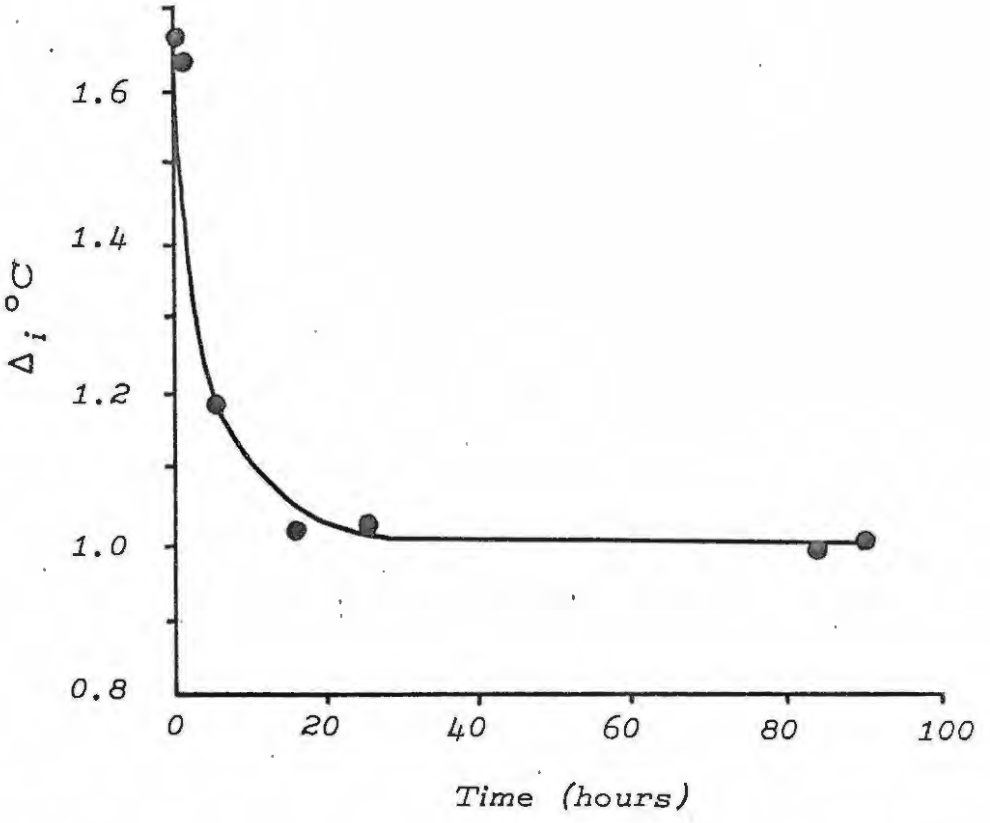

Fig 33: Freezing point depression (Δ_i °C) of blood of prawns after exposure to a medium of freezing point depression 0.19 °C for various periods of time.

depression of blood (Δ_i) of summer prawns which had been kept in a range of salinities. Seven dilutions of sea water were made up and five prawns were put into each. They were kept at a temperature of 20 - 22 °C. After 50 hours samples were withdrawn and the Δ_i and Δ_e determined. The results are summarized in table 8. In addition the Δ_i and Δ_e of two batches of winter prawns kept at 15 - 16 °C in different salinities are shown in table 9.

Table 8: Freezing point depression of the blood of summer prawns after 50 hours exposure to dilutions of sea water.

Δ_e	Max Δ_i	Min Δ_i	Mean Δ_i	Number of observat.
1.91	1.86	1.90	1.87	5
1.47	1.61	1.64	1.62	5
0.97	1.49	1.54	1.52	4
0.49	1.36	1.48	1.43	4
0.14	1.22	1.37	1.31	5
0.10	1.20	1.31	1.28	3
0.02	0.47	0.70	0.57	5

Table 9: Freezing point depression in degrees centigrade of the blood of winter prawns after 50 hours exposure to dilutions of sea water.

Δ_e	Max Δ_i	Min Δ_i	Mean Δ_i	Number of observat.
0.51	1.19	1.03	1.13	4
0.19	1.03	1.00	1.01	4

The Δ_i / Δ_e curve for summer prawns has been plotted in figure 34 and the two values for winter prawns have been superimposed. In summer Upogebia africana was slightly hyposmotic to sea water, but in a salinity of 30 °/oo it was isosmotic. Below this dilution they regulated hyperosmotically. In the salinity range 1.8 - 30 °/oo the internal osmotic concentration as reflected by the Δ_i only changed slightly. This 'plateau' in the Δ_i / Δ_e curve reflects a considerable

degree of independance of environmental salinity. In salinities lower than 1.7°/oo regulation appeared to break down and the Δ_i dropped to the range 0.5 - 0.7°C. The salinity at which this occurred agreed with the critical salinity value found in tolerance experiments described above. In salinities below 1.7°/oo the animals eventually collapsed, the arthrodial membranes swelled out and the prawns died. Thus it appears

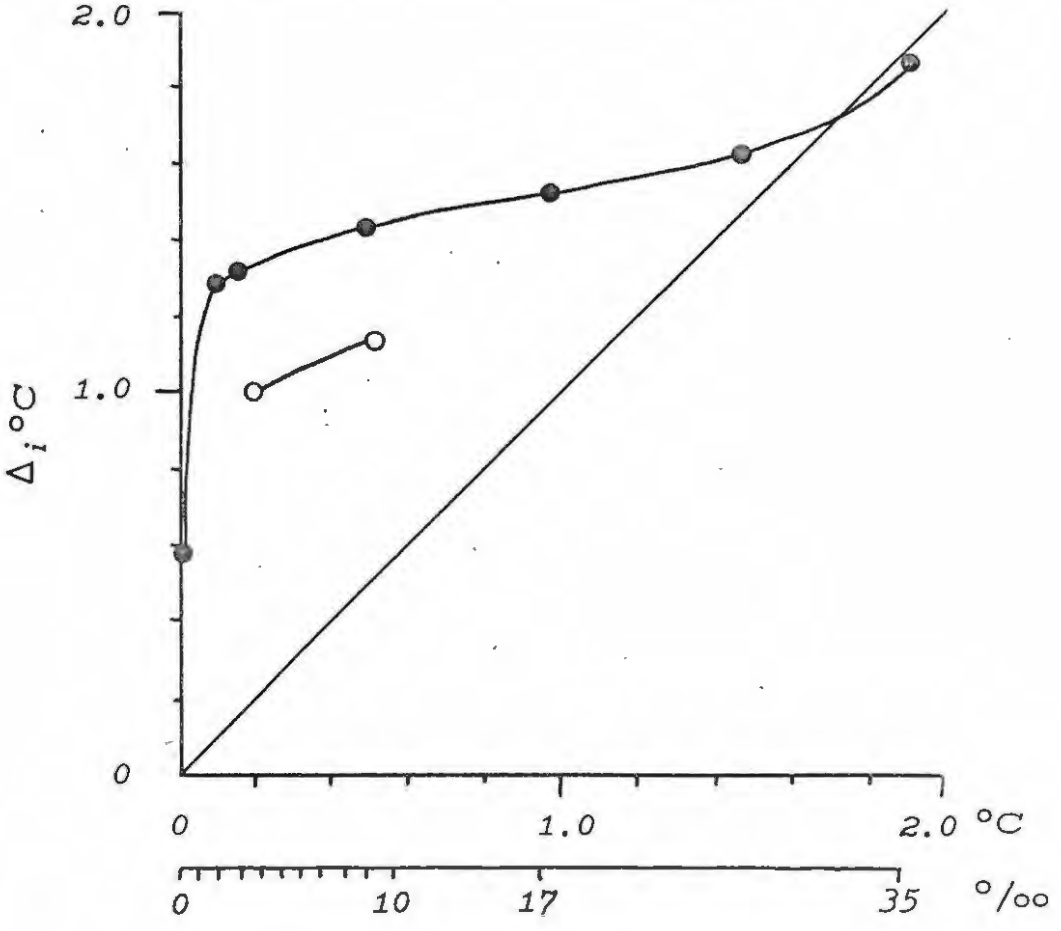

Fig 34: Curve of freezing point depression of the the blood of summer and winter prawns in a variety of salinities.

that *U. africana* can not survive extended periods during which the Δ_i is in the range 0.5 - 0.7 °C.

The two values for winter prawns were well below the Δ_i/Δ_e curve for summer prawns (Figure 34). However the winter and summer measurements were made on prawns which had been held at different temperatures, namely 15 - 16 °C and 20 - 22 °C respectively. The possible effect of temperature on the freezing point depression of the blood was therefore determined.

Five dishes each containing dilute sea water of salinity 0.9 °/oo were kept at different temperatures in constant temperature rooms. Five winter prawns were put into each dish. After 40 hours samples of blood were withdrawn from three prawns in each dish and the Δ_i was determined. The results are shown in table 10 and the means have been plotted graphically in figure 35 in order to facilitate comparison.

Table 10: Freezing point depression of blood of *Upogebia africana* kept at a salinity of 0.9 °/oo at various temperatures for 40 hours.

Temp °C	Δ_e	Δ_i range	Mean Δ_i
9	0.48	0.70-0.85	0.79
15	0.48	1.04-1.15	1.10
21	0.49	1.03-1.48	1.25
24	0.47	1.06-1.47	1.29
28	0.45	1.33-1.57	1.45

The results given in table 10 and in figure 35 show evidence of a temperature effect on the freezing point depression of the blood since in the temperature range 9 - 28 °C the

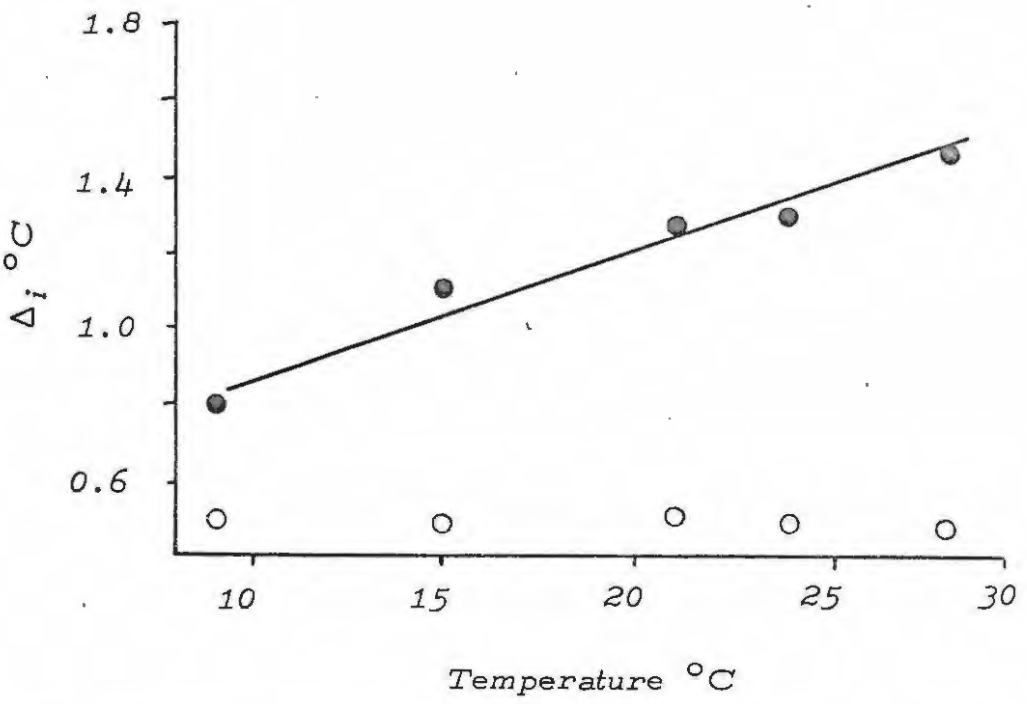

Fig 35: Freezing point depression (Δ_i °C) of blood (solid circles) extracted from prawns kept at different temperatures in low salinity, the freezing point depression of the medium in each case is shown as an open circle.

freezing point depression of the blood nearly doubled. The figure shows a difference of 0.2 °C between the Δ_i of prawns at 15 °C and those at 21 °C. This is not quite as large a difference (0.3 °C) as apparently exists between winter and summer prawns. However it appears reasonable to ascribe the difference in Δ_i between winter and summer prawns to temperature. The significance of this difference will be discussed when dealing with temperature/salinity relations.

In figure 33 it was shown that once prawns had adjusted to a change in the dilution of the medium, the Δ_i remained constant for at least 90 hours. However if prawns

are subjected to low salinity for a long period they might have a completely different Δ_i. In order to test this possibility, twenty prawns were kept in an aquarium in which the salinity was lowered over a period of three months. The apparatus was shown in figure 28 and the salinity changes in the aquarium were recorded in figure 29.

Seventy five days after commencement of the experiment five prawns were removed from the aquarium and the Δ_i was measured. The results are given in table 11 under specimens A. In order to establish whether U. africana can increase its Δ_i when placed in a more concentrated although still hyposmotic medium, four other prawns were transferred to 17°/oo at the same time. After 100 hours in this medium the Δ_i of these prawns was measured and is given in table 11 under specimens B. In the meantime the medium in the aquarium had been further diluted (see figure 29). One hundred days after the start of the experiment the single surviving prawn was removed from the aquarium , the Δ_i of this individual is given in table 11 under specimen C.

Table 11: Freezing point depression of blood of prawns after long term exposure to low salinity.

Specimens	Δ_e	Δ_i range	Mean Δ_i
A	0.31	0.92-1.00	0.97
B	0.94	1.00-1.46	1.22
C	0.11	0.91	0.91

As the experiment ran over the period 14th November to 31st March, it is reasonable to compare the results with those

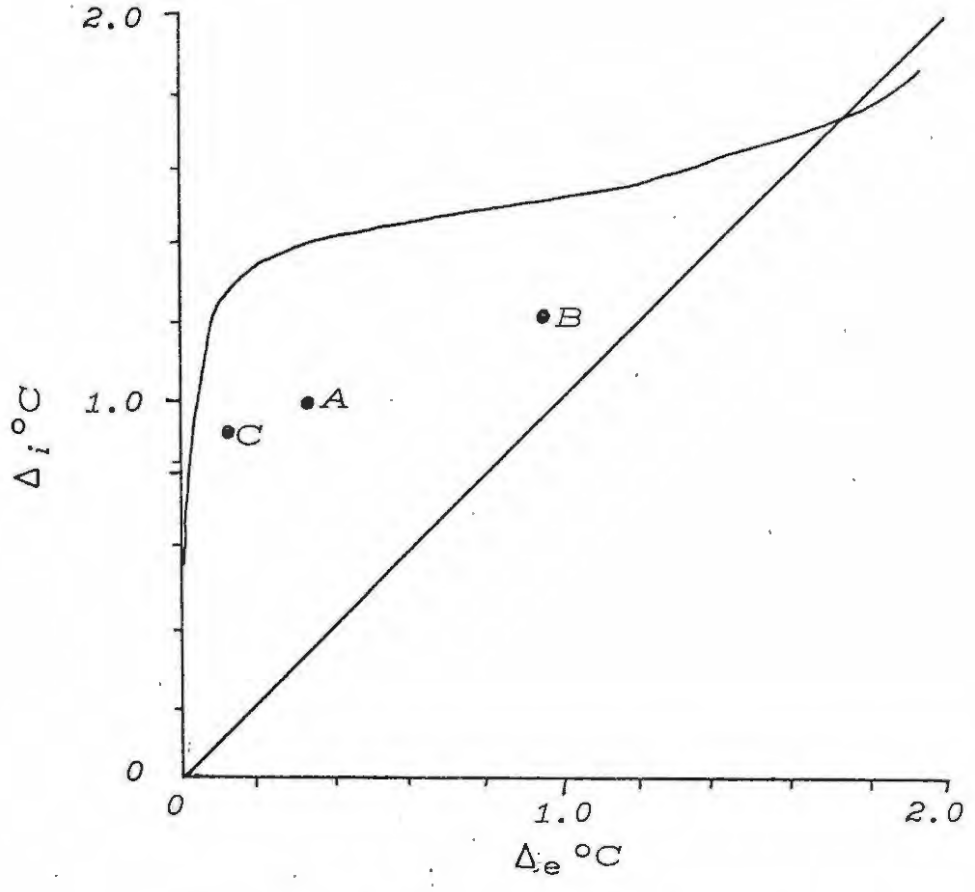

Fig 36: Δ_i/Δ_e *cruve of summer prawns compared with prawns which have been kept in dilute sea water for long periods of time. Fox explanation see text.*

obtained from summer prawns. In order to facilitate this the means in table 11 have been plotted graphically together with the Δ_i/Δ_e *curve of summer prawns in figure 36. The figure shows that the blood of prawns which have been exposed to low salinity for a long period of time had a lower* Δ_i *than that of prawns in the same concentration for 90 hours.*

At low salinities there is a large difference between the osmotic concentration of the blood and the medium. In the

case of short term exposure the osmotic work necessary to maintain this difference is probably outweighed by the advantage of providing a fairly constant internal environment for the tissues. However in the case of long term exposure to low salinity, it would probably be advantageous to reduce the amount of osmotic work. Potts (1954) showed that the most important means whereby a marine animal entering brackish water can reduce the strain upon its osmoregulatory mechanism is by reducing the concentration of its blood. He demonstrated that a small reduction in the difference between internal and external concentration results in a large scale saving of metabolic work. Potts calculated that in the crab Eriocheir in fresh water a fourfold increase in blood concentration would require twenty four times as much work to maintain. In the light of this evidence it is reasonable to assume that the low freezing point depression of specimens A and C in figure 36 represents a drop in internal osmotic concentration in order to reduce the amount of osmoregulatory work.

The freezing point depression of blood of prawns which were transferred to 17°/oo after one month at 5°/oo was shown in table 11 for specimens B. One of these prawns had virtually the same Δ_i as was found in the prawns in 5°/oo. However this prawn had just moulted and was in a 'soft shell' condition when the blood sample was taken. This might have affected the Δ_i. The Δ_i of the other three prawns was higher in 17°/oo than in 5°/oo despite the fact that the prawns were

hyperosmotic to the medium (figure 36 point B). This increase in osmotic concentration is clear proof of an active uptake of salts either from the medium or from the food.

Moulting and Low Salinity

In an experiment described above (page 100), 75 prawns were kept in a salinity of 1.7 °/oo and the survival was recorded. The experiment was finally terminated after 690 hours owing to deaths in the control. If the probits of percentage survival of the experimental and control prawns is plotted against time (on a logarithmic scale) the curve shown in figure 37 is obtained.

During the course of the experiment the first moult in 1.7 °/oo occurred after 339 hours and the newly moulted prawn died at 355 hours. Thereafter every death in 1.7 °/oo was associated with moulting, either at ecdysis or within 24 hours of ecdysis. In contrast 26% of the control prawns in sea water had succesfully moulted before 350 hours. No deaths occurred in the control before 540 hours by which time 43% had succesfully moulted.

The curve of survival in figure 37 shows a distinct change of slope at approximately 350 hours. This change in slope or split probit indicates that there were probably two causes of death in the experiment, one operating before 350 hours and one after this time. The time corresponds almost exactly

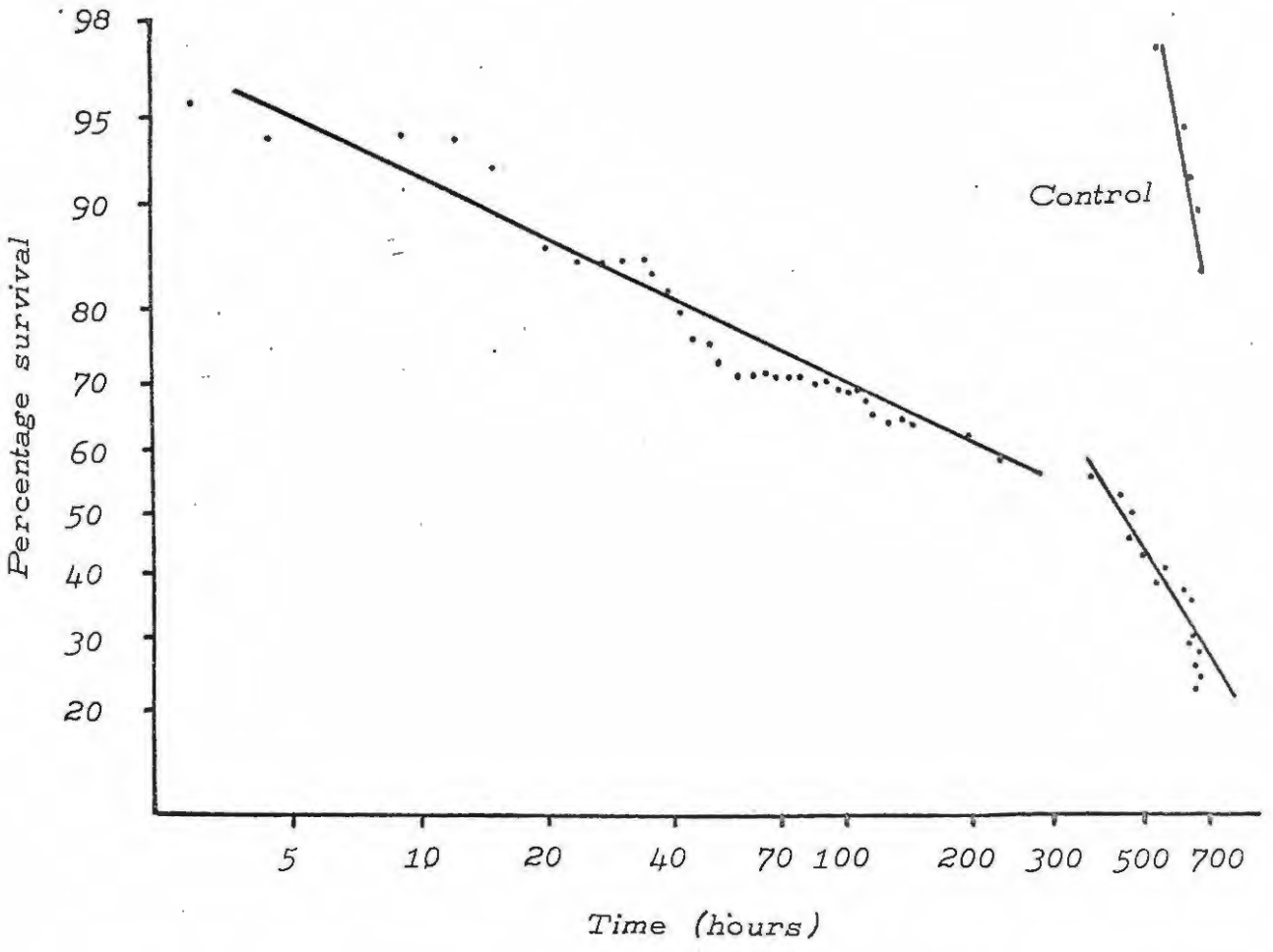

Fig 37: Percentage survival (on a probit scale) of prawns in 1.7°/oo. Control was in sea water.

with the time of 355 hours at which the first moulting death occurred, and as stated above every death in 1.7°/oo after 355 hours was associated with moulting. Thus in figure 37 the change in slope of the curve after 350 hours was a result of the death of newly moulted prawns. Deaths up to 350 hours were probably due to animals succumbing to the general osmoregulatory stress resulting from the low salinity.

Upogebia africana apparently could not survive a moult in a salinity of 1.7°/oo although it could live in this dilution for long periods (Median time of survival 430 hours). In addition it appears that since 26% of the control prawns in sea water had succesfully moulted before the first moult in 1.7°/oo, moulting is delayed in low salinity.

The lowest salinity at which moulting can succesfully occur was determined by keeping four samples of prawns at different salinities. A record was kept of all moults for a period of 50 days. If the moulted prawn survived, the moult was classified as successful. The results have been summarised as follows:

Salinity °/oo:	34	17	8.5	3.4	
1st moult after:	2	2	17	17	days
Total successes:	12	10	7	3	
Total attempts:	13	10	8	5	

The results show that Upogebia africana moulted successfully in salinities down to 3.4°/oo, although two of the five attempted moults in this salinity failed. The number of prawns which attempted to moult in low salinities was less than in higher salinities. In 3.4°/oo only five out of the sample of 18 (28%) had moulted after 50 days, whereas in full sea water thirteen of the 18 (72%) had moulted. This appears to confirm the observation made in an earlier experiment that moulting is delayed in low salinity.

In the experiment involving exposure of prawns to 1.7°/oo (page 110), many of the prawns which moulted, died

within 24 hours of ecdysis. Apparently sensitivity to low salinity was not limited to the actual period of ecdysis but extended for some time afterwards. It was decided to test the sensitivity of newly moulted prawns by transferring them to a lethal salinity (0.3 °/oo) and determining their survival times. Three categories of newly moulted prawns were used. Firstly those prawns which just undergone ecdysis. These prawns would be expected to be at maximum sensitivity to low salinity. Secondly prawns 24 hours after ecdysis. This time was chosen since it was pointed out above that prawns in 1.7 °/oo died within 24 hours of ecdysis. Thirdly prawns 100 hours after ecdysis in order to establish whether after this period they would still be more sensitive to low salinity than intermoult prawns. Prawns which survived transfer to 0.3 °/oo for 48 hours were classified as surviving. The MTS of intermoult prawns in 0.3 °/oo is 60 - 100 hours (figure 31). A control of newly moulted prawns were transferred to 7 °/oo. The results are given in table 12.

Table 12: Survival of newly moulted prawns after transfer to 0.3 °/oo.

Number of prawns tested	Hours after ecdysis	Result
6	0	All died, MTS 2.7 hr
5	24	All died, MTS 7.8 hr
5	100	Four survived
4 (control)	0	All survived.

Clearly prawns were more sensitive to low salinity just after ecdysis. After 24 hours the MTS had increased from 2.7 to 7.8 hours, indicating that the animals were slightly more

resistant probably due to increasing impermeability of the new cuticle. Nevertheless 24 hours after ecdysis U. africana was still extremely sensitive to low salinity. One hundred hours after ecdysis this sensitive phase had passed and the prawns were presumably as resistant as intermoult prawns.

It is well known that at ecdysis decapod Crustacea take up water through the gut in order to increase their total volume. For example Robertson (1937) found that a 50 gm Carcinus absorbed about 35 gm water at moult. Cancer showed a ninefold increase in blood volume during ecdysis (Drach 1939). If the crustacean is hyperosmotic to the medium this uptake of medium should cause a decrease in osmotic pressure of the blood.

Upogebia africana is hyperosmotic in dilute sea water. The effect of moulting on the Δ_i was determined on two prawns which had been kept in 19°/oo (Δ_e 1.0°C). Blood samples were withdrawn within one hour of ecdysis. The freezing point depressions were as follows: 1.22° and 1.27°. Intermoult prawns in this medium have a Δ_i of 1.5°C. Thus the blood of newly moulted prawns had a lower freezing point depression and therefore a reduced osmotic pressure as compared with intermoult prawns in the same salinity. The figures show that at ecdysis the Δ_i dropped to a value halfway between that of the medium and the Δ_i of intermoult prawns.

It was shown earlier that U.africana could not survive a moult in 1.7°/oo. Figure 34 shows that prawns in 1.7°/oo

(Δ_e 1.0 °C) are extremely close to the point at which osmoregulatory breakdown occurs. Presumably this breakdown is the result of an inability to extract sufficient salts from the medium or to cope with the passive inflow of water into the body. Thus when prawns moulted in 1.7 °/oo the increased permeability of the cuticle at ecdysis probably resulted in a flooding of the internal medium. This would cause a drop in Δ_i which would be accentuated by the takeup of dilute medium at ecdysis. The result is a drop in the Δ_i, possibly to the lethal range 0.5 - 0.7 °C with consequent death.

Three out of five prawns survived a moult in 3.4 °/oo (page 112). At this salinity the medium is twice as concentrated as at 1.7 °/oo and this difference is apparently sufficient to enable some prawns to cope with the drop in Δ_i which occurs at ecdysis.

The freezing point depression of blood which results when prawns take up medium at ecdysis will depend upon the Δ_i before ecdysis as well as upon the volume of medium which is taken up. At present nothing is known of either of these two values in U. africana since great difficulty was experienced in trying to predict when moulting would occur. In addition after the animals had been handled in order to extract blood samples, moulting was postponed. Other decapods appear to increase the body weight by over 50% at ecdysis. Baumberger and Olmsted (1928) found that one hour before ecdysis the osmotic pressure of the blood of the crab Pachygrapsus crassipes

increased to nearly double the intermoult value. This increase could result in a much higher Δ_i when the crabs moulted in dilute media than if no increase occured before ecdysis. It is hoped to investigate pre-ecdysial changes in the blood of U. africana at a later date.

When prawns were exposed to 1.7°/oo it was found that the first moult occurred after 339 hours. By this time 26% of the control prawns which were in sea water had already moulted. On the basis of this evidence it was suggested that moulting was delayed in low salinity. In another experiment described above (page 107), four prawns were transferred to 17°/oo after having been kept at 5°/oo for a month. Three of these four prawns moulted within four days of transfer. This result appears to support the suggestion that moulting in U. africana is delayed when conditions are unfavourable.

A delay due to unfavourable conditions has been shown to exist in a number of Crustacea including crabs and hermit crabs. However salinity has not apparently previously been reported to have this effect. For example Passano (1960) reviewed moulting in Crustacea and stated that salinity does not appear to influence moult initiation. It is unlikely that Upogebia africana is the only crustacean in which moulting is inhibited by salinity. Investigation of other crustaceans is obviously necessary in order to establish whether a salinity inhibition occurs.

Interaction between Temperature and Salinity

The experiments on temperature and salinity tolerance were carried out with only one stress factor, for example high temperatures in sea water, or low salinity at moderate temperatures. Both temperature and salinity were shown to act as separate independant limiting factors but the limits of survival may be narrowed if animals are subjected to the double stress of simultaneous high temperature and low salinity. This was determined experimentally in two ways, firstly by exposing prawns to a range of salinities at a lethal temperature, and secondly by keeping prawns at a low salinity in a range of temperatures.

The method used in these experiments was the same as described in the temperature tolerance experiments, namely that randomised samples of prawns were kept in glass dishes which were heated and stirred. Records were kept of survival, the results were plotted on probit/log paper and the median times of survival (MTS) for each experiment were derived from the resultant curves.

Prawns collected in summer (December) were divided into batches of 26. One batch was then put into each of the following salinities: 34.5; 26; 17; 8.5; 3.4; and 1.7 °/oo. They were left in this dilution at 21.8 °C for 19 hours after which the water was replaced and the temperature raised to 34 °C. The MTS values were as follows:

Salinity °/oo	MTS in hours
34.5	20.5
26.0	32.0
17.0	11.0
8.5	9.25
3.4	5.5
1.7	3.5

The prawns in sea water had a MTS of 20.5 hours which agrees with the results of other temperature experiments (see figure 23). Any marked deviation from this time must have been due to the effects of low salinity. Survival in a salinity of 1.7 °/oo at 20 °C is more than 100 hours (see figure 31). Any deviation from this value must have been due to a combination of the effects of temperature and salinity.

The results show that prawns survived longer in 26 °/oo than in full sea water. Measurements of the freezing point depression of the blood have indicated that in the salinity range 26 to 7 °/oo, the blood concentration of summer prawns remains nearly constant (see figure 34). This plateau probably represents some form of optimum internal concentration. Prawns in sea water have an internal concentration 20% higher than this apparent optimum. It is suggested that this departure from the optimum results in a lowered resistance to high temperature.

As the medium is diluted below 26 °/oo the difference between the Δ_i and the Δ_e increases. This probably increases the stress on the osmoregulatory mechanism and presumably at lethal temperatures an increase in osmotic stress results in a lower survival time. Thus the MTS in increasing dilutions show a shorter survival time in lower salinity.

The effect of temperature on salinity tolerance was determined by exposing prawns in dilute sea water to a wide range of temperatures. The experiment was repeated at four different salinities, namely 0.17, 0.5, 1.7, and 34.5 °/oo. Twenty four batches of prawns were tested. In the six experiments at 0.17 °/oo, 23 prawns were used in each batch. In all other experiments a minimum of 30 and a maximum of 34 prawns were used. As only six heater/stirrers were available these experiments could not be carried out simultaneously. In the case of prawns exposed to 1.7 and 34.5 °/oo, periods of three to four weeks were required to complete individual tests. As a result the experiments were necessarily spread over a considerable period of time. The experiments in 1.7 and 0.5 °/oo were carried out from July to October 1967. Experiments in 0.17 °/oo were performed in February. Half of the tests in 34.5 °/oo were done in February, the other half in August. Thus the four parts to the experiment were carried out with prawns from different temperature backgrounds. However the highest temperature used was 30 °C which in earlier experiments (see figure 23) was shown to result in a similar MTS for both winter and summer prawns.

The results of all the experiments are shown in figure 38 in which the MTS derived from the probit of percentage survival/log time curve has been plotted against time. As median survival times varied from 6.5 to over 800 hours it was necessary to use a log time scale.

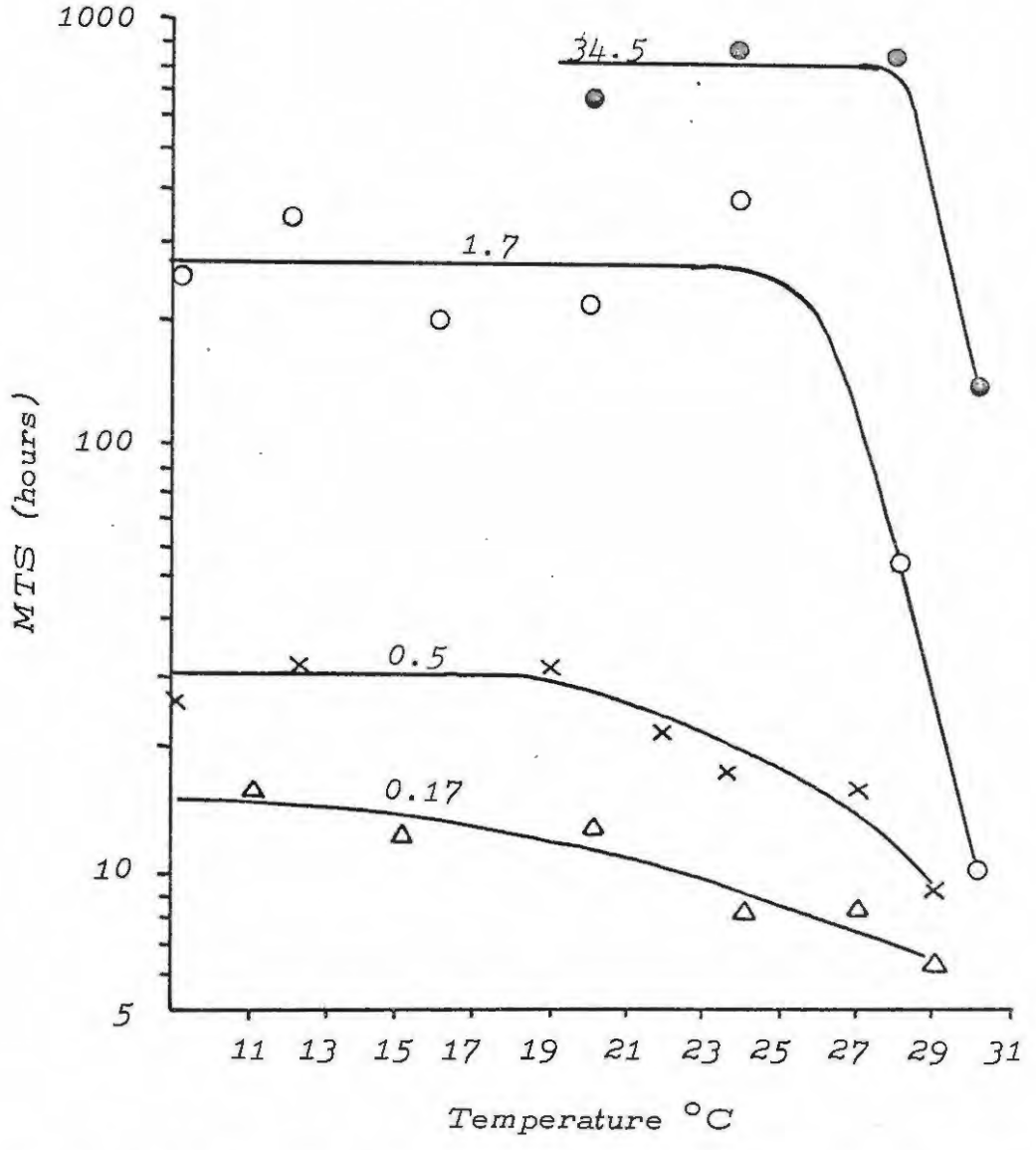

Fig 38: Median times of survival of batches of prawns kept in a series of salinities at a range of temperatures. The salinity (in parts per thousand) of each test is shown next to the respective curve.

Survival at 1.7 °/oo appeared to be temperature independant except in the range 26 - 30 °C. At 28 °C the MTS was only 53 hours as compared to 370 hours at 24 °C. Thus the low salinity appears to have reduced the upper lethal temperature. Mcleese (1956) in Kinne (1964) found a similar effect in the lobster Homarus americanus.

Figure 38 shows that in 0.17 °/oo there was a definite decrease in survival time with increasing temperature over the entire temperature range of 11 - 29 °C. This was also found in 0.5 °/oo except that it was only evident in temperatures above 19 °C.

Discussion of the Temperature Salinity Interaction

Survival of U. africana exposed to very low salinities was apparently dependant upon at least two separate factors. One of these was temperature dependant and its effect was clearly seen in survival at 0.17 °/oo over the entire temperature range. The effect of this factor was partially obscured by a second factor which was temperature independant. Thus in 0.5 °/oo temperature dependance was only seen in temperatures above 20 °C. At even higher salinities such as 1.7 °/oo and 34.5 °/oo, temperature effects were not evident except near the lethal temperature.

In an earlier experiment it was shown that the Δ_i of blood of prawns in a salinity of 0.9 °/oo was temperature dependant (figure 35). The higher the temperature to which

the prawns were exposed the higher the Δ_i. This fact appears to conflict with the results of the temperature/salinity experiments. Since prawns are able to osmoregulate better at high than at low temperatures, they should be able to survive for longer periods at high temperatures than at low temperatures in the same low salinity.

Lockwood (1960) found that in the isopod Asellus aquaticus, an increase in temperature resulted in an increase in the concentration of the blood. He showed that the rate of active Na uptake is directly related to temperature, whereas the rate of passive Na loss is apparently temperature independant. Since the passive loss of Na mentioned by Lockwood is due to a diffusion phenomenon it cannot be completely temperature independant but the methods used by Lockwood were of necessity not critical enough to show this dependance. However in Asellus the effect of temperature on passive Na loss is apparently negligible. Lockwood pointed out that in Asellus a rise in temperature caused an increase in Na uptake whilst the Na loss remained the same, resulting in a higher Na content. He tentatively suggested that this effect might explain the penetration into fresh water in the tropics of animals limited to brackish water in temperate regions, since at higher temperatures the animals would be able to maintain a higher internal concetration.

Lockwood further reported that in Gammarus duebeni the opposite condition exists. The temperature co-efficients of loss and uptake of sodium bear an inverse relationship to

those found in Asellus. Thus it would be expected that G. duebeni would be capable of withstanding low salinity better at low temperatures. This has been confirmed by Kinne (1959) in Lockwood (1960).

However in U. africana a conflicting situation appears to be present. The freezing point depression of the blood increased with rising temperature as in A. aquaticus but survival in low salinity was not greater in high temperatures. Indeed in the case of 0.17 °/oo increasing temperature caused decreasing survival, that is a condition comparable to Gammarus duebeni.

A possible explanation lies in the fact that both Asellus aquaticus and Gammarus duebeni can live in fresh water and must have mechanisms to cope with extremely low environmental concentrations. Upogebia africana on the other hand cannot survive for long at concentrations below 1.7 °/oo. In salinities below 1.7 °/oo although the osmoregulatory mechanism was probably operating at its limit, the passive loss of salts exceeded the active uptake and there was a net loss. If the temperature was raised both rates probably increased and the net loss was more rapid with a resultant rapid drop in the osmotic concentration of the blood. Thus the higher the temperature the shorter was the survival time.

In contrast Asellus can cope with low concentrations and if the temperature is raised the possible increased passive loss will be compensated for by an even greater active uptake.

In salinities of 1.7°/oo and higher, the osmoregulatory mechanism of U. africana is able to maintain the Δ_i above lethal levels although it may vary with temperature. Survival in salinities above 1.7°/oo was thus apparently temperature independant. Thus in general, in Crustacea the effect of temperature on diffusion rates may be obscured by the much greater effect temperature has on active uptake.

Although as shown above, temperature has very little effect on survival in non-lethal salinities, salinity can have a large effect on survival at high temperatures. The cause of this difference almost certainly lies in the way in which osmoregulatory breakdown or high temperature causes death.

The cause of death at high temperature in U. africana is not known. However from what is known of other animals it is probably a multiple effect due to inactivation of enzymes, increasing permeability of cell membranes, protein precipitation or release of toxic substances by cells (Prosser and Brown 1962). The temperatures at which these effects cause death are usually extremely specific and this specificity results in great sensitivity to slight increases above the lethal temperatures. It has already been shown that winter prawns at 30°C have a MTS of 135 hours. At 1° higher the MTS is only 13 hours (see figure 23). At temperatures below lethal biological processes are not drastically affected by temperature changes and in the case of U. africana survival at a salinity of 1.7°/oo

and higher was not temperature dependant except in the region of the lethal temperature. The result is that salinity tolerance in U. africana tended to be temperature independant.

On the other hand, lowering salinity results in an altered blood concentration. This must affect nearly every cell and metabolic function since it alters the medium which surrounds the tissues. Thus a decrease in salinity would be expected to have a general overall effect on those processes which are heat sensitive. The result is that as the salinity is lowered the resistance to high temperature changes and and so temperature tolerance becomes salinity dependant. This was illustrated by the changes in the apparent upper lethal temperature seen in figure 38.

The survival of prawns in 34.5 °/oo showed a marked decline at temperatures greater than 29 °C. Thus the upper lethal temperature in sea water is in the region of 29 °C (cf page 73). In 1.7 °/oo the upper lethal temperature appeared to be in the vicinity of 26 °C. At 0.5 °/oo the upper lethal temperature had apparently dropped to 19 °C and at 0.17 °/oo it appeared to be even lower. Thus the lower the salinity the lower the upper lethal temperature.

Clearly 1.7 °/oo represents a critical salinity to U. africana. Below 1.7 °/oo prawns can only survive for short periods of time due to osmotic stress. In addition at this salinity they become more sensitive to high temperature due to the interaction of salinity and temperature.

In the tropics heavy rainfall results in most estuaries having reduced salinities at least in the rainy season, for example Lagos Lagoon (Webb 1958). In the case of U. africana the increased temperatures of the tropics would not result in greater salinity tolerance, but the lowered salinity would cause a decreased temperature tolerance. As has already been shown the temperature tolerance of U. africana is not very great, the upper lethal temperature lying in the region of 29°C. It can be concluded that U. africana unlike many Crustacea, should not be capable of entering lower dilutions in the tropics than in temperate regions. The distribution of U. africana appears to support this conclusion since it is not found in the tropics.

Experimental Studies on Respiration

It has been shown above that U. africana periodically irrigates its burrow even when not engaged in feeding activities. Presumably this irrigation serves to renew burrow water which has been used for respiratory purposes. It was decided to determine the amount of oxygen which U. africana takes and to determine the effects of temperature and salinity on this uptake in order to supplement information on the effects of these two factors.

Prawns in the intertidal zone cannot irrigate their burrows at low tide. It was found during the course of field studies that the oxygen content of the burrow dropped during

periods of low tide. This finding led to a study of the ability of U. africana to extract oxygen from low oxygen tensions and the behaviour at low tide.

METHODS

Oxygen content was determined on samples of burrow water by using Ohle's iodine difference modification to the standard sea water Winkler. This modification is recommended by Barnes (1959) for estuarine water in order to eliminate errors which might arise from the presence of reducing substances in the water. As the volume of water which can be extracted from a burrow is small, only 35 ml sampling bottles were used.

In the laboratory the oxygen uptake of U. africana was determined in a flowing water respirometer utilising a Beckman Model 777 Laboratory polarographic oxygen analyzer and sensor. Ripplinger and Herold (1966) compared oxygen uptake by snail heart using polarographic and manometric techniques. They found that the two methods gave comparable results and concluded that polarographic techniques could be satisfactorily used in experimental physiology.

The respirometer used in determinations on U. africana is shown in figure 39. Prawns were put into chamber A and water from reservoir B was allowed to flow through the chamber. The rate of water flow was shown by the flowmeter C and controlled by a needle valve D. The oxygen content of water in B could be varied by bubbling nitrogen or air through

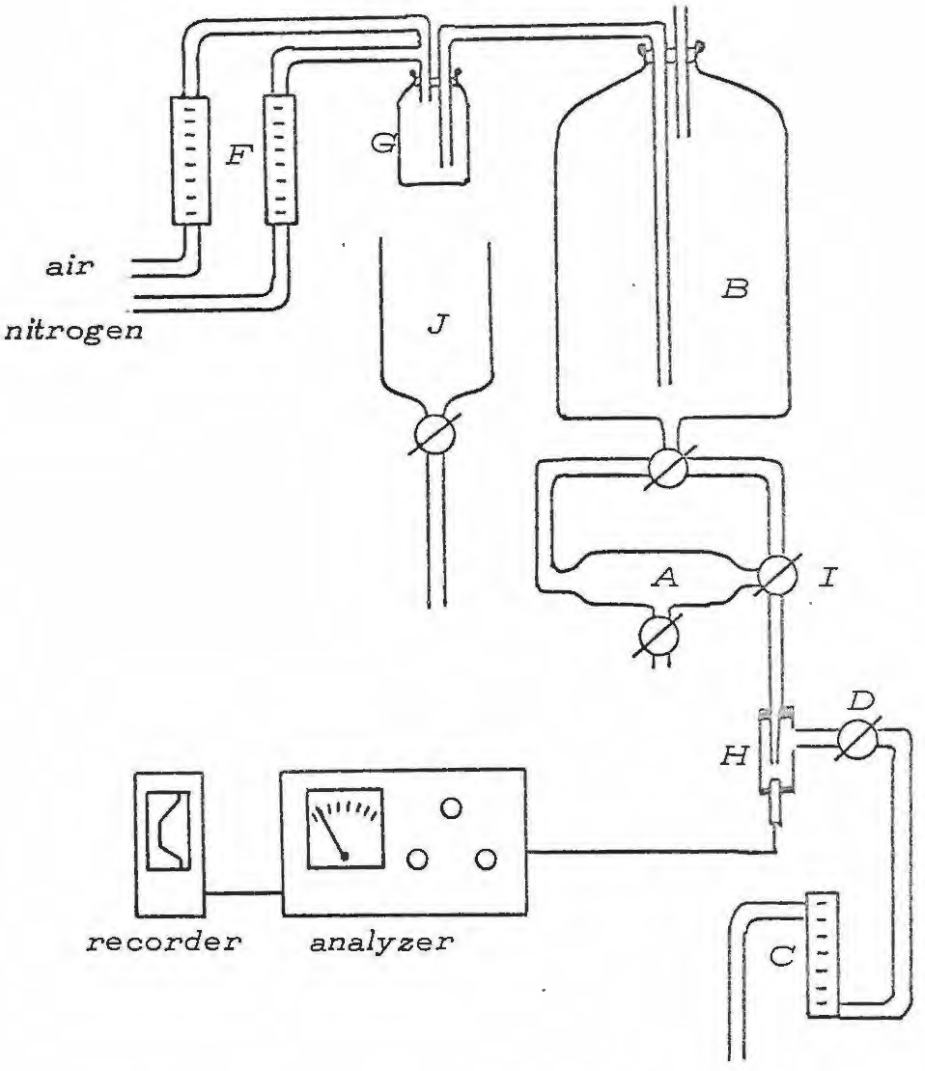

Figure 39: Respirometer used for measuring oxygen uptake by U. africana. A chamber for prawns; B supply reservoir; C and F flowmeters; D needle valve; G manifold for mixing air and nitrogen; H oxygen sensor; I three way valve; J alternate supply of water.

it. Air was obtained from a laboratory air line and nitrogen from a cylinder of the compressed gas. Air and nitrogen flow was controlled by valves and flow rate was indicated by flowmeters F. Nitrogen and air could be mixed in manifold G. The oxygen content of the water was measured by the Beckman sensor at H. This sensor required a fairly rapid movement of water past its tip. It was therefore inserted into a small 'Perspex' chamber with a glass jet placed centrally above it. Water flowing through the system was squirted through the jet onto the sensor. It was found that readout of oxygen was independant of flow rates above 850 ml/hour when this system was used. The lowest flow rate used in any experiment was 1,144 ml/hr. The Analyzer was connected to a Rustrak recorder which continually recorded the oxygen concentration of the water flowing through the system. The manufacturers claim that the accuracy of the Oxygen Analyzer is 1% full scale. On the scale of 0 - 10 ppm dissolved oxygen used in the experiments on Upogebia, the accuracy of the readings was therefore 0.1 ppm.

Neoprene tubing was used for all connections, except for two 3cm pieces of rubber tubing on the three way valve I. These sections of flexible tubing were extremely useful for expelling bubbles from the system.

Each time the apparatus was used the oxygen analyzer was calibrated using the method described by the manufacturers. Theoretical oxygen content of the water at a particular temperature

and salinity was obtained for calibrations from the tables of Truesdale et al (1955) and corrected for atmospheric pressure. Water was allowed to flow through the apparatus for 30 minutes before experiments commenced. During this time the recording trace showed whether there was any fluctuation in the reading of the analyzer meter.

Fluctuations were traced to three causes. Firstly the apparatus tended to build up static charges which resulted in needle deflections when any metal part was touched. This was overcome by earthing all metal parts. Secondly any electrical apparatus which generated a strong electrical field in the vicinity of the analyzer caused a needle deflection. Because of this it was considered inadvisable to employ devices such as magnetic stirrers for moving water past the sensor. Although the deflection caused by a magnetic stirrer appeared to be constant it may not necessarily be linear and thus it could possibly cause errors in the analyzer readings. Thirdly fluctuations in the mains voltage caused the reading to alter slightly. This fluctuation was particularly severe at certain times of the day when maximum use is made of electrical power, for example between 1700 and 2000 hours. Because of this unavoidable factor every experiment was preceded and ended by a calibration check. If the two checks differed by more than 0.15 ppm oxygen, the experiment was rejected. If the difference was less, the oxygen content of inflowing water was taken as the mean of the two calibration readings.

If the water in the system was at a markedly different temperature to ambient, temperature changes occurred in the apparatus. It was essential therefore that ambient be as close as possible to water temperature. In addition the oxygen content of water changes with temperature variation. The analyzer does not register this change since the partial pressure of oxygen remains the same. Because of these temperature effects all experiments were carried out in a temperature controlled room. The operating of the analyzer itself is independant of normal working temperatures and the sensor is temperature compensated in the range 5 - 45 °C.

Although the ideal is to use one prawn at a time, in practice one prawn gave a very small deflection on the analyzer unless extremely low flow rates were used. It was found that five prawns gave a good deflection but if the number of animals was increased above five, difficulties due to variations in behaviour pattern between individuals became too great. The prawn chamber to hold larger numbers would have had to be large and would develop an oxygen gradient from inflow to outflow.

It has been shown that size affects oxygen uptake eg Zeuthen (1953). Thus it is important that in experiments involving more than one animal, all the animals should have the same weight. In experiments on U. africana a large sample of prawns was weighed and sorted into weight classes. Each class consisted of animals within 0.1 gm of each other. Thus

a typical class was prawns weighing between 1.50 and 1.59 gm. This weight class would be referred to as 1.5 gm prawns.

The activity of animals also affects their oxygen consumption. This fact has been used to explain the increased uptake of oxygen by marine animals when exposed to low salinities. It was pointed out by Gross (1957) that at low salinities the animals (in this particular case crabs), struggle and should therefore utilise more oxygen. In order to minimise this effect it was decided to only use readings of oxygen uptake at three standardised activity levels. These levels were defined as follows:

Inactive: No visible movement apart from scaphognathite beat.

Active: Prawns continually changing places, pushing between each other, pleopods beat almost continuously.

Very Active: Occurs mainly during fighting, rapid pleopod beat, escape movements of abdomen, attacking with chela, attempting to push other prawns aside, continually changing position.

In order to carry out an experiment, water was first allowed to flow over the sensor and the oxygen content was noted. Five prawns were then put into the chamber. The water flow was altered to flow through the prawns chamber before it reached the sensor and was allowed to flow for 10 minutes before any observations were made. This ensured

complete flushing of the system. After this period observations of the behaviour of the prawns were related to the trace drawn by the recorder. When a particular behaviour pattern occurred continuously for a few minutes the trace was steady. Bursts of activity and inactivity showed up as a fluctuating trace. For most of the time not all prawns behaved in the same manner. Four prawns might be active whilst one remained inactive, or vice versa. During experiments it was thus necessary to observe the activity of the prawns continuously and only to take readings when all five prawns were behaving similarly. Readings of the oxygen content of the water leaving the chamber were always taken directly from the analyzer.

At the end of an experimental run the water flow was altered and allowed to bypass the prawn chamber. A second reading was then made of the oxygen content of the water in the reservoir. At the same time the tap in the bottom of the prawn chamber was opened to permit a free flow of water through the chamber. This prevented an oxygen deficit building up in the chamber between experiments. If it was desired to expose the prawns to a different type of water between experiments, the water supply to the chamber from reservoir B was disconnected and replaced by a supply from the small container J. Thus for example in experiments involving low oxygen concetrations, water saturated with air could be run over the prawns between experiments. This reduced handling of the experimental animals. At the end of the experiment the

prawns were removed, dried with a towel and weighed.

Upon completion of any experiments the apparatus was flushed out with tap water and drained completely in order to prevent growth of algae in the tubes. The sensor was removed and rinsed with distilled water.

Rates of metabolism of poikilotherms generally increase with increasing temperature. The effect of temperature on overall metabolism in U. africana was investigated using respiratory rate as a measure of metabolism. Prawns were collected at the end of November and sorted into three weight categories, 0.9, 1.6 and 2.3 gm. There were about 10 prawns in each batch. The prawns were held in aerated sea water in plastic dishes in a constant temperature room at 8.3 °C for 24 hours. Five prawns were then taken from each batch and put into the chamber of the respirometer. The prawns were kept under constant observation and measurements were taken with prawns active. Although it would have been more desirable to take readings with inactive animals, insufficient data could be assembled because at higher temperatures the prawns would not remain inactive. At the end of the experiment the prawns were weighed and then put into clean sea water in a constant temperature room at a higher temperature. After 24 hours at this new temperature the respiratory rate was measured again.

It was felt advisable to expose prawns to new temperatures for a fairly long period in order to minimise

possible effects of thermal shock on oxygen uptake.

It was shown above (page 76) that prawns collected in summer have markedly different temperature resistances to those collected in winter. Winter prawns were shown to possess a marked temperature acclimation ability. Prawns collected in June (winter, temperature 15 - 18 °C) were tested for evidence of acclimation in respiratory rate. The prawns were sorted into three size groups and held at 15 °C for 36 hours, followed by 18 °C for six hours. They were then put into the chamber of the respirometer and water at 25 °C was allowed to flow over them. Oxygen uptake was measured within 20 minutes of transfer to the higher temperature. At the end of the experiment the prawns were held at 25 °C for 50 hours after which oxygen uptake was remeasured. All determinations were of the active state.

The effect of low salinity on respiratory rate in U.africana was determined on animals collected in November. Three weight classes were sorted out, namely 1.6, 1.8 and 2.1 gm animals. These were kept in sea water at 20.5 °C for 24 hours to ensure uniformity of background temperature. Oxygen uptake was then measured in sea water. The prawns were subsequently transferred to 30, 17.2, 8.6, 6.0, and 3.5 °/oo for periods of 24 hours in each salinity. Oxygen uptake was measured at the end of each 24 hour period. It has already been shown (page 102) that acclimation to low salinity is apparently complete after 18 hours.

An experiment involving measurement of respiratory rate at low salinity in different temperatures was carried out on prawns collected in February 1967. Two weight classes namely 1.4 and 2.3 gm were used. Half of the prawns in each weight class were transferred to a salinity of 5 °/oo, the balance were kept in sea water.

The prawns were kept in a constant temperature room at 15.5 °C for 24 hours, after which the respiratory rate was determined on five prawns from each of the four groups. They were then transferred successively to higher temperatures for 24 hour periods. Respiratory rate was determined at the end of each 24 hour period.

The effect of low oxygen concentrations on respiratory rate was investigated by bubbling nitrogen/air mixtures through the supply reservoir of the respirometer. Average sized prawns (1.65 - 1.76 gm) were used in batches of five. Their oxygen uptake was measured at a variety of oxygen concentrations. As there was a possibility of an oxygen debt building up in low concentrations, prawns were exposed to aerated sea water for 20 to 30 minutes between each exposure to low concentration. The experiments were carried out at 18.3 °C with a flow rate of 2.25 litres per hour.

Behaviour of prawns in burrows at low oxygen concentrations was studied using the respirometer and an artificial burrow. A glass burrow consisting of a U tube with a 'turn around' at the base was made. This burrow

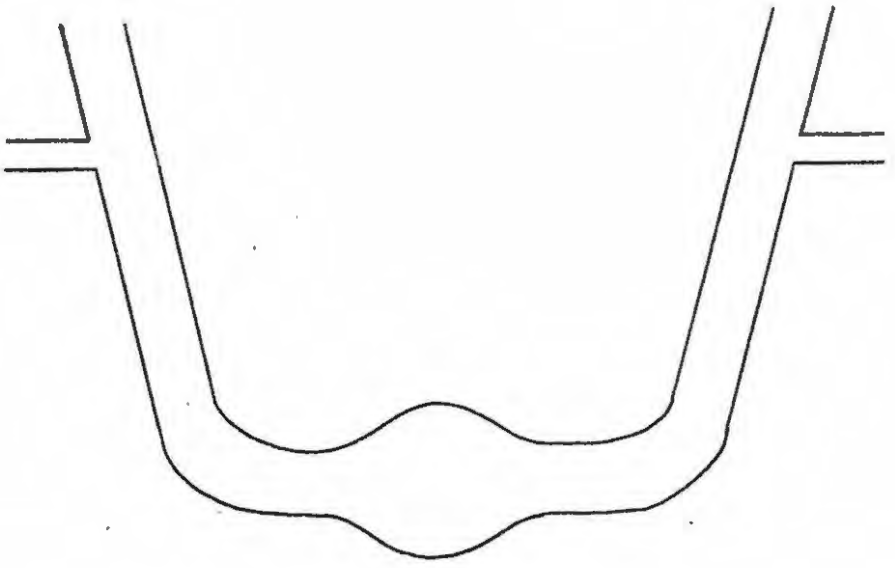

Fig 40: Glass burrow used in the respirometer shown in figure 39 in order to observe the behaviour of U.africana at low oxygen tensions.

had two side arms and is illustrated in figure 40. The prawn chamber of the respirometer was removed and the burrow substituted so that water entered at one of the side arms and left at the opposite one. The burrow was filled with water to just above the side arms. A prawn was put into the burrow which was then corked so as to leave an air space above the water. Water was allowed to flow through the system at a speed of 3 litres per hour. Nitrogen was slowly bubbled through the water in the reservoir and the oxygen content of the water leaving the burrow was recorded. The experiments were performed in dim red light. The experiment was repeated 10 times and the behaviour of the prawns at different oxygen tensions was noted.

RESULTS

In this paper the convention used by Zeuthen (1953) will be adhered to as regards the terms respiration which means the oxygen utilised by the whole organism; and the term respiratory rate which means oxygen uptake (in microlitres or ul) per unit body weight (grams) per hour.

Prawns were always kept in the laboratory for 24 hours before respiration experiments were carried out. No attempt was made to feed them during this period. However since some of the respiration experiments were spread over periods of up to five days it was of importance to establish whether respiratory rate changed over a long period of starvation. Ten prawns were kept in the laboratory at 20 - 22 °C in sea water and the respiratory rate of five of them was measured at irregular intervals. The results are shown below:

Time (hours)	Respiratory rate (ul/gm/hr)
34	189; 175
77	190
151	182
264	184; 161

There appears to have been no significant respiratory rate change over a period of nearly 10 days which is twice as long as the duration of any experiments. A sighting experiment in which the oxygen uptake of five prawns was metered continuously for 24 hours showed no indication of an increase or decrease associated with either time of day or tides.

Wolvekamp and Waterman (1960) pointed out that size of animals must be taken into account in determining respiratory rate. In general small individuals have a low respiration although they may have a high respiratory rate. These authors also point out the paucity of information on the effect of activity on oxygen consumption in crustaceans. Indeed in dealing with high levels of activity they state "no measurements of respiratory rate have ever been made during short bursts of intense activity".

An experiment to determine the effect of size and activity on respiratory rate was carried out using the apparatus and technique outlined above. The experiment was performed at 20 °C. The results are shown in figure 41.

Respiratory rates in the Very Active state were difficult to obtain since the animals were usually Very Active for extremely short periods. Large prawns would not exhibit this activity long enough for accurate readings to be made. The Active and Inactive curves show an increasing respiratory rate with decreasing size. This agrees with previous observations by numerous authors on a wide variety of invertebrates and vertebrates and which have been summarised by Zeuthen (1953). He showed that increase in respiratory rate with decreasing size is common to all organisms from bacteria to large mammals.

Zeuthen (1953) has related total metabolism to body weight using the exponential equation

$$Y = a.X^b$$

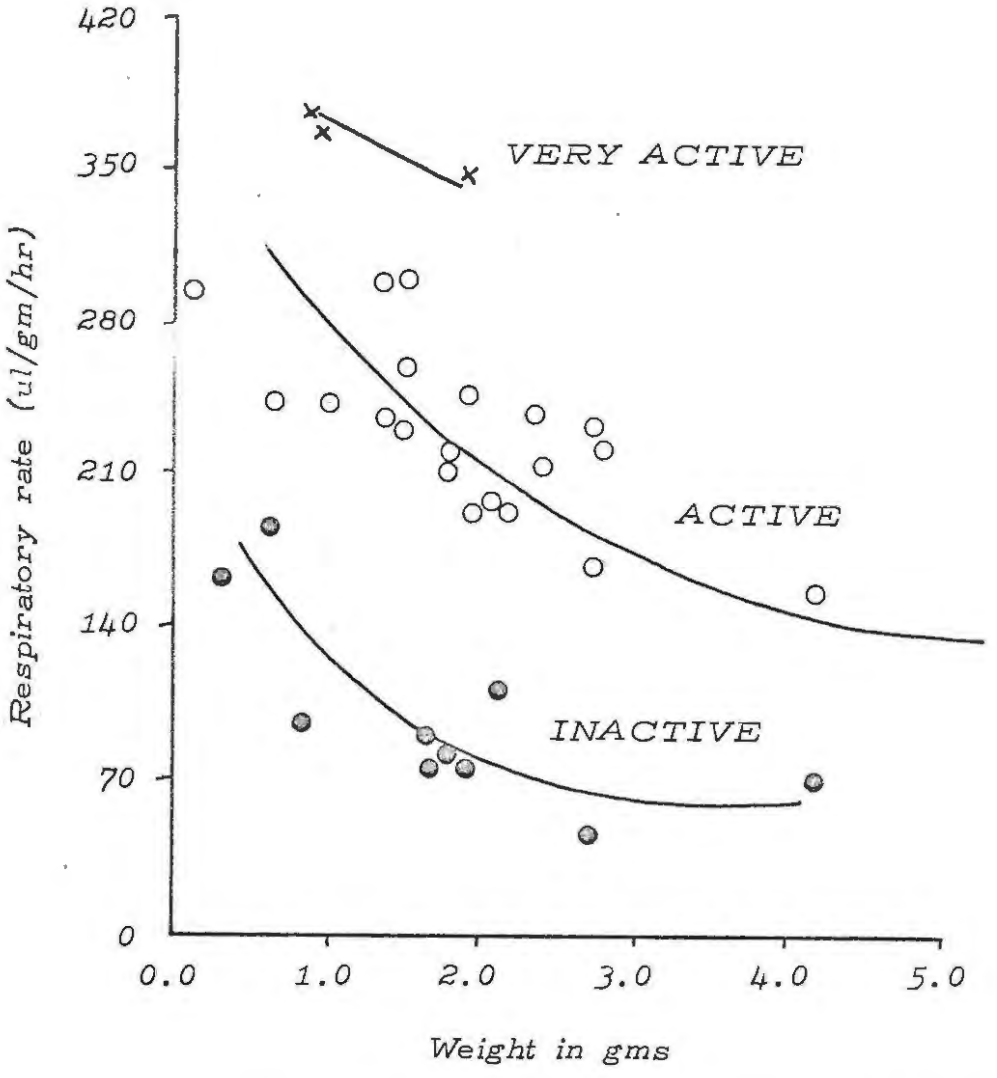

Fig 41: Respiratory rate of U. africana of different weights at three levels of activity. Respiratory rates expressed as microlitres of oxygen per gram wet weight of prawn per hour (ul/gm/hr).

This formula implies that for a constant 'b', the logarithmic change in Y (metabolism) varies directly with the logarithmic change in X (body size). He established that most organisms have a 'b' value between 0.67 and 1.00. However Prosser and Brown (1962) state that 'b' is similar in poikilotherms,

homeotherms and beech trees ! Obviously the value of 'b' lies in pointing out the underlying similarity of tissue processes throughout the animal and plant kingdom. However 'b' also serves as a useful check on respiration experiments, if markedly different values of 'b' are obtained, then either the experimental method is faulty or some other overriding biological factor is intervening.

If the values in the experiment on U. africana are plotted on double logarithmic paper, it is possible using linear regression to fit a straight line to the data for both Active and Inactive states. These lines both have a slope, and therefore a 'b' value of 0.8 which agrees with previous findings for Crustacea (Zeuthen 1953). The fact that in both the Active and Inactive conditions the value of 'b' is the same supports Zeuthen's assumption that it is possible to compare metabolic rates (ie 'b' values) obtained from animals which have been resting with those from active animals. This comparison is of great value since it is not always possible to obtain respiratory rates for inactivity from small swimming crustacea or rates of activity from larger animals under experimental conditions. Recent work by Newell and Northcroft (1967) on a number of animals from different phyla has also shown that b values for maximum and minimum rates of oxygen uptake are not significantly different.

Reference to figure 41 shows that at the extremes of

the size range, namely 0.5 gm and 4 gm, metabolic rates of active prawns were about twice those of inactive animals. Average sized prawns (1 - 2 gm) in the active state had a respiratory rate two and a half times that of inactive prawns. When the curve for Very Active prawns is compared it is seen that a factor of three to four times the inactive rate was involved. Thus in U. africana respiratory rates for active animals were at least twice and could be as much as four times those obtained from inactive animals.

The Effect of Temperature on Respiratory Rate

Measurement of temperature effects on respiratory rate of three sizes of prawns are shown graphically in figure 42. The curve for small prawns (0.9 gm) is much higher than for the two larger groups especially in the temperature range 16 - 29 °C. This is probably due to the size effect described above in which it was shown that small individuals have a higher respiratory rate than large individuals. However the 1.6 gm prawns had a higher respiratory rate than large individuals weighing 2.3 gms. This is the opposite of what has been shown above. However reference to figure 41 shows that considerable variation can exist in respiratory rates. Prawns in the 1.6 gm class at 20 °C had a respiratory rate varying from 200 to 300 ul. Prawns in the 2.3 gm class had respiratory rates varying from 175 to 250 ul. There is thus a considerable overlap in respiratory rate in the two weight classes. However despite

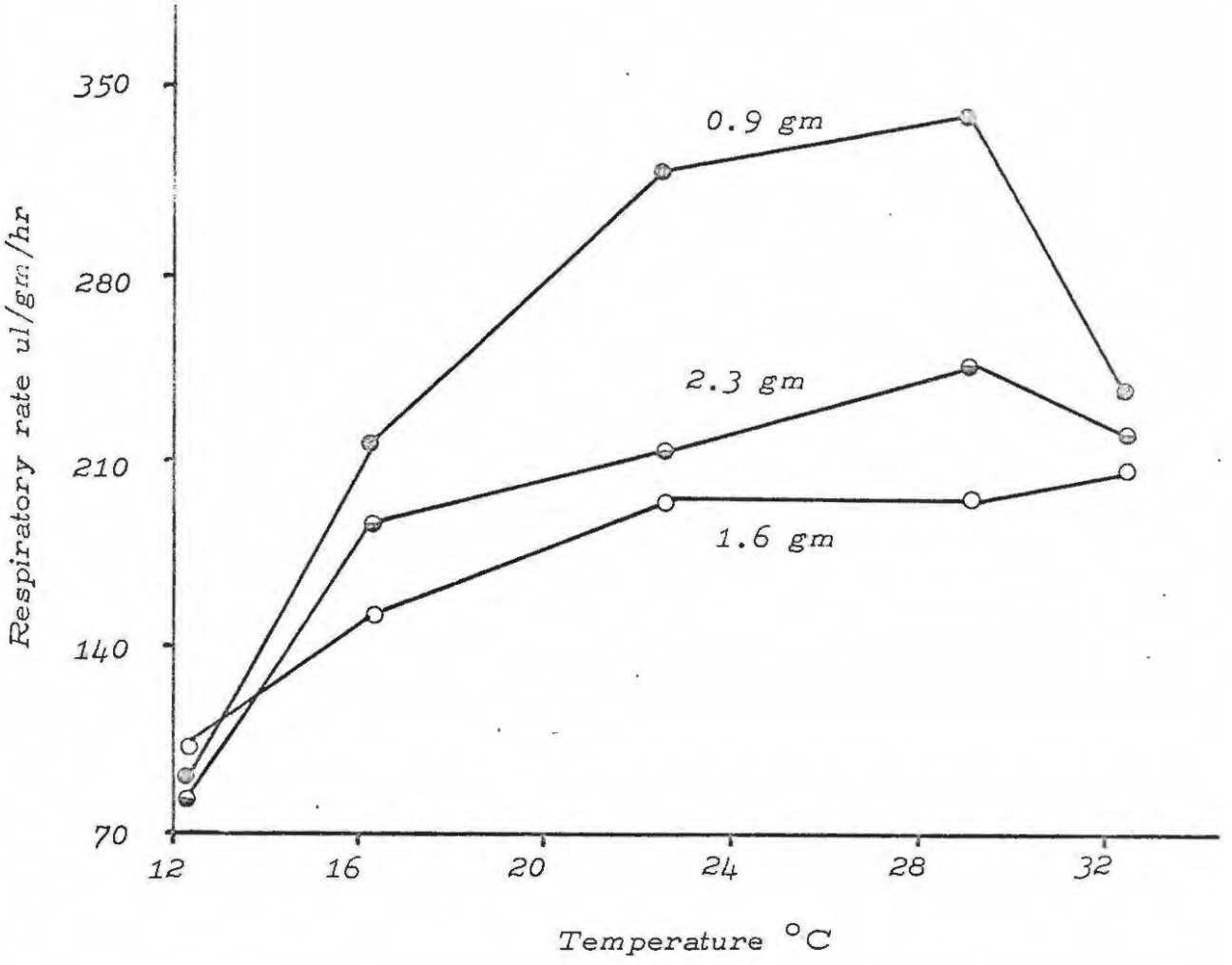

Fig 42: Respiratory rates of three weight classes of prawns determined at a series of temperatures.

this overlap the results obtained from the 1.6 gm prawns are still rather low.

At a temperature of 8.3 °C it was extremely difficult to obtain full activity. Although the prawns made the movements associated with the Active condition, these movements tended to be slower than normal. This is probably the chief cause of the lowered uptake in all three size groups. All size groups showed a gradual increase in respiratory rate between 16 and 29 °C. Except in the case of the smallest prawns this increase

was not large and indicates a degree of independance of the environmental temperature.

The value of Q_{10} was calculated from the respiratory rates of the three weight classes over the temperature range 16 - 29°C. In addition the results of another batch of prawns were utilised to determine the Q_{10} in the range 19.5°C to 29°C. The results were as follows:

Weight of prawn (gm)	Temperature range	Q_{10}
0.9	16 - 29°	1.8
1.4	19.5-29°	1.2
1.6	16 - 29	1.4
2.3	16 - 29	1.5

The value of Q_{10} for small prawns (0.9 gm) indicates that there was only a small degree of independance of environmental temperature. However in the weight range 1.4 - 2.3 gm U. africana showed a moderate temperature independance or compensation. Newell and Northcroft (1967) have shown that although active metabolism in invertebrates increases with temperature, intertidal invertebrates exposed to rapid fluctuations in temperature have a basal metabolic rate with a Q_{10} of approximately 1 over much of the normal environmental temperature range. Unfortunately it was not possible to obtain sufficient measurements of inactive prawns at different temperatures in order to establish a basic metabolic rate for U. africana . However the relatively low value of Q_{10} found in medium and large prawns in the active condition indicates that U.africana is capable of adjusting its metabolism

to compensate for a regime of fluctuating temperature.

Figure 42 shows that there was a sudden decrease in respiratory rate by small and large prawns above 29 °C. Temperature experiments described above have shown that the upper lethal temperature of U. africana is 29 ± 1 °C. Kinne (1963) has previously pointed out that in general, rates of metabolism and activity increase with increasing temperature over most of the temperature range tolerated and then often decrease suddenly near the upper lethal temperature.

An unavoidable interfering factor in this experiment was that with increasing temperature the oxygen concentration of the medium falls. At 8.3 °C the dissolved oxygen content was 8.55 ppm, whilst at 32.4 °C it was only 5.5 ppm. It will be shown that oxygen uptake rates for active prawns are dependant upon oxygen concentrations. Thus in the experiments involving respiratory rates at different temperatures, it is possible that the values obtained at high temperatures were lower than those which were theoretically possible. Of course this does not invalidate the results since prawns in the field exposed to high temperatures will similarly experience lowered oxygen concentrations.

Winter prawns have been shown to possess a marked temperature acclimation ability. An experiment was carried out to determine whether there was any detectable difference in metabolism between acclimated and unacclimated winter prawns. In the following table the respiratory rates of unacclimated

winter prawns measured at 25°C are compared with the respiratory rates of the same prawns after 50 hours acclimation at 25°C:

Weight in gm:	0.90	1.80	2.70	
Unacclimated :	230	225	225	ul/gm/hr
Acclimated:	200	210	230	ul/gm/hr

There appears to be no real metabolic difference between acclimated and unacclimated prawns. Comparison of these results with figure 42 shows that the values obtained fall well within those obtained for summer prawns.

This result has two possible explanations. Firstly that summer prawns show no metabolic adjustment to the generally higher thermal regime in summer. This is unlikely since it has been clearly shown that the temperature resistance of summer prawns is much greater than that of winter prawns. An alternative explanation is that U. africana is capable of extremely rapid metabolic compensation to temperature changes. It has already been shown that the temperature regime in the Kowie estuary is extremely variable and a rapid metabolic compensation to temperature change would be an ability in keeping with the variability of the environment.

The effect of Salinity on Respiratory Rate

The effect of low salinity on respiratory rate in U. africana was determined on animals collected in November. Respiratory rates were measured after the prawns had been

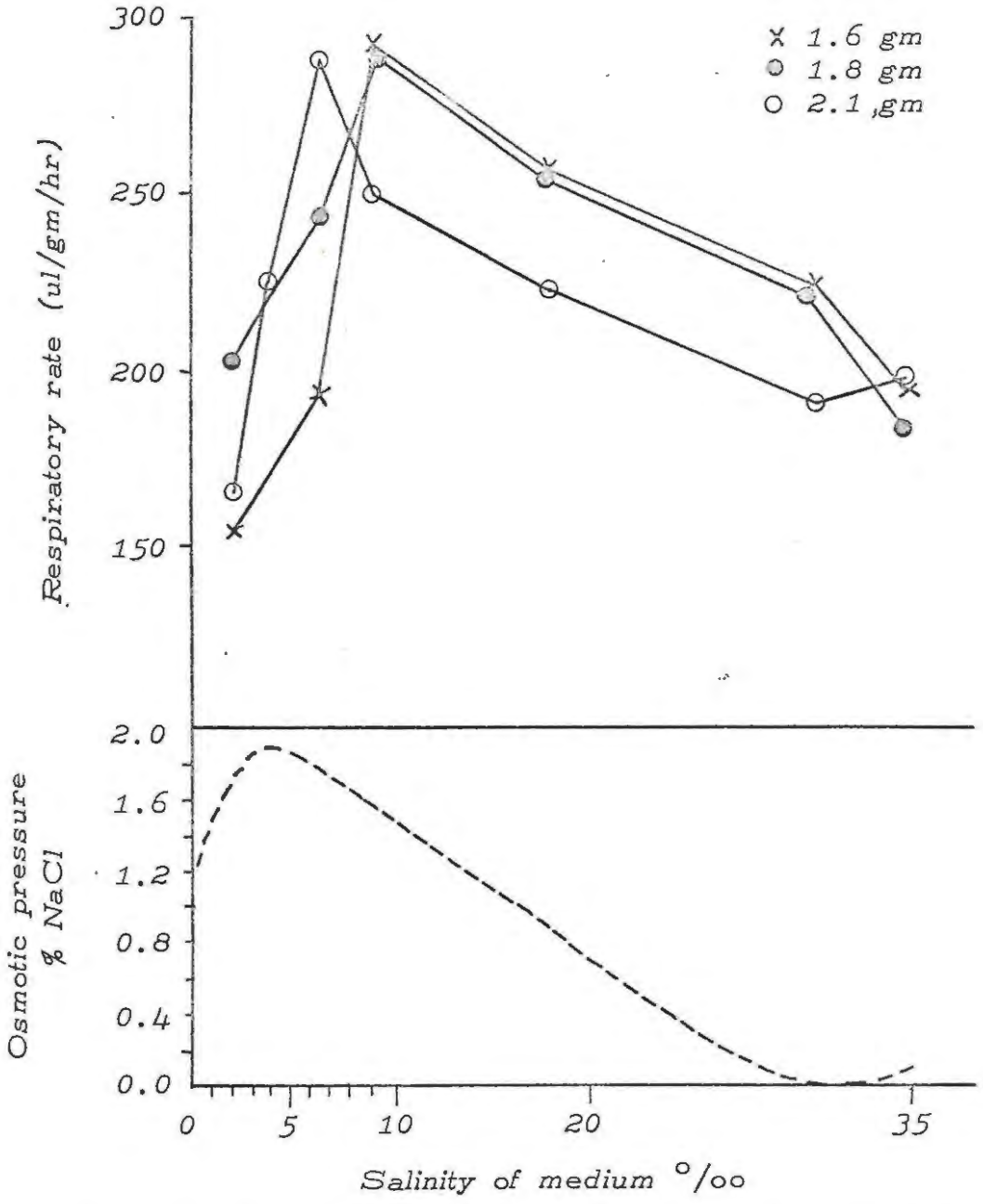

Fig 43: The upper set of curves shows the respiratory rates of three weight classes of prawns in a series of salinities (in parts per thousand). The lower curve indicates the difference in osmotic pressure (expressed as percentage NaCl) between the blood of prawns and the medium at a series of salinities.

exposed to various salinities for 24 hours. The results are expressed graphically in figure 43 together with a curve illustrating the difference (expressed as percentage NaCl) between the osmotic pressure of the blood and that of the medium.

U. africana showed an increased respiratory rate as the salinity of the medium was lowered. The metabolic rate reached a maximum value when the animals were in a salinity of 6 - 8 °/oo. Further dilution of the medium resulted in a fall of respiratory rate to values generally lower than those in full sea water. Comparison of these results with the curve showing the difference in osmotic pressure between blood and medium (figure 43) indicates a rough correspondence between the respiratory rate and the amount by which the blood concentration differs from the medium. As the prawns were put into increasingly dilute media the difference between blood and medium increased. Simultaneously the respiratory rate increased. However respiratory rate dropped rapidly in salinities below 6 - 8 °/oo whereas the difference in osmotic concentration between blood and medium reached a maximum in 3.5 °/oo.

An increase in metabolism as reflected by respiratory rate is known to occur in many marine and estuarine crustaceans when put into dilutions of sea water. Originally this increase was thought to be due to the greater amount of osmotic work. However not all animals shown this higher respiratory rate in

low salinities. Eriocheir for example does not show any difference in respiratory rate in sea, brackish or fresh water despite a considerable difference between the osmotic pressure of the blood and medium. Thus this crab does not apparently require increased oxygen when transferred from sea water to fresh water.

Potts (1954) has calculated the total work required for osmotic work by Eriocheir and Astacus in fresh water. Astacus in freshwater maintains its blood at a Δ_i of 0.9 - 1.0 °C, whilst Eriocheir has a Δ_i of 1.1 - 1.2 °C in fresh water. Despite these large differences between blood and medium only about 0.3% in Astacus and 0.5% in Eriocheir of the total metabolic work was required for osmotic work. It is clear from these figures that in these two species the work required to maintain a large osmotic difference between blood and medium is small and it is therefore understandable that Eriocheir does not show a high respiratory rate in low salinity.

The small amount of osmotic work performed by Eriocheir and Astacus in fresh water has led many authors to suppose that this is applicable to all species of Crustacea. However both species are capable of living in fresh water and it is reasonable to postulate that selection would have favoured osmoregulatory mechanisms which entail a small amount of work.

Robertson (1960) reviewed this problem and quoted the work of Schlieper (1936) who found that when muscle and

hepatopancreas were hydrated they consumed more oxygen. Robertson concluded that increased oxygen uptake in low salinity was caused by hydration of tissues. However Florkin and Schoffeniels (1965) have shown that hydration of tissues when crustaceans are transferred to dilute media, only occurs for a short period. Intracellular regulation results in the osmotic pressure of the intracellular fluid being altered to equal that of the extracellular fluid. Apparently this is accomplished chiefly through the reduction of the free amino acid content of the cells by altering the relative speeds of anabolism and catabolism of amino acids. Thus when first transferred to brackish water, marine crustacea show increased nitrogen excretion.

The increased intracellular regulation postulated by Florkin and Schoffeniels would account for increased oxygen uptake immediately following upon transfer of a euryhaline crustacean to brackish water but it does not occur for the sustained high level of metabolism.

Thus at present no explanation can be offered for the sustained increased respiratory rate exhibited by many crustaceans including U. africana when subjected to osmotic stress, although the possibility of it being due to increased osmotic work cannot be excluded.

The Effect of Temperature on Respiration at Low Salinity

An experiment was carried out to determine the effect of temperature on respiratory rate of two weight classes of

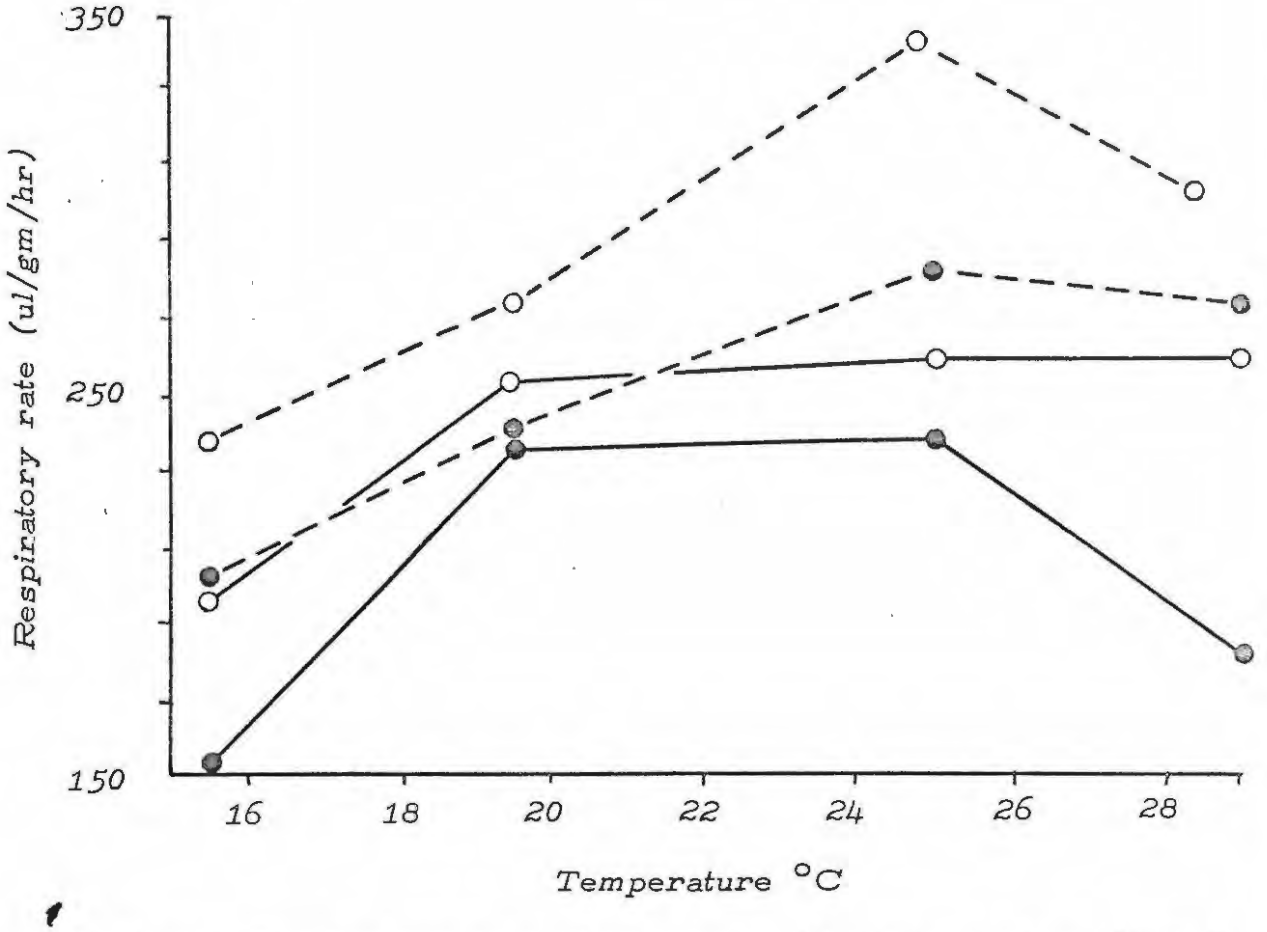

Fig 44: Respiratory rate of prawns in the 1.4gm class (dotted line) and 2.3gm class (solid line) in sea water (solid circles) and in a salinity of 5.2°/oo (open circles).

prawns at low salinity. The respiratory rates of two identical weight classes kept at the same temperatures but in full sea water were also determined for purposes of comparison. The results are shown in figure 44.

In general increasing temperature resulted in higher respiratory rates except at 29°C where nearly all prawns showed a decrease. Both batches of prawns at 5.2°/oo had

higher respiratory rates than the same weight classes in sea water. This applied throughout the temperature range.

These results agree with the determinations of the independant effect of temperature and salinity on respiratory rate and suggest that any interaction between temperature and salinity is not reflected in the respiratory rate in the range studied. It was pointed out when dealing with the interaction of temperature and salinity (page 121), that this interaction only appearsd to act near lethal temperatures and in lethal salinities.

Respiration at Low Tide

It has been shown above (page 138) that Upogebia extracts oxygen from the surrounding water. However a large proportion of the population of U. africana in the Kowie estuary lives in the intertidal zone and during low tide periods it is not possible for these animals to irrigate their burrows. Thus at low tide the oxygen content of the burrow water should drop. In order to establish whether this does occur, water samples were extracted from burrows in the intertidal zone at low tide and the dissolved oxygen content was determined. The oxygen concentrations found were as follows (in parts per million dissolved oxygen):

2.0	0.8	1.1	2.2	0.8
0.3	0.5	0.5	0.3	

Clearly the oxygen concentration of water in the burrows in the

intertidal zone at low tide drops to extremely low values. This drop is probably caused through oxygen withdrawal by the prawn as well as by the micro-organisms on the mud lining the burrow.

In the field it was noticed that at low tide, prawns could occasionally be seen just inside their burrows with the anterior part of the body out of the water. The slightest disturbance caused them to rapidly withdraw. Observations were made on prawns living in burrows in mud in a glass sided aquarium. About an hour after the water had been drained from the aquarium the prawns climbed up the burrow until the carapace was just out of the water with the abdomen still submerged. The hindmost edge of the branchial chamber dipped under the water surface and the chamber remained full of water. The scaphognathite carried on beating and caused a stream of water to flow from the anterior end of the gill chamber. The water ran back along the ventral and lateral surfaces of the prawn and into the burrow water. This mechanism presumably results in aeration of the uppermost layers of water in the burrow and simultaneously enables the prawns to carry on respiration. At intermittent intervals the prawn ducks beneath the surface and then re-emerges. This probably serves to keep the body surface moist.

If this activity is initiated by a respiratory need, then the volume of water in the burrow should affect the time which elapses before the prawns emerge. This was tested by keeping

prawns in glass burrows of various volumes and determining the time which elapsed before they emerged. No correlation was found between the times to emergence and size of prawn probably because the amount of activity in the burrows was erratic. The mean, maximum and minimum times recorded for six replicates were as follows:

Volume of burrow (ml)	Time to emergence (minutes)		
	mean	max.	min.
25	40	57	19
110	123	205	85
150	144	195	100

From these results it is clear that the greater the volume of the burrow the longer the prawn remains submerged. As described above the volume of burrows is probably about 100 - 200 ml (page 33). Most prawns should be able to remain submerged for at the most two to four hours. However in the field the micro-organisms which are almost certainly present on the mud walls of the burrow also take up oxygen from the burrow water. Thus in the field the period before prawns emerge will be shorter than those given above.

Since the low tide emergence appeared to be related to respiration, there were two factors which might have been responsible for initiating it, firstly a drop in the oxygen content of the water in the burrow and secondly an increase in the CO_2 level. The effect of reduction of the partial pressure of oxygen in the burrow water was determined by means of the respirometer described above. Prawns

were kept in a U shaped glass burrow (figure 40) and water at various oxygen tensions was passed through whilst the behaviour of the prawns was noted. The experiment was repeated ten times and the results are summarised below:

Oxygen tension (mm Hg)	Prawn Behaviour
36 - 150	Normal behaviour
17 - 36	Activity decreased, slow pleopod beat, scaphognathite beat normal or slightly increased, often clean gills with periopods.
10 - 14	Inactive, even pleopods may stop beating, scaphognathite beat too rapid for movement to be followed by eye.
7 - 9	Prawns slowly move up burrow, approach surface, occasionally descend again but then gradually move up once more, scaphognathite beat normal
4.5 - 11	Prawns emerge from water and display 'low tide behaviour'.

Although the approach to initial emergence was very slow, once the prawns had come out they stayed out apart from occasional brief duckings. If the burrow was tapped they immediately retreated underwater but would soon emerge again. Once the prawns had emerged the oxygen tension of the water was allowed to rise. If the burrow was tapped at an oxygen tension of 16 - 20 mm the prawns descended and then re-emerged. If the oxygen tension increased above

25 mm Hg the prawns descended and remained underwater.

As the water was flowing through the burrow, no build up of CO_2 or excretory products could occur and thus emergence in this experiment was initiated by low oxygen. Controls in which aerated sea water was run through the system never resulted in emergence, even after 15 hours exposure.

However under natural conditions there might be a build up of CO_2 in the burrow at low tide and this by itself could also possibly initiate emergence. In order to test this possibility CO_2 was bubbled through the water in the supply reservoir. As the CO_2 went into solution it reduced the oxygen and nitrogen content of the water. When the oxygen tension reached about 100 mm the prawns emerged. The gas above the water in the reservoir was then replaced by air and the oxygen tension began to rise as the CO_2 came out of solution. When the oxygen tension reached approximately 110 mm Hg the prawns descended and carried on normal behaviour such as attempting to irrigate the burrow or in one case consolidating the walls of the burrow.

Using the technique described by Barnes (1959) an attempt was made to determine the partial pressure of CO_2 in the water when the oxygen tension had been reduced to 100 mm. However the CO_2 content was far too high to be measured. Estimations based on the partial pressure of oxygen and nitrogen gave a partial pressure of CO_2 of

approximately 250 mm Hg at the concentration at which the prawns emerged and 200 mm when they descended. This is an exceptionally high value. Spencer (1965) reports that the partial pressure of CO_2 in sea water under natural conditions is abour 0.2 mm. Partial pressures as high as 200 - 300 mm can only occur in closed systems, any system open to atmosphere rapidly loses its CO_2 if the partial pressure is raised above 0.2 mm. It is concluded that CO_2 is not normally a factor in causing low tide emergence.

When CO_2 is bubbled through sea water the pH of the water drops. In the experiment described above, when the oxygen tension reached 100 mm, the pH of the water was only 5.28. In order to test whether it might have been pH that induced emergence, a sample of sea water was acidified with concentrated HCl to a pH of 5.20. Fifty ml of this water was put into a glass burrow together with a prawn. On the basis of earlier experiments (page 154) it would be reasonable to expect the prawns to stay underwater for about 50 minutes before emerging. However in four replicates with different prawns, the maximum time of emergence from acid sea water was 20 minutes and the mean 16 minutes. Thus pH can initiate emergence although the mechanism by which it does so is not clear.

Prawns normally only emerge when the oxygen tension drops below 11 mm. However when CO_2 was bubbled through the water and the pH dropped to 5.28 the prawns emerged at

an oxygen tension of 100 mm. Many animals can regulate their oxygen consumption despite fluctuations in environmental oxygen, ie they are oxygen regulators or oxygen independent. However if the oxygen tension drops, a point is reached when the oxygen consumption also drops, ie they become oxygen conformers or oxygen dependent. This point is known as the critical pressure for that animal. The exact value of the critical pressure can be modified by a number of external factors such as temperature and pH.

In oxygen tensions below the critical pressure the animal may compensate for the reduced oxygen uptake by a variety of mechanisms such as inactivity in order to reduce oxygen requirements, or beating of the respiratory appendages to increase supply of oxygen. In the case of U. africana the compensation appears to be associated with emergence which enables the animal to obtain an increased oxygen supply when the oxygen content of the burrow is extremely low.

It is suggested that pH raises the critical oxygen pressure of U. africana and that as a consequence it is unable to obtain sufficient oxygen from the burrow water. The result is that at low pH emergence occurs at a higher oxygen tension than at normal pH. U. africana is apparently extremely insensitive to CO_2 which under natural conditions cannot rise to concentrations high enough to initiate emergence. This agrees with previous work on a variety of animals by Munro Fox and Johnson (1934) and Johnson (1936) who found

that many crustaceans appeared to be insensitive to CO_2 and that respiration as evidenced by respiratory movements was dependant upon oxygen concentration.

Respiration at Low Oxygen Concentration

In order to establish the amount of oxygen which U. africana can extract from the surrounding water and to determine the critical pressure under normal conditions, a series of experiments involving the determination of respiratory rates at low oxygen levels was initiated. Nitrogen/air mixtures were bubbled through the supply reservoir of the respirometer in order to reduce the oxygen concentration of the water to which the prawns were exposed. The respiratory rate at a variety of oxygen concentrations was determined and the results are shown in figure 45.. The percentage of available oxygen which the prawns extracted from the water was calculated using the amount of oxygen extracted (in mg per litre) from the water, relative to the oxygen concentration of the water (in mg per litre). These results are shown in figure 46.

Although at all concentrations of oxygen the level of activity appeared to be the same, figure 45 shows that in fact respiratory rate declined by half over the range recorded. Activity was judged purely on movement of appendages. Since this movement appeared the same, there must have been a large

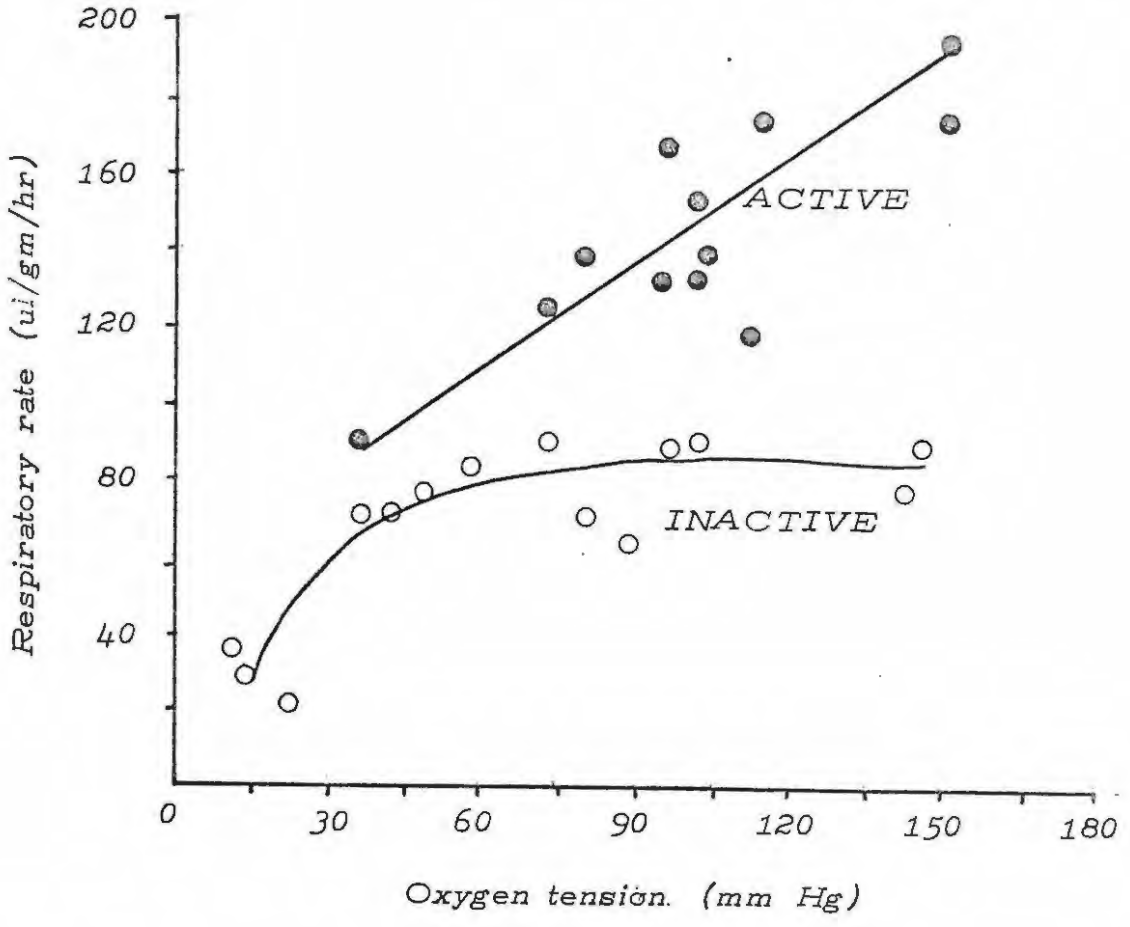

Fig 45: Respiratory rate of U.africana in a series of oxygen tensions at two levels of activity.

reduction in the metabolism in other organs. This probably represents a mechanism for conservation of oxygen in times of stress such as during periods of intense locomotory activity. In the Active state, U. africana is clearly oxygen dependant.

The curve for Inactive animals in figure 45 by contrast indicates oxygen independance. Oxygen uptake remained virtually constant over an environmental partial

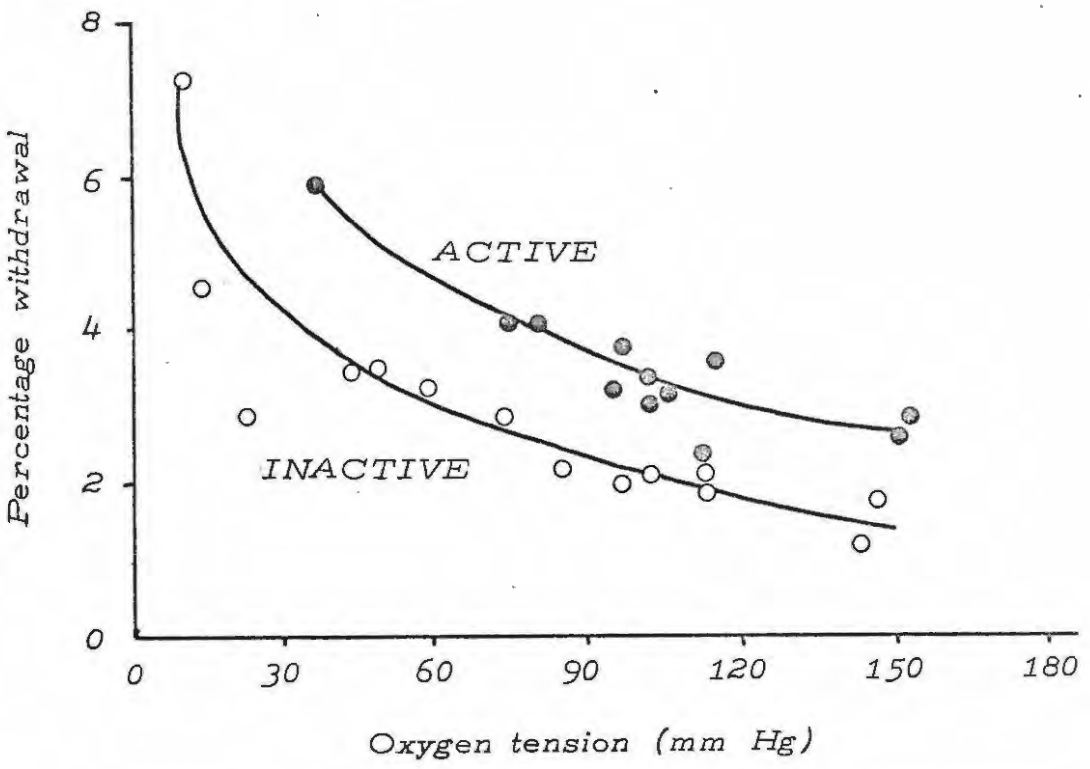

Fig 46: Percentage of oxygen which is withdrawn from water of different oxygen tensions by prawns at two levels of activity.

pressure range of 150 mm to approximately 45 mm Hg. A respiratory rate of 70 - 100 ul/gm/hr probably represents a basic metabolic demand of the prawns. If the oxygen tension dropped below 45 mm Hg the respiratory rate dropped rapidly. Forty five mm Hg must therefore represent the critical oxygen pressure of average sized U. africana at 18.3 °C and in full sea water. This critical pressure was also the tension at which it was no longer possible to induce sustained activity in the prawns. They only exhibited very brief bursts of activity followed by periods of inactivity.

Figure 46 shows that the prawns increased the percentage of oxygen withdrawn from the medium as the oxygen tension dropped. There was a sharp increase in the withdrawal percentage below 25 mm partial pressure in the Inactive state. The percentage withdrawal has been based on the volume of water which flowed through the prawn chamber during the experiment (2.25 litres per hour). Obviously the percentage withdrawal in this case will depend upon the volume of water which is passing through the burrow. Attempts were not made to determine the volume of water which Upogebia pumps through its gill chamber and therefore the percentage withdrawal results should not be compared with any obtained from other animals.

In an experiment on the behaviour of prawns when exposed to low oxygen tensions (page 155) it was stated that the prawns became inactive when the oxygen tension was between 10 and 36 mm Hg. This probably represents an attempt to keep oxygen consumption down, since from figure 45, it can be seen that at this tension the respiratory rate of the prawns declined. When the oxygen tension dropped below 11 mm the prawns emerged from the burrow water, see page 155. Even although they were then extracting as much as 7% of the available oxygen they apparently could not obtain

sufficient for their requirements and some form of drastic action was necessary. This behaviour of emerging may have originated as a stage in the abandonment of the burrow when conditions became unfavourable. With the water no longer able to provide sufficient oxygen the reaction was to move out of the burrow. However once the water/air interface was reached, normal respiratory movements could supply sufficient oxygen. If the animal climbed higher in the burrow water would drain out of the gill chamber and desiccation occurred. If the prawns retreated below the water surface they were once more confronted by low oxygen. The result was that the animals took up a position at the water/air interface and normal beating of the scaphognathite moved water over the gills. In this way a primarily subtidal animal managed to overcome a major obstacle to colonisation of the intertidal zone.

PARASITES OF UPOGEBIA AFRICANA

Virtually nothing is known of the parasites of U. africana. The only reference which was traced was that of Barnard (1950) who recorded a bopyrid isopod of the genus Pseudione in the branchial chamber of a specimen of U. africana collected at Gordon's Bay.

External and internal examination of U. africana from the Kowie estuary revealed four different parasites, namely a bopyrid isopod, an entoniscid isopod, a tetrarhynch cestode and nematodes. The latter are occasionally found in the body cavity and gut but no record was kept of them.

Bopyrid Isopod

The species of isopod which parasitises U. africana from the Kowie estuary has not been identified. It is not a species of Pseudione. Fifty specimens were sent to Dr R.B. Pike in New Zealand, a specialist on isopod parasites but to date he has not identified them.

Bopyrids are easy to find on Upogebia as they cause a swelling of the branchial chamber. The female bopyrid is large and occupies most of the swelling whereas the male is dwarf and is found on the ventral surface of the female.

Examination of samples of prawns totalling 3,600 animals collected for size frequency analysis between February 1965 and December 1966 revealed 60 cases of bopyrid infestation, this

is a parasitization of 1.6%. On three occasions prawns were found with bopyrids in both branchial chambers.

Tucker (1930) carried out a most comprehensive investigation into the effects of a bopyrid Gyge branchialis on the prawn Upogebia littoralis which occurs on the coast of Italy. He found that out of over 1,000 specimens examined, 21.5% carried the bopyrid. This is a far heavier infestation than was found in U. africana.

A record was kept of the total length of the female bopyrid and the total length of its host in each case. The results are shown in figure 47. There was a clear linear relationship between the size of the female parasite and that of the host. This implies that the prawns became infected at a small size and that the parasite grew with the host. On six occasions parasitized prawns moulted in the laboratory. Careful examination of the exuviae and dishes showed no trace of the parasites having moulted simultaneously. In two cases the bopyrids had eggs in the brood pouch and moulting would have resulted in the loss of these eggs. Thus it appears that this particular species of bopyrid does not moult simultaneously with its host. In contrast Caroli (1929) in Caullery (1952) claimed that "the bopyrid Gyge moulted simultaneously with its host Upogebia".

Fifty per cent of the parasites were found to be carrying eggs. There appeared to be no breeding season since eggs were found throughout the year.

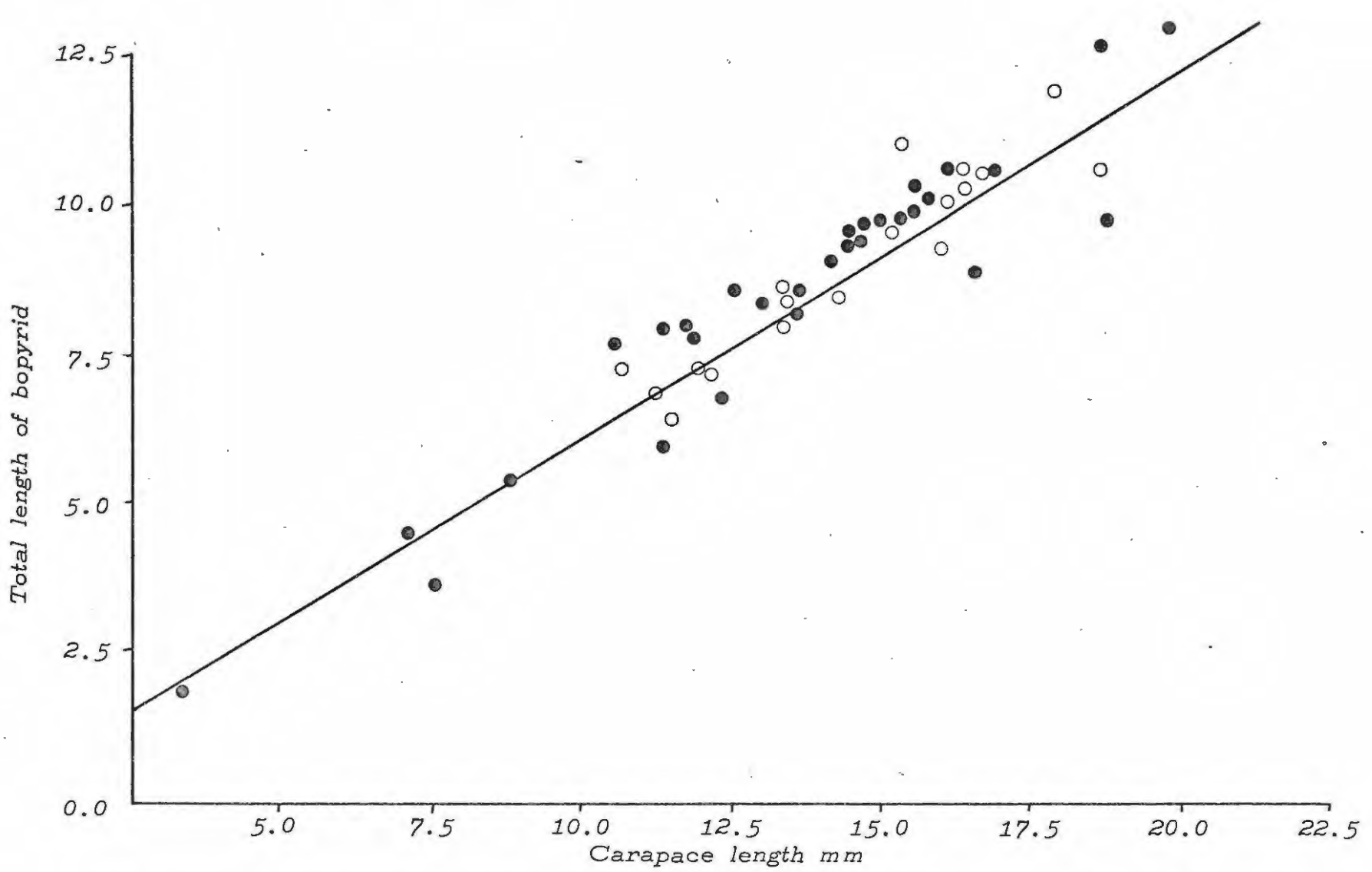

Fig 47: Total length of bopyrid parasites on U.africana compared with the total carapace length of the host. Solid circles indicate female prawns, hollow circles are male prawns.

Tucker found that as in U. africana there was a linear relationship between the size of the female bopyrid and that of its host. He found in addition that the parasite did not affect the size to which the parasitized prawns could grow. In fact the largest specimen of U. littoralis which he measured was parasitized.

Parasitic castration in Crustacea is widespread and frequently leads to alterations in secondary sexual characters. There are two secondary sexual differences in the degree of development of appendages in the genus Upogebia according to Tucker (1930). Firstly the male chela is broader than that of the female, and secondly the females have a pair of rod like first pleopods which are absent in the male. Tucker measured the chela of parasitized and unparasitized male and female U. littoralis and established that the parisitized males had a chela breadth comparable to that of the parasitized and unparasitized females. Tucker found that parasitized males of U. littoralis developed a first pleopod although the degree of development was extremely variable.

Specimens of U. africana were examined in order to establish whether changes occurred in parasitized individuals. No alteration in the first pleopods was detected in parasitized females nor did these pleopods apparently tend to develop in parasitized males. The breadth of the chela as well as the total carapace length was also measured in parasitized and unparasitized males and females and the results are shown in figure 48.

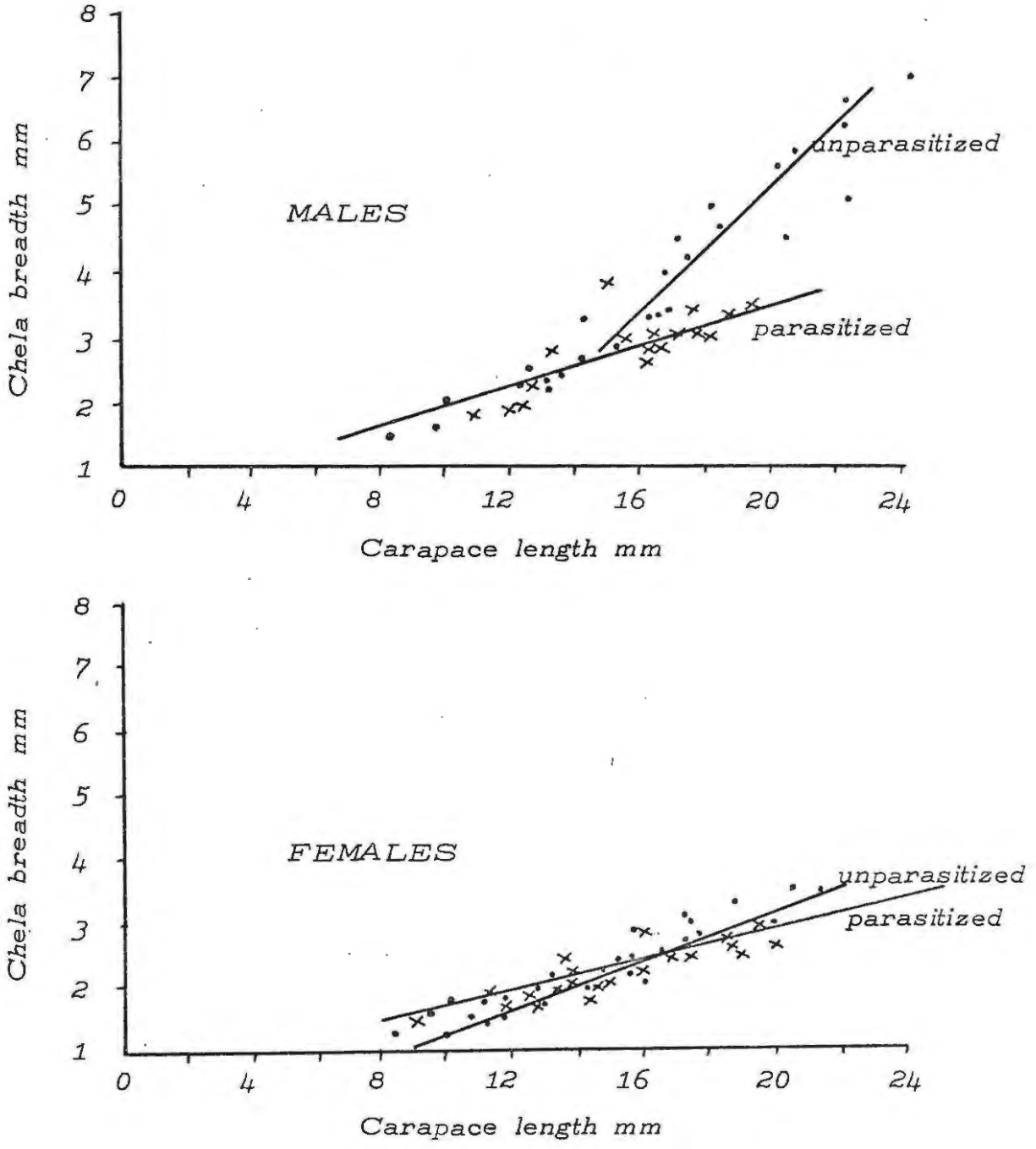

Fig 48: Breadth of the chela of male and female prawns which are parasitized (x) or unparasitized (•) by bopyrids. Lines fitted by linear regression (least squares).

Parasitized and unparasitized females have similar sized chela. There is a slight difference but in view of the

variation it is only trivial. Parasitized males larger than 14 mm total carapace length have a narrower chela than unparasitized males and approximate the chela breadth of the females. It appears the bopyrid does affect this secondary sexual character in the male although it has little effect in the female.

Tucker made a detailed study of the histology of the gonads of parasitized and unparasitized U. littoralis. He found that the testis of parasitized males showed all possible variation from complete normality through all grades of degeneration to complete absence. He suggested that some parasitized males would probably be capable of sexual reproduction. On the other hand he found that in parasitized females the ovary was either invisible or extremely reduced and he concluded that females carrying bopyrids could never breed.

Although nothing is known of the effect of bopyrids on reproduction in U. africana males, the bopyrids do not cause sterility in all females, since on two occasions parasitized females were found to be ovigerous.

In order to determine whether there was any detectable physiological effect of bopyrids on U. africana, parasitized specimens collected in summer were put into dilutions of sea water for 100 hours. Blood samples were then withdrawn from the prawns and the freezing point depression determined in the usual way. The results are shown in figure 49 (closed circles) together with the freezing point depression curve of unparasitized prawns in summer.

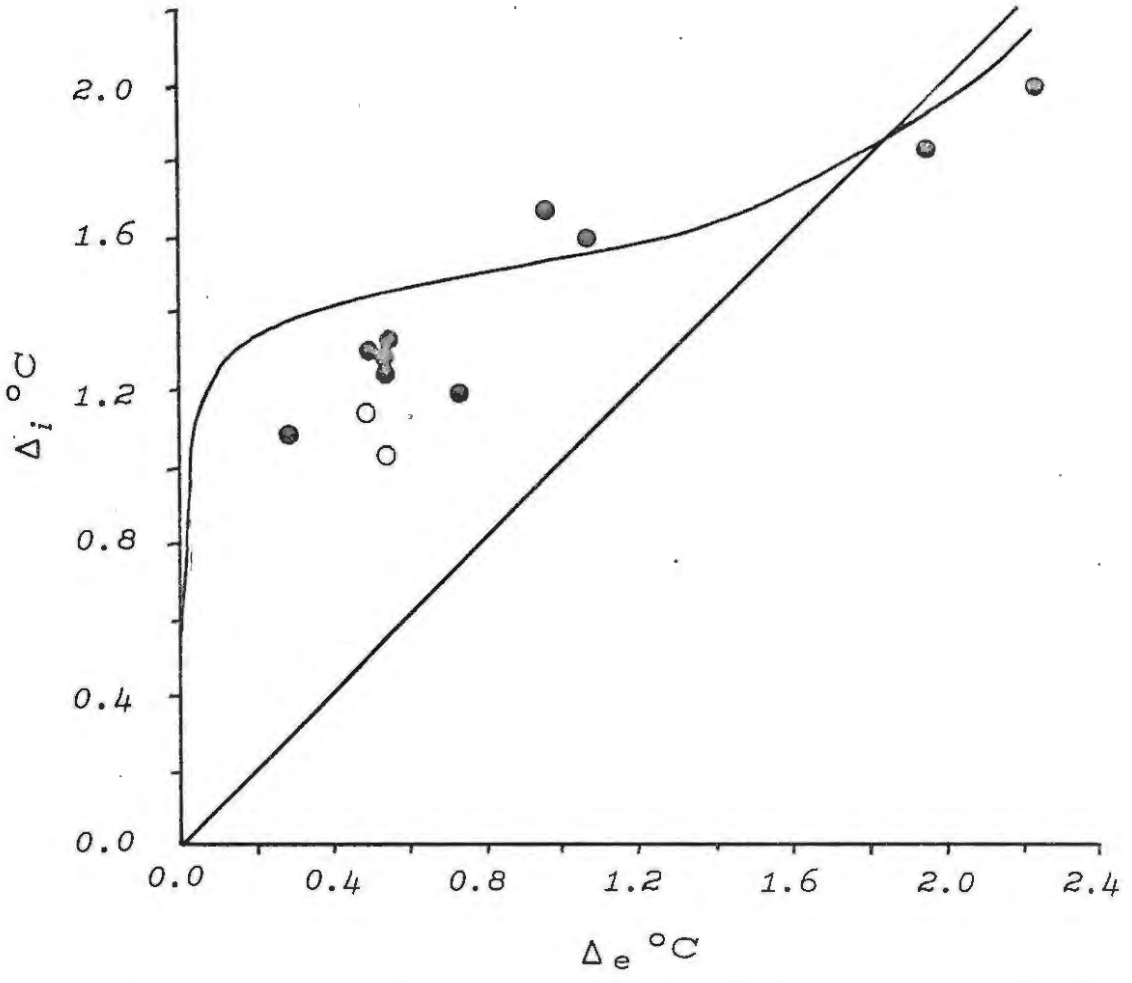

Fig 49: Freezing point depression of blood of prawns (Δ_i °C) parasitized by bopyrids (closed circles) or entoniscids (open circles) in various concentrations of medium (Δ_e °C). The Δ_i/Δ_e curve for summer prawns is superimposed on the figure.

In dilutions below 16 °/oo (Δ_e 0.9 °C), the parasitized prawns had a lower osmotic concentration than the normal individuals. In a medium of salinity 16 - 18 °/oo (Δ_e 1.0 °C), parasitized prawns had a higher osmotic concentration compared with unparasitized animals. In sea water and concentrated sea water (Δ_e 1.95 and 2.2 °C) parasitized prawns were more hyposmotic than unparasitized prawns. In the case of the

parasitized prawn in a medium of Δ_e 1.95°C, the bopyrid was removed after the blood sample was taken. Twenty two hours after the removal of the parasite a second blood sample was withdrawn. This sample had a freezing point depression identical to that of unparasitized prawns indicating that the depression of the freezing point of the parasitized prawn blood from normal values was probably an effect of the bopyrid.

Thus there is a definite effect on the physiology of U. africana as well as upon the morphology. However in general it appears that parasitization by bopyrids does not affect U. africana as severely as U. littoralis.

Entoniscid Isopod

No entoniscid has apparently been previously recorded from Upogebia and specimens found in U. africana are at present being described by Dr R.B. Pike of New Zealand. Entoniscids are internal parasites of Decapod Crustacea, mainly crabs although some have been recorded from pagurids (Caullery 1952). In general entoniscid females consist largely of a brood pouch filled with eggs and juveniles. They fill much of the body cavity of their hosts usually at the expense of the digestive gland.

In the case of U. africana, if the entoniscid is large it presses against the ventral body wall of the abdomen. As this body wall is semi-transparent it is possible to see the entoniscid. However the only way in which positive absence or

presence of the parasite can be determined is by dissecting the prawn. Out of forty one specimens of U. africana dissected, two had entoniscids, an infestation of 4.8%.

Atkins (1933) found that young specimens of the entoniscid Pinnotherion vermiforme did not cause sterility in the crab Pinnotheres pisum, whereas adults did. In U.africana one ovigerous female was found carrying an entoniscid which itself was packed with juveniles indicating that the prawn probably became ovigerous whilst carrying an adult entoniscid.

Two specimens of U. africana infected with entoniscids were put into a salinity of approximately 10 °/oo of different occasions. The freezing point depression of the blood was determined after 100 hours exposure. The results are shown in figure 49 (open circles) together with the Δ_i/Δ_e curve of normal prawns.

Clearly the presence of the entoniscid caused a lower osmotic concentration of the blood. Thus as in the case of bopyrids, entoniscids do have a physiological effect on their hosts. The departures from the normal freezing point depression make it imperative that all prawns used for determination of freezing point depression be examined for these parasites.

Unfortunately the numbers of prawns carrying entoniscids was low and the method of detecting them extremely tedious. Despite these drawbacks an investigation of these parasites should prove most fruitful.

Tetrarhynch Cestode

The plerocercoid of a tetrarhynch cestode was found in U. africana. The percentage of infestation appears to be low since three specimens were found in 41 prawns examined, ie 7.3%. The plerocercoids were identified by Dr J.C. van Hille of Rhodes University, as Parachristianella ?trygonis. Plerocercoids of this species were recorded by Dollfus (1946) in Upogebia stellata from the north coast of France and he found adults of P. trygonis in the elasmobranch Trygon (a stingray).

The plerocercoids in U. africana varied in size from 1.5 to 3.5 mm in length and were usually found inside the lobes of the digestive gland. On two occasions they were found to be free in the body cavity although still lying amongst the lobes of the digestive gland. No effect on the morphology of the host was observed and the freezing point depression of parasitized prawns in 9 and 17 °/oo (one sample in each case) was the same as unparasitized animals.

UPOGEBIA CAPENSIS AND THE VALIDITY OF OF UPOGEBIA AFRICANA AS A SEPARATE SPECIES

According to Barnard (1950), the decisive character separating U.capensis and U.africana is the presence or absence of coxal spines. These are small spines on the coxal joints of the 1st to 3rd periopods. Barnard states in connection with africana, "although opinions may differ as to whether this form should be regarded as merely a variety of capensis, the two forms appear to be localized, one in colder water, the other in warmer water".

The distribution of U. capensis is shown in figure 50 and should be compared with the distribution of U. africana shown in figure 1. Figure 50 is based on the following records:

Barnard (1950): Luderitzbucht; Saldanha Bay; Table Bay; Three localities in False Bay (including Gordon's Bay;) Mossel Bay.

Day (1958): Langebaan Lagoon.

Personal records: Gordon's Bay; Port Alfred; trawling grounds between Port Elizabeth and East London.

At Port Alfred U.capensis was found in the intertidal zone in crevices between rocks. The burrows were in coarse shelly grit but were lined with a thin layer of fine mud. At Gordon's Bay the burrows had been constructed in crevices filled with muddy coarse sand and pebbles. Berrisford

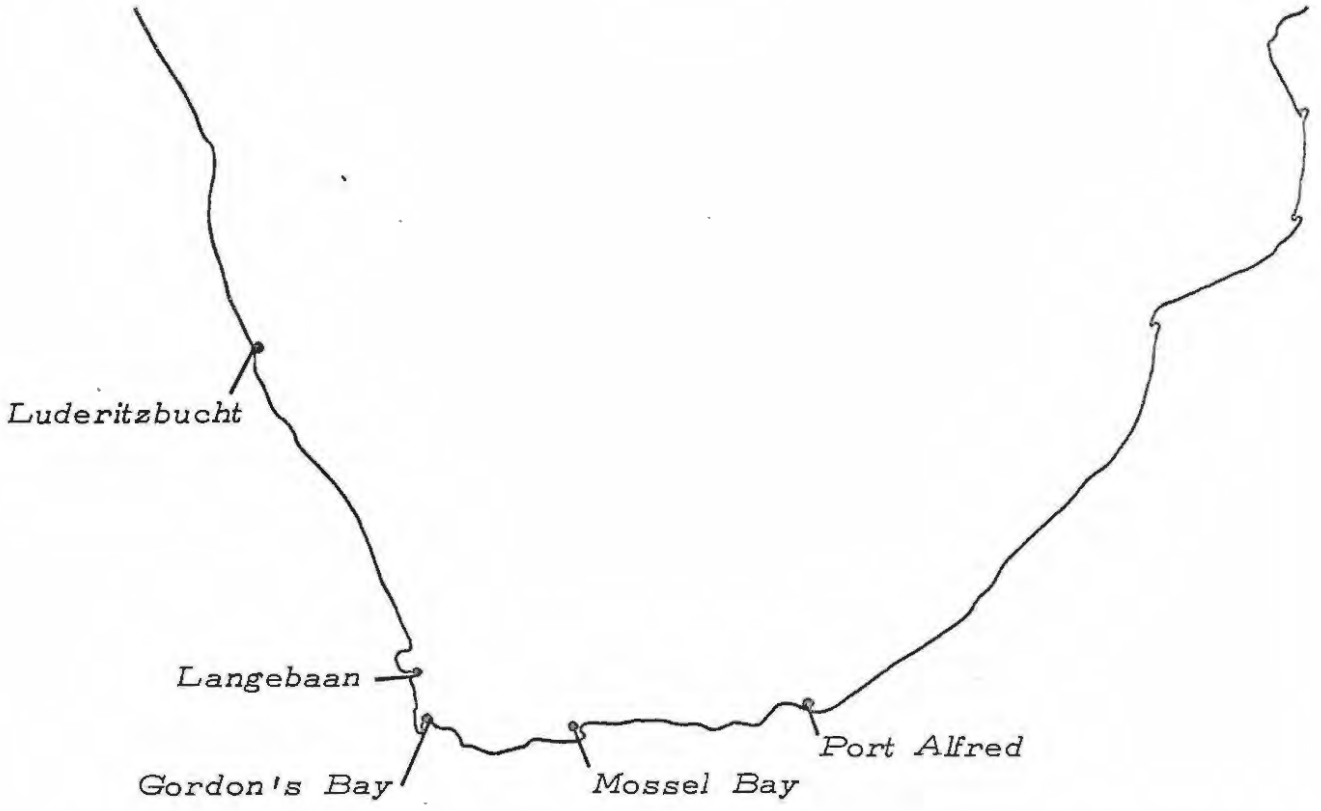

Fig 50: Localities around the southern African coast from which U. capensis has been recorded.

(personal communication) found U.capensis in stony mud flats at the head of the lagoon at Luderitzbucht. At Langebaan Day (1958) recorded U. capensis as occurring intertidally on rocky shores. It appears that at least in the intertidal zone, U.capensis makes its burrows in relatively coarse sediments in areas associated with stones or rocks.

U.capensis apparently extends into deeper water than does U.africana. Berrisford (personal communication) stated that at Luderitzbucht, specimens of U.capensis were obtained in every sample taken at a depth of five metres and that it appeared to be far more abundant subtidally than intertidally. Day (1958) reported that at Langebaan, U.capensis was obtained by dredging whereas U.africana was not. In April 1967 twenty one skates (Raia rhizacanthus) were obtained from a trawler at Port Elizabeth. The skates had been trawled on the grounds 'between Port Elizabeth and East London at a depth of 20 to 40 fathoms'. Thirteen of these skates had specimens of U.capensis in their stomachs. The number of prawns varied from 1 to 8 with a mean of 3.5. This record indicated that U.capensis must be present in large numbers off the south eastern Cape coast. Water temperatures at the depth from which the skates were obtained (20 - 40 fathoms) are 9 - 10 °C (Shannon 1966). These temperatures are similar to those on the West coast.

U.capensis can survive in higher temperatures since specimens were found at Port Alfred where sea temperatures

average 19 - 23 °C in summer and 15 - 17 °C in winter. The specimens collected at Port Alfred were rather small, the largest measured 14.3 mm total carapace length. West coast specimens attain a carapace length of 26 mm (Barnard 1950) and specimens obtained from the skates were up to 20 mm carapace length. The apparent small size of U. capensis in warm water recalls the same condition found in U. africana (page 88).

In view of the apparent absence of U. capensis from estuaries it was decided to determine the osmoregulatory ability of the prawns. Eight prawns collected from the intertidal zone at Port Alfred in August 1966 were exposed to various dilutions of sea water. A second batch of three were collected and put into dilute sea water in March 1967. Freezing point depressions were determined on blood samples withdrawn in the usual way. The individual results together with the exposure time in each case, are shown in the following table:

Date	Medium °/oo	Hours exposed	Δ °C
August	42.7	22	2.31
August	34.3	30	1.92
August	34.3	30	1.91
August	25.7	170	1.54
August	17.1	18	1.35
March	17.5	24	1.44
March	17.5	24	1.43
August	8.6	18	0.90
August	8.6	260	0.86
March	8.7	24	0.90
August	3.4	18	0.57

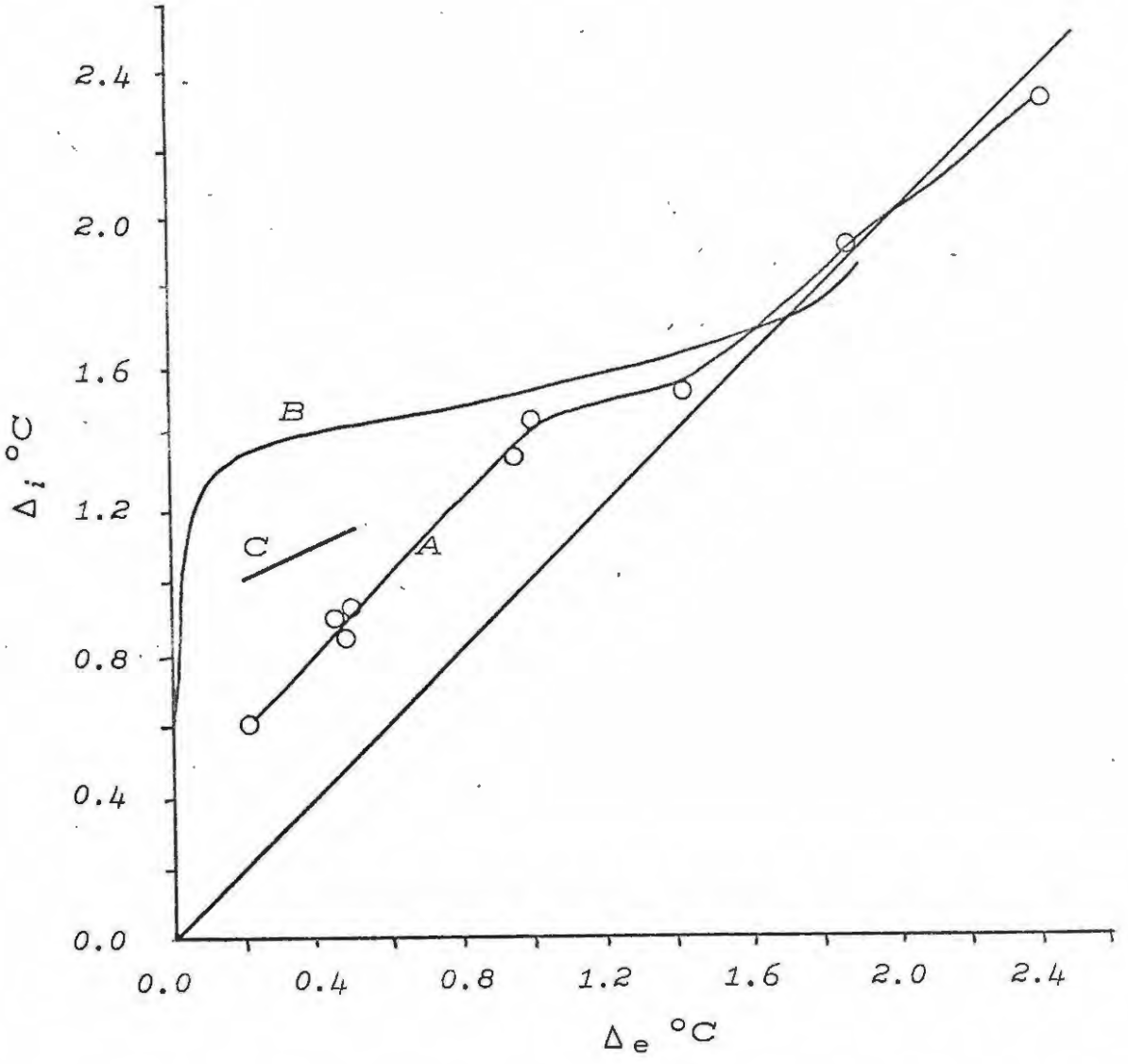

Fig 51: Δ_i/Δ_e *curves for* U.capensis *(open circles, A). The curves for* U.africana *in summer (B) and winter (C) have been superimposed on the figure.*

There appears to be no difference between summer and winter specimens of U.capensis *in the salinities tested since the freezing point depression of blood from prawns in 17.1 - 17.5 °/oo and 8.6 - 8.7 °/oo was extremely close in both summer (March) and winter (August).*

The results have been used to draw a Δ_i/Δ_e *curve for* U.capensis *as shown in figure 51. The curve for* U.africana

has been superimposed on the figure. Although the number of U.capensis used was extremely limited, the following tentative conclusions are based upon the results obtained.

U.capensis showed a definite osmoregulatory ability. It was hyposmotic in concetrated sea water (42.7 °/oo) but nearly isosmotic in sea water. In salinities of 18 to 27 °/oo it was hyperosmotic and it showed a narrow 'plateau' of internal concentration, indicating a slight degree of independance of environmental salinity. Below 18 °/oo the internal concentration dropped as the medium was diluted. The prawns maintained a difference in freezing point depression of 0.4 °C between blood and medium in the salinity range 3 to 18 °/oo.

If the curve for U.capensis is compared with that for U.africana it is seen that the difference is quantitative rather than qualitative. Both species were nearly isosmotic in sea water and both were hyperosomtic in salinities less than 30 °/oo. U.africana and U. capensis both maintain the internal concetration fairly constant (Δ_i 1.4 - 1.6 °C) in a limited salinity range below 30 °/oo. However in salinities below 18 °/oo the concetration of U.capensis falls off more rpaidly than that of U. africana .

Three specimens of U.capensis in a salinity of 3.4 °/oo all died within 31 hours of exposure. In a salinity of 3.4 °/oo the Δ_i is 0.57 according to the table given above. It has been shown above (page 105) that U.africana cannot survive extended periods during which the blood concentration drops to a Δ_i of

0.5 - 0.7°C. Apparently U.africana and U.capensis have a common basic tissue sensitivity to dilutions of the blood although this critical internal concentration occurs at different environmental salinities in the two species.

A single ovigerous female of U.capensis was collected from Gordon's Bay in September 1965. A second ovigerous female was found at Port Alfred in August 1966. These females were kept in sea water and the eggs hatched. The stage 1 larva obtained are typical of the genus Upogebia as described by Gurney (1942). Larvae of U.africana have also been hatched in the laboratory and thus it has been possible to compare the larvae of the two species.

The telsons of stage 1 larvae of U.capensis and U.africana are shown in figure 52. The different position of the central pair of spines was extremely characteristic and appeared to be constant in all the larvae examined. If this difference is valid for all individuals of the two species it should be possible to distinguish stage 1 larvae of U.africana and U.capensis. This difference could be confirmed or rejected by analysis of plankton samples from Luderitzbucht where only U.capensis occurs. No further stages of U.capensis larvae have been obtained and it is not known whether all stages are separable.

It is thus possible to distinguish U.capensis and U.africana morphologically (coxal spines) and physiologically (osmoregulatory ability), they have different geographical

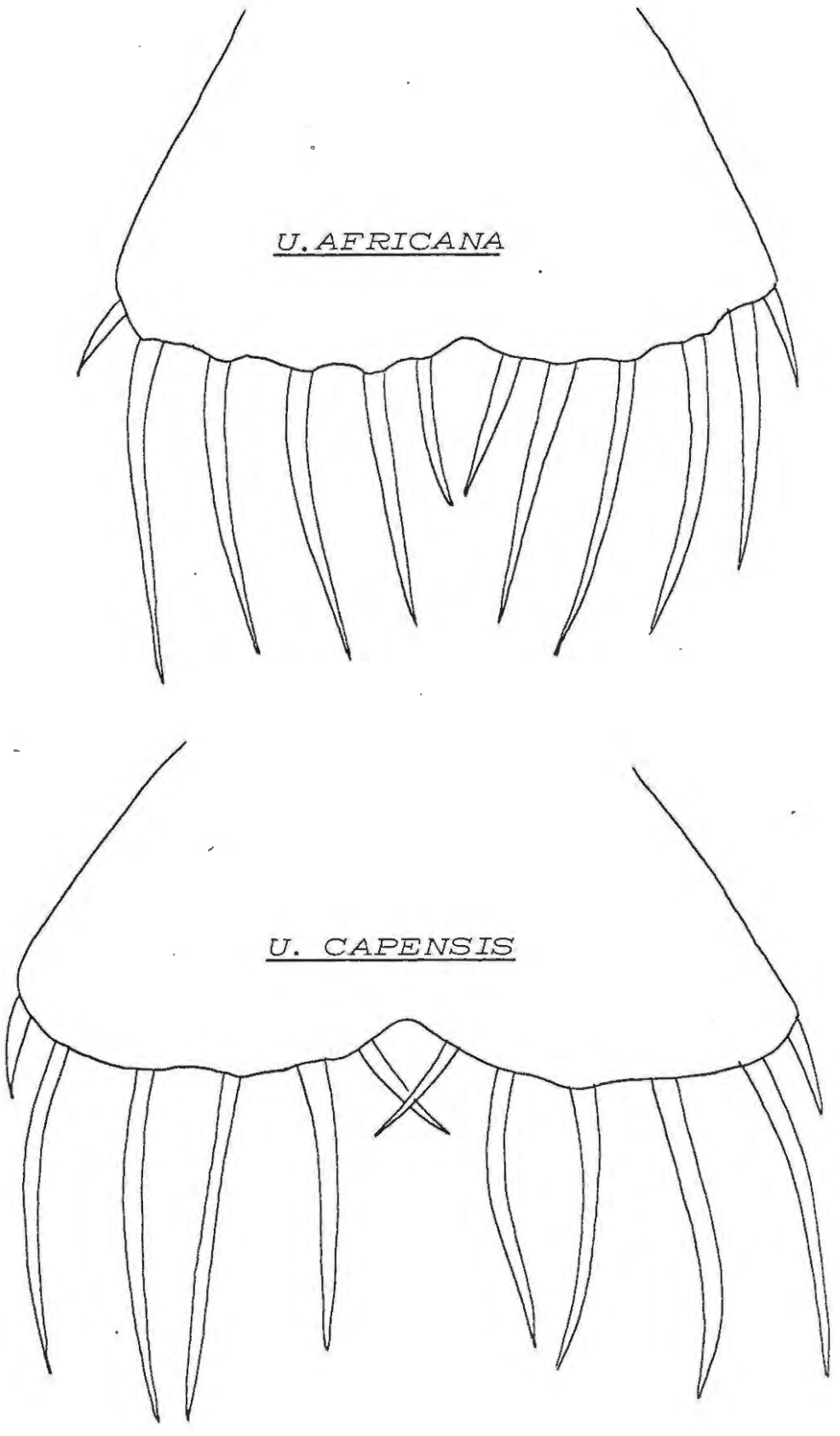

Fig 52 Telsons on stage 1 larvae of *U. africana* and *U. capensis*.

distributions and occupy different ecological niches and apparently the first stage larvae are distinguishable. In the light of the above information it appears that the division into two species is completely valid.

DISCUSSION

Evolution and Distribution of Upogebia africana

According to Borradaile (1903) most of the members of the tribe Thalassinidea are burrow dwellers. This burrowing habit probably originated very early in the history of the group since even the most primitive members, the Axiidae, are burrowers.

Life in burrows requires the solving of several problems associated with living in tubes. The tube has to be irrigated and requires a certain amount of maintainance such as the removal of debris and faeces. In addition the tube has to be periodically enlarged as the inhabitant increases in size and it may also have to be repaired. The setose nature of the anterior appendages found in the tribe was possibly first associated with these functions. They later became associated with filter feeding, an ability greatly facilitated by the irrigation of the tube for respiratory purposes. An important advantage of filter feeding is that the animal does not have to leave its home to forage for food.

In the genus Upogebia the most common habitat appears to be burrows in mud or sand. In contrast the subgenus Calliadne

is found in galleries in sponges. However this is a rather specialised group which has no larval stages. Obviously if an animal can inhabit a burrow in sand or mud it is in a position to take advantage of other tubes. Many species of Upogebia construct their burrows between crevices in rocks or on mudflats in association with stones. Macginitie (1930) recorded that in California, U.pugettensis was more abundant on rocky mud flats than in areas with no rocks. Dr P.Castle has informed me that in New Zealand a species of Upogebia is found in the crevices between rocks in the intertidal zone. It has already been stated that U.capensis is almost invariably associated with rocks, at least in the intertidal zone. Presumably the capability of burrowing in mud completely independant of supporting structures such as stones represents an advance on this condition. This is the stage which has been attained by U.africana.

Although U.africana appears to be a distinct species from U.capensis, there are both morphological and physiological similarities. It appears that the two species are related and it is tentatively suggested that U.africana evolved from U.capensis. The experimental evidence presented in this paper points to the separation having occurred mainly as a result of the colonisation of shallow water.

It has been shown that suitable substrates for burrow construction in shallow water are found mainly in sheltered areas such as quiet bays and estuaries and especially in the intertidal

zone of these areas. The closed estuaries were not colonised due to the lack of suitable food but in the open estuaries food and mud are available.

Despite the protection afforded by the burrow, three important problems associated with the colonisation of estuaries had to be overcome. These were, firstly high temperatures associated with shallow water, secondly occasional periods of low salinity during flooding and thirdly, in the case of animals living in the intertidal zone, survival at low tide when water cannot be pumped through the burrows for respiratory purposes.

Evidently there has been an upward shift in the temperature limits of U.africana in comparison with U.capensis. This has enabled U.africana to invade the east coast as far as Inhambane whereas U.capensis has not been recorded further along the east coast than Port Alfred. However the results of experiments on prawns from the Kowie estuary indicated that in summer, U.africana on the east coast may be living at the limits of its temperature acclimation ability. Exposure to temperatures over 30 °C for long periods is deleterious as shown by the temperature tolerance and sizes of prawns living in the heated pond at Knysna. In addition it was shown that a temperature/salinity interaction would probably effectively prevent U.africana from colonising tropical estuaries.

The apparent upward shift in the upper temperature limits of U.africana appears to have also raised the temperatures

at which breeding occurs. The cessation of breeding in the Uilenkraal estuary in winter suggested that low temperature inhibited breeding. A similar inhibition of short duration was found to occur in the Kowie estuary in winter. This temperature inhibition of breeding might be the cause of an inability to survive on the West Coast except in areas in which temperatures are higher than in the sea, such as at Langebaan. On the other hand U.capensis is able to breed at low temperatures since it occurs both on the West Coast and in cold deep water on the south east coast.

Life in the sublittoral or lower intertidal zone of the open coast requires very little osmoregulatory ability as there are only small variations in salinity. Gross (1957) found that U.pugettensis which lives in this zone was apparently isosmotic over a wide range of salinities. Significant salinity variations can occur in the higher levels of the intertidal zone and in order to inhabit this zone requires some degree of osmotic regulation or tolerance. It was found that U.capensis from the intertidal zone at Port Alfred showed a clear ability to osmoregulate.

In estuaries salinities drop during periods of flooding and a considerable osmoregulatory ability is required in order to survive. Selection operating through the medium of frequent flooding could have acted on an osmoregulatory ability of the type already existing in U.capensis. U.capensis can maintain an osmotic difference between its blood and the medium but

U.africana can maintain a much larger difference. Both species are hyposmotic in sea water and isosmotic in a salinity of 30 °/oo. Both species are also sensitive to a decreased blood concentration with a freezing point depression in the region of 0.6 to 0.7 °C. However osmoregulation in U.africana has not progressed to the point where the prawns can enter fresh water.

It was shown that in the estuaries, substrata suitable for burrows are found in quiet waters and especially in the intertidal zone. However at low tide prawns in this zone cannot irrigate their burrows. U.africana exhibits a low tide behaviour which enables it to carry on respiration at low tide. It was suggested that this behaviour might have originated as a stage in the abandonment of the burrow due to unfavourable conditions at low tide. U.capensis also occurs in this intertidal and must also be faced with this problem. Thus the low tide behaviour seen in U.africana probably originated in U.capensis.

The overall distribution of U.africana in the light of the above arguements has been summarised in figure 53. The distribution is clearly limited by a number of separate factors each of which can act independantly. In the case of temperature there are two distinct effects, firstly high temperatures are lethal to prawns, and secondly low temperatures inhibit breeding. U.africana is obviously a quiet water species as defined by Day (1964) and is limited by wave action and strong currents. This restriction is indirect since it acts on the substrate which

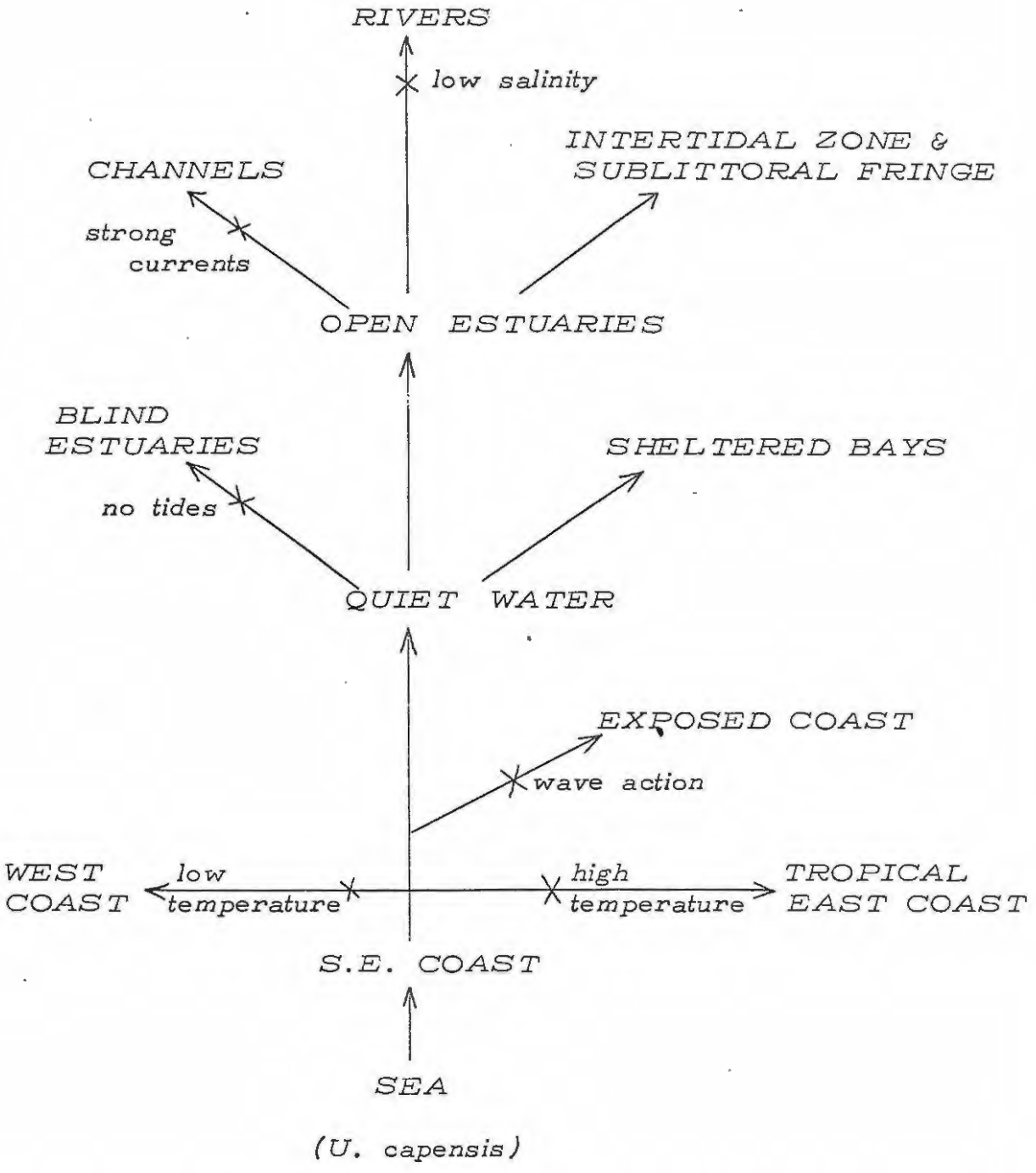

Figure 53: *Diagrammatic representation of the distribution of* *U.africana* *and the factors which control this distribution. Arrows indicate the possible direction the distribution could have taken. The crosses represent barriers, the nature of which is specified alongside the cross.*

is made unsuitable for the construction of burrows.

The occurrence of several distinct limiting factors in the ecology of U.africana emphasizes the importance of a broad approach in the understanding of the ecology of a species.

The Importance of Upogebia africana in the Economy of the Estuary

As stated earlier U.africana is abundant in many South African estuaries and it is often the dominant animal in the lower intertidal zone. Some idea of the vast numbers of prawns in the estuary is given by the fact that between 5,000 and 48,000 are removed from the Kowie estuary every fortnight with very little effect on the total population.

The importance of Upogebia in the overall economy of the estuary has three aspects. Firstly U.africana feeds on detritus and micro-organisms living on the mud. Thus Upogebia stands near the base of the food chain of the estuary.

Secondly the burrowing habit results in substrate being brought to the surface and the lower layers of the mudbanks being irrigated. In areas of dense colonisation this aspect must result in an increased rate of aeration and exchange of interstitial water. A consequence of this exchange is probably a richer interstitial fauna.

The third aspect of Upogebia's role in the economy of the estuary is that it serves as food for certain predatory animals. Day (1967) stated that several animals - polychaets (Glycera convoluta); a nemertine (Gorgonorhynchus sp); and

several fish such as white stumpnose (Rhabdosargus globiceps); white steenbras (Lithognathus lithognathus); and kob (Johnius hololepidotus); all prey on Upogebia. Thus in the overall economy of the estuary, U.africana is an important link in the food chain between basic food supplies and predators.

General Comments on Laboratory Studies in Ecology

It has been shown in this investigation that field ecology can and should be supported by laboratory studies and vice versa. Much of the research to date on lethal temperatures in Crustacea has been based on the use of a single temperature which causes death within a certain arbitrary time. However the work by Orr (1955) showed that this approach is far too rigid since there are a whole series of temperatures which will kill an animal provided it is exposed to them for long enough. The approach of establishing temperature/survival time curves has been adopted in the present investigation but an important additional factor has emerged. This is that summer and winter animals may have different temperature tolerances. Although this phenomonen is well known in other animals, temperature acclimation has been poorly documented in Crustacea.

The interpretation of temperature survival curves is occasionally questioned on the basis that these laboratory studies bear little relation to conditions in the field. However in the present study it was shown that predictions based on the results of temperature

experiments agreed exactly with actual findings in the field in the case of prawns exposed to heated water in the Knysna power station cooling pond. On the other hand evidence was presented to show that frequent exposure to lethal temperatures for short periods is deleterious and this long term aspect should be borne in mind when interpreting laboratory data.

In the determination of freezing point depression of blood it was found that the history of the animals affected the osmotic pressure of the blood. It was shown that the freezing point depression was to a large extent dependant upon the length of exposure of the animals to a particular medium. In addition in many Crustacea, the temperature of the medium may affect the osmotic pressure of the blood. In the case of U. africana *this temperature effect may have been the cause of a difference in freezing point depression of the blood of winter and summer animals. Finally the presence of parasites can have a significant effect on the osmotic pressure of the blood.*

U. africana *was shown to be more sensitive to low salinity at ecdysis than at other periods. This important fact has previously been overlooked in determinations of the lower lethal salinity based on survival experiments. Low salinity was also shown to inhibit moulting, this has not previously been reported to occur in Crustacea but it is extremely unlikely that* U. africana *is unique in this respect and further work on other Crustacea is obviously required.*

Many workers in determining respiratory rates have

utilised closed systems from which water samples are periodically withdrawn and the oxygen content determined. However this method suffers from the fact that the oxygen concentration of the medium decreases during the course of the experiment. In order to overcome this drawback most authors recorded the activity of the experimental animals and assumed that if the activity remained constant, the overall metabolism also remained constant. However it was shown that the respiratory rate of U. africana varied widely depending upon the oxygen tension of the medium even when the level of activity remained constant. Apparently metabolism may be reduced in some organs or tissues although locomotory activity remains unaltered. Clearly the method of closed systems for determination of respiratory rate is not satisfactory and should be replaced whereever possible by flowing water systems. Flowing water respirometers also have the advantage of not being subject to build up of CO_2 or excretory products. A build up in CO_2 causes a drop in pH which might affect the ability of the experimental animals to withdrawn oxygen from the medium.

It is felt that the explanation of the increase in respiratory rate which is exhibited by many crustaceans including U. africana when exposed to low salinity is not satisfactory. Physiological differences occur between the osmoregulatory ability of a euryhaline form such as U. africana and crustaceans like Eriocheir and Astacus which can live in fresh water. There is a distinct possibility that different

grades of osmoregulation can occur and that animals which are not continually exposed to low salinity are not at the same level of efficiency as those which can survive in fresh water. Surely it is not unreasonable to suppose that these differences extend to the respiratory requirements of the two types when in low salinity ?

This investigation has given possible answers to some of the problems associated with the ecology of U.africana; much still remains to be done. Probably the most important aspect is the elucidation of the life cycle. There is at present no information on the duration of the planktonic stages, nor where they occur. A great deal of comparative work on U.capensis is also required in order to establish both its distribution and physiology. Of special interest would be its temperature limits since it appears to be capable of breeding at lower temperatures than U.africana and might well have a lower high temperature tolerance. The work on osmoregulation by U.capensis was unfortunately limited to animals obtained at Port Alfred, its validity should be tested on animals from the West coast.

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