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Temperature tolerance of the estuarine prawn *Upogebia africana* (Anomura, Crustacea)

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Abstract

Continuous temperature measurements were made in a typical South East African estuary. Mean summer (November to March) temperatures were in the range 19° to 24 °C, and in winter (June to August) from 13° to 16 °C. Large daily temperature fluctuations of 6° to 10 °C occurred in summer; these appear to result from tidal movement of cool sea water into the estuary. In winter, temperature fluctuations were much smaller (3° to 5 °C). The burrowing prawn *Upogebia africana* (Ortmann) was found to have an upper lethal temperature of 29 °C in both winter and summer. The resistance time of prawns to temperatures above 30 °C was much greater in summer than in winter. It was possible to acclimate winter prawns and increase their resistance time to a level comparable to that of summer individuals. A latent period of 40 h occurred before acclimation effects were detectable. Long-term exposure of prawns to high temperatures did not increase their resistance above that of summer prawns. Water at a temperature above this upper lethal temperature is not pumped through the burrows. This avoidance behaviour considerably increases the ability of *U. africana* to withstand short-lived temperature extremes.

Introduction

Species inhabiting the intertidal zone are exposed to wider temperature fluctuations than species living in the sea. As a result, there has been considerable interest in the temperature tolerance of intertidal animals and speculation on the effects of temperature on their distribution. Estuaries are also subject to large temperature fluctuations but, in general, work on estuarine animals has been concerned only with the epifauna. Little attention has been paid to the infauna — those forms which habitually burrow into the substrate — despite the fact that they make up a large proportion of the estuarine intertidal fauna.

A series of ecological surveys (Day, 1964) has shown that, in southern Africa, one of the most abundant intertidal estuarine species is the burrowing prawn *Upogebia africana* (Ortmann). It inhabits U-shaped burrows in the intertidal zone and is an important member of the intertidal infauna. At one place, *U. africana* was also found in a pond containing heated power-station effluent.

A study of the temperature tolerance, acclimation ability and behavioural reactions to elevated temperatures, was carried out to determine the temperature limits which govern, in part, the geographical distribution of the species. The temperature regime in a typical South East African estuary is given as a background to this study.

Material and methods

Temperatures in the Kowie Estuary (35° S, 27° E) were recorded continuously for one year (1967) by means of an Oceanographic Engineering Corporation Model 401 Temperature Monitor and Recorder. The thermistor probe was attached 10 cm below the water surface on the end of a floating jetty, located 2.5 km from the mouth of the estuary, which is tidal for 18 km.

Temperatures over mud flats were measured on several occasions using a portable battery-operated thermistor thermometer. This apparatus had 6 waterproof probes in the ends of long electrical leads, enabling temperatures to be measured up to 30 m from the readout unit. The probes were placed at points between low and high tide mark, and the water temperature recorded at 5 min intervals from the time when each probe was first covered by the rising tide.

The prawns used for temperature tolerance studies were collected by digging in the intertidal mud banks 3 to 4 km from the mouth. This method results in very few young specimens (less than 10 mm carapace length) being collected. The prawns used in experiments were, therefore, predominantly in the size range 10 to 20 mm carapace length. In the laboratory, they were randomised into batches of 25 to 30 using the technique described by Allanson and Noble (1964) and placed in covered 25 cm diameter borosilicate glass dishes containing 4 l of sea water (34 to 35‰ S) at ambient temperature. The water was heated by means of 750 watt Buhler heater-stirrers and maintained to within ± 0.1 C° of the desired value. When the heaters were switched on, the temperature rose at between 2.6 and 2.8 C°/min. Temperatures were measured with a −10° to +50 °C mercury-in-glass thermometer graduated in 0.1 C° and standardised by the South African Bureau of Standards. All other temperature measuring instruments were checked against this thermometer. The starting time of the experiment was taken from when the final experimental temperature was reached. Water in dishes at a temperature of above 30 °C was changed every 24 h, while at lower temperatures a change was made every 48 h. Replacement water was preheated to the experimental temperature before substitution.

The approach of death was marked by collapse of the prawns, which rolled over onto their sides. Some time after collapse, the time varying with the degree of stress, the scaphognathite beat ceased. Beating was occasionally resumed if the prawns were handled at this stage, and in this case they were regarded as alive and were returned to the experiment. If the scaphognathite did not resume beating when the prawns were handled, they were discarded and recorded as dead. The time from the commencement of the experiment until death occurred for any individual or group is referred to as the survival time for that individual or group.

The prawns used in the experiments were not separated into sex or size groups, as preliminary experiments indicated no detectable difference in survival time either between male and female prawns or between prawns of different sizes.

The results were plotted graphically as the probit of percentage survival against the logarithm of the survival time in hours, using the method described by Finney (1952). These graphs were used to estimate the time required to kill 50% of the sample, a value subsequently referred to as the median time of survival (MTS). The terms upper lethal temperature, zone of resistance and zone of tolerance are used in accordance with previous work on fish (Fry, 1964), in addition, the survival time of prawns in the zone of resistance is referred to as the resistance time.

The behavioural reaction to high temperatures was studied by circulating heated water through an aquarium containing mud into which prawns had burrowed. Direct observations of the prawns could be made because burrows occasionally adjoined the glass sides. Temperatures within the burrows were measured by means of a miniature thermistor probe.

Temperature tolerance experiments were also carried out on specimens collected in April, 1967 at Knysna (34° S, 23° E), from a pond containing sea water which had been heated by circulation through the heat exchangers of an electricity generating power station.

Results

Estuarine temperatures

A clear seasonal variation was seen in the mean weekly temperatures in the Kowie Estuary. Peak values (19° to 24 °C) occurred from November to March, while the lowest temperatures (13° to 16 °C) were found between June and August. Considerable daily variations were found in summer as shown in Fig. 1, these variations could be related to tidal movements of water in the estuary. Water within the estuary was warmed by the sun and temperatures tended to be higher than in the sea. When the tide rose, cool sea water flooded into the estuary and temperatures dropped to values comparable to those of the sea. Thus, high temperatures coincided with low tide and low temperatures with high tide. In winter, temperature fluctuations were not as great (Fig. 1) due to a smaller difference between sea and inland

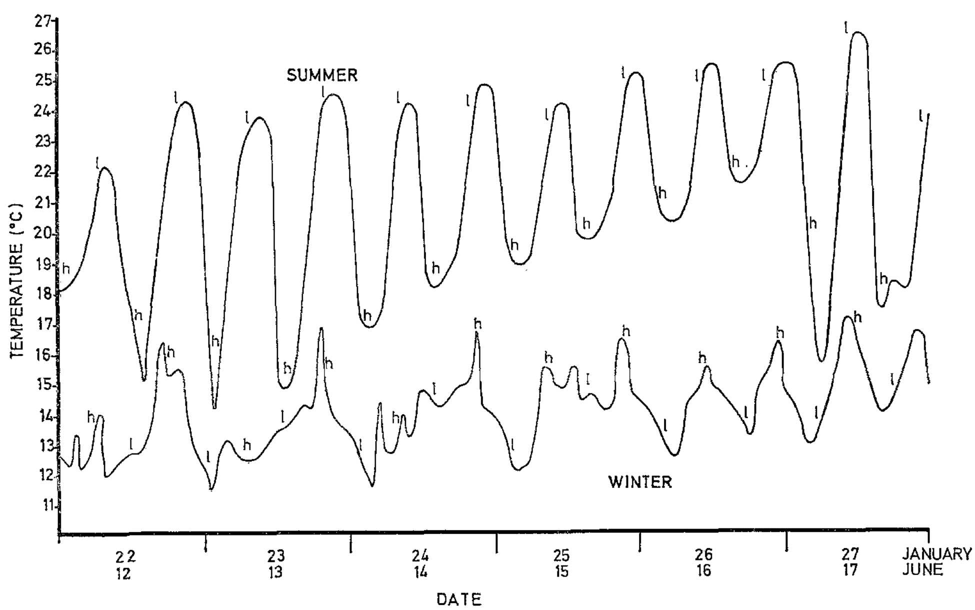

Fig. 1. Temperatures in the Kowie Estuary, S. Africa, over a typical 6 day period in summer (22—27 January) and winter (12—17 June). Predicted times of high (*h*) and low (*l*) tides are indicated

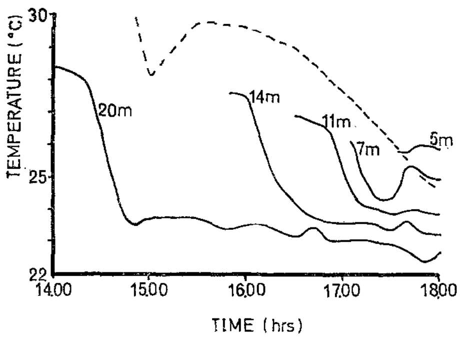

Fig. 2. Temperatures of water overlying tidal bank in the Kowie Estuary, S. Africa, on 10th March, 1966. Horizontal distance of each probe from high-water spring-tide level is shown next to appropriate trace. Probe at 20 m was at low-water spring-tide level. Dashed line: air temperature

water temperatures. At this time the temperature of water high up in the estuary dropped below that of sea water. This resulted in reduced temperatures at low tide. The lowest temperature recorded was 11.5 °C (13th June).

On a hot summer's day there was noticeable warming of shallow water on the margins of mud banks, and temperatures of up to 33 °C were measured. This feature was investigated in detail on several occasions, and typical results are shown in Fig. 2. This figure shows that a narrow band of heated water moved up the mud flat as the tide rose. This band of water gradually cooled from 28.5 °C at the bottom of the shore to 26 °C at the top. The water immediately behind the heated band was several degrees cooler and, as the tide rose, caused a sudden drop in temperature at each probe.

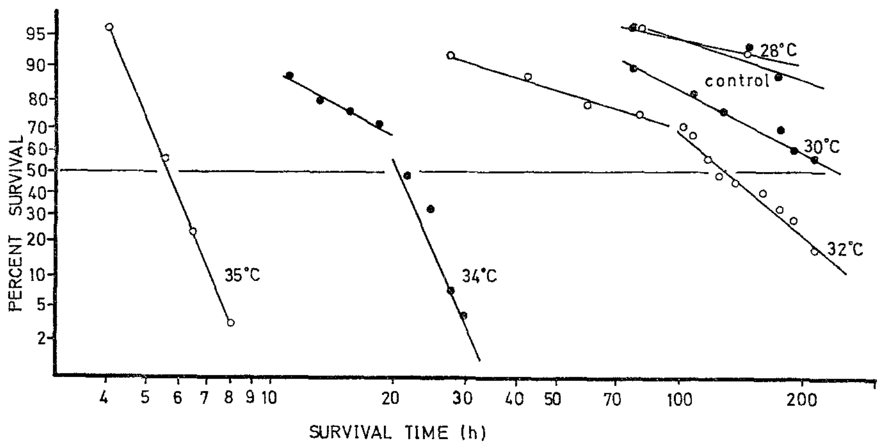

Fig. 3. *Upogebia africana.* Survival at high temperatures of prawns collected in summer (February, 1967). Percentage survival is plotted on probit scale

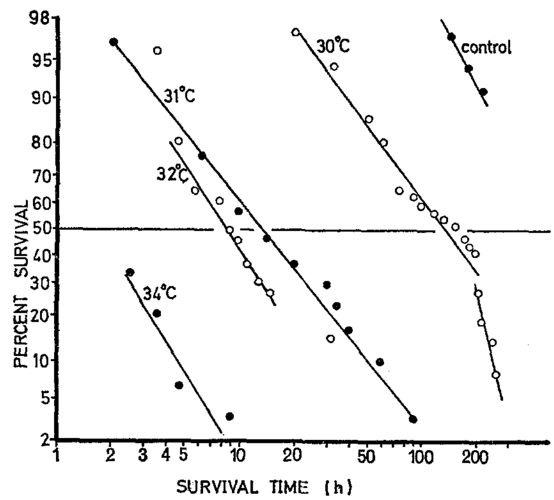

Fig. 4. *Upogebia africana.* Survival at high temperatures of prawns collected in winter (August, 1967). Percentage survival is plotted on probit scale

Tolerance experiments

When the results of high-temperature tolerance experiments on prawns collected in summer are plotted as probits of percentage survival against time (Fig. 3), a break in probit line is seen at temperatures of 34° and 32 °C. Finney (1952) pointed out that, provided these breaks occurred early on in the experiments, they could be ignored. Gibson (1954), working on temperature tolerance of goldfish, also found split probits which she interpreted as indicating that there is more than one cause of death operating. At the present time we have no information on the cause of death in *Upogebia africana,* but the possibility of two causes of death at high temperatures cannot be excluded.

The curves in Fig. 3 show that small temperature increases resulted in marked changes in the survival time. Thus, at 35 °C, all the prawns were dead before 10 h had elapsed, whereas the first deaths in 34 °C occurred only after 10 h exposure. The survival curve for animals kept at 28 °C is similar to that of the

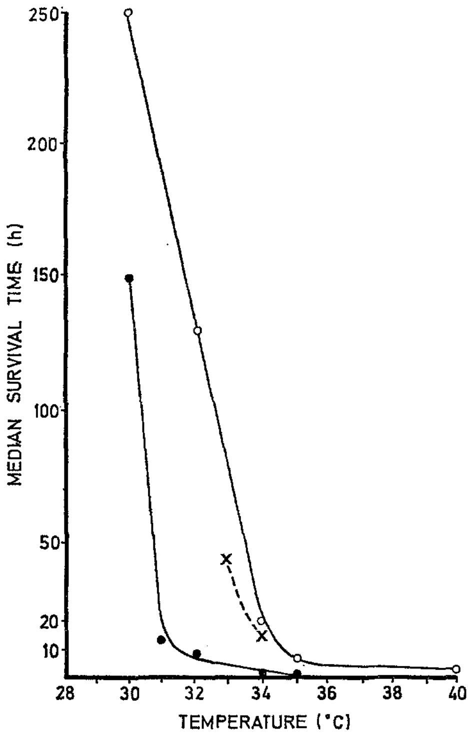

Fig. 5. *Upogebia africana*. Median times of survival of winter (●) and summer (○) prawns collected from Kowie Estuary, S. Africa. MTS of prawns from heated pond at Knysna (×) in April, 1967, are shown for comparison

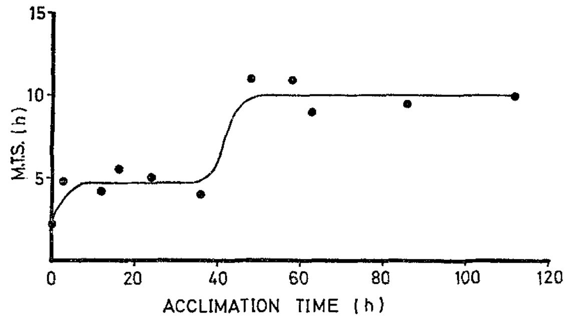

Fig. 6. *Upogebia africana*. Median survival times at 34 °C after acclimation for various periods at 24 °C

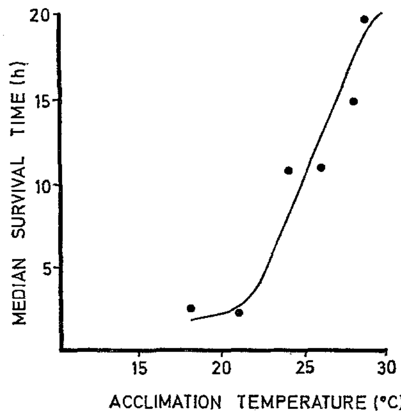

Fig. 7. *Upogebia africana*. Median survival times at 34 °C after acclimation for 58 h at various temperatures. Batch of prawns at 28.6 °C (MTS 20 h) were acclimated for 72 h

control group, but very different to that of animals at 30 °C. This suggests that the upper lethal temperature of summer individuals is in the region of 29 °C.

Survival experiments carried out on *Upogebia africana* collected in winter (Fig. 4) showed a split probit only at 30 °C. Deaths at 34 °C occurred extremely rapidly, more than half the prawns having died within 2 h of the start of the experiment. A marked increase in survival time occurred with a 1 C° difference in temperature between 31° and 30 °C.

There is a clear difference in MTS between prawns studied in winter and summer at temperatures higher than 30 °C (Fig. 5). Below 30 °C, the survival times are similar, suggesting that the upper lethal temperature of both summer and winter individuals is in the region of 29 °C. Thus, the upper lethal temperatures of both summer and winter prawns is similar, although the zone of resistance of summer individuals is much larger.

The difference in thermal history between summer and winter prawns probably accounts for the increased resistance time of summer individuals to high temperatures. The influence of thermal history was investigated by acclimating 10 batches of winter prawns at 24 °C for different periods of time. After acclimation, the various groups were transferred to 34 °C and their MTS determined; the results are shown in Fig. 6. This figure shows that there appeared to be a latent period of about 40 h before acclimation effects were detectable. Acclimation at 24 °C for more than 40 h did raise the temperature tolerance of winter prawns significantly, but not to the level of summer individuals.

The effect of acclimation temperatures other than 24 °C was examined by exposing batches of winter prawns to various temperatures for 58 h. When tested at 34 °C, these groups showed that temperatures below 21 °C did not result in any apparent acclimation effect after 58 h exposure (Fig. 7). Winter prawns exposed to temperatures above 21 °C showed increased resistance. The higher the acclimation temperature, the longer the MTS at 34 °C. In the case of winter prawns acclimated at 28.6 °C for 72 h, the MTS was the same as that of summer individuals transferred to 34 °C directly after being collected. Attempts to increase the resistance of summer prawns by acclimation at high temperatures failed to increase the MTS at 34 °C. When *Upogebia africana* was held at high temperatures for long periods the gills became black, suggesting microbial infection, and the prawns died shortly after. Thus, long-term high temperature could not be pursued further in the laboratory. The population living in the heated pond at Knysna is exposed to continual high temperatures and the resistance of these prawns to high temperatures was therefore determined.

The Knysna power station pond is divided into two distinct areas. The first section receives water only from the power station; in this region temperatures are in the range of 30° to 35 °C for about 8 h each day, dropping to 24° to 28 °C at night. There were no *Upogebia africana* living in this section of the pond. Water from this section flows into the second part of the pond which also receives an inflow of estuary water. This water is eventually pumped into the power station. This area of the pond has large numbers of *U. africana* living in the bottom. The temperature regime in this section is extremely complicated, but in general along the bottom in April 1967 when experiments were conducted, night temperatures varied between 19° and 23 °C and day temperatures between 24° and 29 °C. Temperatures 2.5 cm into burrows were between 24.1° and 28.1 °C during the day, and when the thermistor probe was pushed into the mud, temperatures ranging between 23.8° and 24.8 °C were measured at depths down to 14 cm.

The MTS of *Upogebia africana* collected from the pond and exposed to 34° and 33 °C are superimposed on Fig. 5. Despite the high temperature regime to which these prawns had been exposed, the MTS is slightly less than that of summer prawns from the Kowie estuary.

Behaviour at high temperatures

When water at 24 °C was circulated through an aquarium containing *Upogebia africana* living in burrows in mud, the prawns continued normal irrigation of their burrows. As a result, the temperature in the burrow corresponded closely to that of the overlying water. If water at 27.5 °C was circulated over the mud, the prawns decreased the irrigation rate. As the mud of the burrow walls was cooler (18 °C) than the water in the aquarium, the temperature of the water in the burrow dropped slightly to between 25° and 26.5 °C. An example of the temperatures recorded in a single burrow are shown in Fig. 8. When the overlying water temperature was increased above 32 °C, the prawns did not irrigate the burrow continuously. Pleopod beat lasted for 3 to 5 sec and then ceased for several minutes, with the result that only a small amount of water entered the burrow and the temperature rose only to 20° to 21 °C (Fig. 8). After about 30 min, most of the prawns began to close one of the entrances to the burrow by plastering mud around the hole. The temperature in the burrow gradually rose to 23° to 25.5 °C, due probably mainly to occasional weak irrigation and movements of the prawns which

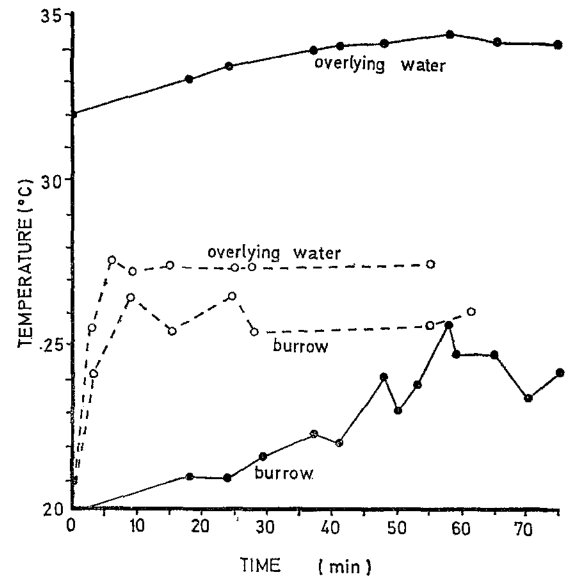

Fig. 8. *Upogebia africana.* Temperature of water in burrows compared with temperature of overlying water when warm water (dashed line) and hot water (solid line) flow over mud

caused some water to be moved in and out of the burrow entrance.

Discussion

As would be expected in a warm temperate estuary, there is not a great difference between average summer (19° to 24 °C) and winter temperatures (13° to 16 °C). On the other hand, large semidiurnal temperature fluctuations occur; these are associated with the tides and, in summer, changes of 6° to 10 °C in a few hours are common.

Although the temperatures are moderate, animals living in South East African estuaries must be able to cope with these rapid changes. In the case of *Upogebia africana,* average summer temperatures are well within its tolerance range except for brief periods. Brett (1956) has pointed out the significance of the zone of resistance in allowing animals to tolerate some diurnal fluctuations in which the peaks of environmental temperature exceed the lethal temperature. In addition, *U. africana* exhibits an interesting behavioural avoidance of heated water. *U. africana* enters its zone of resistance only if temperatures of water outside the burrow exceed 30 °C for long periods of time. Behavioural avoidance of high temperature is, of course, well known in terrestrial vertebrates and has also been reported in aquatic vertebrates such as the desert pupfish *Cyprinodon macularis* (Lowe and Heath, 1969). Intertidal crustaceans are also known to avoid high temperatures. Reese (1969) noted that hermit crabs would crawl out of intertidal pools when temperatures were high. The burrow of *U. africana* clearly offers considerable protection from transient high temperatures. This form of protection has been reported by EDNEY (1961) who stated that *Uca* burrows were several degrees cooler than exposed mud flats.

The correspondence between the upper lethal temperatures of winter and summer prawns despite the marked difference in zone of resistance can be attributed to acclimation occurring during the course of the experiment. At a temperature of 30 °C, winter individuals have an MTS of 130 h, whilst acclimation is apparently complete after only 60 h.

Upogebia africana exhibits a clear latent period of about 40 h before acclimation effects are detectable. MCLEESE (1956) reported a latent period of 10 days before acclimation effects became evident in the lobster *Homarus americanus*. He could not suggest a reason for this latent period. In contrast, a latent period of 40 h in *U. africana* could have considerable advantage. If it is assumed that the lowered temperature resistance is in some way advantageous, it would be undesirable for a winter individual to initiate acclimation immediately it is exposed to high temperatures. This is especially important in the case of an estuarine animal such as *U. africana* which, even in winter, is exposed to considerable temperature fluctuations.

Sustained high temperatures as used in the laboratory to acclimate prawns do not normally occur in their natural habitat. An alternative trigger suggested by LOWE and HEATH (1969) is the cyclic increasing extreme of daily temperature in spring together with increasing photoperiod.

It is tempting to speculate that the absence of *Upogebia africana* from that part of the Knysna power-station pond in which daily temperatures exceed 30 °C confirms the results of the temperature-tolerance experiments. Unfortunately, one cannot be sure that temperature is the limiting factor. There are several alternatives, since this very hot area receives only water which has been through the heat exchangers, whereas the rest of the pond receives an addition of cool estuary water. This could possibly result in differences other than temperature, such as food content.

Long-term exposure to high temperatures near the upper lethal limit either experimentally in the laboratory or in the case of prawns living in the power-station pond, does not increase the resistance time beyond that shown by summer individuals. This apparent inability to increase thermal resistance may well account for the absence of *Upogebia africana* from tropical estuaries. High temperatures can act as limiting factors in distribution. READ (1969) reported large scale mortality of the bivalve *Modiolus modiolus* due to high temperatures in a tidal pool, a finding which tends to support HODGKIN's (1959) contention that, on Australian reefs, annual mortality due to high temperature may be a potent factor in maintaining shore zonation. *U. africana* has, to date, been reported from only two places on the East African coast, at Inhaca (26 °S, 33° E) by MACNAE and KALK (1958), and at Morrumbene (24° S, 35° E) by DAY (personal communication). In both cases, the prawns were found in mud densely shaded by mangroves, an area which is undoubtedly cooler than the open mud flats. Thus, although *U. africana* in the Kowie Estuary lives well within its zone of tolerance, it appears capable of living at temperatures close to the upper lethal limit, but may well be limited by high temperatures on the East Coast.

Summary

1. Detailed temperature measurements were made in a South East African estuary.

2. Mean summer (November/March) temperatures were in the range 19° to 24 °C, winter (June/August) in the range 13° to 16 °C.

3. In summer, temperatures fluctuate rapidly due to tidal movements, changes of 6° to 10 C° occurring within a few hours.

4. In winter, daily temperature fluctuations are smaller (3° to 5 C°).

5. In *Upogebia africana* (ORTMANN), the upper lethal limit of both summer and winter prawns was 29 °C, but the zone of resistance of summer prawns is larger than that of winter individuals.

6. It was possible to acclimate winter prawns to the same resistance level as summer prawns.

7. It was not possible to increase the resistance of summer individuals. Prawns living in a heated pond did not have a greater resistance.

8. *U. africana* avoids water at a temperature above the upper lethal limit by cessation of pumping activity in its burrow.

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