Biology of *Hymenosoma orbiculare* Desm. in Lake Sibaya

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Hymenosoma orbiculare, (Crustacea: Brachyura: Hymenosomatidae) a crab common in estuaries in south- and south east Africa occurs in freshwater in Lake Sibaya at depths down to 40 m. This is the only known freshwater record of this species. The population density in the lake is fairly uniform declining in shallow and very deep water with an average of 2,5 m^{-2} (134 Jm^{-2}). The proportion of females in the population increases with depth. Females carry fewer eggs than estuarine populations and breeding appears to occur throughout the year. Both zoeae and adults differ morphologically from estuarine populations. These differences in breeding, biology and morphology raise the possibility that the Lake Sibaya population is specifically distinct from estuarine populations and this is discussed in relation to other instances of hymenosomatid invasion of freshwater habitats.
S. Afr. J. Zool. 14: 75-79 (1979)

Hymenosoma orbiculare, (Crustacea: Brachyura: Hymenosomatidae) 'n krap wat algemeen voorkom in riviermondings in suid en suidoos Afrika, word ook aangetref in die varswater van die Sibayameer tot op 'n diepte van 40 m. Dit is die enigste bekende geval van hierdie spesie se voorkoms in varswater. Die populasiedigtheid is redelik eenvormig en neem af vanaf vlak tot baie diep water met 'n gemiddeld van 2,5 m^{-2} (134 Jm^{-2}). Die verhouding van wyfies tot mannetjies neem toe met toename in diepte. Wyfies dra minder eiers as die in riviermondings en voortplanting vind blykbaar dwarsdeur die jaar plaas. Beide die zoeae en volwassenes verskil morfologies van die in riviermondings. Hierdie verskille in teling, biologie en morfologie dui op 'n moontlike spesieverskil tussen die bevolking in die Sibayameer en die in riviermondings. Hierdie aspekte word bespreek in die lig van ander gevalle van toetreding tot varswaterhabitatte onder die Hymenosomatidae.
S. Afr. Tydskr. Dierk. 14: 75-79 (1979)

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Accepted 26 October 1978

The Hymenosomatidae are an Indo-Pacific family of small crabs which occur in marine and brackish-water conditions. Some species - Holthuis (1968) listed six - may also or only occur in freshwater. In South Africa three species of Hymenosomatidae have been recorded (Barnard 1950). Of these *Hymenosoma orbiculare* is commonly found in estuarine and sheltered marine conditions along the southern African coast from Luderitz to Zanzibar (Barnard 1950), but was also recorded from freshwater in Lake Sibaya by Allanson *et al.* (1966). The bathymetry and possible origin of this lake has been described by Hill (1969), while the physics and chemistry have been discussed by Allanson & van Wyk (1969). Forbes & Hill (1969) investigated the osmoregulatory physiology of this freshwater population and compared it with populations from brackish and marine habitats. The present paper describes further studies on *H. orbiculare* from Lake Sibaya undertaken to obtain information on the reproduction, distribution, population density, activity and biomass, as well as differences in morphology of larvae and adults from fresh and sea water.

Methods

No suitable method was found for quantitative sampling of adult *H. orbiculare*. Underwater observations indicated that on approach of a net or a trawl many crabs swam upwards or sideways thereby avoiding capture. The best alternative procedure was counting or collecting by scuba divers. Unfortunately this method could only be used on limited visits to the lake and in addition diving at night had to be restricted due to the increased danger of attack by crocodiles. Counts of the crabs were made in July 1970 and January 1971 and quantitative sampling was carried out in January 1977. Counts and collections were made by two divers swimming at a speed of approximately 3 m min^{-1} for a measured distance of 38 m along the bottom. The divers raked the sand bottom by sweeping back and forth with their fingers to a distance of 1 m on either side of the line. Crabs were easily caught by hand and transferred to a plastic bag. Six counts at depths between 8 m and 20 m were made in July 1970 and four in January 1971. In January 1977 a more detailed survey was undertaken when all depths of the lake were sampled. Crabs were sexed,

carapace length measured and the presence of ovigerous females noted. Measurements were classified into 1 mm size classes, e.g. crabs between 6,0 and 6,9 mm are referred to as 6 mm crabs. The number of eggs carried by females in each of three size classes (6, 7 and 8 mm) was determined by counting the eggs scraped off five females from each class. The diameter of 50 of these eggs was measured using a micrometer eyepiece on a microscope.

The energy content of crabs collected in January 1977 was estimated by burning in a Gallenkamp Ballistic Bomb Calorimeter and expressed as kJg^{-1} ash-free dry mass (AFDM). Determinations were made on lumped samples consisting of 25 to 30 crabs from a single size class and dried to constant mass at 80° C. Ovigerous females in the 7 and 8 mm size classes were bombed separately. Ash (mainly $CaCO_3$) content of two batches, each of 25 crabs initially dried to constant mass at 80° C, was determined by ashing at 525° C for 14 hours. In view of the high ash content of the crabs (34%), a correction of 2,5% for endothermy was applied (Paine 1966). Adult *H. orbiculare* were collected from Lakes Nhlange and Mpungwini in the Kosie system of northern Natal and from Poelela in order to compare adult morphology with that of Lake Sibaya crabs. Ovigerous females collected from Lake Poelela in July 1973 and from Knysna Estuary in September 1977 were used for determining number and size of eggs carried by *H. orbiculare* from different areas.

Activity of *H. orbiculare* from Lake Sibaya was recorded in January 1971. Crabs were kept in a glass-sided aquarium 900 x 300 mm containing 400 mm depth of water at a temperature of 22 to 25° C. The aquarium was situated so that it received daylight but was shaded from direct sunlight. A 50 mm-deep layer of sand collected from the lake at a depth of 10 m and containing detritus and amphipods was spread over the bottom of the aquarium. Thirty-five crabs (6,0 to 9,9 mm carapace length), collected by divers from a depth of 9 to 15 m were introduced into the tank in the morning. The number of crabs which were on the surface of the sand or swimming, i.e. not buried, was then counted at intervals for 48 hours from 12h00. The experiment was repeated twice using different batches of crabs. Light intensity in the aquarium was measured by means of a Hydro-Bios submersible luxmeter.

The occurrence of *H. orbiculare* larvae in the lake was monitored by means of monthly plankton hauls taken from July 1970 to July 1971. Collections were made one to three hours after sunset by towing a 300 mm-diameter plankton net with 158 μm mesh for 10 minutes at the surface, over a water depth of 20 to 30 m, 1 km offshore. Vertical migration of zoeae was investigated by means of a closing vertical plankton net in January 1971 at a site 1 km offshore where the water was 30 m deep. Vertical 5 m hauls were made from 30 m to the surface. Morphology of zoeae was described using specimens sorted from Sibaya plankton samples and compared with stages obtained by rearing larvae from an estuarine population of *H. orbiculare* from the Knysna Estuary.

Results

A size-frequency analysis of *Hymenosoma orbiculare* collected in January 1977 is shown in Fig. 1. The sampling method was selective since few small crabs, and none smaller than 4 mm, were collected. Adult crabs were found

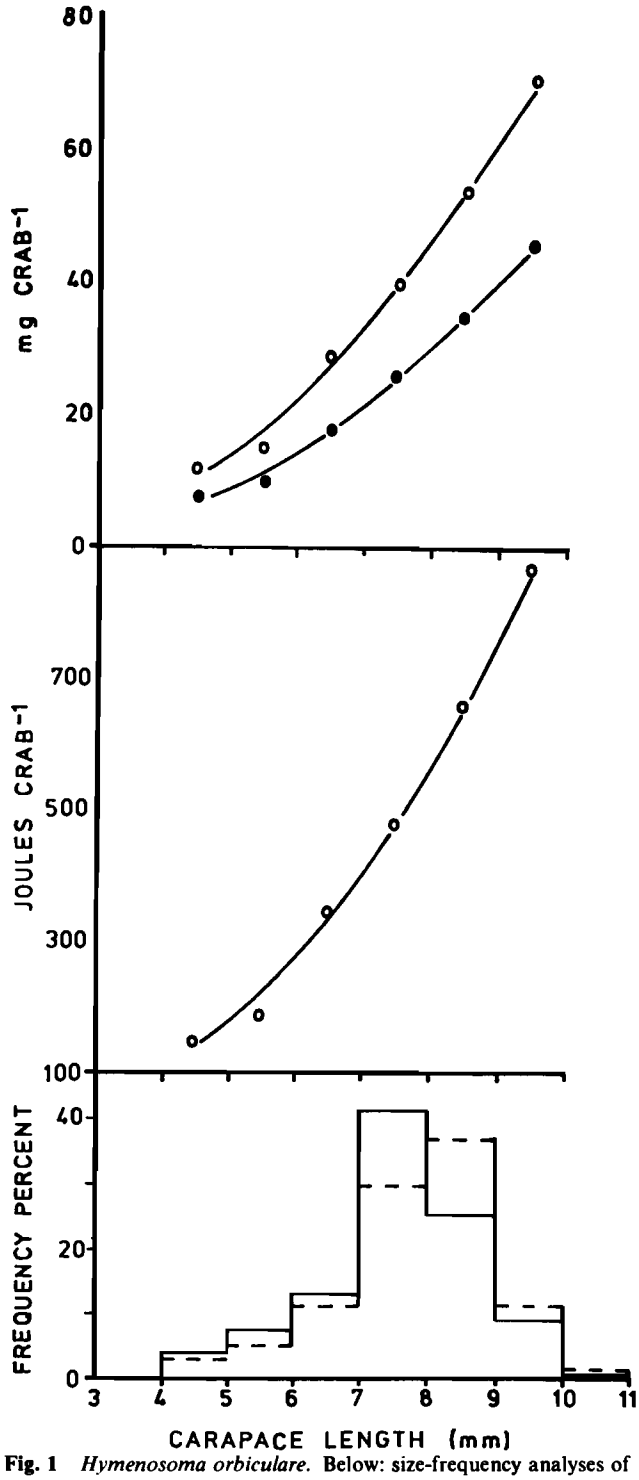

Fig. 1 *Hymenosoma orbiculare*. Below: size-frequency analyses of crabs collected from Lake Sibaya in January 1977 (males - dashed line; n = 333), (females - solid line; n = 307). Middle: size-energy content g^{-1} and size weight curve. Top: relationship between size and dry mass (DM) and ash-free dry mass (AFDM). (DM power curve: a = 0,44; b = 2,31; v = 0,99; n = 6 grouped samples).

at all depths (Table 1) although slightly fewer crabs were caught in very shallow (3-4 m) and very deep water (33-40 m). The density of crabs was fairly uniform over the lake bottom averaging 2,5 crabs 10 m^{-2} in January 1977 (Table 1). A similar density was found in July 1970 but in January 1971 it was twice as high (Table 2). Ash-free dry mass (AFDM) of *H. orbiculare* is 66% of dry mass. Mass and energy content of *H. orbiculare* increased rapidly with size (Fig. 1); the mean energy content of adult crabs (males and non-ovigerous females) was 18,86 kJg^{-1} AFDM. The standing stock of *H. orbiculare* in Lake Sibaya averaged 134 Jm^{-2} (Table 1). The modal size of females (7 to 7,9 mm) was slightly smaller than that of males (8 to 8,9 mm) (Fig.

Table 1 *Hymenosoma orbiculare:* details of samples of crabs collected in Lake Sibaya in January 1977. Calculation of standing stock energy content m^{-2} takes into account the size distribution of crabs at each depth, as well as the higher energy content of ovigerous females

Depth m	Area searched m^2	No. crabs collected	No. crabs 10 m^{-2}	Percentage female	Percentage females ovigerous	Standing stock J m^{-2}
3-4	360	48	1,3	31,2	6,7	45
7-9	360	89	2,5	37,0	45,5	133
10-12	360	91	2,5	50,5	50,0	143
13-17	360	91	2,5	42,8	53,8	150
22-24	480	144	3,0	54,8	65,0	176
26-29	240	113	4,7	49,6	48,2	206
33-35	240	36	1,5	58,3	57,1	92
39-40	90	15	1,7	46,7	14,3	109
Mean			2,5	48,0	50,1	134

Table 2 *Hymenosoma orbiculare:* population density of crabs in Lake Sibaya on three different dates

Date	Area (m^2) searched	Number of crabs found	Number of crabs 10 m^{-2}
July 1970	457	119	2,6
January 1971	152	78	5,1
January 1977	2 490	627	2,5
Total/Mean	3 099	824	2,7

1). Sexes were virtually equally distributed, 48% of the crabs collected being female. Sex ratio did however show a change with depth. Of 315 crabs collected at depths shallower than 10 m, 27,6% were female. This trend was also shown in a sample collected in January 1972 when 35% of 137 crabs collected shallower than 10 m were females, compared to 51,5% of 503 crabs collected deeper than 10 m. If all the samples of *H. orbiculare* collected from Lake Sibaya are grouped, the following percentages are female: 30,7% (n= 296) shallower than 10 m; 47,7% (n= 694) between 10 and 30 m; and 62,8% (n= 113) deeper than 30 m. These grouped values are significantly different at the one percent level, thus there is an increase in the proportion of females in the population in deep water.

Ovigerous females from Lake Sibaya carried fewer eggs than those from Knysna Estuary (Fig. 2). Extrapolation of the regression line fitted to the Knysna data indicates that the difference is not entirely due to the smaller size of Sibaya crabs. Thus an 8 mm crab from Knysna would, theoretically, carry 1 187 eggs as compared to a mean of 358 carried by the same size crab from Sibaya. There was no significant difference between the sizes of eggs carried by *H. orbiculare* from the various areas (Table 3).

In January 1977, 52,7% of females larger than 5 mm were ovigerous. The proportion ovigerous is related to size since 8% of 5 mm carried eggs (n = 24), while this proportion increased to 39% of 6 mm (n= 38) and to 62% of 7 mm (n = 126) females. The overall proportion of females carrying eggs was relatively constant at all depths except at 3-4 m and 39-40 m where it was less (Table 1).

The numbers of zoeae caught in plankton tows were extremely variable (Fig. 3) but the results indicate that

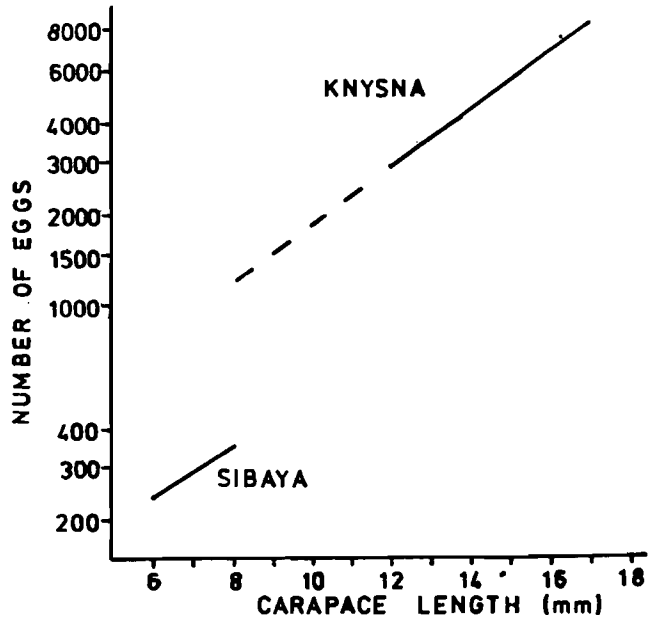

Fig. 2 *Hymenosoma orbiculare.* The number of eggs carried by females at different sizes from Lake Sibaya (exponential regression a a = 74,6; b = 0,19; r = 0,64; n = 14) and from Knysna Estuary (exponential regression a = 139; b = 0,25; r = 0,87; n = 8). Dashed line represents an extrapolation of the relationship of Knysna crabs.

Table 3 *Hymenosoma orbiculare:* sizes of eggs carried by crabs from different localities

Locality	Mean Diameter mm	Standard Deviation mm	n
Knysna Estuary	0,41	0.021	50
Lake Sibaya	0,39	0,019	24
Lake Mpungwini	0,44	0,047	30
Lake Poelala	0,45	0,036	50

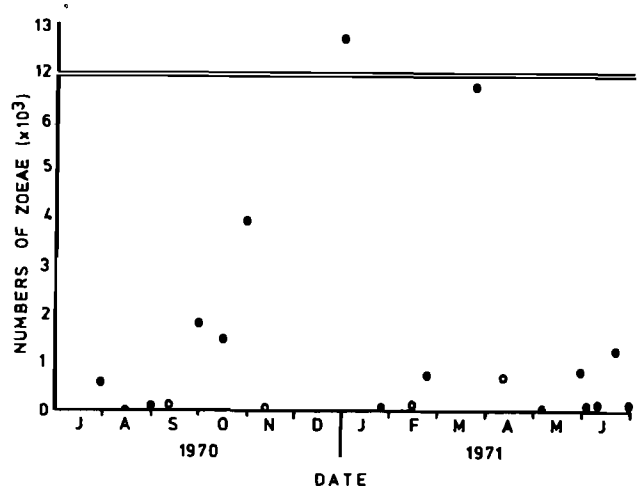

Fig.3 *Hymenosoma orbiculare.* Numbers of zoeae caught in plankton nets in Lake Sibaya. Catches indicated by open circles were made on bright moonlight nights.

breeding occurs throughout the year with a peak in summer. Some of the variability in the catches may have been caused by bright moonlight since field records showed that low numbers in November, January and February coincided with nights of full or nearly full moon. *H. orbiculare* zoeae appear to be sensitive to bright light since major concentrations were found where light intensities were below 10 lux (Fig. 4). Light is probably the

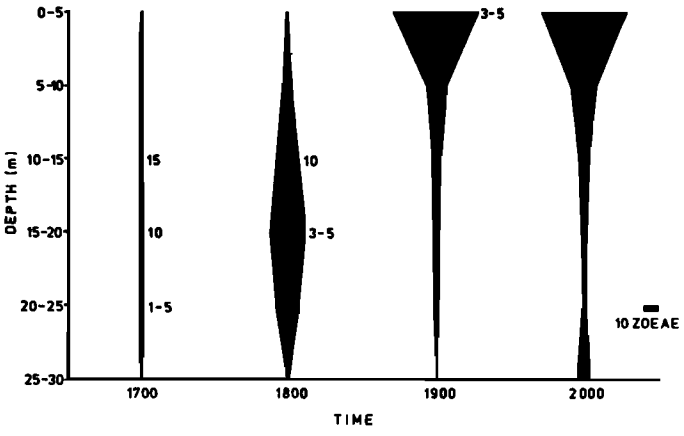

Fig. 4 *Hymenosoma orbiculare*. Vertical distribution of larvae at different times. Numbers are the lux values at various depths. Time is in hours.

controlling factor in the very marked vertical migration shown by the zoeae. Three distinct zoeal stages occurred in *H. orbiculare* from both estuarine and freshwater conditions. Zoeae from freshwater (Lake Sibaya) have far longer rostral and carapacial spines than do those from estuarine water (Fig. 5). This difference occurred in all three zoeal stages. Adult *H. orbiculare* from Lake Sibaya also show a morphological difference as compared to crabs from the Kowie (eastern Cape) and Swartvlei (southern Cape) estuaries and figured by Broekhuysen (1955). Adult male crabs from Lake Sibaya have two flattened posterior

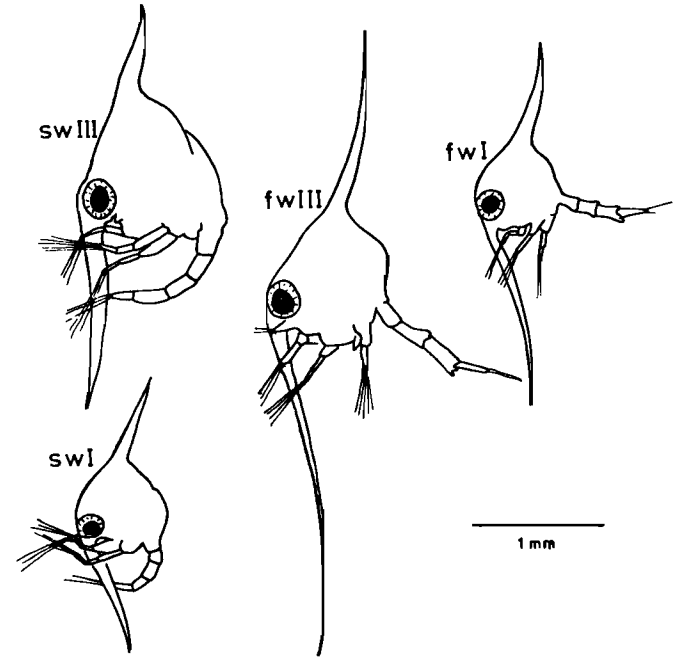

Fig. 5 *Hymenosoma orbiculare*. Zoeae I and III from Knysna Estuary (sw) and from Lake Sibaya (fw).

projections (Fig. 6 upper). These projections are absent on *H. orbiculare* from southern estuaries and from Sibaya females larger than about 7 mm carapace length (Fig. 6 lower). Rudimentary projections were found on small females from Sibaya (Fig. 6 centre). Adult male *H. orbiculare* collected from Lakes Nhlange (n = 32) and Poelela (n = 138) also had these projections but adult females did not. A small collection of *H. orbiculare* from Lake Mpungwini similarly showed no projections on females (n= 7), but half the males (four out of nine) had no projections. Thus this lake has an intermediate condition between that of the other three lakes in the region and the estuarine *H. orbiculare* found further south.

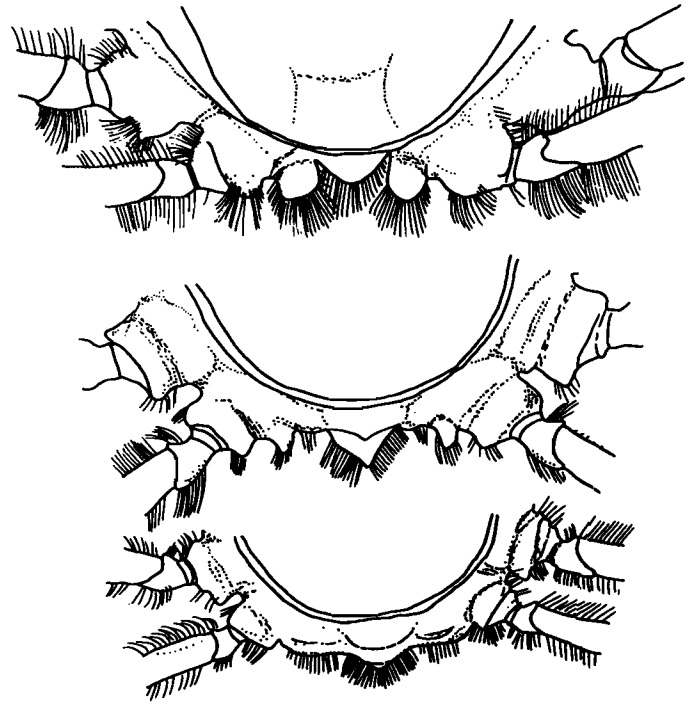

Fig. 6 *Hymenosoma orbiculare*. Posterior margin showing projections on adult males from Lake Sibaya (above), rudimentary projections on juvenile females (centre) as compared to adult females (below).

H. orbiculare showed a clear cycle of nocturnal activity (Fig. 7). They emerged around 18h00 as light values declined below 30 lux and buried themselves once again around 06h00 the following morning. During the night most crabs walked around on the surface of the substrate and foraged for food using the chelae to catch sand-dwelling amphipods. Many crabs also spent long periods swimming. *H. orbiculare* were seen by divers at night swimming in the water column. Adult crabs were also occasionally caught in plankton nets. During the day *H. orbiculare* remain buried in the sand. Divers noticed, however, that, at depths greater than 24 m, where daytime light levels are below 10 lux, many crabs could be seen walking on the surface of the sand. Thus in deep water *H. orbiculare* may not show a diurnal cycle of emergence.

Discussion

Forbes & Hill (1969) showed that zoeae of estuarine *Hymenosoma orbiculare* could not survive in freshwater. Thus there appears to be a physiological difference between zoeae from fresh and salt water. Lucas (1971) found that the freshwater hymenosomatid *Halicarcinus*

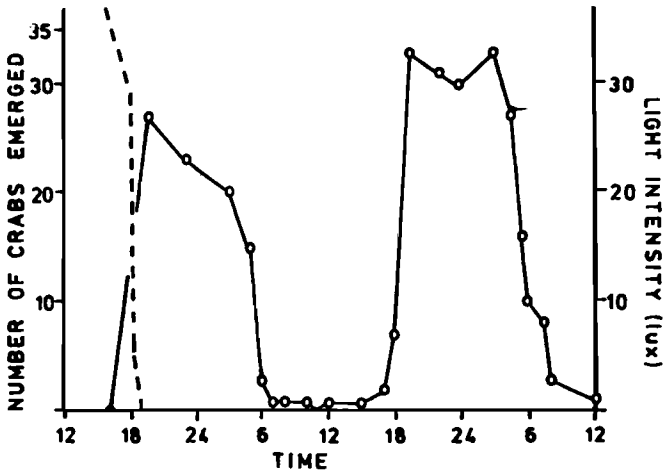

Fig. 7 *Hymenosoma orbiculare*. Number of crabs emerged from sand in a tank containing 35 crabs. Dashed line indicates light intensity. Time is in hours.

lacustris differed from estuarine and marine species in having lost the larval stages and having much larger eggs. These differences do not occur in *H. orbiculare* populations living in freshwater. *H. orbiculare* in Lake Sibaya has the same number of zoeal stages as it has in estuaries, and eggs from all localities are of similar size. The only morphological adaptation lies in the longer carapacial and rostral spines of freshwater zoeae. Lucas (1971) noted a similar difference between estuarine and marine zoeae of Australian species of hymenosomatids.

In Lake Sibaya, *H. orbiculare* breeds throughout the year with a peak in summer. This is different from the condition in Cape estuaries where Broekhuysen (1955) reported winter breeding. In both areas breeding coincides with the rainy season. Lucas & Hodgkin (1970) also recorded winter breeding in the Australian hymenosomatid *Halicarcinus lacustris*. They stated that breeding was not triggered by low salinity, similarly it could not act as a trigger in Lake Sibaya. Nevertheless it appears that rainfall may in some way be associated with breeding. Lucas & Hodgkin (1970) found large numbers of dead zoeae in plankton samples, apparently caused by low salinity (Lucas 1972). Broekhuysen (1955) pointed out that breeding by *H. orbiculare* in the rainy season results in considerable mortality due to larvae being washed out to sea and to their inability to tolerate salinities below 5 $^{0}/_{00}$. The coincidence of breeding with the rainy season therefore remains a puzzle.

Despite the large numbers of zoeae in the plankton of Lake Sibaya the population density of adults was low – a mean of 2,5 adults $10m^{-2}$. In the Kowie estuary in the eastern Cape the population density of *H. orbiculare* is much higher - about 40 crabs $10m^{-2}$ (Hill, *unpubl. data*). Lake Sibaya possesses two planktivorous fish – *Gilchristella aestuarius* and *Atherina breviceps*, which are capable of eating crab zoeae. Bruton (1977) found that adult *H. orbiculare* was a preferred food item of the barbel *Clarias gariepinus*. Thus predation may be partly responsible for the low numbers of adult crabs.

Although most information on hymenosomatid crabs is derived from shallow-water populations, several species do enter deep water. Broekhuysen (1955) for example recorded *H. orbiculare* at a depth of 22 m in the sea in False Bay and Barnard (1950) quotes records down to 80 m. Lucas (1975) reported two species of *Halicarcinus* in an 18 m-deep sound on the west coast of Australia. Studies by Lucas on these populations dealt with the larvae. These showed a vertical migration similar to that found for *H. orbiculare* in Lake Sibaya. There is no published information on change in adult population structure with depth. In Lake Sibaya there was a clear tendency for the proportion of females to increase with depth. Females made up 30,7% of crabs collected shallower than 10 m; this percentage increased to 62,8% in samples collected deeper than 30 m.

H. orbiculare in southern African waters is either a very plastic species and the morphological variations discussed by Barnard (1950) bear this out, or we are dealing with more than one species. Several differences have now appeared between southern and northern populations. These include physiological, morphological and behavioural characters. Clearly a thorough investigation is required to clarify the systematic position of this abundant and widespread crab. Most information on northern *H. orbiculare* is based upon the Lake Sibaya population and further research is now necessary upon estuarine populations in this region.

Acknowledgements

The authors wish to express their thanks to the Institute for Freshwater Studies, Rhodes University, for the use of facilities at Lake Sibaya.

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