Population biology of *Ilyoplax stevensi* (Brachyura: Ocypodidae) on a Kuwait mudflat

R. J. Snowden*, D. A. Clayton, E. Y. Al-Taher

Department of Zoology, Kuwait University, PO Box 5969, 13060 Safat, Kuwait

ABSTRACT: The ocypodid *Ilyoplax stevensi* was sampled every 6 wk between May 1988 and March 1989 in the upper eulittoral of a mudflat in Sulaibikhat Bay, Kuwait. A total of 770 males and 765 females of 2.5 to 10 mm carapace width (CW), were collected. CW frequency data indicated that instar number was either variable, or fixed with widely overlapping size ranges, and that 4.75 to 6.25 mm (an increment of 31.5%) was the puberty moult in males and in a proportion of females. There was a significant male bias in the pre-pubertal size class and a female bias in the main ovigerous classes (7 to 8 mm). Overall, 36% of the females were ovigerous; ovigerous females were present throughout the year, but in significantly higher proportions in September to March. Density and biomass were also significantly higher in winter which was therefore the ecologically active season, contrary to the normal cycle of warm temperate species.

INTRODUCTION


In the north of Kuwait there are extensive intertidal mudflats, the upper levels of which are dominated by ocypodids (Clayton 1986, Jones 1986). Kuwaiti shores experience wider annual temperature changes than those of similar latitude (Jones & Clayton 1983) and in combination with a general hypersalinity this creates an unusually harsh environment for the inhabiting organisms (Clayton 1986, Jones 1986). Apart from the work of Jones & Clayton (1983) on *Paracleistostoma* and *Cleistostoma* spp. and Collins et al. (1984) on *Uca sindensis*, very little is known of the effects of the extreme environmental conditions on the ecology of the mudflat fauna. In the present survey, this was investigated by the study of *Ilyoplax stevensi* (Kemp, 1919), one of the smallest and most numerous of the mudflat ocypodids. This species has long been reported from Pakistan (Kemp 1919, Tweedie 1937), but there appears to have been no previous work on its ecology.

MATERIALS AND METHODS

Three transects, 200 m apart, were established across the upper eulittoral zone of western Sulaibikhat Bay (29° 21.5' N, 47° 49.25' E) and 2 stations, at mean high tide level (MHTL) and mean lower high water (MLHW), were located along each transect. Every 6 wk, between May 1988 and March 1989, the substrate within 15 randomly placed 0.05 m² quadrats was extracted to 20 cm depth at each station. In the laboratory the samples were washed through sieves of 2 and 1 mm mesh and the macrofauna from the upper sieve plus the residue on the lower sieve were stored in 5% formyl seawater. *Ilyoplax stevensi* (Kemp) individuals were subsequently removed, counted and preserved in 90% ethanol. Maximum
carapace width (CW) was measured to the nearest 0.1 mm using an eyepiece micrometer under 60× magnification. All individuals were sexed, and for females the presence or absence of eggs was noted. Sexing of individuals < 3.5 mm CW required examination under 120 or 250× magnification to detect the slight indentation at the base of abdominal segment 5 which indicates the subsequent development of the narrow male abdomen. All intact individuals were oven-dried at 80 °C for 48 h and weighed separately. Throughout the survey, surface water temperature and salinity were measured at high water at the collection site at approximately monthly intervals.

RESULTS

Population dynamics

There were 2 modes, at 4.75 and 6.25 mm, in the CW frequency histogram of all males collected during the survey (Fig. 1a) and a single mode, at 7.25 mm, in the female data set (Fig. 1b). The 2 sexes were present in almost identical numbers (7706, 7650) and size ranges (6.25 to 10 mm CW, 9.25 to 9.5 mm), but in females there was a higher proportion of large individuals, around the 7.25 mm mode. The variances of the 2 data sets were heterogeneous (χ² = 9.7, p < 0.01; Bartlett test; Sokal & Rohlf 1981), and the mean CW of females (y ± s = 6.31 ± 1.33 mm) was significantly greater than that of males (6.01 ± 1.49 mm; t = 4.17, p < 0.001). Thirty-six % of the females were ovigerous (Fig. 1b), and these were present in all size classes > 5 mm, comprising between 45 and 70 % of the females in the classes > 6 mm (Fig. 2a). Males significantly outnumbered females in the 2.75, 3.25 and 4.75 mm CW classes (χ² tests; Fig. 2b) and females outnumbered males at 7.25 and 7.75 mm CW. In the remaining 10 classes and for the total population, sex ratios did not differ significantly from 1:1 (p > 0.10).

![Fig. 1. *Ilyoplax stevensi* carapace width frequency distributions of total (a) males, (b) females (black = ovigerous females)](image1)

![Fig. 2. *Ilyoplax stevensi*. (a) Ovigerous females as a percentage of total females in each CW class; (b) males as a percentage of total no. of individuals in each CW class. Asterisks indicate significant departures from 1:1 sex ratio (*p* < 0.05, **p** < 0.01, ***p*** < 0.001)](image2)

![Fig. 3. *Ilyoplax stevensi* carapace width frequency distributions of total (a) males and (b) females (black = ovigerous females) during each sampling period. Ratios = males females)](image3)
The CW frequency distributions of males (Fig. 3a) and females (Fig. 3b) during each of the sampling periods show varying numbers of modes, few of which can be followed through successive sampling periods. The population tended to be concentrated in the larger size classes during the first half of the survey, and there were more individuals in the smaller and mid-range size classes from November 1988 to March 1989. Ovigerous females were present throughout the year (Fig. 3b) and the only sex ratios to differ significantly from 1:1 were in June 1988 when there was a male bias ($\chi^2 = 4.12, p < 0.05$) and in September 1988 when there was a female bias ($\chi^2 = 4.18, p < 0.05$).

**Temporal variations**

Salinity was 40% in the early and late periods of the survey and 42% between July and October 1988 (Fig. 4a). Water temperatures were above 30 °C from mid-May to late September 1988, and at a maximum of 32.5 to 33.5 °C between June and August (Fig. 4b). There was then a gradual decline to the annual minimum (14 °C) in February 1989, followed by an increase to 22 °C in March.

At all stations *Ilyoplax stevensi* densities remained below 60 ind. m$^{-2}$ between May and November 1988 (Fig. 5) and began to increase in December. Slight reductions in February 1989 were followed, at all MLHW stations and at Transect 3 MHTL, by increases to maxima of 120 to 190 ind. m$^{-2}$ in March. At Transects 1 and 2 MHTL the maxima were lower and occurred earlier, in December and February. Between May and August 1988, 20 to 26% of the mature females (> 5 mm; Fig. 1b) were ovigerous (Fig. 6a), after which there was a sudden increase to a maximum of 66% in September. The ovigerous percentage then declined gradually to 45% at the end of the survey in March 1989. Individuals < 3.5 mm CW were only present during the last 4 sampling periods (November 1988 to March 1989).
March 1989), when they comprised between 2 and 5% of the total sample (Fig. 6b).

The regressions of $\log_{10}$ dry weight against $\log_{10}$ CW for the dried and weighed males, non-ovigerous and ovigerous females produced significant correlations ($p < 0.001$; Fig. 7), which were significantly different from each other. The equations were applied to the data of Fig. 3 showing the number of each type of individual in each size class, to estimate the biomass of the 3 groups during each sampling period. Fig. 8 shows that total biomass was low during the first half of the survey, although there was a minor peak of 0.68 g m$^{-2}$ in June. Biomass increased from September to December 1988, and, following a slight decrease in February, values increased in March 1989 to a maximum of 1.74 g m$^{-2}$.

Throughout the survey males and females each contributed around 50% to the total biomass and the contribution of ovigerous females was < 15% between May and August 1988, 40% in September and constant at around 25% from November 1988 to March 1989.

**DISCUSSION**

The fact there were only 2 rather indistinct modes in the male CW frequency histogram and one in females indicates that in *Ilyoplax stevensi* there is no clear size definition of moultng, and that the number of instars is either variable, or fixed but occurring over wide size ranges. However, even in such species the size of sexual maturity is generally clearly delimited (Hartnoll 1982). The increment between the 4.75 and 6.25 mm modes in males (31.5%) is similar to that recorded during moults in other crabs (cf. Hartnoll 1982, 1983, Bellwood & Perce 1989) and it is around this size that the male chelae enlarge, and the level of allometry of ambulatory limbs changes (Clayton & Snowden 1991). The female abdomen also enlarges at this size (Clayton & Snowden 1991), and the CW of the smallest ovigerous female was 5 mm. This suggests that 4.75 to 6.25 mm probably represents the puberty moult in most males and in at least a proportion of females.

Many authors have reported deviations from 1:1 sex ratios in brachyurans, and differential growth has frequently been suggested as a causative factor (Wenner 1972, Haley 1979, Conde & Diaz 1989, Diaz & Conde 1989). Female bias is generally thought to result from reproductively active females deferring somatic growth and therefore accumulating in the main reproductive size classes (Colby & Fonseca 1984, Conde & Diaz 1989, Diaz & Conde 1989). The highly significant female bias at 7.25 and 7.75 mm, in the centre of the unimodal size distribution of ovigerous females, suggests that this is the case in *Ilyoplax stevensi*. Fig. 2 certainly indicates a high commitment to reproduction, with 40 to 70% of females in the CW classes > 6 mm being ovigerous. The preponderance of males at 4.75 mm CW might also be due to differential growth; possibly the morphological changes associated with puberty require a greater commitment of bodily resources in males, which therefore spend longer in the prepubertal size class. No data are available to assess other causative factors (cf. Wenner 1972), but these observed variations in sex ratio produced differences in the CW frequency distributions such that females were found to be significantly larger than males.

Reproduction occurred throughout the year but was of a strongly seasonal nature, with the percentage of ovigerous females being significantly higher in September 1988 to March 1989 (56% to 45%), than in May to August 1988 (26% to 20%) (Mann-Whitney U-test: $n_1 =$
3, \( n_1 = 5, n_2 = 5, U = 0, p < 0.05 \). No information is available on the size of the megalopa/first crab stages of *Ilyoplax stevensi*. However it is not unreasonable to assume that settlement would occur at around the same size (1 to 2.5 mm CW; Wada 1981, 1983a) as in the ecologically and morphometrically similar *I. pusillus*. The 1 mm mesh sieve retained 1 mm CW crabs of other species, and the complete lack of *I. stevensi* individuals < 2.5 mm CW, and the very low numbers in the 2.5 to 3.5 mm classes, suggests that the majority of settlement occurred outside the area studied. As this was an upper eulittoral population, in a typically laterally uniform mudflat, preferential settlement downshore is the most likely. This would ensure shorter periods of emersion, which could be important in promoting the survival of individuals passing through early benthic stages in July and August when air temperatures can rise above 55°C (see below). The fact that individuals < 3.5 mm CW were only present between November and March 1989, during which time numbers in the mid-range size classes also increased, suggests that there was migration into the upper shore population as temperatures fell during winter. The occurrence of smaller individuals downshore is not uncommon in brachyurans, and amongst ocyopids has been observed by Hartnoll (1973), Frith & Brunenmeister (1980) and others. In the Red Sea, where summer air temperatures reach 45°C, Fishelson (1983) recorded this phenomenon in *Dotilla sulcata*, and in Kuwait Jones & Clayton (1983) found the smallest juvenile *Cleistostoma kuwaitense* individuals at the lower edge of the adult zone, around MHTL. Establishing the existence and extent of migrations in *I. stevensi* and examining their possible adaptive significance seem profitable topics for future study.

Population density and biomass were also strongly seasonal and were significantly higher in December 1988 to March 1989 than in May to November 1988 (Mann-Whitney U-test: \( n_1 = 5, n_2 = 3, U = 0, p < 0.05 \)). Seasonality in invertebrate populations is well known in temperate environments where, primarily as a result of elevated temperature, spring and summer are the main seasons of ecological activity (Kinne 1970, Levinson 1982). Increasing evidence suggests that seasonality is also a phenomenon of tropical waters, where salinity differences between dry and rainy seasons appear to be the major controlling factor (Livingston et al. 1975, Broom 1982, Conde & Diaz 1989, Snowden & Ekweozor 1990). Although Kuwait occupies a warm temperate latitude, the seasonality observed in *Ilyoplax stevensi*, where the main periods of reproduction and population growth occurred during the cooler months, is the opposite of the cycle normally associated with such waters (Raymoni 1983). Because of Kuwait's position at the northwestern edge of the shallow semi-enclosed Arabian Gulf, which is surrounded by desert, sea temperatures are equivalent to those of the tropics in summer and the subtropics in winter (Fig. 4; cf. Kinne 1970). However, although density, biomass and the percentages of ovigerous females and small individuals all increased in the period in which salinities fell from 42 to 40% and sea temperatures from 30 to 14°C, none of the parameters was significantly correlated with salinity, and only the percentage of crabs < 3.5 mm was significantly correlated with water temperature (\( r_s = -0.812, p < 0.05 \); Spearman Rank Correlation Test, Sokal & Rohlf 1981). Of possibly greater significance could be the harsh atmospheric climate, in which daytime temperatures can rise above 55°C in summer and fall to 5°C in winter. *Ilyoplax stevensi* occupies burrows of 20 to 30 cm depth in the upper eulittoral zone and feeds on the surface sediment around the opening during periods of emersion. Like most similar ocyopids (cf. Hartnoll 1973, Wada 1981, Henmi 1984), *I. stevensi* does not appear to leave the burrow when immersed or during darkness. Our unpublished observations suggest that individuals also do not emerge when air temperatures are below 15°C or above ca 45°C. Although daytime temperatures do fall below 15°C in December to February, and may remain below this level for 2 or 3 successive days, such an event is relatively infrequent. Much more common is the occurrence in summer of temperatures above 45°C. Between mid-June and mid-September, temperatures rise above this level for ca 50% of the daylight hours almost every day (Al-Kulaib 1975). This means that for a 3 mo period, *I. stevensi* would only be able to conduct its surface activities for about 4.5 h in the morning (05:30 to 10:00 h) and 2.5 h in late afternoon (16:00 to 18:30 h), provided the upper eulittoral is emersed during this time. This represents a considerable curtailment of surface activities, including feeding and courtship, and it is therefore not surprising that strategies have evolved whereby winter is the more ecologically active season. Further studies will determine how widespread such a pattern is amongst other species on the Kuwait mudflats.

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**LITERATURE CITED**

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