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Dynamics of juvenile shrimp *Crangon crangon* in a tidal-flat nursery of the Wadden Sea after mild and cold winters

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ABSTRACT: Juvenile shrimp *Crangon crangon* (L.) were sampled frequently on a tidal flat in the westernmost part of the Wadden Sea during spring and summer from 1983 to 1991. High densities (several tens per m^2) of small shrimp (length range 5 to 25 mm, mean generally <15 mm) were observed at low tide during late spring, summer and early autumn. The low numbers (ca 1 m^{-2}) of overwintered shrimps observed on the tidal flats in March were positively correlated with the mean temperature of the foregoing months. Settlement of a new generation of postlarvae (ca 5 mm) started in April after mild winters and in May after cold winters. Maximal densities were observed in June after mild winters and in July after cold winters. Settlement continued with fluctuating intensity throughout summer and early autumn. Growth was rapid: as early as ca 1 mo after settlement the shrimps reached a length of 20 to 25 mm, at which point they leave (the higher parts of) the tidal flats. Thus, juvenile shrimp use tidal flats as a transit nursery, where several successive cohorts grow up during any one summer season. Earlier published estimates of time of recruitment, mean size and growth rate of shrimp living in the same area are refuted. In spring (up to mid-June), shrimp biomass on the tidal flat was much lower after cold than after mild winters. This difference could also help explain the generally highly successful recruitment of the bivalve *Macoma balthica* after cold winters.

INTRODUCTION

Shallow parts of estuaries and coastal bays serve as important nursery areas for young stages of several epibenthic animals such as flatfish (Zijlstra 1972, Berghahn 1983, Cyrus & Martin 1991, Reichert & Van der Veer 1991), crabs (Klein Breteler 1976b, Pihl & Rosenberg 1982) and shrimps (Boddeke 1978, Berghahn 1983, Kuipers & Dapper 1984, Henderson & Holmes 1987). After hatching in offshore areas, postlarvae of these species invade shallow coastal areas in spring and summer, when such areas are relatively warm and rich in food. This is especially true of tidal flats. Such sand and mud flats in the Wadden Sea are inhabited by huge numbers of juvenile plaice (Kuipers 1977, Van der Veer 1986), flounder (Van der Veer et al. 1991), shore crabs (Klein Breteler 1976b, Beukema 1991) and brown shrimp (Kuipers & Dapper 1984). Juveniles of all of these species grow rapidly on the flats for some months and subsequently leave the intertidal for deeper waters, at first during low tide and later on permanently (plaice: Kuipers 1977; shore crabs: Klein Breteler 1976a; shrimps: Janssen & Kuipers 1980).

During their stay in the nurseries, juvenile brown shrimp *Crangon crangon* (L.) feed on a variety of mostly small members of the infauna, particularly the meiofauna and young stages of the macrofauna (Plagmann 1939, Pihl & Rosenberg 1984). Due to their huge numbers, they exert a significant influence on the survival of their prey (Evans 1984, Pihl & Rosenberg 1984, Pihl 1985, Reise 1985) and are, therefore, an important structuring force of benthic shallow-water communities (Reise 1985, Mattila et al. 1990). More knowledge about the variation in their abundance and predation pressure would contribute to our understanding of the dynamics of such communities.

Young bottom-dwelling stages of the brown shrimp are numerous in the shallow parts of coastal areas in summer, often reaching densities of several tens per m^2 (Wadden Sea: Kuipers & Dapper 1981, 1984; eastern Denmark: Muus 1967; Swedish west coast: Pihl & Rosenberg 1982). Obtaining detailed knowledge on their stay in the nurseries, however, is hampered by some features of their life cycle. Their almost continuous spawning (46 wk yr^{-1} according to Boddeke 1982) and recruitment during most of the year make distinc-

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tion and following of separate cohorts difficult. Not only their arrival in the nurseries, but also their departure is a continuous and very gradual process (Janssen & Kuipers 1980). There is the added handicap that the reliability of much of the published data on juvenile shrimp is questionable due to the frequent use of coarse netting and inadequate correction for the capture efficiency of these nets.

The present study deals with small (postlarval) stages of brown shrimp only. Up to a size of about 2.5 cm, these shrimp stay permanently on the tidal flats (Janssen & Kuipers 1980, Berghahn 1984), hiding in the wet sediment at low tide. They can then easily and accurately be sampled by sieving sediment cores. An extensive sampling programme was executed at low tide during a 9 yr period (1983 to 1991). This period included 3 distinctly mild and 3 severe winters. The emphasis was on differences in abundance and time of appearance after winters with different character. Low abundance (Beukema 1990) and late appearance (Beukema 1991) of several predatory species during springs and summers following cold winters help explain the generally high reproductive success of bivalves after such winters (Möller 1986, Beukema 1982, 1992).

STUDY AREA AND METHODS

The 3 sampling stations, A, B, and C (square plots of 1000 m^2 each, marked by iron poles), are located on Balgzand, a tidal-flat area in the westernmost part of the Wadden Sea (ca 53° N, 5° E). The mean tidal range in the area extends from +0.6 to −0.8 m. The stations differ slightly in their intertidal level (from about 0.1 m above to 0.4 m below MTL), silt content of their sediment (2 to 10 % of particles <60 µm) and distance from the coast (0.5 to 1 km) and a major tidal channel (0.3 to 1 km).

Samples were taken at low tide, 2 to 4 times a month during the mid-April to late-September periods of 1983 to 1991. At each of the 3 stations 40 core samples of 88 cm^2 each were taken to a depth of ca 5 cm. These 120 core samples approximate 1 m^2 (10 560 cm^2). Data for other seasons (particularly winter) were obtained from a long-term sampling programme (started in 1969) for macrozoobenthos at 15 stations scattered all over Balgzand (see Beukema 1988: Fig. 2). Stns A and B are among these 15 permanent stations; Stn C is situated between Stn B and the nearby tidal channel.

The cores were sieved in the field on 1 mm mesh screens and sorted in white trays with seawater to catch the shrimp alive. Total length from the tip of the rostrum to the tip of the telson was measured to the nearest mm. Ash-free dry weight (AFDW) values were determined for several mm groups at several dates; the relationships obtained between length and weight were used to convert lengths to weights in the other samples.

Results (no. of individuals m^{-2} and g m^{-2}) were evaluated by the Wilcoxon test; samples taken in the same period of the year (generally 1 or 1/3 mo) were allotted to 2 groups depending on the character of the foregoing winter. Such groups usually had a size of $n_1 = n_2 = 9$ (i.e. 3 stations × 3 years, when 10 d periods were compared) or more (when months were compared). Correlations were evaluated by the Spearman rank test. Nonparametric tests were chosen because the data were highly variable and not always normally distributed.

RESULTS

Temperature

Among the 9 winters of the 1983 to 1991 period, 3 were distinguished by high temperatures (1988, 1989, and 1990) and 3 by low temperatures (1985, 1986, and 1987). Mean winter-quarter (January to March) temperatures in all 6 of these extreme winters deviated by 2 to 4 °C from the long-term average (air temperatures at a nearby weather station of the KNMI, the Royal Dutch Meteorological Institute). Such deviations for seawater temperatures in the main tidal inlet of the western Wadden Sea amounted to 2 to 3 °C (see Table 1 in Beukema 1991). The mild winters were the first, second, and sixth mildest of the century. The cold winters were less exceptional, as about 10 % of the winters from 1890 to 1990 were even more severe. Water temperatures after the cold (or mild) winters remained relatively low (or high) up to and including June (Fig. 1).

Seasonality of shrimp on tidal flats

In winter, nearly all shrimps retreat to deeper, generally more offshore waters (Havinga 1930, Boddeke 1975, 1976). Numbers of shrimp observed on the tidal flats were indeed very low in winter, on average 0.02 and 0.2 m^{-2} in January/February and March, respectively, at both Stns A and B (means of annual samples taken over 22 yr). At lower tidal flats (well below MTL), and in particular near the LW line at short distances from tidal channels, slightly higher densities were observed in winter Averages for all 15 stations sampled in March amounted to 1.2 ± 0.3 m^{-2} (or 0.021 ± 0.004 g AFDW m^{-2}). As no small (< 10 mm) postlarvae were encountered during the winter season, shrimp observed in March must have originated from larvae settled during the previous autumn.

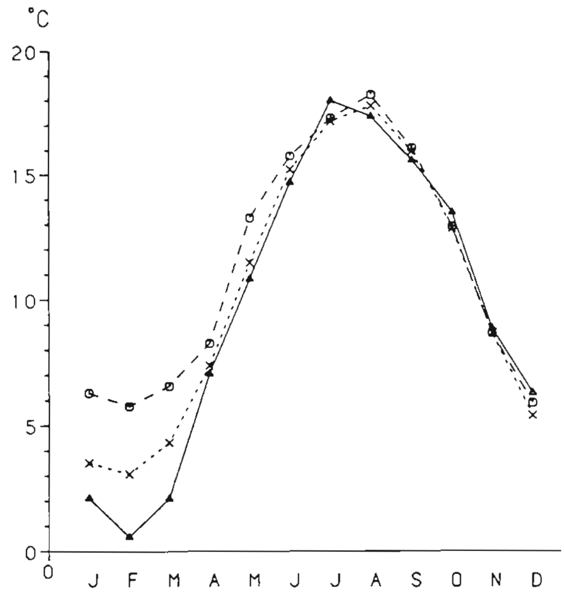

Fig. 1. Monthly averages of water temperature (°C) in the westernmost inlet of the Wadden Sea for 3 groups of years: long-term average for the last 30 yr (×- - -×), average for the 3 mild winters of 1988 to 1990 (o— —o), and average for the 3 cold winters of 1985 to 1987 (△——△). Data from Van der Hoeven (1982), completed with recent data from files of Rijkswaterstaat

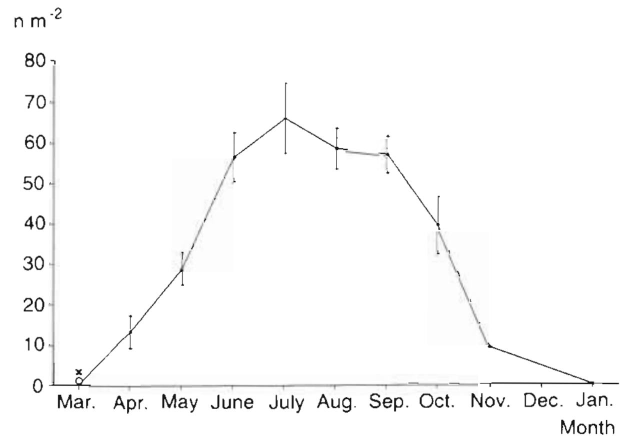

Fig. 2. *Crangon crangon*. Seasonal course of densities (monthly means, no. m^{-2}) of brown shrimp sampled at low tide on tidal flats in the westernmost part of the Wadden Sea: 9 yr averages of 3 (small points) or 2 (circle) stations ± 1 SE and 20 yr average of 15 stations (×)

In April and May, densities of shrimp on the tidal flats showed a rapid increase (Fig. 2), due to settlement of postlarvae at a size of about 5 mm. High densities (on average about 60 m^{-2}) were observed throughout June to September. Shrimp abundance on the higher tidal flats declined during autumn to become virtually nil in winter.

Changes in length-frequency distributions

Changes in numbers (expressed as densities, D = no. m^{-2}) of shrimp of various lengths (mm) are shown in detail in Fig. 3 for both a year starting with a cold winter (1986: Fig. 3A) and one starting with a mild winter (1989: Fig. 3B). The data included in Fig. 3 are representative of the seasonally changing composition of tidal-flat stocks of shrimp in different years.

After the mild winter of 1989 (Fig. 3B), high numbers of postlarvae (5 to 10 mm) were already found in mid-April (the one specimen of 20 mm must have overwintered). By early May 1989, D had increased from 27 to 44 m^{-2} through further settlement, and mean postlarval length had increased from 6.9 to 9.4 mm. By mid-May, mean length had further increased to 12.9 mm (or 13.1 mm if the one very small, newly settled specimen is excluded). During most of May and early June densities remained almost constant, but it became more and more difficult to track the shifts in the tops of the frequency distributions. New settlers had arrived in late May (the group of 5 to 6 mm postlarvae on 29 May) and particularly between 5 and 12 June (the large group of postlarvae on 12 June). At the right-hand side (larger individuals) of the frequency distributions, the shrimp disappeared from the samples at a size of slighly more than 20 mm. This was particularly clear between 29 May and 5 June, and during all of June (Fig. 3B).

After the cold winter of 1986, shrimp dynamics proceeded in a different way (Fig. 3A). Postlarvae were scarce during the first half of May (D = 2 to 4 m^{-2}). Their numbers gradually increased during the second half of May to reach high densities in early June (3 June: 78 m^{-2}; 9 June: 59 m^{-2}). The disappearance of larger postlarval shrimp was particularly clear between 24 June and 3 July. In early July a new wave of postlarvae settled (see the peak of 5 to 9 mm shrimp on 3 July).

Similar data are available for the 2 other years starting with a cold winter and the 2 other years starting with a mild winter. Shrimp dynamics in these 2 groups of 3 years each were examined (see following section) to determine whether the above examples represent general differences in timing and numbers of juvenile shrimp after winters of different character.

Data as shown in Fig. 3 could also be used to estimate growth rates in the field. However, the (almost) continuous settlement of postlarvae plus the gradual disappearance of shrimp at a size of >20 mm hamper and restrict analysis of growth. By following the rightward shifts of peaks in the frequency distributions, some impression of growth rates may be obtained, but for the 2 reasons mentioned above these shifts may underesti-

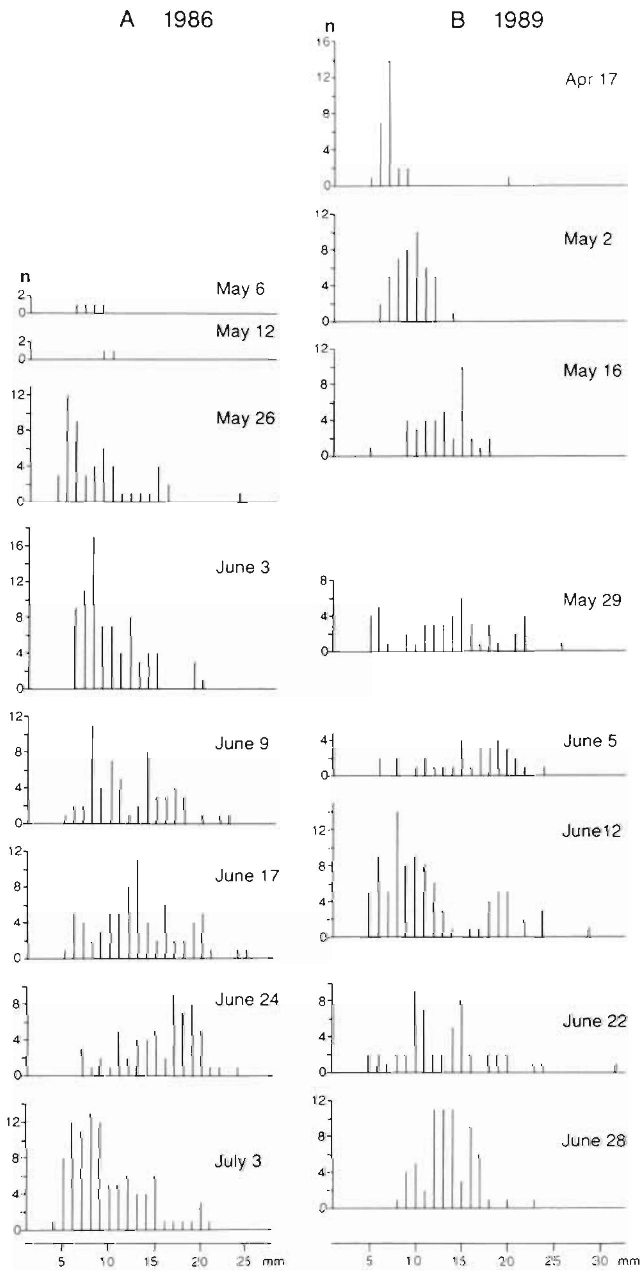

Fig. 3. *Crangon crangon*. Size-frequency distributions (length in mm; no. m^{-2}) of brown shrimp sampled at low tide at 3 stations on a tidal flat during spring of (A) 1986 (after a cold winter) and (B) 1989 (after a mild winter)

mate real individual growth. Nonetheless, growth of young shrimp must have been rapid: from 7 mm on 17 April to 10 mm on 2 May, 15 mm on 16 May, and at least 22 mm on 29 May 1989, i.e. a rate of 0.2 to 0.5 mm d^{-1} at initially relatively low temperatures (mean water temperatures during April and May 1989 were 8 and 13 °C, respectively). Because of the probable bias of such values as estimates of growth rate, and the arbitrary nature (Grant et al. 1987) of the identification of peaks, further analysis of the length-frequency distributions was not attempted.

Differences between years starting with cold and mild winters

Densities of overwintered shrimps observed in March on tidal flats were particularly low after cold winters: $< 1\ m^{-2}$ at the end of all winters colder than average (Fig. 4). The milder the winter had been, the higher were the densities of shrimps at the tidal flats in March (Fig. 4: $r = +0.71$, $n = 23$, $p < 0.001$; Spearman rank test).

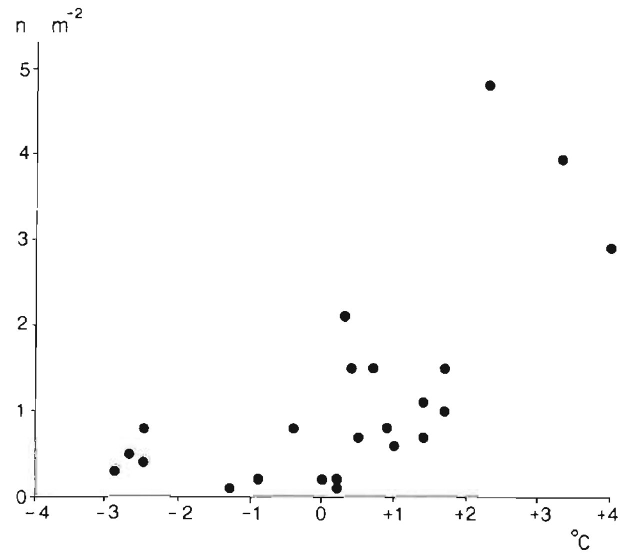

Fig. 4. *Crangon crangon*. Relationship between winter temperatures (expressed in °C as deviations from long-term averages of mean air temperatures between January and March) and March densities (no. m^{-2}) of brown shrimp for 23 yr (1969 to 1991). Means of data from 15 tidal-flat stations

Comparison of the shrimp densities observed in the first half of May in 1986 and 1989 (Fig. 3) suggests that settlement of postlarvae occurred earlier after the mild winter (1989) than after the cold winter (1986). This was generally the case: postlarvae were absent in April after all 3 cold winters, but present after all 3 mild winters. After the cold winters, shrimp densities in spring lagged behind by about 1 mo as compared to the densities observed in years starting with mild winters (Fig. 5). During April, shrimp densities were significantly higher after mild than after cold winters ($p < 0.01$, Wilcoxon test). This was so also during each of the 3 decades of May ($p < 0.01$, < 0.01, and < 0.05 respectively). During June these differences were either non-significant or hardly significant ($p < 0.1$, 2-sided). Maximal densities were reached in late June

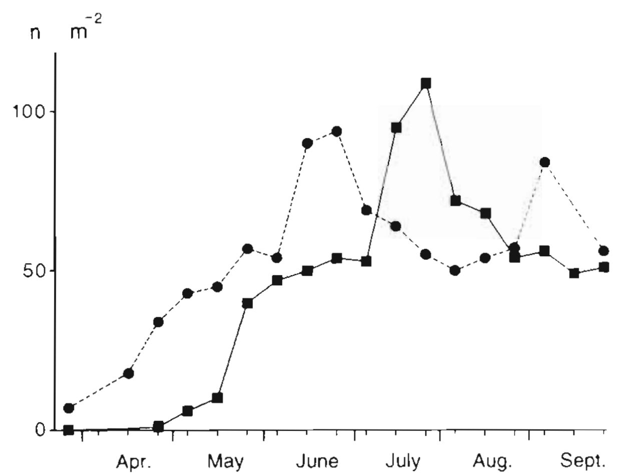

Fig. 5. *Crangon crangon.* Seasonal course of numerical densities (no. m^{-2}) of brown shrimp on a tidal flat after mild (●----●) and cold (■——■) winters. Data from 3 years (mild: 1988, 1989 and 1990; cold: 1985, 1986 and 1987) and 3 stations averaged over 10 d period

after mild winters but not until late July after cold winters (Fig. 5). These maxima were caused by late 'waves' of settling postlarvae (cf. Fig. 3: high numbers must have settled shortly before 3 July 1986 and 12 June 1989). Such strong settlement waves must have also occurred shortly before 13 and 28 June 1988 (after a mild winter) and shortly before 30 July 1985 and 27 July 1987 (after cold winters). Thus, the strong early-summer waves were observed about 1 mo later following cold than following mild winters.

Most of the few shrimp already present in March were between 10 and 25 mm in size, with an average of about 13 mm (Fig. 6a). After cold winters, the only shrimp present in April were relatively large and thus were probably also overwintered individuals. After mild winters, mean lengths dropped to between 8 and 10 mm in the course of April, due to the arrival of newly settled postlarvae. This did not happen until May after cold winters. Shrimps present in May on the tidal flats were significantly larger ($p < 0.01$) after mild than after cold winters. Most of them had a lead in growth of about 1 mo after a mild winter as compared to those settled after a cold winter. This difference disappeared in summer, when mean lengths of the shrimps collected at the sampling stations remained generally between 12 and 15 mm (Fig. 6a). These low values for mean length can be explained by the observed continuous settlement of postlarvae throughout summer and early autumn and the continuous disappearance of the shrimps once they had reached a size of ca 20 mm.

Mean weights per individual showed a similar pattern (Fig. 6b): in springs after mild winters the same mean weights were reached several weeks earlier than in springs after cold winters. From mid-June on, consistent differences disappeared and mean weights per individual remained generally between 3 and 6 mg in the 2 groups of years.

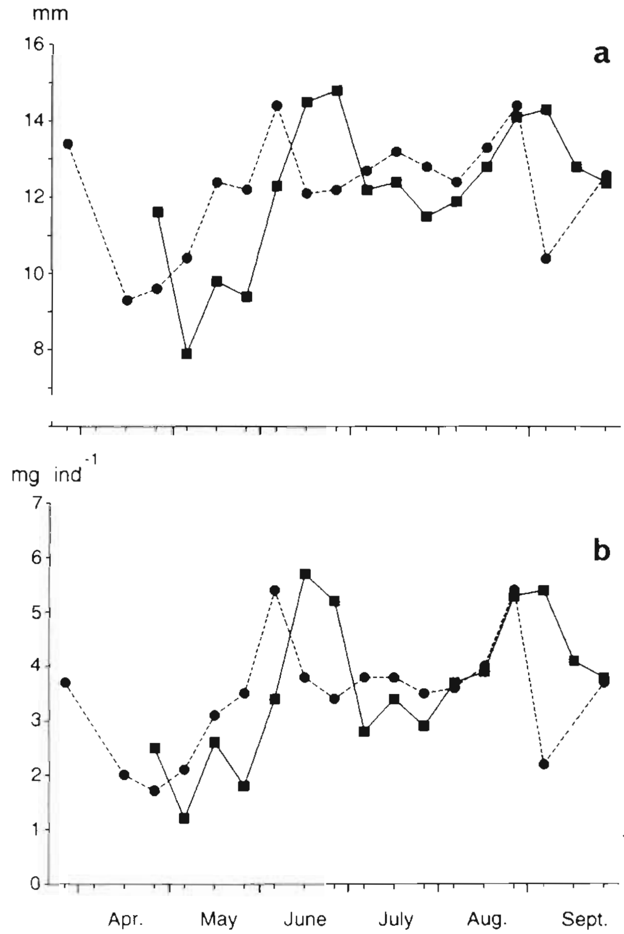

Fig. 6. *Crangon crangon.* Seasonal course of (a) mean length (mm) and (b) mean weight (mg ash-free dry weight) of brown shrimp on a tidal flat after mild (●----●) and cold (■——■) winters. Data as in Fig. 5

As a consequence of the above differences in density and size between years with a mild or a cold start, shrimp biomass values in spring were significantly higher after mild than after cold winters. This was the case (Fig. 7) in April ($p < 0.05$), each of the 3 decades of May ($p < 0.01$), and the first 2 decades of June ($p < 0.05$). In summer, biomass reached similar values (0.2 to 0.3 g AFDW m^{-2}) in the 2 groups of years.

DISCUSSION

The character of the winter season affects brown shrimp in the Wadden Sea area at several stages of their life cycle. Mature shrimp leave the shallow coastal waters in winter, and in cold winters they migrate further offshore (up to 90 km) than in mild winters

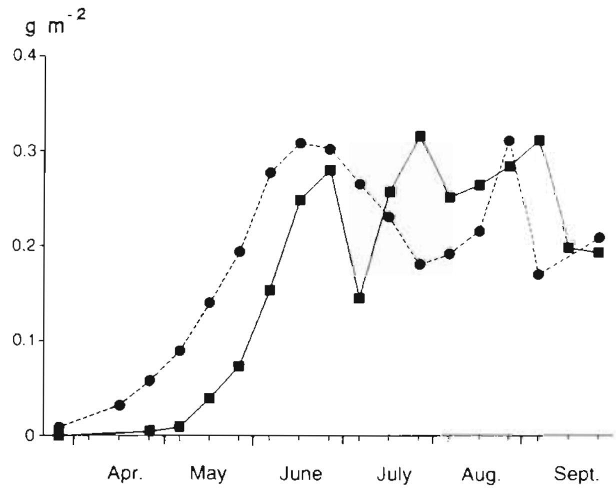

Fig. 7. *Crangon crangon.* Seasonal course of biomass (g AFDW m^{-2}) of brown shrimp on a tidal flat after mild (●- - - -●) and cold (■——■) winters. Data as in Fig. 5

(Boddeke 1975, 1976). Some of the immature shrimp stay in the gullies between the tidal flats or even on the lower tidal flats of the Wadden Sea during winter. This is particularly so during mild winters (Boddeke 1976). Indeed, numbers of shrimp found on the tidal flats of Balgzand each year in March during the 1970 to 1991 period were higher after mild than after cold winters (Fig. 4).

Eggs of brown shrimp develop more slowly at the lower water temperatures of cold winters (Tiews 1970, Wear 1974). Moreover, since the eggs hatch at longer distances from the shore, larvae arrive later in coastal areas after cold than after mild winters. During a 12 yr study of brown shrimp larvae in the Elbe estuary (German Wadden Sea), Kühl & Mann (1964) found no larvae in January and February. In March larvae were observed only after mild winters. After the close-to-normal winter of 1981, Heiber (1988) did not observe shrimp larvae in the German Wadden Sea until April. Maximal larval abundance was not reached until May (Heiber 1988) or June (Kühl & Mann 1964). According to Kühl & Mann (1964), abundance of shrimp larvae in May in this area is positively related to temperature (even in May, water temperatures appear to be lower after cold than after mild winters; see Fig. 1 and the more elaborate data in Van der Hoeven 1982). Thus, in the Wadden Sea area, shrimp larvae appear both to occur earlier and to be more numerous throughout the spring periods after mild than after cold winters.

Settlement of postlarvae on the tidal-flat sampling stations was found to start around mid-April after mild winters, but not until May after cold winters (Fig. 5). These differential periods are in accordance with the arrival time of high numbers of shrimp larvae in coastal waters as observed by Kühl & Mann (1964).

The statement by Kuipers & Dapper (1984) that the arrival of newly settled brown shrimp in the western Wadden Sea starts as early as February and is completed in August (with the main period of arrival between March and June) was not corroborated by any direct observation. They derive these (too early) periods by back-calculation from length-frequency distributions of shrimp in catches made from April to September. As these catches were made using 5 × 5 mm mesh trawl nets, they must have missed nearly all of the smaller postlarvae. Berghahn (1984) estimated the efficiency of such nets for shrimps of various size classes and for the smallest groups of shrimps (5–10 and 10–15 mm) found values of only 0.1 and 6.1 %, respectively. Similarly low values for the smallest size classes were found by Van Lissa (1977). Conversion factors based on retention rates of 27 and 53 %, as used by Kuipers & Dapper (1981) and apparently also applied in Kuipers & Dapper (1984), are therefore far too low. Indeed, their diagrams (Fig. 3 in Kuipers & Dapper 1984) show that their catches contained several times more shrimp of 10–15 and 15–20 mm than of 5–10 mm. Such a size distribution is not (Fig. 3, and figures in Günther 1990) and cannot be a genuine reflection of the actual composition of the shrimp population on tidal flats. The unrealistically high estimate of mean length of ca 20 mm (Fig. 1c in Kuipers & Dapper 1984) instead of <10 mm (Fig. 6a) or ca 10 mm (Günther 1990) for shrimp living on the tidal flats in April–May inevitably leads to a back-calculated time of settlement (at a length of ca 5 mm) that is too early.

As would be expected from the lower winter temperatures in more northern areas, settlement of postlarval shrimp there takes place later. Pihl & Rosenberg (1982) did not observe the first new settlers in western Swedish bays until the second half of June or in July (in the normal years 1977 and 1978) or even later after a cold winter (1979). Peak densities of shrimp in this area were found as late as late July (1977 and 1978) or late August (1979). Thus, in this area as well, a delay was observed after a cold winter.

Relatively high values for growth rate were estimated, amounting to ca 0.5 mm d^{-1} at ca 15 °C (from the clearest shifts of peaks in Fig. 3). Using the same method, Van Lissa (1977) observed a length increase of 6.7 mm (from an average of 10.8 to 17.5 mm) in 14 d (second half of May), i.e. 0.48 mm d^{-1}. By essentially the same method (but applied to mostly larger shrimps), Kuipers & Dapper (1981) arrived at lower estimates (a mean of 0.23 mm d^{-1}) for the growth rate of shrimp living in the same area. Extrapolation of these data to field temperature conditions (Fig. 2 of Kuipers & Dapper 1984) would lead to an estimated length of 40 mm reached in early October by shrimp settling in early May at 5 mm. Such a low estimate cannot be representative, because it is not consistent with the time of the annual maximum of the stock size of consumption shrimps (length >55 mm) in September–October (Boddeke & Becker 1979, Boddeke 1982, Boddeke et al. 1986). Therefore, the higher growth rate estimate of ca 0.5 mm d^{-1} would be more appropriate. In the laboratory, such a rapid growth has been observed only in small shrimp and at relatively high temperatures, around 20 °C (M. F. Fonds pers. comm.).

Nearly all of the smallest shrimp present in the Wadden Sea in spring and summer appear to live permanently on the tidal flats. Shrimp smaller than 15 or 20 mm are hardly ever found in subtidal parts of the Wadden Sea (Van Lissa 1977, Janssen & Kuipers 1980). Only when they reach a size of 20 to 25 mm do they start living more or less permanently in subtidal areas, some of them initially migrating up and down the edges of the tidal channels with the tides (Janssen & Kuipers 1980; author's obs.). Emigration from the tidal flats appears to proceed both gradually and in waves, in the form of 'exodus' migrations on hot days (Berghahn 1983).

It is debatable whether the densities of small shrimp observed during low-tide sampling reliably reflect shrimp abundance on the flats throughout the tidal cycle. Even at high tide, large shrimp (> 30 mm) are rarely observed on tidal flats (Janssen & Kuipers 1980, Günther 1990), and when they have been caught in significant numbers this has been within only a few tens of meters away from a tidal channel (Keus 1986) or on very low tidal flats which are not drained at most low tides (own obs.). Thus underestimates due to sampling shrimp at low tide only will be restricted to a minor part of the total tidal-flat area. In conclusion, dynamics of the smallest size classes of shrimp (< 20 to 25 mm) living permanently on tidal flats can be studied adequately by accurate core sampling, which is feasible only on drained tidal flats.

The responses of brown shrimp in the Wadden Sea to cold and mild winters resemble those of shore crabs *Carcinus maenas* in the same area (Beukema 1991): after cold as compared to mild winters lower densities of overwintered individuals are observed, recruitment of the new generation starts later and abundance (numbers and biomass) and mean size throughout spring (and early summer) are lower. In shore crabs, the delays observed after cold winters appear to be even longer.

A consequence of the higher abundance of shrimps and shore crabs in springs after mild than after cold winters is the relatively low predation pressure exerted by epibenthic predators during the first half of the years starting with a cold winter. According to extensive studies by Plagmann (1939), Evans (1983) and Pihl & Rosenberg (1984), shrimps are omnivorous and feed on all kinds of available small prey, including microbenthos, meiobenthos and young stages of macrobenthos. Little is known on dynamics of small prey species, but annual variability in recruitment of bivalves has been studied in the Wadden Sea (Beukema 1982, 1992). Most bivalve species in the Wadden Sea spawn too late in the season to experience differential predation by shrimps in their early bottom-dwelling stages after winters of different character, because shrimp biomass values were no longer affected by the character of the foregoing winter after mid-June (Fig. 7). Only in *Macoma balthica* do larvae reach peak numbers as early as April or May (Heiber 1988) and start settling in high densities as early as May, as observed by Günther (1991) on a tidal flat near Borkum, and by R. Dekker (pers. comm.) in the western part of the Wadden Sea. Keus (1986) found *M. balthica* spat ca 1 mm in size in the stomachs of shrimp 10 to 20 mm in length on Balgzand. From shrimp densities, numbers of spat per stomach and stomach clearance rates, Keus estimated a considerable predation exerted by shrimps on juvenile *M. balthica* in this area. Based on results of cage experiments with different shrimp densities, Mattila et al. (1990) concluded that shrimp predation seriously reduces densities of *M. balthica* spat. Recruitment in this species is, therefore, likely to be favoured by cold winters via lower shrimp predation. Indeed, the high spat densities of *M. balthica* observed in August on tidal flats in the westernmost part of the Wadden Sea in years starting with cold winters, as opposed to those starting with very mild winters (Beukema 1992), suggest that such a relationship exists.

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