Vol. 71: 219-225, 1991 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published April 30

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

Ecological work on the Ocypodidae has been concentrated on relatively few genera (*Uca*: Crane 1975, Icely & Jones 1978, Frith & Brunenmeister 1980, Colby & Fonseca 1984, Thurman 1984, 1987; *Ocypode*: Barass 1963, Hughes 1966, Haley 1972, Jones 1972, Rao et al. 1986; *Dotilla*: McIntyre 1968, Hartnoll 1973, Hails & Yaziz 1982, Fishelson 1983; *Macrophthalmus*: Ono 1962, 1965, Simons & Jones 1981, Jones & Simons 1982, Henmi & Kaneto 1989; *Scopimera*: Ono 1962, 1965, Yamaguchi & Tanaka 1974, Wada 1981, 1983a, b, c, Suzuki 1983, Henmi & Kaneto 1989). Little has been written about the ecology of *Tylodiplax* and *Ilyoplax*, species of which can numerically dominate the shores on which they occur (Al-Taher 1990). The only *Ilyoplax* species to have been studied in any detail is *I. pusillus* in Japan by Ono (1962, 1965), Wada (1981, 1983a, b, c, 1984, 1987a, b) and Henmi & Kaneto (1989).

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 m^2 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

* Present address: Environmental Sciences Department, Sir William Halcrow & Partners, Burderop Park, Swindon SN4 0QD, Wiltshire, UK

0171-8630/91/0071/0219/$ 03.00

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 (770♂, 765♀) and size ranges (♂2.5 to 10 mm CW, ♀2.5 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 ($\chi^2 = 9.7$, $p < 0.01$; Bartlett test; Sokal & Rohlf 1981), and the mean CW of females ($\bar{x} \pm s = 6.31 \pm 1.33$ 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 (χ^2 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 ($p > 0.10$).

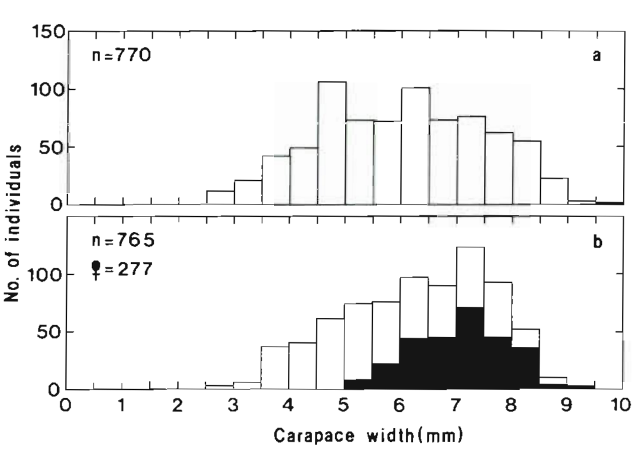

Fig. 1. *Ilyoplax stevensi* carapace width frequency distributions of total (a) males, (b) females (black = ovigerous females)

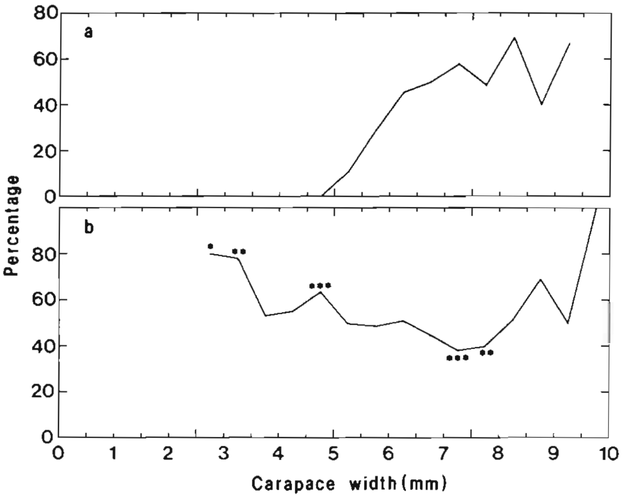

Fig. 2. *Ilyoplax stevensi.* (a) Ovigerous females as a percentage of total females in each CW class; (b) males as a percentage of total no. of individuals in each CW class. Asterisks indicate significant departures from 1:1 sex ratio (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

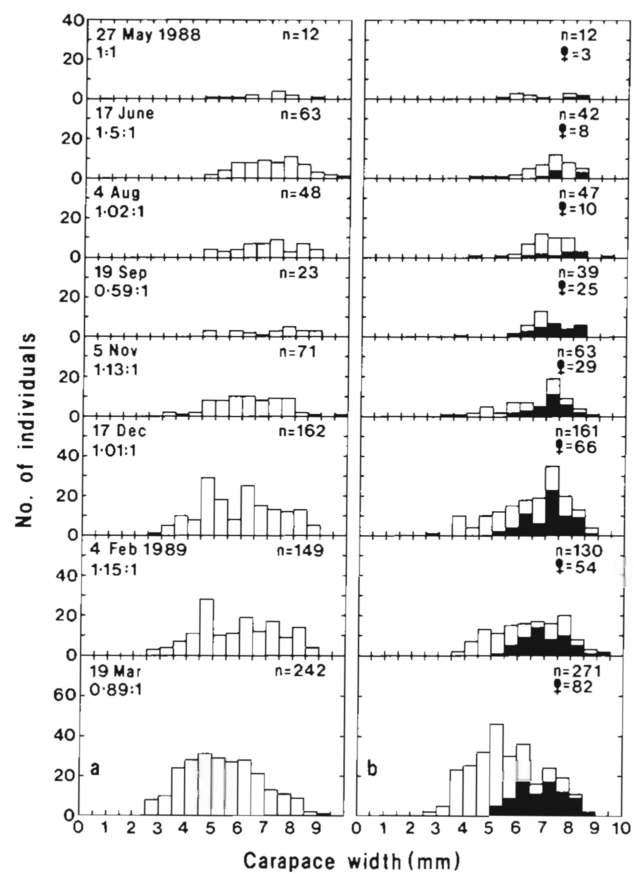

Fig. 3. *Ilyoplax stevensi* carapace width frequency distributions of total (a) males and (b) females (black = ovigerous females) during each sampling period. Ratios = males:females

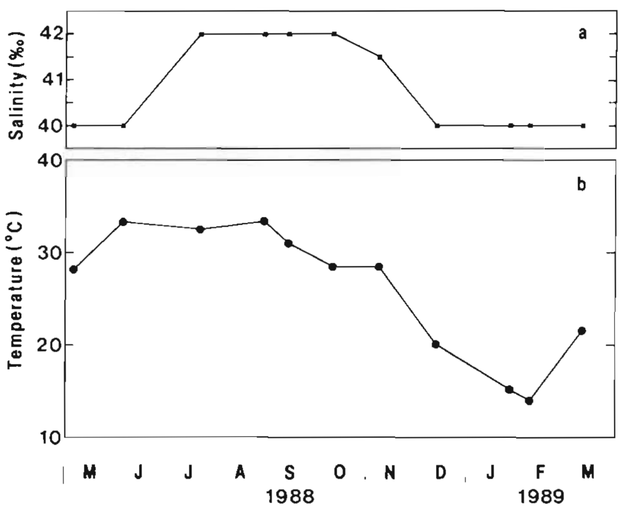

Fig. 4. (a) Salinity and (b) temperature at high water in western Sulaibikhat Bay, May 1988 to March 1989

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 ($\chi^2 = 4.18$, $p < 0.05$).

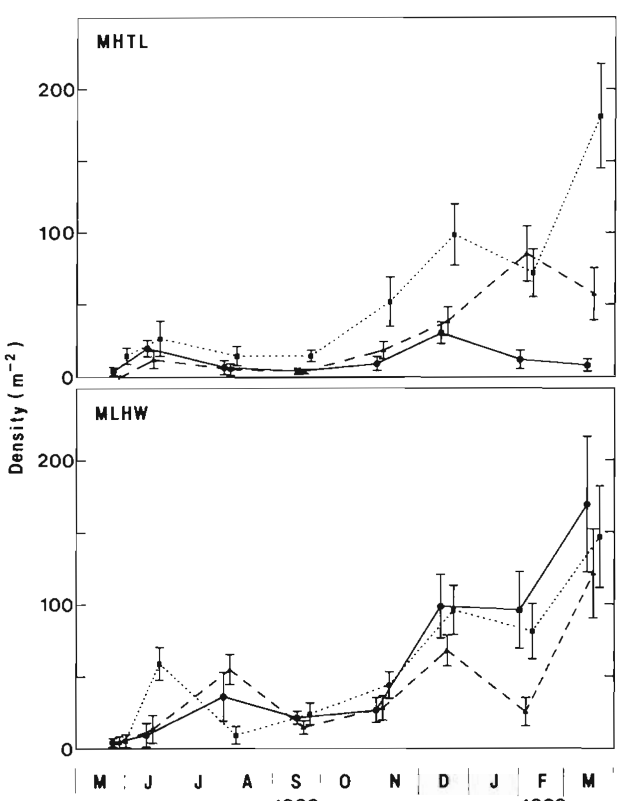

Fig. 5. *Ilyoplax stevensi* population density (m^{-2}), at mean high tide level and mean lower high water May 1988 to March 1989. (●—●) Transect 1; (▲---▲) Transect 2; (■·····■) Transect 3; vertical bars indicate standard errors

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

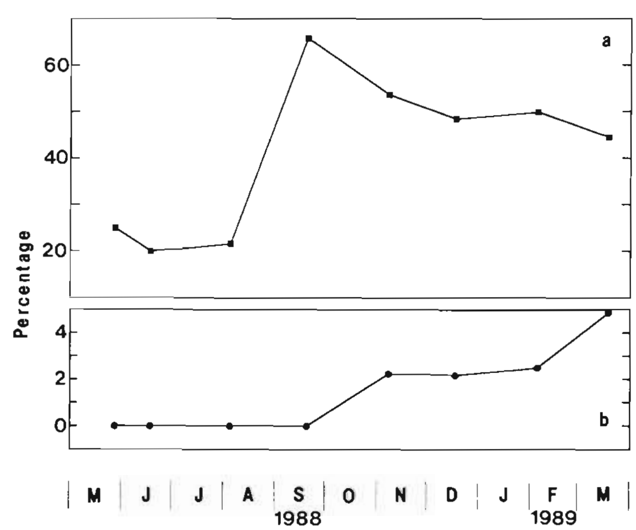

Fig. 6. *Ilyoplax stevensi*. (a) Ovigerous females as a percentage of mature females (> 5 mm CW); (b) individuals < 3.5 mm CW as a percentage of total individuals, May 1988 to March 1989

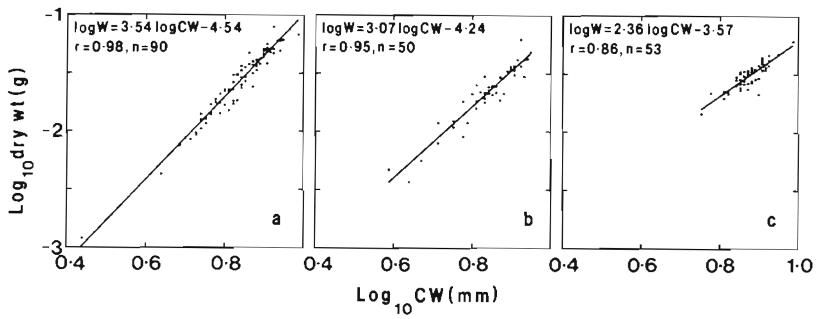

Fig. 7. *Ilyoplax stevensi*. Regressions of $\log_{10}$ dry weight against $\log_{10}$ carapace width for (a) males, (b) non-ovigerous females, (c) ovigerous females

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

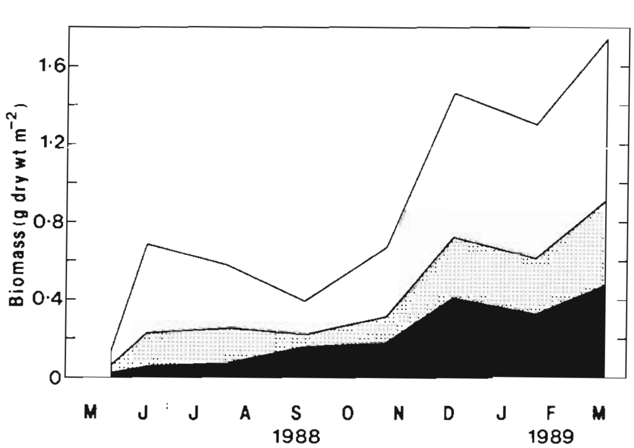

Fig. 8. *Ilyoplax stevensi* biomass (g dry wt m^{-2}) May 1988 to March 1989. Upper (open): males; middle (stippled): non-ovigerous females; lower (black): ovigerous females

definition of moulting, 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 & Perez 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 (66 to 45 %), than in May to August 1988 (26 to 20 %) (Mann-Whitney *U*-test: n_1 =

3, $n_2 = 5$, $U = 0$, $p < 0.05$). 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 typical 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 ocypodids 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, Levinton 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 (Raymont 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 ocypodids (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.

Acknowledgements. This work was funded by Kuwait University research Grant KU SZO32 (D.A.C. & R.J.S.) and a Graduate Research Grant (E.Y.Al-T.). We thank J. M. Wright for temperature and salinity data and Mrs Y. M. Snowden for typing the manuscript.

LITERATURE CITED

Al-Kulaib, A. M. (1975). Weather and climate of Kuwait. Director General of Civil Aviation, Meteorological Section, Kuwait

Al-Taher, E. Y (1990). The impact of the Doha West Power Station effluent on the upper eulittoral benthos of western Sulaibikhat Bay, Kuwait. M. Sc. thesis, Kuwait University

Barass, R. (1963). The burrows of *Ocypode ceratophthalmus* (Pallas) (Crustacea, Ocypodidae) on a tidal wave beach at Inhaca Island, Moçambique. J. Anim. Ecol. 32: 73–85

Bellwood, D. R., Perez, O. S. (1989). Sexual differences in the absolute growth pattern of the Indo-Pacific sandy shore crab *Matuta lunaris*. J. Zool. Lond. 218: 603–608

Broom, M. J. (1982). Structure and seasonality in a Malaysian mudflat community. Estuar. coast. Shelf Sci. 15: 135–150

Clayton, D. A. (1986). Ecology of mudflats with particular reference to those of the northern Arabian Gulf. In: Halwagy, R., Clayton, D. A., Behbehani, M. (eds.) Marine environment and pollution, Proceedings of the First Arabian Gulf Conference on Environment and Pollution. Kuwait University, Faculty of Science, p. 83–96

Clayton, D. A., Snowden, R. J. (1991). Allometric growth in *Ilyoplax stevensi* (Brachyura: Ocypodidae). Crustaceana (in press)

Colby, D. R., Fonseca, M. S. (1984). Population dynamics, spatial dispersion and somatic growth of the sand fiddler crab *Uca pugilator*. Mar Ecol. Prog. Ser. 16: 269–279

Collins, M. J., Jones, D. A., Clayton, D. A. (1984). Redescription of *Uca sindensis* (Alcock, 1900) (Brachyura: Ocypodidae) with notes on the ecology of a population from Kuwait. J. Crust. Biol. 4: 318–328

Conde, J. E., Diaz, H. (1989). The mangrove tree crab *Aratus pisonii* in a tropical estuarine coastal lagoon. Estuar. coast. Shelf Sci. 28: 639–650

Crane, J. (1975). Fiddler crabs of the world. Ocypodidae: Genus *Uca*. Princeton University Press, New Jersey

Diaz, H., Conde, J. E. (1989). Population dynamics and life history of the mangrove crab *Aratus pisonii* (Brachyura, Grapsidae) in a marine environment. Bull. mar Sci. 45: 148–163

Fishelson, L. (1983). Population ecology and biology of *Dotilla sulcata* (Crustacea, Ocypodidae) typical for sandy beaches of the Red Sea. Dev. Hydrobiol. 19: 643–654

Frith, D. W., Brunenmeister, S. (1980). Ecological and population studies of fiddler crabs (Ocypodidae, genus *Uca*) on a mangrove shore at Phuket Island, western peninsular Thailand. Crustaceana 39: 157–183

Hails, A. J., Yaziz, S. (1982). Abundance, breeding and growth of the ocypodid crab *Dotilla myctiroides* (Milne-Edwards) on a West Malaysian beach. Estuar. coast. Shelf Sci. 15: 229–239

Haley, S. R. (1972). Reproductive cycling in the ghost crab *Ocypode quadrata* (Fabr.) (Brachyura, Ocypodidae). Crustaceana 23: 1–11

Haley, S. R. (1979). Sex ratio as a function of size in *Hippa pacifica* Dana (Crustacea, Anomura, Hippidae): a test of the sex reversal and differential growth rate hypothesis. Am. Nat. 113: 391–397

Hartnoll, R. G. (1973). Factors affecting the distribution and behaviour of the crab *Dotilla fenestrata* on East African shores. Estuar coast. mar Sci. 1: 137–152

Hartnoll, R. G. (1982). Growth. In: Abele, L. G. (ed.) The biology of Crustacea, Vol. 2, Embryology, morphology and genetics. Academic Press, New York, p. 111–196

Hartnoll, R. G. (1983). Strategies of crustacean growth. Mem. Aust. Mus. 18: 121–131

Henmi, Y (1984). The description of wandering behavior and its occurrence varying in different tidal areas in *Macrophthalmus japonicus* (DeHaan) (Crustacea: Ocypodidae). J. exp. mar. Biol. Ecol. 84: 211–224

Henmi, Y., Kaneto, M. (1989). Reproductive ecology of three ocypodid crabs I. The influence of activity differences on reproductive traits. Ecol. Res. 4: 17–29

Hughes, D. A. (1966). Behavioural and ecological investigations of the crab *Ocypode ceratophthalmus* (Crustacea: Ocypodidae) J. Zool., Lond. 150: 129–143

Icely, J. D., Jones, D. A. (1978). Factors affecting the distribution of crabs of the genus *Uca* on an East African shore. Estuar. coast. mar. Sci. 6: 315–325

Jones, D. A. (1972). Aspects of the ecology and behaviour of *Ocypode ceratophthalmus* (Pallas) and *O. kuhlii* (DeHaan (Crustacea: Ocypodidae). J. exp. mar. Biol. Ecol. 8: 31–43

Jones, D. A. (1986). A field guide to the seashores of Kuwait and the Arabian Gulf. University of Kuwait

Jones, D. A., Clayton, D. (1983). The systematics and ecology of crabs belonging to the genera *Cleistostoma* DeHaan and *Paracleistostoma* DeMan on Kuwait mudflats. Crustaceana 45: 183–199

Jones, M. B., Simons, M. J. (1982). Habitat preferences of two estuarine burrowing crabs *Helice crassa* Dana (Grapsidae) and *Macrophthalmus hirtipes* (Jacquinot) (Ocypodidae). J. exp. mar. Biol. Ecol. 56: 49–62

Kemp, S. (1919). Notes on Crustacea Decapoda in the Indian Museum. XII – Scopimerinae. Rec. Ind. Mus. 16: 305–348

Kinne, O. (1970). Temperature; Animals; Invertebrates. In: Kinne, O. (ed.) Marine ecology, Vol. 1, Part 1. Wiley, London, p. 407–514

Levinton, J. S. (1982). Marine ecology. Prentice-Hall, New Jersey

Livingston, R. J., Kobylinski, G. J., Lewis, F. G., III., Sheridan, P. F. (1975). Long-term fluctuations of epibenthic fish and invertebrate populations in Apalachicola Bay, Florida. Fish. Bull. U.S. 74: 311–321

McIntyre, A. D. (1968). The meiofauna and macrofauna of some tropical beaches. J. Zool., Lond. 156: 377–382

Ono, Y (1962). On the habitat preference of ocypoid crabs. Mem. Fac. Sci. Kyushu Univ. Ser E (Biol.) 3: 143–163

Ono, Y. (1965). On the ecological distribution of ocypoid crabs in the estuary. Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol.) 4: 1–60

Rao, C. A. N., Sundari, K. S., Rao, K. H. (1986). Reproductive cycle of the crab *Ocypoda macrocera* Milne-Edwards (Crustacea: Brachyura) from Visakhapatnam coast. Proc. Indian Acad. Sci. (Anim. Sci.) 95: 1–6

Raymont, J. E. G. (1983). Plankton and productivity in the oceans, 2nd edn. Pergamon Press, Oxford

Simons, M. J., Jones, M. B. (1981). Population and reproductive biology of the mud crab *Macrophthalmus hirtipes* (Jacquinot, 1853) (Ocypodidae), from marine and estuarine habitats. J. nat. Hist. 15: 981–994

Snowden, R. J., Ekweozor, I. K. E. (1990). Littoral infauna of a West African estuary: an oil pollution baseline survey. Mar Biol. 105: 51–57

Sokal, R. R., Rohlf, F. J. (1981). Biometry, 2nd edn. Freeman, San Francisco

Suzuki, H. (1983). Studies on the life history of sand bubbler crab, *Scopimera globosa* DeHaan, at Tomioka Bay, West Kyushu – I Seasonal changes of population structure. Mem. Fac. Fish., Kagoshima Univ. 32: 55–69

Thurman, C. L., II. (1984). Ecological notes on fiddler crabs of south Texas, with special reference to *Uca subcylindrica*. J. Crust. Biol. 4: 665–681

Thurman, C. L., II. (1987). Fiddler crabs (genus *Uca*) of eastern Mexico (Decapoda, Brachyura, Ocypodidae). Crustaceana 53: 94–105

Tweedie, M. W F. (1937). On the crabs of the family Ocypodidae in the collection of the Raffles Museum. Bull. Raffles Mus. 13: 140–170

Wada, K (1981). Growth, breeding, and recruitment in *Scopimera globosa* and *Ilyoplax pusillus* (Crustacea: Ocypodidae) in the estuary of Waka River, middle Japan. Publ. Seto mar biol. Lab. 26: 243–259

Wada, K. (1983a). Spatial distributions and population structures in *Scopimera globosa* and *Ilyoplax pusillus* (Decapoda: Ocypodidae). Publ. Seto mar. biol. Lab. 27: 281–291

Wada, K. (1983b). Temporal changes of spatial distributions of *Scopimera globosa* and *Ilyoplax pusillus* (Decapoda: Ocypodidae) at co-occurring areas. Jap. J. Ecol. 33: 1–9

Wada, K. (1983c). Movement of burrow location in *Scopimera globosa* and *Ilyoplax pusillus* (Decapoda: Ocypodidae). Physiol. Ecol. Japan 20: 1–21

Wada, K. (1984). Barricade building in *Ilyoplax pusillus* (De Haan) (Crustacea: Brachyura). J. exp. mar Biol. Ecol. 83: 73–88

Wada, K. (1987a). Neighbor burrow-plugging in *Ilyoplax pusillus* (Crustacea: Brachyura: Ocypodidae). Mar. Biol. 95: 299–303

Wada, K. (1987b). Use of barricades as foraging sites by *Ilyoplax pusillus* (Crustacea: Brachyura: Ocypodidae). J. Ethol. 5: 161–164

Wenner, A. M. (1972). Sex ratio as a function of size in marine Crustacea. Am. Nat. 106: 321–350

Yamaguchi, T., Tanaka, M. (1974). Studies on the ecology of a sand bubbler crab, *Scopimera globosa* DeHaan – I Seasonal variation of population structure. Jap. J. Ecol. 24: 165–174

This article was submitted to the editor

Manuscript first received: September 3, 1990
Revised version accepted: January 18, 1991