

Climate-related changes in recruitment of the bivalve *Macoma balthica*

Catharina J. M. Philippart,¹ Hendrik M. van Aken, Jan J. Beukema, Oscar G. Bos, Gerhard C. Cadée, and Rob Dekker

Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg (Texel), The Netherlands

Abstract

Population dynamics of common intertidal bivalves (*Cerastoderma edule*, *Macoma balthica*, *Mya arenaria*, *Mytilus edulis*) are strongly related to seawater temperatures. In northwestern European estuaries, series of mild winters followed by low bivalve recruit densities lead to small adult stocks. In this study, we examine temperature-induced effects on reproductive output (eggs m⁻²), onset of spawning (day of the year), and the juvenile instantaneous mortality rate (per day) of *M. balthica*. Data analysis was based on an extensive long-term data set (1973–2001) originating from the western Wadden Sea. Our results strongly suggest that rising seawater temperatures affect recruitment by a decrease in reproductive output and by spring advancement of bivalve spawning. Apparently, global warming upsets the evolved reproductive strategy of this marine bivalve to tune its reproduction to the most optimal environmental conditions for the first vulnerable life stages, most importantly the match/mismatch of time of spawning with that of the phytoplankton bloom and the settlement of juvenile shrimps on the tidal flats. It is hypothesized that the observed density-dependent mortality of juvenile bivalves may act via competition for food, a behavioral response of shrimp to low spat densities, or be the result of the response of age and size at metamorphosis of marine bivalves to resource variability. It is to be expected that prolonged periods of lowered bivalve recruitment and stocks will lead to a reformulation of estuarine food webs and possibly a reduction of the resilience of the system to additional disturbances, such as the depletion and disturbance by shellfish fisheries.

In northwestern European estuaries, severe winters are often followed by high densities of intertidal bivalve recruits, whereas densities after mild winters are usually low. This negative relationship between winter temperature and bivalve recruitment has been reported for cockles (*Cerastoderma edule*), Baltic tellins (*Macoma balthica*), gaper clams (*Mya arenaria*), and blue mussels (*Mytilus edulis*) (e.g., Beukema 1992a; Young et al. 1996). Large and covarying fluctuations in bivalve recruit densities largely determine the year-to-year variation in the size of the adult stocks (e.g., Beukema et al. 2001; Van der Meer et al. 2001). If global warming shifts the winter character toward higher temperatures, bivalve stocks as well as their predators may be affected (Beukema 1992a).

Although species have responded to climatic changes throughout their evolutionary history, a primary concern for wild species living today is the current rapid rate of the temperature increase (Mac et al. 1998). Two recent articles show that present biological trends, i.e., shifts in range boundaries, phenological (timing) shifts, and changes in species abundances, are consistent with predicted effects of climate warming (Parmesan and Yohe 2003; Root et al. 2003). The synergism of rapid temperature rise and other stresses

could easily disrupt the connectedness among species and lead to a reformulation of species communities and possibly extinctions (Root et al. 2003). In the Wadden Sea, e.g., a series of mild winters (1988–1990) led to a prolonged period of low bivalve recruitment, which ultimately resulted in mass emigration, starvation, and mortality of bivalve-eating birds (Beukema and Cadée 1996; Camphuysen et al. 2002). Knowledge of the underlying mechanisms of failure of bivalve recruitment following mild winters is necessary to predict and manage the consequences of global warming for marine ecosystems.

Under the assumption that recruitment takes place in a closed system, i.e., the pelagic larvae are retained in proximity to their natal population (see reviews in Warner and Cowen 2002) and that the instantaneous mortality rate (z ; per day) is constant during the development from egg to postlarval recruit, the relationship between reproductive output (N_0 ; eggs m⁻²) and recruitment (N_t ; recruits m⁻²) densities at a particular age of the juvenile bivalve (t) can be described as $N_t = N_0 e^{-zt}$. Under these assumptions, low recruitment levels (N_t) following mild winters must be caused by either relatively low egg densities (small N_0), a relatively long period between spawning and assessment of recruitment levels (large t) and/or high instantaneous mortality rates (high z) during the development from egg to recruit. Juvenile mortality rates may, however, differ for different phases, e.g., the pelagic larval and the bottom-dwelling recruit phase (Thorson 1966). If so, the phase mortality rates and the duration of the successive phases must be taken into account.

During cold winters, bivalves show a lower metabolism, resulting in a higher preservational biomass (Zwarts 1971; Honkoop and Beukema 1997; Beukema 1992a) and consequently in the production of more eggs in early spring (Honkoop and Van der Meer 1997, 1998). Similarly, well-fed bi-

¹ Corresponding author (katja@nioz.nl).

Acknowledgments

We thank W. de Bruin, J. Hegeman, D. Waasdorp, and J. Zuidewind for their help in collecting the phytoplankton and macrozoobenthos samples during the past decades. Furthermore, we acknowledge J. Drent, M. F. Leopold, J. van der Meer, I. Williams, and two anonymous reviewers for their critical comments on earlier versions of this manuscript. Funding for this study was provided by research grants from the Netherlands Organisation for Scientific Research (Priority Program on Sustainable Use and Conservation of Living Marine Resources), the Netherlands Bremen Oceanography (NEBROC), and Rijkswaterstaat (Rijksinstituut voor Kust en Zee).

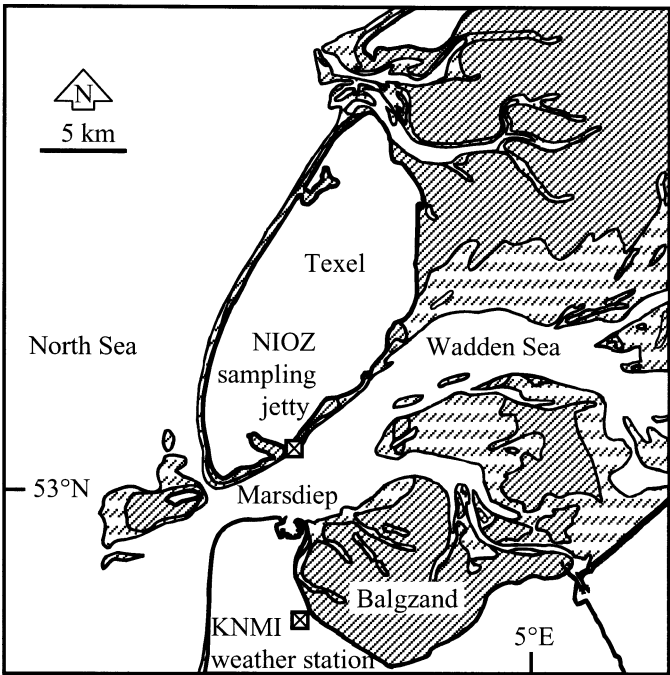


Fig. 1. Location of study area showing sampling stations for wind direction and speed (KNMI weather station), water temperature and chlorophyll *a* (NIOZ sampling jetty), and marine bivalves and shrimps (Balgzand). Dark-hatched areas indicate tidal flats, i.e., depth <0 m (relative to mean lower low-water springs); lighter-hatched areas indicate a water depth between 0 and -2 m.

valves produce more and larger eggs (Bayne et al. 1978). However, long-term field observations (1970–1996) on population dynamics of *Macoma* showed that the substantial year-to-year variation in egg production in late winter could only explain a minor part (7%) of the observed variation in recruit density (Honkoop et al. 1999).

For some species, cold winters delay the time of spawning (t_0) and consequently shorten the period (t) of the time between spawning and a given moment in late summer when recruit densities are assessed. Bivalve spawning is triggered when the seawater temperature reaches a threshold value in spring (e.g., Giese 1959). Recently, *Macoma* was found to be triggered into spawning at 8.3°C (Drent and Luttkhuizen unpubl. data). If the instantaneous mortality rate (per day) of bivalve postlarvae is approximately 0.05 d⁻¹, as has been

shown for *Cerastoderma*, *Macoma*, and *Mya* (Beukema et al. 1998; Van der Veer et al. 1998), an earlier onset of spawning by 1 month would result in a more than 75% decrease of recruit densities at a fixed sampling date in summer.

Optimizing the time of spawning is necessary to match reproduction with the most optimal environmental conditions for the first vulnerable life stages (i.e., the settlement-timing hypothesis by Todd and Doyle [1981]). Mortality of juvenile bivalves appears to be related to food availability (Beukema et al. 2002). In temperate waters, most bivalve larvae are more or less planktotrophic, i.e., their food stores are not sufficient to survive the pelagic phase without ingesting exogenous food (Thorson 1950). Although the peak and magnitude of the phytoplankton spring bloom shows strong year-to-year variation (Philippart et al. 2000), not much attention has been paid to a possible causal relationship between this food supply, larval mortality rates, and resulting bivalve recruitment. There is still much debate on whether growth and development of invertebrate larvae are food limited under natural conditions (e.g., Strathmann 1996).

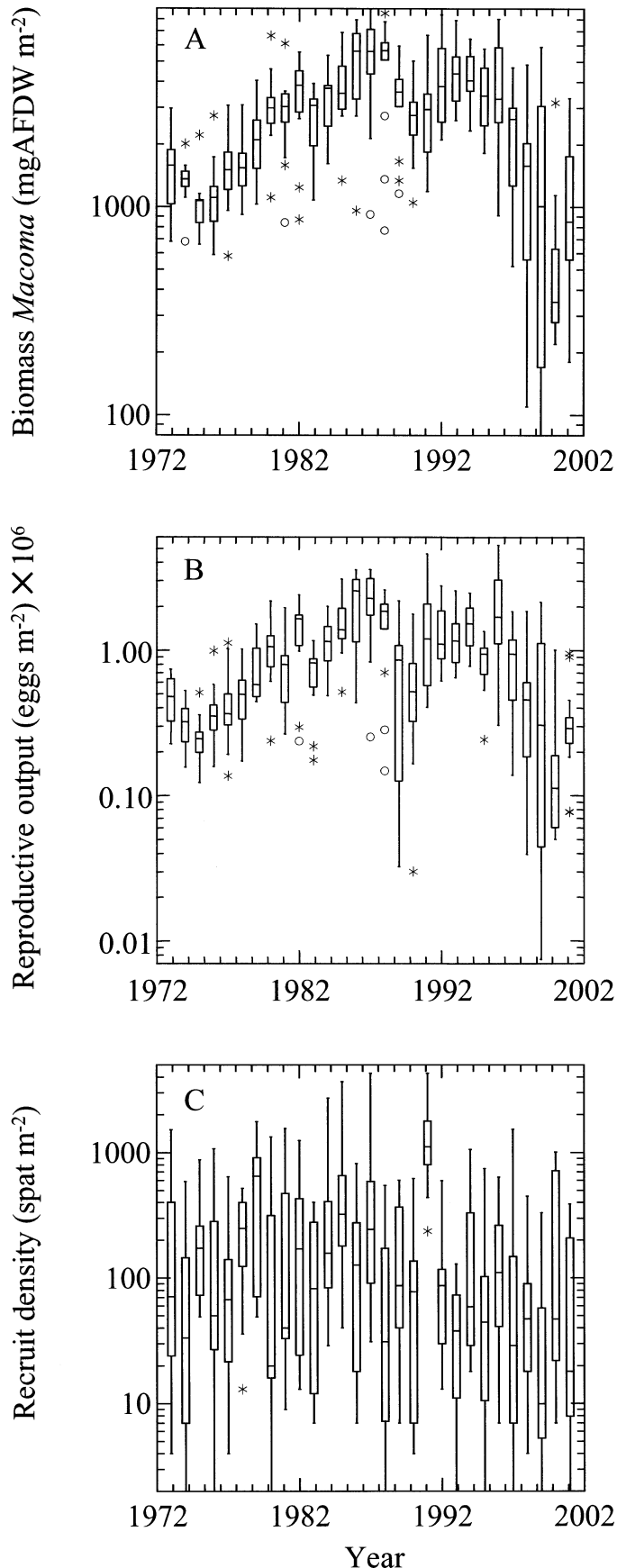
The main predators of settled recruits of *Macoma* are 0-group shrimp, *Crangon crangon* (Beukema et al. 1998; Van der Veer et al. 1998). These shrimps selectively prey on small (<3 mm) bivalve spat (e.g., Beukema et al. 1998; Hiddink et al. 2002). Cold winters delay the onset of the crustacean reproduction in the North Sea and subsequent settlement of new-born shrimps onto the tidal flats of the Wadden Sea (Beukema 1992b). This delay enables the bivalve recruits to escape predation by outgrowing their predators (Beukema et al. 1998).

Other known temperature-correlated sources of mortality of juvenile bivalves are advection of pelagic larvae toward the open sea and interference by adult bivalves. In the Wash estuary (England), cold winters (January–February) were followed by an increased frequency of easterly winds from April to July. Under these conditions, induced currents enhanced retention of *Cerastoderma* larvae close to suitable settlement sites and, ultimately, enhanced recruitment (Young et al. 1996). For the western Wadden Sea, strong easterly winds effect an increase of the outflow to the North Sea (H. Ridderinkhof unpubl. data) and therefore potentially decrease the retention of bivalve larvae.

The cockle *C. edule* is an important component of the

Table 1. List of variables included in the linear regression analyses of instantaneous mortality rate of *Macoma balthica* (per day) in the western Wadden Sea between 1973 and 2001 (Period I) and between 1983 and 2001 (Period II).

| Factor | Code | Period | | Variable |
|---------------------|----------------|--------|----|--|
| | | I | II | |
| Density dependence | N ₀ | + | + | Reproductive output (eggs m ⁻²) |
| Food availability | V ₁ | + | + | Match with phytoplankton spring bloom (days) |
| | V ₂ | + | + | Magnitude of phytoplankton spring bloom (mg Chl <i>a</i> m ⁻³) |
| | V ₃ | – | + | Match with <i>Crangon crangon</i> predation (days) |
| Shrimp predation | V ₄ | – | + | Magnitude of <i>Crangon crangon</i> predation pressure (m ² m ⁻²) |
| | V ₅ | + | + | Wind stress (m ² second ⁻²) |
| Estuarine retention | V ₆ | + | + | Biomass <i>Cerastoderma edule</i> (mg AFDW m ⁻²) |



bivalve community. Adult stocks vary greatly as cockles are very sensitive to low temperatures (Beukema 1979, 1985; Strasser et al. 2001). Very cold winters can decimate adult stocks (Beukema 1985) and this may enhance the survival of bivalve recruits (Young et al. 1996). Adult cockles would otherwise filter settling larvae out of the water column (Thorson 1950; Woodin 1976; André and Rosenberg 1991) and compete for space, food, and other resources (Young et al. 1996).

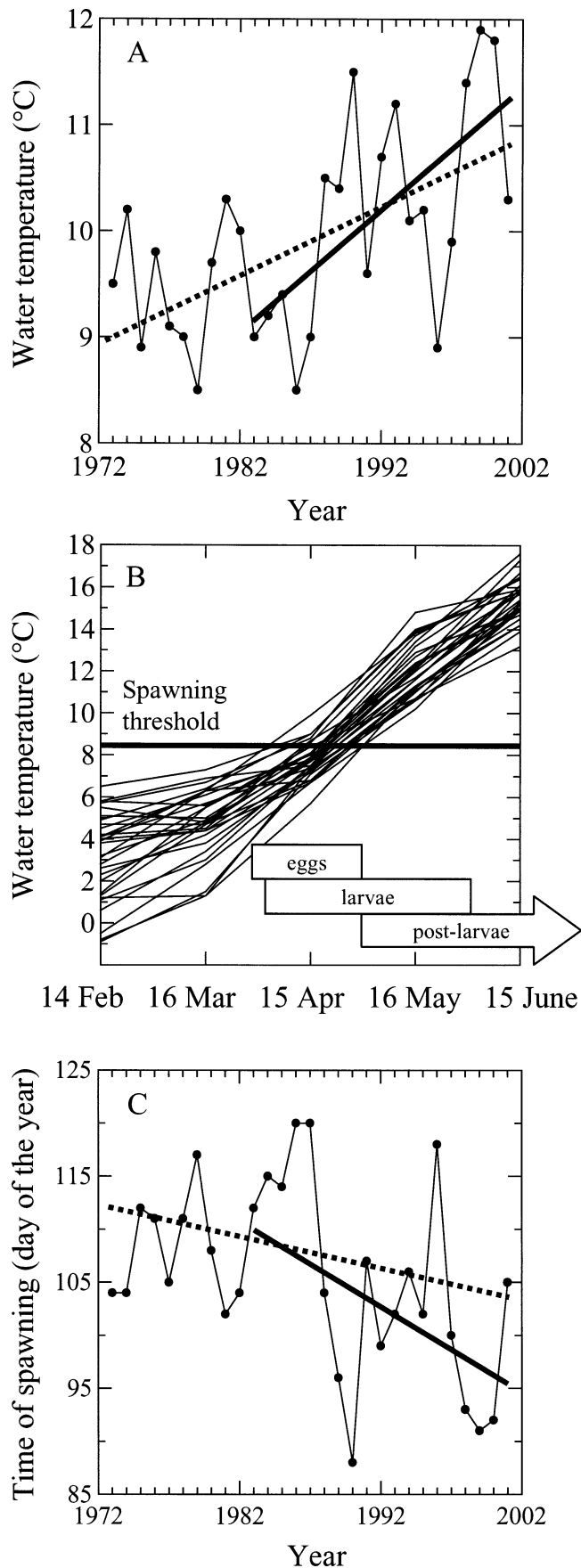
The present article deals with possible effects of rising temperatures on recruitment of *M. balthica*. Data analysis is based on long-term datasets (temperature, wind, phytoplankton, bivalves, and shrimps) originating from one area (western Wadden Sea) over a study period of 29 years (1973–2001). First, we examine the temperature-induced effects on reproductive output (eggs m⁻²), onset of spawning (day of the year), and the juvenile instantaneous mortality rate (per day) of *M. balthica*. Second, we analyze the combined effects of the temperature-related environmental variables (viz. time and magnitude of food availability, time and magnitude of predatory shrimps, advection of larvae toward the open sea, and interference by cockle stock) on the instantaneous mortality rate by means of stepwise multiple regression. Third, we discuss the dominant structuring factors in the light of reproductive strategy of *M. balthica* and possible consequences of global warming for temperate estuarine ecosystems.

Materials and methods

Stock, eggs, and recruits—Since 1970, the macrozoobenthos community has been monitored at 13 tidal stations located at the Balgzand in the western Wadden Sea (Fig. 1). Sampling, sorting, and further analysis have been carried out in a consistent way throughout the entire study period. Data on bivalve recruits are available since 1973 (Beukema et al. 2001). Samples of macrobenthos (>1 mm) were taken each year in late winter (mostly in March, at the time of the lowest abundance; see Beukema 1974) and in late summer (August–September, to include bivalve recruits). Sampling procedures were described earlier in detail by Beukema (1974). **Recruitment or year class strength (N_t ; recruits m⁻²) was assessed as the number of recruits (0-year class individuals, no year-ring) per m² during the late-summer sampling period.**

←

Fig. 2. Stock and recruitment of *M. balthica* at the Balgzand tidal flats in the western Wadden Sea between 1973 and 2001 ($n = 13$ tidal stations). (A) Biomass in late winter (mg AFDW m⁻²). (B) Reproductive output in late winter (eggs m⁻²). (C) Recruit density in late summer (spat m⁻²). **The horizontal line within the box marks the median of the sample.** The length of each box shows the range within which the central 50% of the values fall, with the hinges (box edges) at the first and third quartiles. H is the absolute value of the difference between the values of the two hinges. The whiskers (vertical lines) show the range of values that fall within 1.5 H, values between the inner (>1.5 H) and outer (<3 H) fences are plotted with asterisks, values beyond the outer fences (>3 H) are plotted with open circles.



Reproductive output (N_0 ; eggs m^{-2}) was calculated as the summed egg production of all females, multiplied by their density. The egg production of a female (eggs ind^{-1}) is related to her shell length (SL; cm) and body mass index (BMI; mg AFDW SL^{-3}) in late winter, according to $N_{ind} = 7,739(SL^3/1.5^3)(BMI - 5.6)$ (Honkoop and Van der Meer 1997). Females do not produce eggs if the BMI falls below 5.6 mg AFDW cm^{-3} , so egg production was set to zero when $BMI < 5.6$ mg AFDW cm^{-3} , thus preventing negative values for fecundity. Furthermore, it was assumed that females < 1 cm are immature and therefore do not reproduce and that half of the adult population consisted of females (Honkoop et al. 1999).

When information on the local stock (e.g., eggs m^{-2}) is included in an analysis of recruitment patterns at a relatively small area (50 km^2), it is implicitly assumed that recruitment takes place in a closed system, i.e., the pelagic larvae are retained in proximity to their natal population. Mounting evidence suggests that some populations of benthic marine organisms are more demographically closed than previously thought (see reviews in Warner and Cowen 2002). Recent mitochondrial DNA sequence analyses showed that European populations of *M. balthica* are highly subdivided (viz. in French, Atlantic, and Baltic population assemblages), meaning that they are numerically and evolutionarily independent (Luttikhuisen et al. 2003). More detailed analyses of quantitative and molecular traits revealed genetic differences between adult populations of *M. balthica* living in the western Wadden Sea and the adjacent North Sea (Luttikhuisen et al. 2003b). Even if part of the larvae originate from neighboring areas (or are lost to such areas), this would not seriously distort the analysis because temporal patterns in bivalve recruitment and stock biomass are synchronous in the Dutch and German Wadden Sea (Beukema et al. 2001).

Onset of spawning—Field observations and laboratory experiments showed that *M. balthica* spawns (criterion: 50% spent) in spring when the gradual increase of the mean (monthly averaged) water temperature surpasses 8.3°C (Drent and Luttikhuisen unpubl. data). Since 1947, bucket water samples have been collected daily at 0800 h from the so-called NIOZ jetty, located at the northern shore of the Marsdiep tidal inlet (Fig. 1). The temperature was assessed using a calibrated seawater thermometer. Since March 2000,

←

Fig. 3. Water temperatures and bivalve spawning in the western Wadden Sea between 1973 and 2001. (A) Annual averaged water temperatures (April–May). Dotted line (Period I): linear increase of 0.07°C yr^{-1} ($n = 29$; $r^2 = 0.33$; $P = 0.001$); solid line (Period II): linear increase of 0.11°C yr^{-1} ($n = 19$; $r^2 = 0.37$; $P = 0.006$). (B) Monthly averaged water temperatures (February–June). Solid horizontal line: threshold temperature for bivalve spawning (8.3°C). Potential presence (depending on the actual time of spawning) of bivalve eggs, pelagic larvae and bottom-dwelling postlarvae is indicated. (C) Time of bivalve spawning viz. day of the year at which water temperatures reaches the threshold value of 8.3°C. Dotted line (Period I): linear decrease of -0.44 d yr^{-1} ($n = 29$; $r^2 = 0.19$; $P = 0.019$); solid line (Period II): linear decrease of -0.99 d yr^{-1} ($n = 19$; $r^2 = 0.31$; $P = 0.013$).

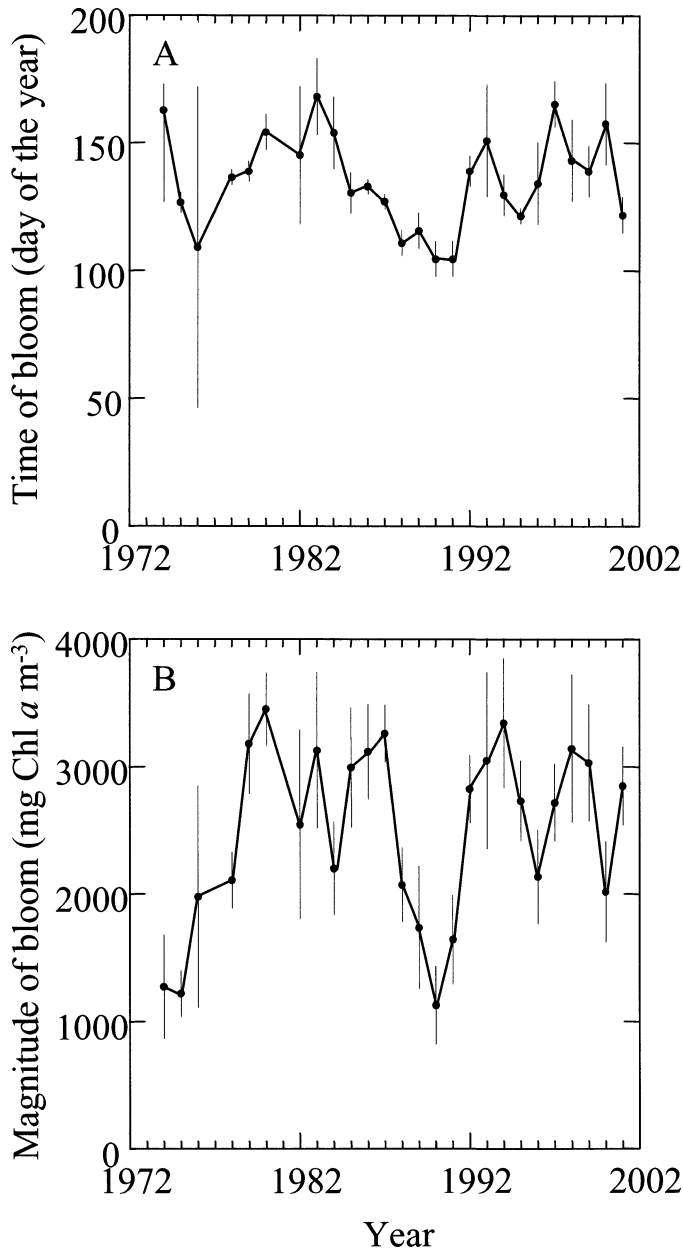


Fig. 4. Time of the peak and magnitude of the phytoplankton spring bloom (estimated values ± 1 standard error) in the western Wadden Sea between 1973 and 2001. (A) Time of the peak (day of the year). (B) Magnitude ($\text{mg Chl } a \text{ m}^{-3}$).

temperature is measured continuously by means of electronic sensors. Monthly values have been derived from daily observations (Van Aken in press). In accordance with the empirical relationships based on field observations (Drent and Luttkhuizen unpubl. data), we calculated the day number at which the threshold temperature of 8.3°C for *Macoma* spawning was reached by means of linear regression of monthly averaged water temperatures between March and June ($n = 4$). Finally, the age of the recruits at the time of the assessment of recruitment levels (t) was calculated as the number of days between the calculated time of spawning in spring (t_0) and that of the actual sampling in summer (t_s),

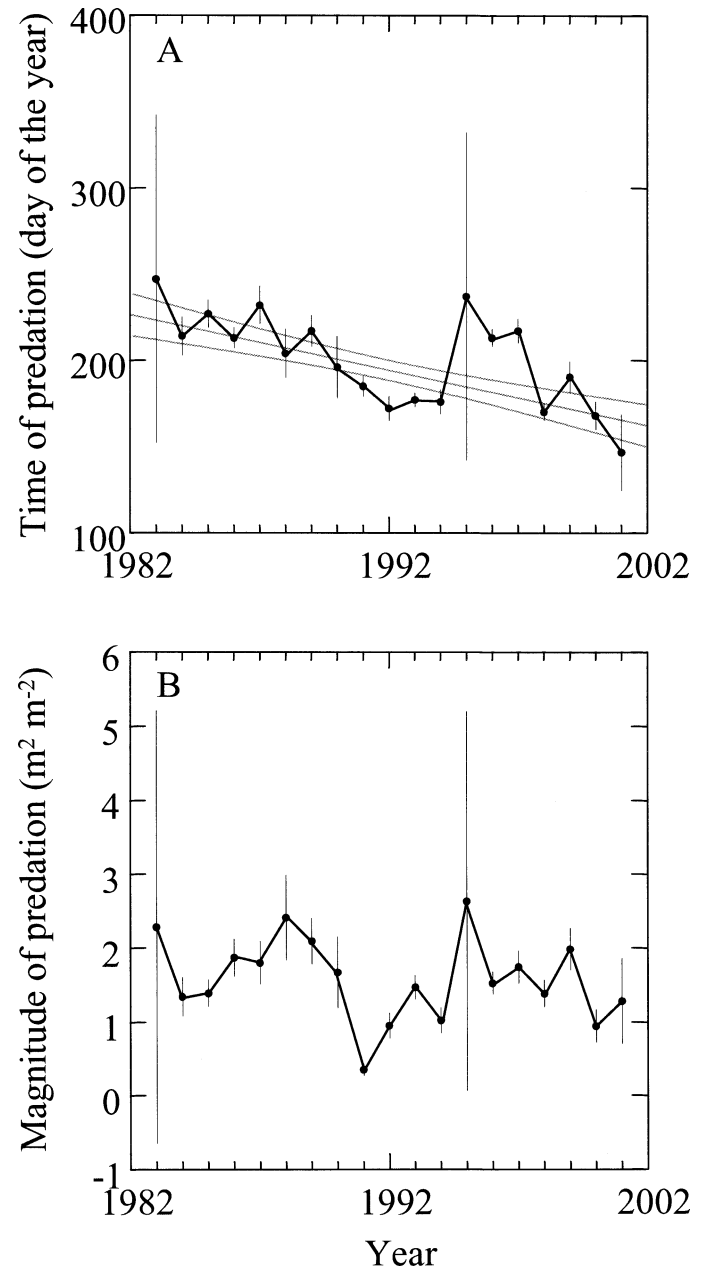


Fig. 5. Time of the peak and magnitude of predation pressure by 0-group *C. crangon* (estimated values ± 1 standard error) in the western Wadden Sea between 1983 and 2001. (A) Time of the peak (day of the year). (B) Magnitude ($\text{m}^2 \text{ m}^{-2}$).

which was more or less fixed throughout the entire study period.

Food availability—From 1974 onwards, bucket water samples have been collected at high water from the NIOZ sampling jetty (Fig. 1). Phytoplankton sampling frequency is 50–60 times yr^{-1} , varying from once or twice a month in winter up to twice a week during phytoplankton spring blooms (e.g., Cadée and Hegeman 2002). Chlorophyll *a* concentrations ($\text{mg Chl } a \text{ m}^{-3}$) were averaged for every month from 1974 to 2001. Missing values within the phytoplankton

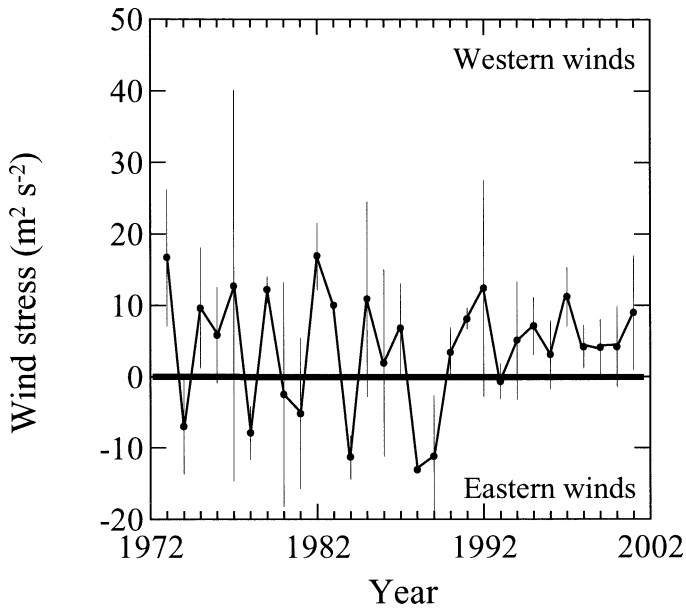


Fig. 6. Wind stress ($\text{m}^2 \text{s}^{-2}$) in the western Wadden Sea between 1973 and 2001 in spring (vertical lines: values of April and May; dots: average values). Western winds have a positive sign (indicating enhanced retention of larvae in the study area), eastern winds a negative (indicating enhanced outflow of larvae toward the open sea).

data set were filled in under the assumption that the expected monthly averaged density of each species was a product of a year effect and a month effect (see Philippart et al. 2000). We had to exclude 2 yr (1977 and 1981) from further analysis because of their relatively high proportion of missing values. For the remaining 26 years, the monthly concentrations of chlorophyll *a* were based on 292 actual averages and 20 imputed values.

The time of the peak and the magnitude of the phytoplankton bloom were derived from the 12 monthly means from January to December of the chlorophyll *a* contents of the water (c_i ; $\text{mg Chl } a \text{ m}^{-3}$) by fitting a normal density function according to $c_i = S_{\text{chl}} / \sigma(2\pi)^{1/2} \exp(-(t - \mu_{\text{chl}})^2 / 2\sigma^2)$, where μ_{chl} is the day of the year at which the phytoplankton bloom is at its maximum (time of the peak in chlorophyll *a*) and S_{chl} is the annual sum of the daily chlorophyll contents (magnitude of the bloom). The match between the peak in phytoplankton blooming (μ_{chl}) and that of bivalve spawning (t_0) was calculated as the length of the period (number of days) between the peak in spawning and that in chlorophyll *a* concentration (viz. food match = $\mu_{\text{chl}} - t_0$).

Shrimp predation—Since 1983, densities of juvenile 0-group shrimps *C. crangon* on the Balgzand tidal flats (Fig. 1) have been measured between April and August. Samples were taken at low tide mostly at about 10-d intervals at three permanent stations at the high tidal flats, located between 0.5 and 1.0 km from the coast between 10 cm above and 40 cm below mean tidal level. The samples were taken at low tide using 0.009 m^2 cores. The total area per sampling date (three stations per date, four samples per station, 10 cores per sample) is 1.08 m^2 . Shrimps were counted and individual

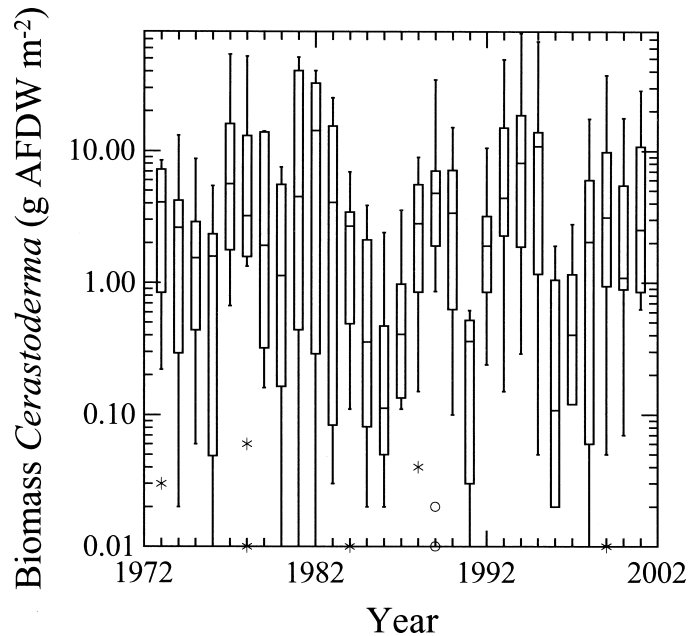


Fig. 7. Late winter biomass of *C. edule* (g AFDW m^{-2}) at the Balgzand tidal flats in the western Wadden Sea between 1973 and 2001 ($n = 13$ tidal stations). See legend of Figure 2 for explanation of the box-and-whisker plots.

lengths (in millimeters) were measured. See Beukema (1992b) for further details on sampling and population dynamics. Since 1998, shrimps are sampled at two additional sites at the lower tidal flats. Comparison of shrimp abundance at the low and high tidal flats showed that year-to-year variation in shrimp dynamics at the high tidal flats is representative for that over the entire Balgzand area (Dekker unpubl. data).

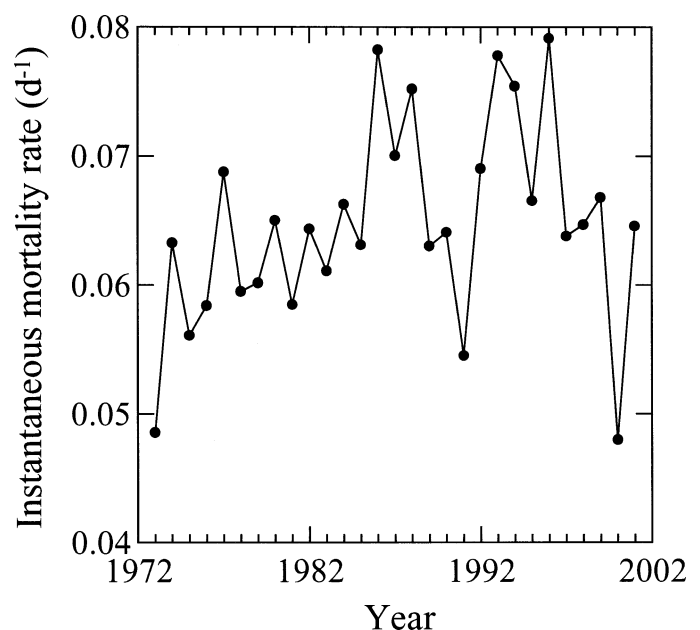


Fig. 8. Instantaneous mortality rates of juvenile *M. balthica* (per day) in the western Wadden Sea between 1973 and 2001.

Table 2. Multivariate linear regression analysis ($n = 26$; $r^2 = 0.62$) of instantaneous mortality rate of *Macoma balthica* (per day) between 1973 and 2001 (Period I) as a function of reproductive output (eggs m^{-2} ; \ln transformed), match (number of days after spawning), and magnitude (mg Chl $a \text{ m}^{-3}$) of the spring phytoplankton bloom, wind stress ($\text{m}^2 \text{ second}^{-2}$), and cockle stock biomass (mg AFDW m^{-2} ; \ln transformed). Variables that contribute significantly to the model ($P < 0.05$) are shown in bold. SS = sum of squares, MS = mean squares.

| Variable | Coefficient | SE | <i>t</i> | <i>P</i> (two tail) | |
|-----------------------------|---------------------|-------|---------------------|---------------------|----------|
| Constant | −0.050 | 0.029 | −1.22 | 0.102 | |
| Reproductive output | 0.008 | 0.002 | 3.79 | 0.001 | |
| Match spring bloom | 0.000 | 0.000 | 0.041 | 0.968 | |
| Magnitude spring bloom | 0.000 | 0.000 | 0.844 | 0.409 | |
| Wind stress | −0.000 | 0.000 | −1.74 | 0.097 | |
| Biomass <i>Cerastoderma</i> | 0.002 | 0.001 | 1.07 | 0.296 | |
| Analysis of variance | | | | | |
| Source | SS | df | MS | <i>F</i> | <i>P</i> |
| Regression | 8.7×10 ⁴ | 5 | 1.7×10 ⁴ | 6.54 | 0.0009 |
| Residual | 5.3×10 ⁴ | 20 | 0.3×10 ⁴ | | |

Assuming that ingestion rate is related to the surface area of the predator (e.g., Kooijman 2000), shrimp predation pressure ($\text{m}^2 \text{ m}^{-2}$) was indexed as the summed squared lengths of the individuals per m^2 . Time of the peak and magnitude of the predation pressure by shrimps were derived from the 10-d measurements of the predatory index (p_i ; $\text{m}^2 \text{ m}^{-2}$) by fitting a normal density function $p_i = S_{\text{shrimp}} / \sigma(2\pi)^{1/2} \exp(-(t - \mu_{\text{shrimp}})^2 / 2\sigma^2)$, where μ_{shrimp} is the day number at which the species-specific predatory index is at its maximum (time of the peak) and S_{shrimp} is the sum of the daily predation indices (annual magnitude of predation pressure). The match between the peak in shrimp predation (μ_{shrimp}) and that of bivalve spawning (t_0) was calculated as the length of the period (number of days) between the peak in spawning and that in shrimp predation (viz. predation match = $\mu_{\text{shrimp}} - t_0$).

Estuarine retention—The ferry that frequently crosses the Marsdiep tidal inlet (Fig. 1) has been equipped with an Acoustic Doppler Current Profiler since 1998. Data analysis showed that the net mean tidal flow is outward to the North Sea. Its magnitude was found to be correlated with wind forcing. Strong easterly winds affect an increase of the outflow, while strong westerly winds may even cause a net inflow from the North Sea into the Wadden Sea (Ridderinkhof et al. 1990; H. Ridderinkhof unpubl. data).

We indexed the wind stress ($\text{m}^2 \text{ per second}^2$) by multiplying the scalar wind velocity (m per second) by the east–west

component of the wind velocity (m per second). Winds blowing from the west have a positive sign, eastern winds a negative. Wind direction and speed are routinely measured at the weather station of the Royal Dutch Meteorological Organisation (KNMI) close to the Balgzand tidal flats (Fig. 1). Monthly mean values were calculated from the daily observations, downloaded from the KNMI web site (<http://www.knmi.nl/voorl/weer/>). The average value of the wind stress index of the most likely period for the presence of pelagic *Macoma* larvae was considered, viz. during April and May (see Results on onset of spawning).

Cockle stock interference—The interference of the cockles was indexed by the late-winter biomass (g AFDW m^{-2}) of the *Cerastoderma* stock, averaged for the 13 intertidal stations at Balgzand tidal flats (Fig. 1).

Calculation and analysis of mortality—The instantaneous mortality rate (z ; per day) was calculated as the natural logarithm of egg survival (=recruits m^{-2} /eggs m^{-2}), divided by the length of the period (number of days) between the peak in spawning (t_0) and the time of assessment of recruitment level (t_s) according to

$$z = \ln(N_t/N_0)/(t_s - t_0)$$

To evaluate the combined effects of the temperature-related environmental variables (Table 1) on the instantaneous

Table 3. Stepwise linear regression analysis ($n = 29$; $r^2 = 0.45$) of instantaneous mortality rate of *Macoma balthica* (per day) between 1973 and 2001 (Period I) as a function of reproductive output (eggs m^{-2} ; \ln transformed), match (number of days after spawning), and magnitude (mg Chl $a \text{ m}^{-3}$) of the spring phytoplankton bloom, wind stress ($\text{m}^2 \text{ second}^{-2}$), and cockle stock biomass (mg AFDW m^{-2} ; \ln transformed). Only variables with $P < 0.05$ were included. SS = sum of squares, MS = mean squares.

| Variable | | Coefficient | SE | <i>t</i> | <i>P</i> (two tail) |
|----------------------|---------------------|-------------|---------------------|----------|---------------------|
| Constant | | −0.041 | 0.022 | −1.89 | 0.082 |
| Reproductive output | | 0.008 | 0.002 | 4.70 | 0.000 |
| Analysis of variance | | | | | |
| Source | SS | df | MS | <i>F</i> | <i>P</i> |
| Regression | 7.8×10 ⁴ | 1 | 7.8×10 ⁴ | 22.08 | 0.0001 |
| Residual | 9.5×10 ⁴ | 27 | 0.4×10 ⁴ | | |

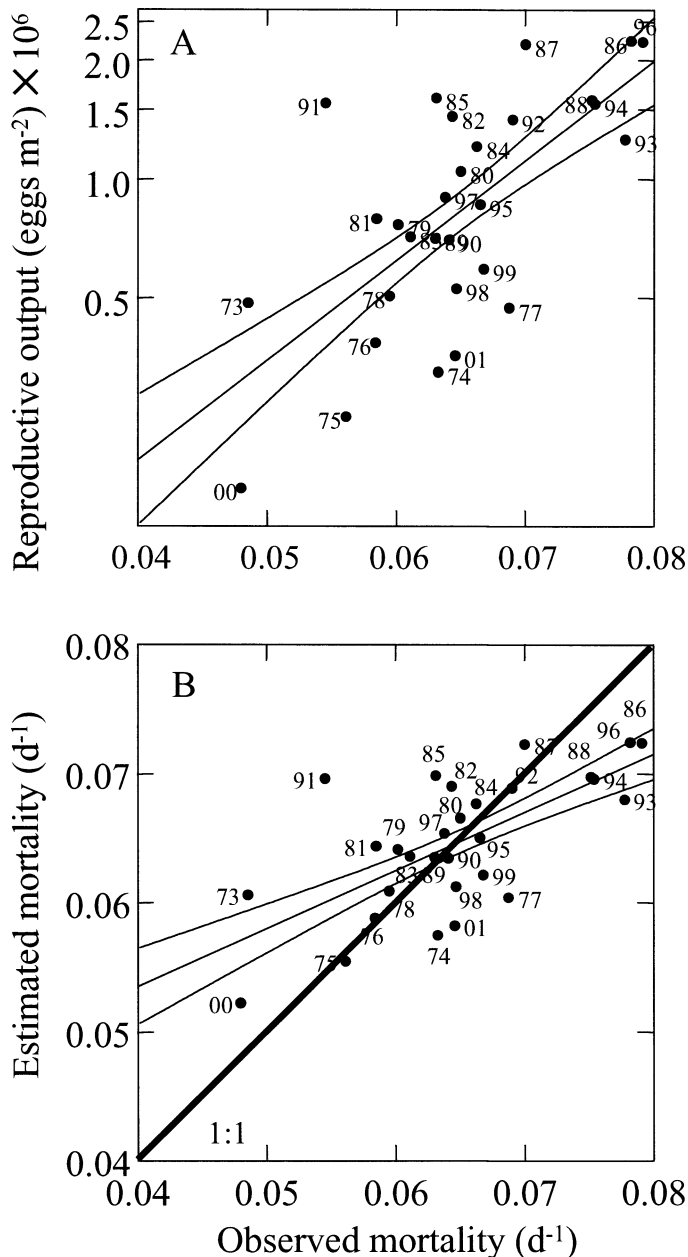


Fig. 9. Model results on the relationships between the instantaneous mortality rate of juvenile *M. balthica* (per day) and environmental factors for Period I (1973–2001). (A) Linear relationship between mortality rate (per day) and reproductive output (eggs m⁻²). (B) Linear relationship between observed and estimated mortality rates (per day). The univariate stepwise linear regression model includes density dependence (see Table 3).

mortality rate (z ; per day), stepwise multiple regression with forward and backward elimination was employed. In order to take density-dependent processes into account, the instantaneous mortality rate was fitted according to

$$z = e_0 - \beta N_0 + e_1 V_1 + e_2 V_2 + \dots + \varepsilon$$

where e_0 , e_1 , e_2 , etc. are constants, β is a density-dependent parameter, V_1 , V_2 , etc. are the environmental variables (see Table 1), and ε is the residual (Wilderbuer et al. 2002). The

analysis was performed for two different periods, i.e., (1) the full period (Period I: 1973–2001), for part of which no data on shrimp abundance were available, and (2) a restricted period (Period II: 1983–2001), for which the data set for all variables was complete. Statistical analyses were performed with SYSTAT (2000), version 10.

Results

Stock, eggs, and recruits—Between 1973 and 2001, the average biomass of the total stock of *M. balthica* was 2.89 g AFDW m⁻² (Fig. 2A). Highest values occurred around 1987 (>5 g AFDW m⁻²) and the stock significantly declined thereafter with an average rate of -0.26 g AFDW m⁻² yr⁻¹ ($n = 15$; $r^2 = 0.67$; $P = 0.0002$). Within the study period, the reproductive output of *M. balthica* was on average almost 1×10^6 eggs m⁻² (Fig. 2B). Since 1987, the reproductive output of the stock declined with a rate of $-8,363$ eggs m⁻² yr⁻¹ ($n = 15$; $r^2 = 0.35$; $P = 0.021$). Within the study period, the average spat densities varied between more than 1,400 m⁻² in 1991 to less than 50 m⁻² in 1993 (Fig. 2C). The exceptionally high spatfall in 1991 was considered to be a consequence of the almost complete removal of commercially exploited bivalve stocks from the western Wadden Sea, resulting in strong reduction of the competition for food and space for the recruits (Beukema and Cadée 1996; Beukema et al. 2002). In contrast with the trends in stock and reproductive output, the recruit densities did not significantly decline during the past 15 yr. However, average spat densities were significantly higher before (1973–1987) than after (1988–2001) the onset of the decline in reproductive output, respectively 359 ± 257 and 144 ± 64 recruits m⁻² (two-sample t -test; $P = 0.007$; data 1991 excluded).

Onset of spawning—Average water temperature in spring (April–May) varied between 8.5°C in 1979 and 1986, and almost 12°C in 2000 and 2001 (Fig. 3A). Between 1973 and 2001 (Period I), spring temperatures increased with a rate of $0.07^\circ\text{C yr}^{-1}$ ($n = 29$; $r^2 = 0.33$; $P = 0.001$). Between 1983 and 2001 (Period II), the rate of increase was $0.11^\circ\text{C yr}^{-1}$ ($n = 19$; $r^2 = 0.37$; $P = 0.006$). On average, the threshold temperature for bivalve spawning was reached at 16 April, but could be as early as 29 March and as late as 30 April (Fig. 3B). The day number at which bivalve spawning took place showed a significant declining trend with a rate of -0.44 d yr⁻¹ ($n = 29$, $r^2 = 0.19$, $P = 0.019$) for Period I, and -0.99 d yr⁻¹ ($n = 19$, $r^2 = 0.31$, $p = 0.013$) for Period II (Fig. 3C).

Food availability—The average time of the peak of the phytoplankton bloom was 16 May (Fig. 4A), i.e., 30 d after the average time of onset of bivalve spawning (Fig. 3C). The length of this period between spawning and blooming varied between -2 and $+66$ d. The magnitude of the phytoplankton blooms varied between more than 1,000 and almost 3,500 mg Chl *a* m⁻³, with an average value of approximately 2,500 mg m⁻³ (Fig. 4B). The time of the peak in chlorophyll *a* and the magnitude of blooming were not correlated ($n = 26$, $r^2 = 0.11$, $P = 0.096$).

Table 4. Linear regression analysis ($n = 19$; $r^2 = 0.92$) of instantaneous mortality rate of *Macoma balthica* (per day) between 1983 and 2001 (Period II) as a function of reproductive output (eggs m^{-2} ; \ln transformed), match (number of days after spawning), and magnitude (mg Chl *a* m^{-3}) of the spring phytoplankton bloom, match (number of days after spawning), and magnitude ($\text{m}^2 \text{m}^{-2}$) of predation pressure by 0-group shrimp, wind stress ($\text{m}^2 \text{second}^{-2}$), and cockle stock biomass (mg AFDW m^{-2} ; \ln transformed). Variables that contribute significantly to the model ($P < 0.05$) are shown in bold. SS = sum of squares, MS = mean squares.

| Variable | Coefficient | SE | <i>t</i> | <i>P</i> (two tail) |
|------------------------------------|--------------------|-------|-------------------|---------------------|
| Constant | -0.112 | 0.025 | -4.54 | 0.001 |
| Reproductive output | 0.013 | 0.002 | 7.44 | 0.000 |
| Match spring bloom | 0.000 | 0.000 | 2.74 | 0.019 |
| Magnitude spring bloom | -0.000 | 0.000 | -1.19 | 0.258 |
| Match <i>Crangon</i> predation | -0.000 | 0.000 | -5.76 | 0.000 |
| Magnitude <i>Crangon</i> predation | 0.013 | 0.002 | 5.36 | 0.000 |
| Wind stress | 0.000 | 0.000 | 0.45 | 0.661 |
| Biomass <i>Cerastoderma</i> | 0.001 | 0.001 | 1.31 | 0.216 |
| Analysis of variance | | | | |
| Source | SS | df | MS | <i>F</i> |
| Regression | 10.7×10^4 | 7 | 1.5×10^4 | 18.67 |
| Residual | 0.9×10^4 | 11 | 0.1×10^4 | <i>P</i> |
| | | | | 0.00003 |

Shrimp predation—The average time of peak in juvenile shrimp at the high tidal flats was 19 July (Fig. 5A), and, on average, 96 d after the average time of bivalve spawning (Fig. 3C). Between 1983 and 2001, the number of days between onset of bivalve spawning and the peak in shrimp predation pressure decreased significantly with a rate of -2.2 d yr^{-1} ($n = 19$, $r^2 = 0.26$, $P = 0.026$). Shrimp predation pressure was, on average, $1.58 \text{ m}^2 \text{m}^{-2}$ (Fig. 5B). For shrimp, the time and magnitude of predation pressure were positively correlated ($n = 19$, $r^2 = 0.41$, $P = 0.003$), i.e., a late peak of the juvenile shrimp density on the tidal flats coincided with a relatively high predation pressure.

Estuarine retention—The winds in spring (April–May) blew predominantly from the east in 1973, 1977, 1980, 1981, 1985, 1998, and 1990, and from the west in all other years (Fig. 6). Assuming a direct relationship between wind stress and estuarine retention (H. Ridderinkhof unpubl. data), the outflow of larvae from the Wadden Sea toward the North Sea was relatively high in 1988 and relatively low in 1973 and 1982.

Cockle stock interference—Between 1973 and 2001, the average biomass of *C. edule* was 5 g AFDW m^{-2} (Fig. 7). Lowest mean biomass values occurred in 1991 and 1996 ($<0.2 \text{ g AFDW m}^{-2}$) and highest mean values of more than 15 g AFDW m^{-2} were found in 1981 and 1994.

Mortality—The instantaneous mortality rate (per day) of *M. balthica* between spawning and sampling was, on average, 0.065 d^{-1} and varied between less than 0.050 d^{-1} in 1973 and 2000 and more than 0.075 d^{-1} in 1986, 1988, 1993, 1994, and 1996 (Fig. 8).

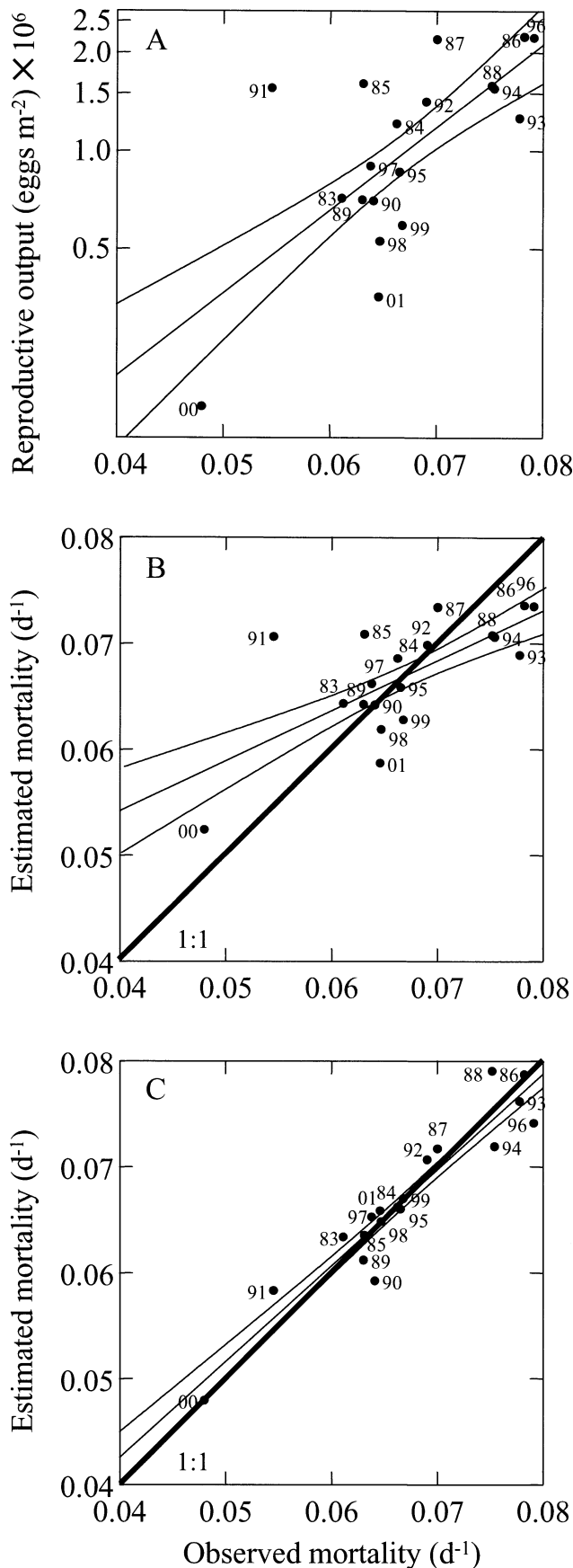
For Period I (1973–2001), the full model (including five variables) explained 62% of the variation in mortality rates of juvenile *M. balthica* (Table 2). The height of the reproductive output (eggs m^{-2}) was the only factor that contributed significantly to this model, the other factors (match and magnitude of the phytoplankton bloom, western wind stress,

and cockle stock biomass) did not (Table 2). Stepwise linear regression analysis resulted in a univariate model that explained 45% of the variation in bivalve juvenile mortality rates by the height of the reproductive output between 1973 and 2001 (Table 3; Fig. 9).

For Period II (1983–2001), the full model (including all seven variables) explained 92% of the variation in mortality (Table 4). Four factors (height of the reproductive output, match with spring bloom, and match and magnitude of shrimp predation) contributed significantly to this model; the other three factors (magnitude of the phytoplankton bloom, wind stress, and cockle stock biomass) did not. Also for this restricted period, the mortality rate is mainly related to the height of the reproductive output (Fig. 10A). A univariate linear regression model explains 47% of the variation in bivalve mortality rates by the height of the reproductive output alone (Fig. 10B). Stepwise linear regression analysis resulted in a multivariate model that explained 90% of the variation in bivalve juvenile mortality rates by egg density, the match with food and predation, and the magnitude of predation between 1983 and 2001 (Table 5; Fig. 10C).

Discussion

Indices and assumptions—Although the environmental factors we studied were the most likely ones (see the introduction) and other potentially explaining factors such as turbidity, tidal range, emersion time of tidal stations, and sediment composition hardly changed during the study period (Beukema and Cadée 1997), the actual explanatory value of the regression models must still be questioned. First, the selection of factors to be included into the stepwise linear regression was not only based on the plausibility of the temperature-induced concepts but also on the availability of relevant data. For example, we did not test the possibility of temperature-induced effects of macroalgae on recruitment levels (e.g., Raffaelli 2000) nor the potential role of parasites, bacteria, and fungi in recruit survival (e.g., De Montaudouin et al. 2000). Second, although some factors were



very indicative for the hypothesis to be tested (e.g., time and magnitude of shrimp predation based on local and high-frequency measurements), other factors were only rough approximations for the hypothesis, e.g., wind stress as an index for the strength of estuarine retention of bivalve larvae. Third, the significant relationships between temperature-induced factors and recruitment may in fact be spurious, i.e., due to associated variations in other factors that were not included in the analysis. Actual model validation can only be achieved by means of dedicated experiments.

Pre- and postlarval mortality—The calculation of the instantaneous mortality rates was based on the assumption that mortality was constant and phase-independent, i.e., similar mortality rates during the larval phase, at settlement and during the postlarval phase. At the study site, Beukema et al. (1998) and Van der Veer et al. (1998) observed constant rates of change in postlarval densities of *Macoma* ranging from -0.009 to -0.045 d^{-1} . These measurements were performed at the high tidal flats, where the rate of change of density of postlarval *Macoma* is a combination of mortality and immigration (Beukema et al. 1998), implying that at this location the actual mortality rate is higher than the rate of change in abundance. From our calculations, based on 13 stations at the study site and covering the full development time from egg to postlarval recruit, we derived an average instantaneous mortality rate of 0.065 d^{-1} for *Macoma* between 1973 and 2001. From these results, we suspect that mortality of *Macoma* is higher during the pelagic egg and larval phase ($>0.10 \text{ d}^{-1}$) than during the bottom-dwelling postlarval phase ($<0.05 \text{ d}^{-1}$).

Climate and recruitment—Our results indicate that rising seawater temperatures affect the stocks of *M. balthica* by lowering the reproductive output (Fig. 11) and moving the spawning period to an earlier time in the year (Fig. 12A). The onset of the phytoplankton bloom is not related to temperature (Fig. 12B). Therefore, the period between spawning and maximum food will be extended and food availability during the pelagic phase will be reduced (cf. the match/mismatch hypothesis by Cushing 1990). In addition, mild winters advance the onset of the crustacean reproduction in the North Sea, and newborn shrimps subsequently settle earlier on the tidal flats of the Wadden Sea (Fig. 12C). A rise in seawater temperature of 1°C causes an advancement of the peak in bivalve spawning of 8 d and in shrimp predation

←

Fig. 10. Model results on the relationships between the instantaneous mortality rate of juvenile *M. balthica* (per day) and environmental factors for Period II (1983–2001). (A) Linear relationship between mortality rate (per day) and reproductive output (eggs m^{-2}). (B) Linear relationship between observed and estimated mortality rates (per day). The univariate model includes density dependence. (C) Linear relationship between observed and estimated mortality rates (per day). The multivariate stepwise linear regression model includes density dependence, match of phytoplankton bloom, and match and magnitude of predation by 0-group *C. crangon* (see Table 5).

Table 5. Stepwise linear regression analysis ($n = 19$; $r^2 = 0.90$) of instantaneous mortality rate of *Macoma balthica* (per day) between 1983 and 2001 (Period II) as a function of reproductive output (eggs m^{-2} ; \ln transformed), match (number of days after spawning), and magnitude (mg Chl a m^{-3}) of the spring phytoplankton bloom, match (number of days after spawning), and magnitude ($\text{m}^2 \text{m}^{-2}$) of predation pressure by 0-group shrimp, wind stress ($\text{m}^2 \text{second}^{-2}$), and cockle stock biomass (mg AFDW m^{-2} ; \ln transformed). Only variables with $P < 0.05$ were included. SS = sum of squares, MS = mean squares.

| Variable | Coefficient | SE | t | P (two tail) |
|------------------------------------|--------------------|-------|-------------------|----------------|
| Constant | -0.085 | 0.017 | -4.93 | 0.000 |
| Reproductive output | 0.011 | 0.001 | 9.21 | 0.000 |
| Match spring bloom | 0.000 | 0.000 | 2.68 | 0.015 |
| Match <i>Crangon</i> predation | -0.000 | 0.000 | -7.08 | 0.000 |
| Magnitude <i>Crangon</i> predation | 0.013 | 0.002 | 7.38 | 0.000 |
| Analysis of variance | | | | |
| Source | SS | df | MS | F |
| Regression | 10.4×10^4 | 4 | 2.6×10^4 | 32.91 |
| Residual | 1.1×10^4 | 14 | 0.1×10^4 | |
| | | | | P |
| | | | | 0.000001 |

pressure of 16 d (Table 6), narrowing the time gap between spawning and predation by 8 d.

Density-dependent mortality—The instantaneous mortality rates of juvenile *Macoma* were predominately related to height of the reproductive output (Tables 2–5), which implies that powerful density-dependent controls are operative during the pelagic and/or early benthic phase (Beukema et al. 2001; Van der Meer et al. 2001). Our results indicate that this density-dependent mortality is enhanced by the extension of the period between spawning and blooming, the shortening of the period between spawning and the peak in juvenile shrimp predation, and increase of the magnitude of the shrimp predation pressure. Based on the significant contribution of the phenological (timing) shifts of food and predation to the instantaneous mortality rate, we hypothesize

that density-dependent mortality of juvenile bivalves may act via (1) competition for food, (2) a strong behavioral (prey switching) response of predators to prey densities, or (3) the response of age and size at metamorphosis of marine bivalves to resource variability.

1. Competition for food: Food is considered to be the prime limiting factor for benthic biomass in shallow well-mixed estuarine systems (e.g., Herman et al. 1999). At the study site, a doubling in food availability (primary production and biomass of phytoplankton) at the end of the 1970s was followed by a doubling in the total zoobenthic biomass at the beginning of the 1980s (Beukema and Cadée 1997; Beukema et al. 2002). The carrying capacity of the study site for bivalve stocks and consequently for their recruitment is strongly related to the primary productivity of the system (Beukema et al. 2002).

In the surface waters at the study site, densities of marine bivalve larvae can be up to 200–300 L^{-1} (De Vooy 1999; Bos unpubl. data). At an individual clearance rate of 0.001 L d^{-1} (Sprung 1984), the proportion of water cleared by larvae can be up to 0.3 d^{-1} . Assuming that the specific growth rate of phytoplankton is 0.5 d^{-1} (Parsons et al. 1977), larvae would consume 40–60% of the total primary production. Moreover, shallow marine systems such as the western Wadden Sea (mean depth 3.3 m; Ridderinkhof et al. 1990) are not barren but inhabited by benthic filter feeders, such as cockles and mussels. Assuming population filtration rates of 1–10 $\text{m}^3 \text{m}^{-2} \text{d}^{-1}$ (Riisgård and Larsen 2000), the proportion of water cleared by the adult stocks is 0.3–3 d^{-1} . The total consumption of the bivalve community (larvae and adult stocks) would then add up to 100–600% of the total primary production. These estimates indicate that the growth and development of invertebrate larvae can be food limited under natural conditions. Recruit densities will then be determined by the height of the reproductive output, the size of the total bivalve stock, and the availability of specific food items for pelagic larvae and/or bottom-dwelling recruits.

2. Predation thresholds: The common shrimp *C. crangon* is able to feed on a suite of bottom-dwelling organisms, including polychaetes, bivalve spat, and juvenile flatfish (Oh

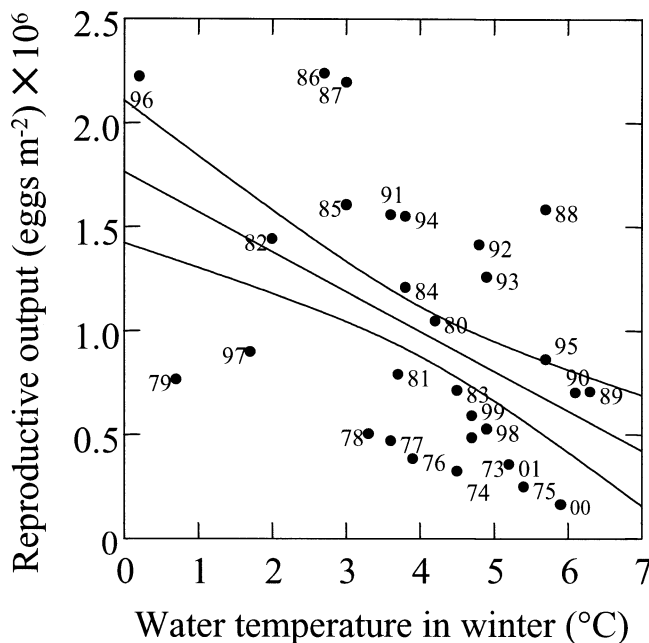
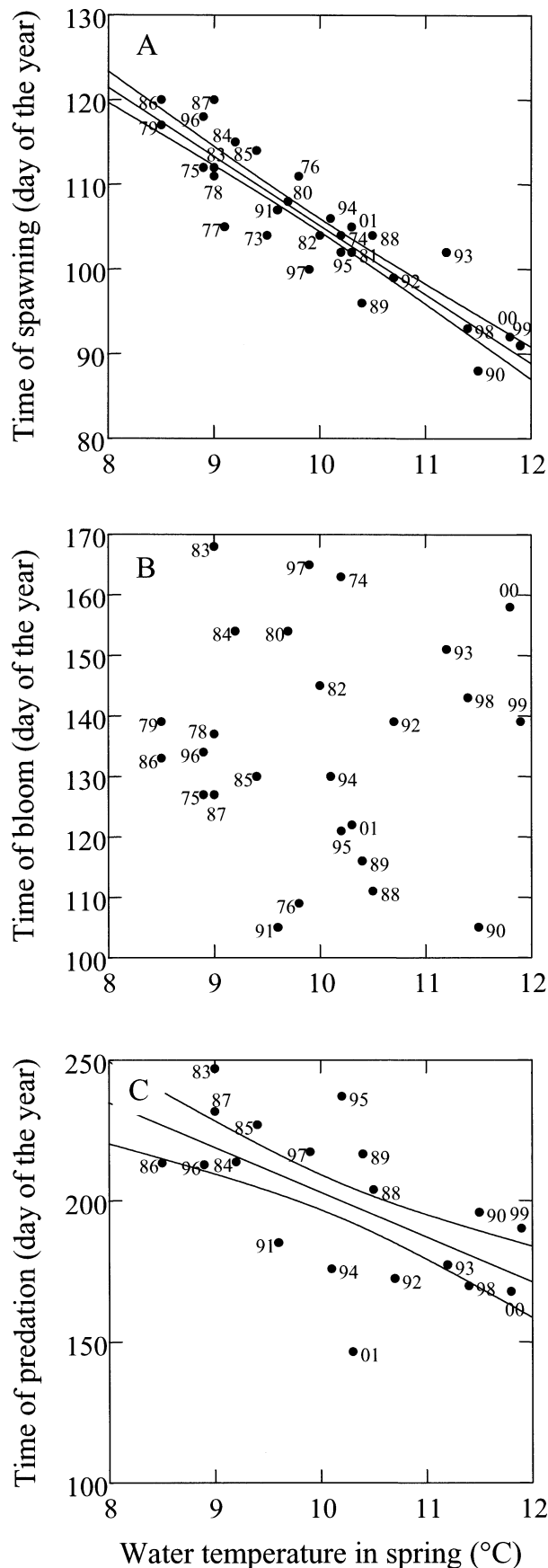


Fig. 11. Relationship between water temperature in winter ($^{\circ}\text{C}$; December–February) and reproductive output of *M. balthica* (eggs m^{-2}) in the western Wadden Sea between 1973 and 2001.



et al. 2001). Its actual diet, however, is mainly determined by the spatial and temporal availability of its prey (Ansell et al. 1999). In the Wadden Sea, predation of the common shrimp on bivalve spat is size selective (Beukema et al. 1998; Van der Veer et al. 1998; Hiddink et al. 2002). In these highly productive benthic environments, bivalve spat are relatively dense, which makes size selection cost effective (Oh et al. 2001). Shrimp predation may contribute to the observed density-dependent mortality of bivalve spat, if shrimp stop feeding when the abundance of edible bivalve spat falls below a threshold density. The threshold density of a forager that is behaving optimally should correspond to a harvest rate that just balances the metabolic costs of foraging, the predation cost of foraging, and the missed opportunity cost of not engaging in alternative activities (Brown 1988). When the threshold density is reached, the predator may then leave to find other patches with higher prey densities (e.g., tidal gullies) or shift to other prey items. If the density-dependent mortality of juvenile bivalves is determined by predation thresholds, the recruit densities in late summer would be regulated by the timing, abundance, and behavior of predatory shrimp, rather than by the height of the reproductive output of the bivalve stock.

3. Age and size at metamorphosis: One of the more conspicuous interactions between growth and early-life development of marine bivalves is the effect of growth rate on the age and size at metamorphosis. For *M. balthica*, decreased food levels reduce larval growth rate, and result in delayed metamorphosis at a smaller size (Bos and Philippart unpubl. data). Depending on the food availability, we found that the age at metamorphosis varied between 14 and 23 d, and the size of the primary settlers ranged from 228 to 287 μm . These findings are in agreement with reaction norms observed for a variety of taxa (e.g., review of Morey and Reznick 2000).

The temperature-induced mismatch between spawning and the phytoplankton bloom is assumed to effect a reduction of the food availability for the pelagic larvae, cf. the match/mismatch hypothesis (see Cushing 1990). Subsequent reduction of the growth rate of planktotrophic larvae will result in an increase of the age and a decrease of the size of the competent larvae. Metamorphosing at a later age will enhance larval mortality because the larvae are exposed longer to advection to the open sea and pelagic predation. Metamorphosing at a smaller size will enhance postlarval mortality because smaller bottom-dwelling recruits are less

←

Fig. 12. (A) Relationship between water temperature in spring (°C; April–May) and time of spawning of *M. balthica* (day of the year) in the western Wadden Sea between 1973 and 2001 ($n = 29$; $r^2 = 0.82$; $P = 0.000$). (B) Relationship between water temperature in spring (°C; April–May) and time of the peak of the phytoplankton bloom (day of the year) in the western Wadden Sea between 1973 and 2001 ($n = 26$; $r^2 = 0.00$; $P = 0.927$). (C) Relationship between water temperature in spring (°C; April–May) and time of the peak in shrimp predation pressure (day of the year) in the western Wadden Sea between 1983 and 2001 ($n = 19$; $r^2 = 0.37$; $P = 0.006$).

Table 6. Linear relationships between average water temperature in winter (°C; Dec–Feb) or spring (°C; Apr–May) and bivalve reproductive output (eggs m⁻²), time of bivalve spawning (day of the year), time of phytoplankton bloom (day of the year), and time (day of the year) and magnitude (m² m⁻²) of predation pressure by 0-group shrimp in the western Wadden Sea. Significant relationships ($P < 0.005$; corrected for multiple comparisons) are shown in bold.

| Variable | Season | <i>n</i> | Origin | Slope | <i>r</i> ² | <i>P</i> (two tail) |
|------------------------------------|--------|----------|-----------------------|-----------------------|-----------------------|---------------------|
| Reproductive output | Winter | 29 | 17.64×10 ⁵ | -1.91×10 ⁵ | 0.29 | 0.003 |
| Time <i>Macoma</i> spawning | Spring | 29 | 186.61 | -8.15 | 0.82 | 0.000 |
| Time spring bloom | Spring | 26 | 138.63 | -0.31 | 0.00 | 0.927 |
| Time <i>Crangon</i> predation | Spring | 19 | 362.13 | -15.91 | 0.37 | 0.006 |
| Magnitude <i>Crangon</i> predation | Spring | 19 | 2.08 | -0.05 | 0.01 | 0.715 |

protected against redistribution by tidal currents (Hunt and Mullineaux 2002) and predation by juvenile shrimp (e.g., Beukema et al. 1998; Hiddink et al. 2002). Recruit densities will then be determined by competition for food (reproductive output, total bivalve stock, and availability of specific food items) as well as the predation by shrimp (timing, abundance, and possibly behavior).

Reproductive strategy—The reproductive strategy of *Macoma* appears to be dedicated to fully profit from the phytoplankton bloom in spring and to escape shrimp predation in summer by means of a temperature-induced onset of spawning, cf. the settlement-timing hypothesis (Todd and Doyle 1981). In order to be able to spawn before the phytoplankton spring bloom, the gonads of *Macoma* are built up from autumn onward up to the moment of spawning (Honkoop and Van der Meer 1997; Drent pers. comm.). Recruitment can only be successful if the bivalves do not have to reallocate this energy for maintenance during winter. Furthermore, the threshold temperature must be an accurate predictor for the time of the phytoplankton bloom and the settlement of the juvenile shrimps on the tidal flats. Apparently, global warming upsets the evolved reproductive strategy of this marine bivalve to tune its reproduction to the most optimal environmental conditions for the first vulnerable life stages. Selection for a lower threshold temperature for spawning to escape shrimp predation will take the bivalve recruits further away from the peak in food availability.

Implications—Based our results and long-term observations on other marine intertidal communities (Southward et al. 1995; Sagarin et al. 1999), we expect that a cold-water species such as *Macoma* will further decline and warm-water species will take over. For example, the northwestern European shores are presently invaded by the introduced Pacific oyster *Crassostrea gigas* for which, at the time of its introduction in the 1960s, ambient water temperatures were considered too low for natural reproduction and settlement (e.g., Wehrmann et al. 2000). Lowered adult stocks of edible cold-water species such as *Macoma* may reduce the carrying capacity of the system for bivalve-eating predators such as birds (for which these oysters are hardly edible; Cadée 2001), making it more vulnerable to depletion and disturbance as the result of shellfish fisheries (e.g., Camphuysen et al. 2002; Stillman et al. 2001).

References

- ANDRÉ, C., AND R. ROSENBERG. 1991. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*. Mar. Ecol. Prog. Ser. **71**: 227–234.
- ANSELL, A. D., C. A. COMELY, AND L. ROBB. 1999. Distribution, movements and diet of macrocrustaceans on a Scottish sandy beach with particular reference to predation on juvenile fishes. Mar. Ecol. Prog. Ser. **176**: 115–130.
- BAYNE, B. L., D. L. HOLLAND, M. N. MOORE, D. M. LOWE, AND J. WIDDOWS. 1978. Further studies on the effects of stress in the adult on the eggs of *Mytilus edulis*. J. Mar. Biol. Assoc. U.K. **58**: 825–841.
- BEUKEMA, J. J. 1974. Seasonal changes in the biomass of the macrobenthos of a tidal flat area in the Dutch Wadden Sea. Neth. J. Sea Res. **8**: 94–107.
- . 1979. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: Effects of a severe winter. Neth. J. Sea Res. **13**: 203–223.
- . 1985. Zoobenthos survival during severe winters on high and low tidal flats in the Dutch Wadden Sea, p. 351–361. In J. S. Gray and M. E. Christiansen [eds.], Marine biology of polar regions and effects of stress on marine organisms. Wiley.
- . 1992a. Expected changes in the Wadden Sea benthos in a warmer world: Lessons from periods with mild winters. Neth. J. Sea Res. **30**: 73–79.
- . 1992b. Dynamics of juvenile shrimp *Crangon crangon* in a tidal-flat nursery of the Wadden Sea after mild and cold winters. Mar. Ecol. Prog. Ser. **83**: 157–165.
- , AND G. C. CADÉE. 1996. Consequences of the sudden removal of nearly all mussels and cockles from the Dutch Wadden Sea. PSZN I. Mar. Ecol. **17**: 279–289.
- , AND ———. 1997. Local differences in macrozoobenthic response to enhanced food supply caused by mild eutrophication in a Wadden Sea area: Food is only locally a limiting factor. Limnol. Oceanogr. **42**: 1424–1435.
- , G. C. CADÉE, AND R. DEKKER. 2002. Zoobenthic biomass limited by phytoplankton abundance: Evidence from parallel changes in two long-term data series in the Wadden Sea. J. Sea Res. **48**: 111–125.
- , R. DEKKER, K. ESSINK, AND H. MICHAELIS. 2001. Synchronized reproductive success of the main bivalve species in the Wadden Sea: Causes and consequences. Mar. Ecol. Progr. Ser. **211**: 143–155.
- , P. J. C. HONKOOP, AND R. DEKKER. 1998. Recruitment in *Macoma balthica* after mild and cold winters and its possible control by egg production and shrimp predation. Hydrobiologia **375–376**: 23–34.
- BROWN, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behav. Ecol. Sociobiol. **22**: 37–47.

- CADÉE, G. C. 2001. Herring gulls learn to feed on a recent invader in the Dutch Wadden Sea, the Pacific Oyster *Crassostrea gigas*. *Basteria* **65**: 33–42.
- , AND J. HEGEMAN. 2002. Phytoplankton in the Marsdiep at the end of the 20th century, 30 years monitoring biomass, primary production, and *Phaeocystis* blooms. *J. Sea Res.* **48**: 97–110.
- CAMPHUYSEN, C. J., AND OTHERS. 2002. Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: Starvation in a commercially exploited wetland of international importance. *Biol. Cons.* **106**: 303–317.
- CUSHING, D. H. 1990. Plankton production and year class strength in fish populations: An update of the match/mismatch hypothesis. *Adv. Mar. Biol.* **26**: 249–293.
- DE MONTAUDOUIN, X., I. KISIELEWSKI, G. BACHELET, AND C. DESCLAUX. 2000. A census of macroparasites in an intertidal community, Arcachon Bay, France. *Oceanol. Acta* **23**: 453–468.
- DE VOOYS, C. G. N. 1999. Numbers of larvae and primary planigrades of the mussel *Mytilus edulis* in the western Dutch Wadden Sea. *J. Sea Res.* **41**: 189–201.
- GIESE, A. C. 1959. Comparative physiology: Annual reproductive cycles of marine invertebrates. *Ann. Rev. Physiol.* **21**: 547–576.
- HERMAN, P. M. J., J. J. MIDDELBURG, J. VAN DE KOPPEL, AND C. H. R. HEIP. 1999. Ecology of estuarine macrobenthos. *Adv. Ecol. Res.* **29**: 195–240.
- HIDDINK, J. G., S. A. E. MARIJNISSEN, K. TROOST, AND W. J. WOLFF. 2002. Predation on 0-group and older year classes of the bivalve *Macoma balthica*: Interaction of size selection and intertidal distribution of epibenthic predators. *J. Exp. Mar. Biol. Ecol.* **269**: 223–248.
- HONKOOP, P. J. C., AND J. J. BEUKEMA. 1997. Loss of body mass in winter in three intertidal bivalve species: An experimental and observational study of the interacting effects between water temperature, feeding time and feeding behaviour. *J. Exp. Mar. Biol. Ecol.* **212**: 277–297.
- , AND J. VAN DER MEER. 1997. Reproductive output of *Macoma balthica* populations in relation to winter-temperature and intertidal-height mediated changes of body mass. *Mar. Ecol. Prog. Ser.* **149**: 155–162.
- , AND ———. 1998. Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea. *J. Exp. Mar. Biol. Ecol.* **220**: 227–246.
- , ———, J. J. BEUKEMA, AND D. KWAST. 1999. Reproductive investment in the intertidal bivalve *Macoma balthica*. *J. Sea Res.* **41**: 203–212.
- HUNT, H. L., AND L. S. MULLINEAUX. 2002. The roles of predation and postlarval transport in recruitment of the soft shell clam (*Mya arenaria*). *Limnol. Oceanogr.* **47**: 151–164.
- JENSEN, K. T., AND J. N. JENSEN. 1985. The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *J. Exp. Mar. Biol. Ecol.* **89**: 157–174.
- KOOIJMAN, S.A.L.M. 2000. Dynamic energy budgets in biological systems, 2nd ed. Cambridge Univ. Press.
- LUTTIKHUIZEN, P. C., J. DRENT, AND A. J. BAKER. 2003a. Disjunct distribution of highly diverged mitochondrial lineage clade and population subdivision in a marine bivalve with pelagic larval dispersal. *Mol. Ecol.* **12**: 2215–2229.
- , ———, W. VAN DELDEN, AND T. PIERSMA. 2003b. Spatially structured genetic variation in a broadcast spawning bivalve: Quantitative versus molecular traits. *J. Evol. Biol.* **16**: 260–272.
- MAC, M. J., P. A. OPLER, N. PUCKETT HAECKER, AND P. D. DORAN. 1998. Status and trends of the nation's biological resources, part I. U.S. Geological Survey.
- MOREY, S., AND D. REZNICK. 2000. A comparative analysis of plasticity in larval development of three species of spadefoot toads (Anura: Pelobatidae: Scaphiopus). *Ecology* **81**: 1736–1749.
- OH, CH.-W., R. G. HARTNOLL, AND R. D. M. NASH. 2001. Feeding ecology of the common shrimp *Crangon crangon* in Port Erin Bay, Isle of Man, Irish Sea. *Mar. Ecol. Prog. Ser.* **214**: 211–223.
- PARMESAN, C., AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
- PARSONS, T. R., M. TAKAHASHI, AND B. HARGRAVE. 1977. Biological oceanographic processes, 2nd ed. Pergamon.
- PHILIPPART, C. J. M., G. C. CADÉE, W. VAN RAAPHORST, AND R. RIEGMAN. 2000. Long-term phytoplankton-nutrient interactions in a shallow coastal sea: Algal community structure, nutrient budgets, and denitrification potential. *Limnol. Oceanogr.* **45**: 131–144.
- RAFFAELLI, D. 2000. Interactions between macro-algal mats and invertebrates in the Ythan Estuary, Aberdeenshire, Scotland. *Helgol. Mar. Res.* **54**: 71–79.
- RIDDERINKHOF, H., J. F. T. ZIMMERMAN, AND M. E. PHILIPPART. 1990. Tidal exchange between the North Sea and Dutch Wadden Sea and mixing time scales of the tidal basins. *Neth. J. Sea Res.* **25**: 331–350.
- RIISGÅRD, H. U., AND P. S. LARSEN. 2000. Comparative ecophysiology of active zoobenthic filter feeding, essence of current knowledge. *J. Sea Res.* **44**: 169–193.
- ROOT, T. L., J. T. PRICE, K. R. HALL, S. H. SCHNEIDER, C. ROSENZWEIG, AND J. A. POUNDS. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.
- SAGARIN, R., J. P. BARRY, S. E. GILMAN, AND C. H. BAXTER. 1999. Climate-related change in an intertidal community over short and long time scales. *Ecol. Monogr.* **69**: 465–490.
- SOUTHWARD, A. J., S. J. HAWKINS, AND M. T. BURROWS. 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *J. Thermal. Biol.* **20**: 127–155.
- SPRUNG, M. 1984. Physiological energetics of mussel larvae (*Mytilus edulis*). 2. Food uptake. *Mar. Ecol. Prog. Ser.* **17**: 295–305.
- STILLMAN, R. A., AND OTHERS. 2001. Predicting shorebird mortality and population size under different regimes of shellfishery management. *J. Appl. Ecol.* **38**: 857–868.
- STRASSER, M., A. HERTLEIN, AND K. REISE. 2001. Differential recruitment of bivalve species in the northern Wadden Sea after the severe winter of 1995/96 and of subsequent milder winters. *Helgol. Mar. Res.* **55**: 182–189.
- STRATHMANN, R. R. 1996. Are planktonic larvae of marine benthic invertebrates too scarce to compete within species? *Oceanol. Acta* **19**: 399–407.
- THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* **25**: 1–45.
- . 1966. Some factors influencing the recruitment and establishment of marine benthic communities. *Neth. J. Sea Res.* **3**: 267–293.
- TODD, C. D., AND R. W. DOYLE. 1981. Reproductive strategies of marine benthic invertebrates: A settlement-timing hypothesis. *Mar. Ecol. Prog. Ser.* **4**: 75–83.
- VAN AKEN, H. M. In press. 140 years of daily observations in a tidal inlet (Marsdiep). ICES Mar. Sci. Symp.
- VAN DER MEER, J., J. J. BEUKEMA, AND R. DEKKER. 2001. Long-term variability in secondary production of an intertidal bivalve

- population is primarily a matter of recruitment variability. *J. Anim. Ecol.* **70**: 159–169.
- VAN DER VEER, H. W., R. J. FELLER, A. WEBER, AND J. I. J. WITTE. 1998. Importance of predation by crustaceans upon bivalve spat in the intertidal zone of the Dutch Wadden Sea as revealed by immunological assays of gut contents. *J. Exp. Mar. Biol. Ecol.* **231**: 139–157.
- WARNER, R. R., AND R. K. COWEN. 2002. Open vs. closed marine populations—synthesis and analysis of the evidence. *Bull. Mar. Sci.* **70**: 245–396.
- WEHRMANN, A., M. HERLYN, F. BUNGENSTOCK, G. HERTWECK, AND G. MILLAT. 2000. The distribution gap is closed—first record of naturally settled Pacific oysters *Crassostrea gigas* in the East Frisian Wadden Sea, North Sea. *Senckenb. Marit.* **30**: 153–160.
- WILDERBUER, T. K., A. B. HOLLOWED, W. J. INGRAHAM, P. D. SPENCER, M. E. CONNERS, N. A. BOND, AND G. E. WALETERS. 2002. Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. *Prog. Oceanogr.* **55**: 235–247.
- WOODIN, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: Patterns of abundance. *J. Mar. Res.* **34**: 25–42.
- YOUNG, E. F., G. R. BIGG, A. GRANT, P. WALKER, AND J. BROWN. 1996. A modelling study of environmental influences on bivalve settlement in The Wash, England. *Mar. Ecol. Prog. Ser.* **172**: 197–214.
- ZWARTS, L. 1971. Seasonal variation in body weight of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden Sea. *Neth. J. Sea Res.* **28**: 231–245.

Received: 14 December 2002

Accepted: 22 July 2003

Amended: 11 August 2003