



FEATURE ARTICLE

Variability in predator abundance links winter temperatures and bivalve recruitment: correlative evidence from long-term data in a tidal flat

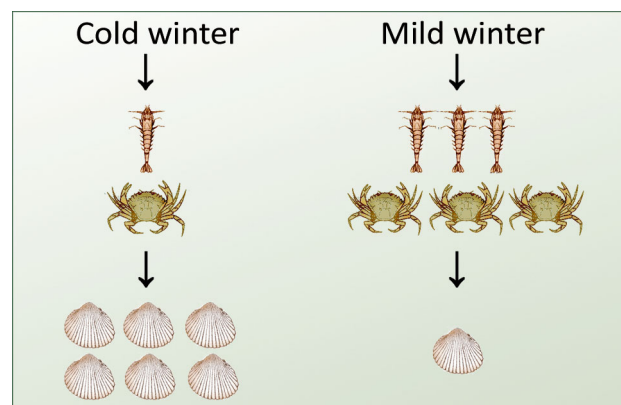
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ABSTRACT: In the Wadden Sea, annual recruitment in the major bivalve species is mostly successful in summers following severe winters, whereas it usually fails after mild winters. On the basis of a 40 yr data series, we corroborated this relationship between winter temperatures and subsequent summer abundance of recruits in 3 bivalves: *Macoma balthica*, *Cerastoderma edule*, and *Mytilus edulis*. A 30 yr data series showed that annual abundance of their main epibenthic predators (0-group shrimp *Crangon crangon* and 0- and 1-group shore crabs *Carcinus maenas*) was higher in springs after mild winters compared to cold ones. Summer recruit numbers in 4 bivalve species (the above and *Mya arenaria*) were higher when predator biomass had been lower in the preceding spring. We argue that the latter relationship was probably of a causal nature and might explain not only the relationship between winter temperatures and bivalve recruitment success, but also the observed synchronies of annual recruitment success between bivalve species and between distant parts of the Wadden Sea. Shrimp abundance in May showed a significantly increasing long-term trend that might partly explain the declining trends in recruitment success, biomass, and annual production observed in the western Wadden Sea in *M. balthica* and *M. edulis*. We conclude that top-down effects by predation on early bottom stages of bivalves strongly affect biomass and production of some of the most important members of the benthic community of the Wadden Sea, keeping this system well below its carrying capacity for bivalves in nearly all years.

KEY WORDS: *Crangon crangon* · *Carcinus maenas* · Temperature rise · Tidal flats · Wadden Sea · *Macoma balthica* · *Cerastoderma edule* · *Mytilus edulis* · *Mya arenaria*

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The positive influence of cold winters on bivalve recruitment comes from the negative effects of low winter temperatures on the spring abundance of shrimps and shore crabs. These predators prey upon the tiny just-settled bivalve spat. They leave few spat by summer when their abundance is high after mild winters.

Image: D. Mosk

INTRODUCTION

Bivalves play a key role in the functioning of coastal ecosystems: they are connected to primary producers by their high filtration capacity (Philippart et al. 2007) and to higher trophic levels by offering an indispensable food source for predators such as fishes and birds. As they do in most other coastal areas, bivalves dominate zoobenthic biomass in the Wadden Sea (Beukema 1976, Dekker 1989, 2012). Because bivalve abundance varies from year to year, the significance of their role also differs from year to year (e.g. Beukema et al. 1993, Dekker 2012). In some years, this can even lead to serious food shortages for bivalve-eating birds (Camphuysen et al.

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1996, 2002, Smit et al. 1998, Kraan et al. 2009). Such shortages appear to originate from recruitment failures leading to low stocks (Beukema 1982, 1993, Beukema & Dekker 2005). Among the processes that govern variability in biomass and production of bivalves on tidal flats of the Wadden Sea, year-to-year variation in recruitment success is of greater importance than between-year variability in either mortality later in life or growth (Van der Meer et al. 2001, Beukema et al. 2010). Infrequently occurring strong year classes usually dominate biomass and annual production for some years, whereas a succession of years with failing recruitment leads to low bivalve stocks. Therefore, the functioning of the Wadden Sea ecosystem can be understood only with a better understanding of the processes behind recruitment variation, including an identification of the main causes of recruitment failure or success in bivalves.

Year-class strength in bivalves is notoriously variable, but not entirely unordered. In several species, strong and weak cohorts were found to arise with some synchrony over the entire Wadden Sea, and favorable and unfavorable years for different species often coincided (Beukema et al. 2001). This double synchrony provides a clue as to the cause of recruitment variability in bivalves: it points to a common causal factor that is effective over extensive areas. The incidence of severe winters may be such a factor, as winter temperatures are synchronized over extensive areas (hundreds or even >1000 km; MacKenzie & Schiedeck 2007), and successful bivalve recruitments after cold winters appear to be strikingly frequent (see references in Beukema et al. 2001 and in Strasser et al. 2003). Another factor that has frequently been proposed to explain bivalve recruitment variability is predation pressure on early life stages (Reise 1985a, Beukema et al. 1998, Strasser 2002, Philippart et al. 2003, Beukema & Dekker 2005, Andresen & Van der Meer 2010, Andresen et al. 2013).

These 2 factors, viz. winter temperatures and predation pressure, are intertwined, as 2 of the most important predators on newly settled bivalves appear later in spring and are less abundant on tidal flats after a cold winter than after a mild one: the brown shrimp *Crangon crangon* (Beukema 1992b) and the shore crab *Carcinus maenas* (Beukema 1991). It is imaginable that the frequently noticed positive influence of cold winters on subsequent bivalve recruitment is exerted via a lower predation pressure on their just-settled post-larvae after such winters, caused by lower predator abundance. Another explanation might be a mismatch in the timing of abundances of epibenthic predators and early benthic life stages of

their prey, as suggested by Strasser & Günther (2001), Philippart et al. (2003), and Durant et al. (2013). However, Dekker & Beukema (2014, this volume) found little evidence for such a temporal mismatch in a Wadden Sea tidal-flat area.

In their review, Ólafsson et al. (1994) concluded that post-settlement processes play a significant role in the regulation of populations living in marine soft sediments and that recruitment limitation (by limited input of larvae to the system) may not be the dominant factor, thus stressing the importance of studying the process of predation after settlement. So far, studies underpinning the importance of predation after settlement of post-larvae were mostly of an experimental nature, either in the laboratory (e.g. Andresen & Van der Meer 2010) or at a small scale in the field (e.g. Reise 1978, 1985a,b, Peterson 1979, Andresen et al. 2013), using predator-exclusion cages. These studies produced abundant and convincing evidence for the importance of predation for survival and ultimate abundance of bivalve recruits, but they were executed only at small scales and for relatively short periods. Long-term and large-scale studies to relate variation in predation pressure on early benthic stages to variability in subsequent bivalve cohort strength appear to be scarce. Reise (1985a) already predicted that exceptionally strong year classes of bivalves could arise only in the (near-) absence of predators on their small early bottom stages. Years with substantial predation pressure resulting in small or completely failing recruitment would be the rule.

The main hypothesis of our paper concerns the prediction that year-to-year variability in predation pressure in spring by shrimps and crabs offers an explanation for (1) the year-to-year variability in bivalve recruitment success or failure on tidal flats and (2) the generally observed relationship of recruitment success with the severity of the preceding winter. Bivalve species included in the present study are the 4 most important species (in terms of biomass) in the intertidal part of the Wadden Sea (Beukema 1976): the Baltic tellin *Macoma balthica*, the cockle *Cerastoderma edule*, the blue mussel *Mytilus edulis*, and the gaper clam *Mya arenaria*. Predator species are the 2 most abundant epibenthic predators: the shrimp *Crangon crangon* and the shore crab *Carcinus maenas*. Bivalve recruitment success was assessed in August in each of 40 successive years and was related to abundance of their predators in the months that the bivalves were present on the tidal flats as recently settled tiny post-larvae. Our long-term data series now includes a 30 yr set of results of consistent sampling of these predators. Our earlier publications on the relationships between

epibenthic predation and bivalve recruitment success (Beukema et al. 1998, Beukema & Dekker 2005) dealt with shorter data series and did not yet include shore crabs or total (shrimp + crab) predator abundance.

MATERIALS AND METHODS

Data on recruitment success of the 4 selected bivalve species were obtained as part of a long-term program (started around 1970) involving twice-annual sampling of macrozoobenthos at 15 permanent sampling stations located on Balgzand, a 50 km² tidal flat area in the westernmost part of the Wadden Sea (at about 53° N, 5° E). Further details on the sampling area, the stations, and the methods can be found in Beukema & Cadée (1997). Annual recruitment was estimated beginning in 1973 as a 15-station mean of densities (n m⁻²) of 0-group (spat, summer recruits) found in late summer (nearly all summer samples were taken in August), a few months after their settlement as post-larvae on the tidal flats (see Dekker & Beukema 2014). The sieves (1 mm mesh size) that we used retained spat of a shell length of more than about 1.5 mm.

Since 1983, we have run a special sampling program for shrimp and shore crabs during the months when high numbers of just-settled bivalve post-larvae are present on the tidal flats. The program involves about twice monthly sampling from late April to at least late June at low tides at 3 intertidal stations on Balgzand. For practical reasons, these stations were chosen at nearby locations (within about 0.5 km of each other), but at different intertidal heights (from +1 dm to -4 dm, relative to mean-tide level) and with different sediments (from 2 to 10% silt content), thus covering a wide range of environmental conditions occurring in the Balgzand area. Small shrimps (up to a length of 2.5 cm), and probably also small crabs, do not migrate with the tide, being equally abundant on the tidal flats at low and high tide. Big shrimps and crabs were not considered, as they are abundant only at high tide and in small parts of the tidal flats close to the tidal channels (Janssen & Kuipers 1980). Sampling was performed at low tide, when precise samples can easily be taken by corers (at each station, 40 samples of 88 cm² each were taken on each sampling occasion). Abundance of these epibenthic predators was expressed in g ash-free dry mass (AFDM) m⁻², separately for shrimps and for 0- and 1-group shore crabs. For further details on the locations of stations and methods see Beukema (1991, 1992b).

Because annual densities of bivalve recruits observed in August covered a wide range (from close to 0 to >1000 m⁻²) and the distribution of these numbers was far from normal in all species, we applied a log₁₀ transformation of these numbers for regressions and statistical tests. To be on the safe side, we also tested using a non-parametric test, i.e. the Spearman rank correlation test that assigns equal weight to the data of all single years.

RESULTS

Variability in bivalve recruitment

During the 40 yr of annual counts, the August numbers of spat (0-group) m⁻² found on Balgzand varied strongly in all 4 species studied: *Macoma balthica* (Fig. 1a), *Cerastoderma edule* (Fig. 1b), *Mytilus edulis* (Fig. 1c), and *Mya arenaria* (Fig. 1d). In all 4 species, mean numerical densities of spat could differ by 3 orders of magnitude. Years with real recruitment failures, with at most some tens of spat m⁻², were numerous in all species. On the other hand, recruitments that were highly successful, with around 1000 spat m⁻², occurred only rarely.

In *M. balthica*, the declining long-term trend was strong and the Pearson *r* value was statistically significant. In 2 additional species (*C. edule* and *M. edulis*), the declining trends were statistically significant only when evaluated by the Spearman rank correlation test (Table 1). Other tests would easily overweight peak values, such as the 2011 figure for *C. edule* in Fig. 1b. Therefore, we considered the non-significant Pearson correlation shown in Fig. 1b as having been unduly influenced by the 1 data point for 2011. However, such extremely high values should not be omitted as outliers because they are meaningful in the present context of explaining the variability in recruitment success.

There was some synchrony in the occurrence of successful and failing years in the 4 species. For instance, the 1979 year class was large in all species, whereas the 3 years 1988, 1989, and 1990 showed failing recruitment in all 4 species. Synchrony proved to be statistically significant in all 6 pairs of between-species comparisons (Table 2).

Variability in abundance of epibenthic predators

Abundance of the main epibenthic predators on the tidal flats of the Balgzand area, viz. the shrimp *Cran-*

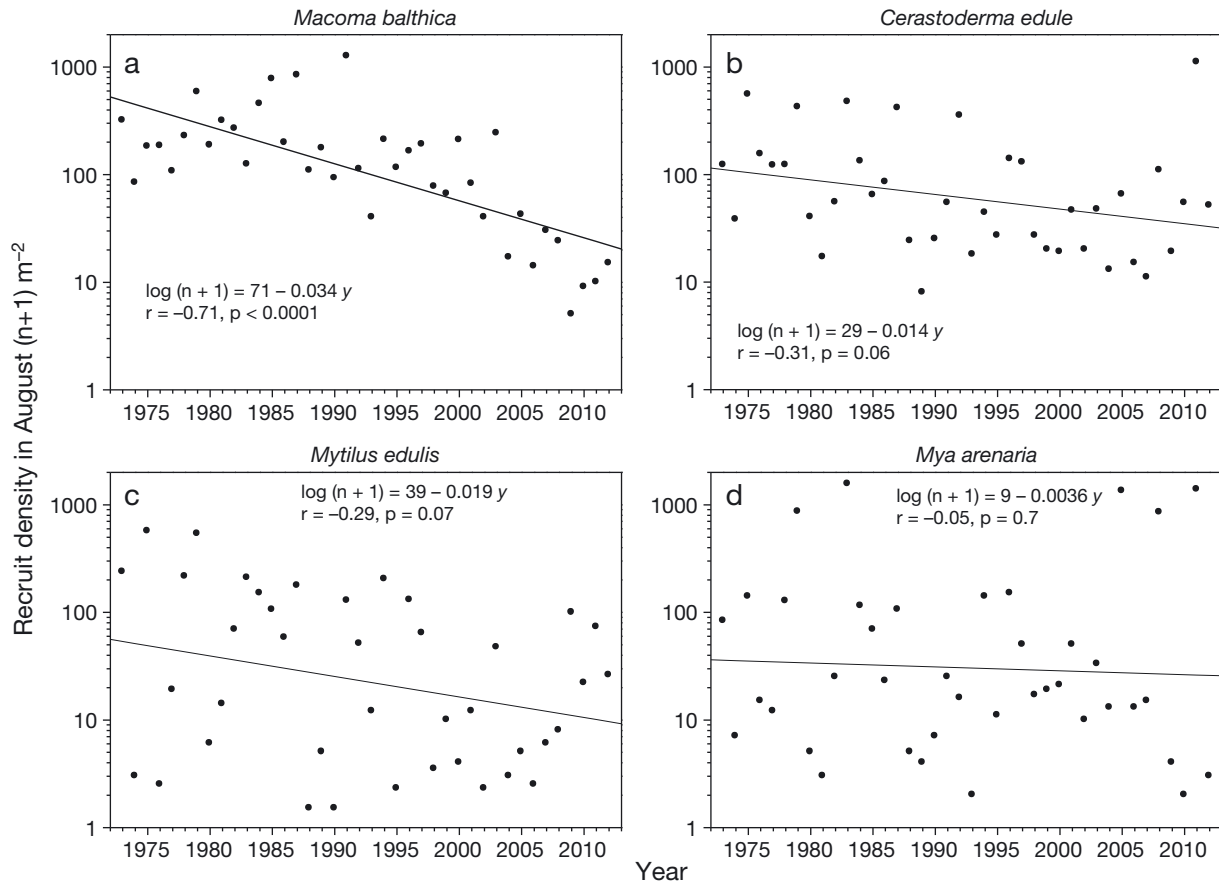


Fig. 1. Changes over a 40 yr (y) period (1973–2012) in annual recruitment (numerical densities, $n \text{ m}^{-2}$ of spat as assessed in August) on Balgzand (means of 15 sites) in 4 species of bivalves, expressed in $\log_{10}(n+1) \text{ m}^{-2}$. The lines depict best linear fits with $n = 40$. (a) *Macoma balthica*, (b) *Cerastoderma edule*, (c) *Mytilus edulis*, and (d) *Mya arenaria*

Table 1. Relationships (expressed in Spearman rank correlation coefficients) between the factors year number and temperature in the preceding winter and (top 4 lines) numerical densities of recruits in 4 bivalve species in August and (lower 7 lines) biomass of 2 predator species in the 2nd half of April (A), in May (M), and in June (J). Data are for 30 yr (1983–2012) for predator abundance and 40 yr (1973–2012) for bivalve recruitment. Winter temperatures were means of daily observations of water temperature in the 2 coldest months, January and February. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Species	Year	Winter temperature
<i>Macoma balthica</i>	-0.68***	-0.42**
<i>Cerastoderma edule</i>	-0.34*	-0.46**
<i>Mytilus edulis</i>	-0.30*	-0.58***
<i>Mya arenaria</i>	+0.12	-0.24
<i>Crangon crangon</i> (A)	+0.33	+0.64***
<i>C. crangon</i> (M)	+0.44*	+0.58**
<i>C. crangon</i> (J)	+0.02	+0.45*
<i>Carcinus maenas</i> (0-yr, J)	+0.28	+0.83***
<i>C. maenas</i> (1-yr, A)	+0.15	+0.49**
<i>C. maenas</i> (1-yr, M)	-0.07	+0.38*
<i>C. maenas</i> (1-yr, J)	+0.09	+0.34*

Table 2. Spearman rank correlation coefficients of relationships between annual spat densities ($n \text{ m}^{-2}$) of the 4 most important bivalve species on Balgzand (means of 15 sampling sites) observed in August for 40 yr (1973–2012). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

	<i>Cerastoderma edule</i>	<i>Mytilus edulis</i>	<i>Mya arenaria</i>
<i>Mytilus edulis</i>	0.67***		
<i>Mya arenaria</i>	0.70***	0.59***	
<i>Macoma balthica</i>	0.37*	0.50**	0.37*

gon crangon and the shore crab *Carcinus maenas*, was expressed in units of biomass (g AFDM m^{-2}), separately for each of the spring months April, May, and June. Both species showed substantial between-year variability in their abundance in spring (Fig. 2a,b).

Shrimps are abundantly present on the tidal flats in spring and summer, usually in densities of tens to hundreds m^{-2} (Beukema 1992b). Over the course of spring, shrimp biomass significantly (t -tests) increased, from

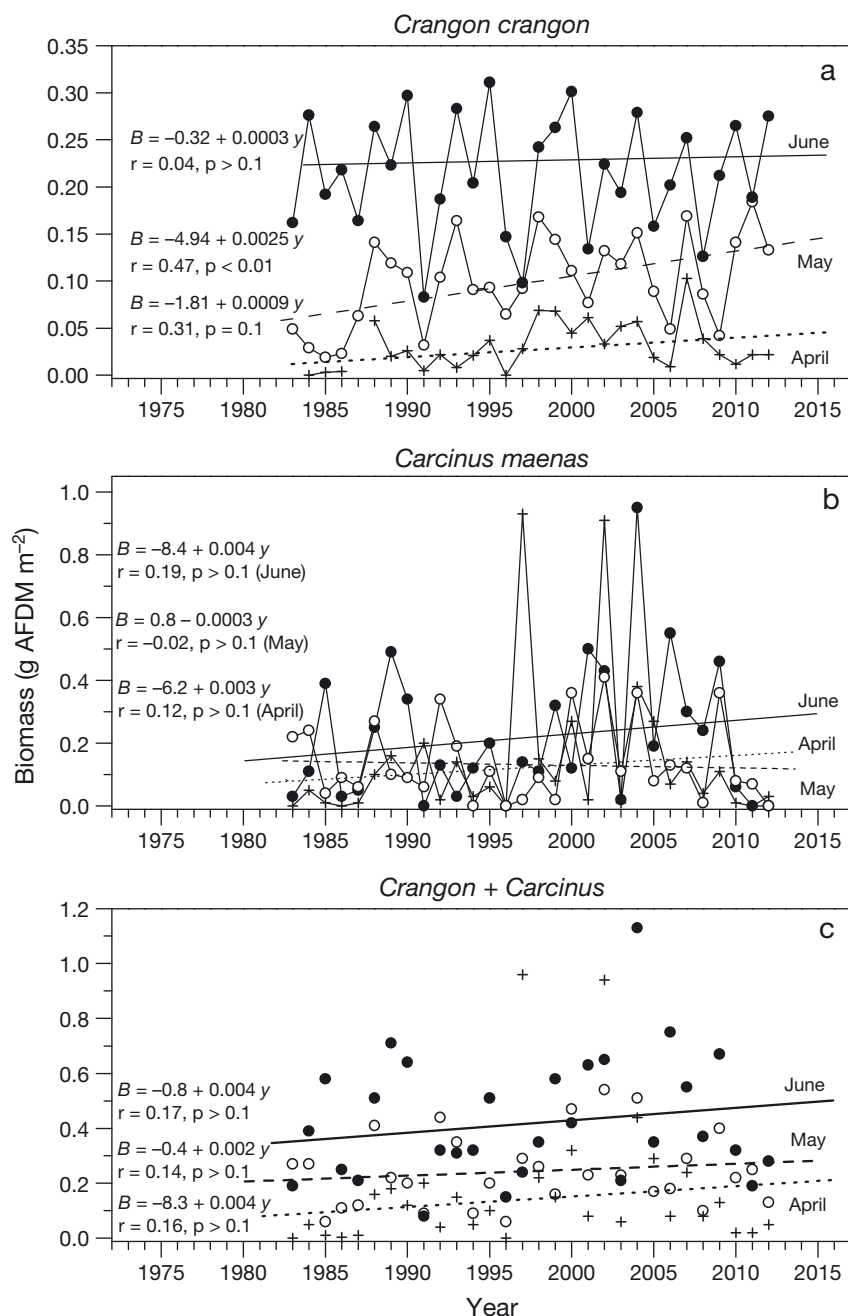


Fig. 2. Changes over a 30 yr period (1983–2012) in abundance (biomass, B) of 2 important epibenthic predator species on Balgzand (means of 3 sites), expressed in g ash-free dry mass (AFDM) m^{-2} : (a) the shrimp *Crangon crangon*, (b) the shore crab *Carcinus maenas*, and (c) totals of the 2 epibenthic predator species in the 2nd half of April (crosses), May (open circles), and June (closed circles). The lines depict best linear fits with $n = 30$ for April (dotted), May (dashed), and June (solid)

0.03 ± 0.005 g AFDM m^{-2} in the second half of April, to 0.10 ± 0.009 g AFDM m^{-2} in May and to 0.21 ± 0.011 g AFDM m^{-2} in June (30 yr means ± 1 SE). A significantly increasing long-term trend was observed only in the May values (Table 1), with roughly tripled

values in the most recent years as compared to the earliest years of observation (Fig. 2a).

Shore crab biomass on tidal flats in spring is dominated by ~1 yr olds with a carapace width of up to 2 cm (after reaching this size, they leave the tidal flats) which are mostly present at a density of only a few individuals m^{-2} (Klein Breteler 1976, Beukema 1991). Their long-term mean biomass as assessed on the tidal flats at low tide in the second half of April, in May, and in June amounted to 0.14 to 0.20 g AFDM m^{-2} . No significant differences were found between these long-term mean values, nor were any long-term trends in this species significant. Young-of-the-year (0-group) crabs were usually totally absent in April and May, arriving on the tidal flats only in late spring, usually in June. As a consequence of their small size, mean biomass of 0-group shore crabs was still low in June, with values of zero in 15 out of the 30 yr. On average, their biomass in June amounted to 0.02 ± 0.005 g AFDM m^{-2} . Only in July did numbers and individual weights of 0-group crabs increase to such an extent that their biomass could surpass that of 1-group crabs, whose numbers declined following mortality and migration away from the flats when reaching a size of about 2 cm (Beukema 1991). Total (0- + 1-group) shore crab biomass values for April, May, or June did not show significant long-term trends (Fig. 2b, Table 1), nor did the sums of shrimp and crab biomass values (Fig. 2c).

Relationships with winter temperatures

For the last 3 decades, Wadden Sea water temperatures in all seasons clearly reflected the trend of a warming climate (Van Aken 2008, 2010). During the 40 yr observation period of the present study, annual mean water temperatures (solid points in Fig. 3) significantly increased at a rate of about $0.04^{\circ}C$ yr^{-1} . The increasing

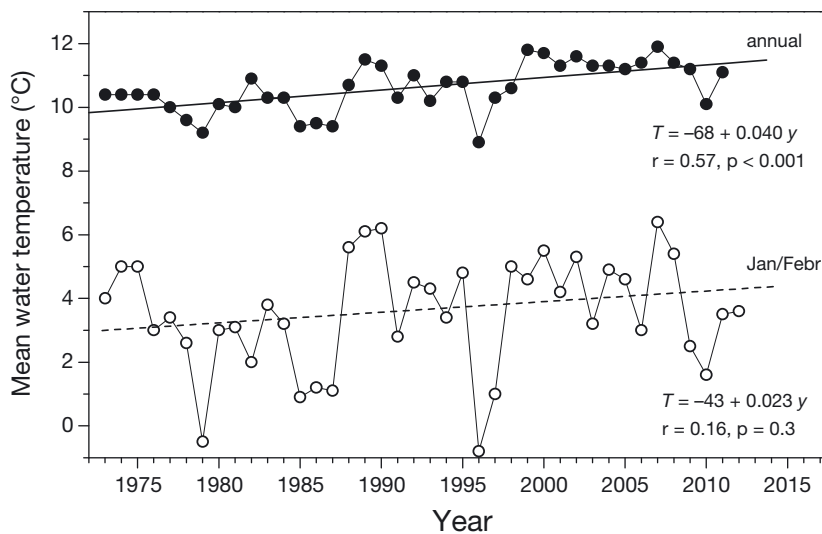


Fig. 3. Changes over a 40 yr period (1973–2012) in water temperatures (T , °C) in the Marsdiep tidal inlet (courtesy of H. van Aken, NIOZ) in winter (open points; means of January and February, the 2 coldest months) and for the entire year (solid points)

trend of the more variable winter temperatures (open points) happened to be non-significant for this 40 yr period, but is actually significant when evaluated for longer periods (Van Aken 2008).

Both in shrimps as well as in shore crabs, the biomass values observed in spring were significantly positively correlated with water temperatures in the preceding winter. Stronger correlations were found in early than in late spring in shrimps and in 1-group shore crabs (Table 1). In May and June, shrimp biomass was about twice as high after mild than after cold winters (Fig. 4a). Strongest relationships between winter temperature and biomass of epibenthic predators were found in 0-group shore crabs, which were still totally absent in June after the 8 coldest winters, but arrived at the tidal flats sometimes already by late May or (more frequently) early June after milder winters (Fig. 4b). Biomass values of older

crabs also significantly increased with water temperatures in the preceding winter when evaluated by the Spearman rank test (Table 1), although the Pearson r values for this relationship were non-significant (Fig. 4c).

In 3 out of the 4 bivalve species, recruitment success tended to be higher when preceding winters had been colder: *M. balthica* (Fig. 5a), *C. edule* (Fig. 5b), and *M. edulis* (Fig. 5c). Spearman rank tests (Table 1) as well as Pearson r values after \log_{10} transformation of bivalve recruit densities (Fig. 5a–c) showed that the negative relationships in these 3 species were significant. In *M. arenaria*, we found no significant relationship between winter temperature and recruitment success (Fig. 5d, Table 1).

Predator abundance and bivalve recruitment

In all 4 bivalve species studied, we found negative relationships between numerical densities of their recruits in August and biomass of their predators (shrimps, 0- and 1-group shore crabs, and sums of these groups) in the preceding spring months, i.e. at the time these recruits started their benthic life on the tidal flats at a very small size (Table 3). Most of the 28 correlation coefficients shown in Table 3 are statistically significant. However, not all of them are independent, because abundances of the predator groups did not vary independently between the years; all were positively correlated with preceding winter temperatures (cf. Fig. 4). Moreover, in all predator groups, biomass values for May and June were positively correlated. Thus, only 4 out of the 28

Table 3. Strength of relationships (expressed in Spearman rank correlation coefficients) between numerical densities ($n\ m^{-2}$) of recruits of 4 bivalve species found in August on Balgzand and biomass (g ash-free dry mass [AFDM] m^{-2}) of age groups of 2 predator species observed in May or June. Relationships for later months were not included, because at that time bivalve spat would have grown to sizes no longer suitable as food for the small predators. Data are for a 30 yr period (1983–2012). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Bivalve	Predators						
	Shrimps		0-yr crabs June	1-yr crabs		Shrimps + crabs	
	May	June		May	June	May	June
<i>Macoma balthica</i>	-0.54**	-0.22	-0.31	-0.16	-0.28	-0.30	-0.40*
<i>Cerastoderma edule</i>	-0.41*	-0.53**	-0.64**	-0.42*	-0.58**	-0.34	-0.73***
<i>Mytilus edulis</i>	-0.54**	-0.51*	-0.72***	-0.36*	-0.50**	-0.44*	-0.65***
<i>Mya arenaria</i>	-0.42*	-0.66***	-0.44*	-0.28	-0.25	-0.32	-0.43*

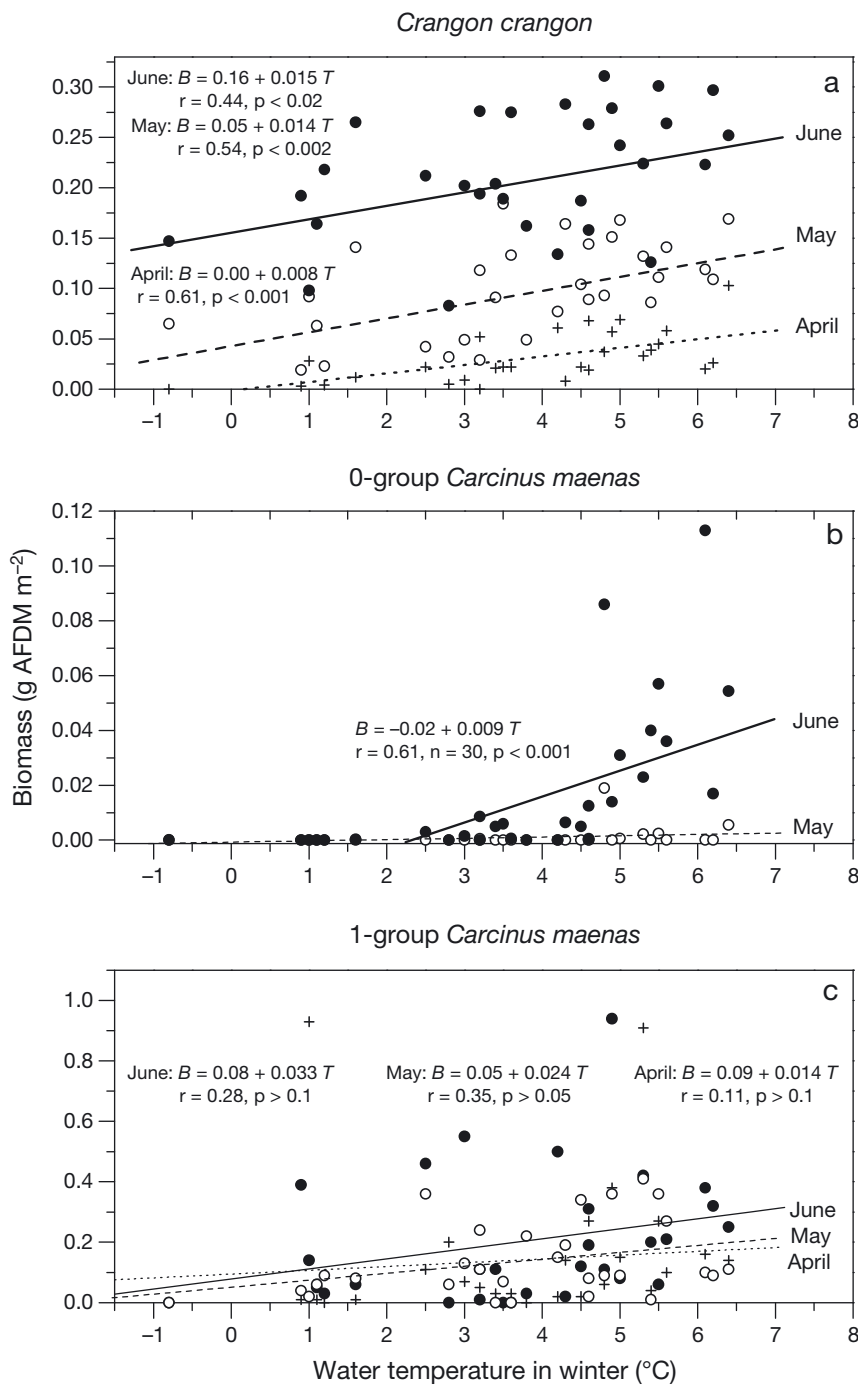


Fig. 4. Relationships between water temperatures (T) in winter (means of January and February, in °C) in the main tidal inlet and biomass (B ; in g AFDM m⁻²) of epibenthic predators in a Balgzand tidal flat area, as assessed in the 2nd half of April, in May, and in June for 30 yr (1983–2012). The lines depict best linear fits with $n = 30$ for April, May, and June. Statistical tests are on Pearson r values with $n = 30$. (a) Shrimp *Crangon crangon* biomass in April (crosses, dotted line), May (open circles, dashed line), and June (closed circles, solid line). (b) Young-of-the-year (0-group) shore crabs *Carcinus maenas* in May (open circles, dashed line) and June (closed circles, solid line). (c) ~1 yr old shore crabs in April (crosses, dotted line), May (open circles, dashed line), and June (closed circles, solid line)

correlation coefficients shown (1 for each bivalve species) can be considered as genuinely independent. In each of these 4 species, at least 1 coefficient was highly significant ($p < 0.01$ or < 0.001), others invariably showing the same sign and often also being significant (Table 3).

In *M. balthica*, recruit densities were significantly negatively correlated in particular with shrimp biomass in May and also with total predator biomass in June, but there were no significant correlations with June biomass of any of the 3 separate groups of predators (top line of Table 3). In *C. edule*, spat densities were significantly negatively correlated with biomass of shrimps as well as of 1-group shore crabs in both May and June. The correlations with predator abundance were stronger for June than for May values, and the strongest correlation was with total predator abundance in June (Table 3). In *M. edulis*, the strongest correlation was observed with abundance of 0-group shore crabs, but the data on which this correlation was based included no less than 15 (out of a total of 30 data points) zero values. Nevertheless, it remained statistically significant after a correction for equal values. As in *C. edule*, recruitment in *M. edulis* was significantly negatively correlated with biomass of shrimps as well as shore crabs in both May and June, again with a particular strong correlation with total predator abundance in June. In *M. arenaria*, recruit densities were significantly correlated with shrimp abundance in both May and June (with the strongest correlation for the latter month), but not significantly with 1-group shore crab biomass.

Separately for each of the 4 bivalve species, Fig. 6 shows the strongest (Spearman) correlation out of the above relationships, with recruit densities plotted on a log₁₀ scale. We excluded relationships with 0-group crabs when selecting relationships to be shown in Fig. 6, because of the pre-

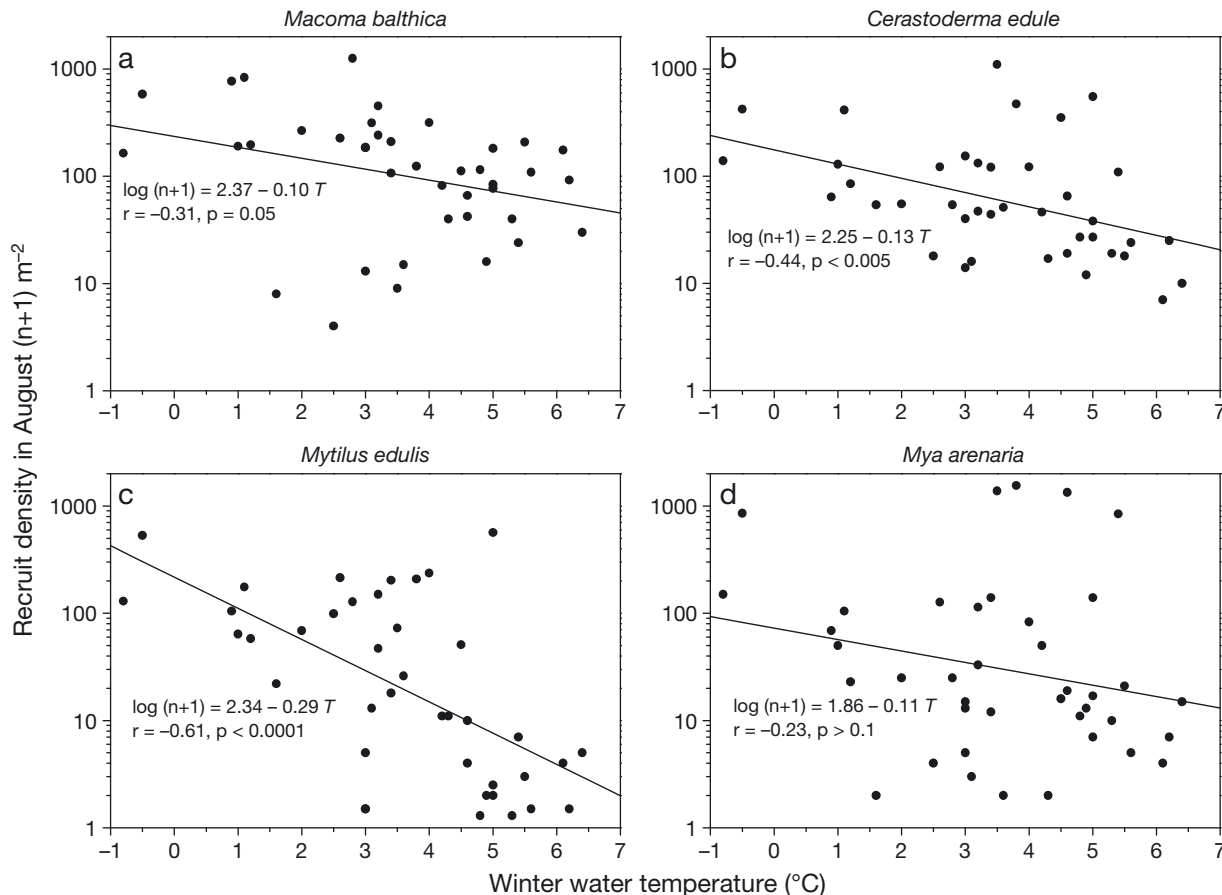


Fig. 5. Relationships between water temperatures (T) in winter (means of January and February, in $^{\circ}\text{C}$) in the main tidal inlet and recruit abundance (n), expressed as $\log_{10}(n+1)$ of spat m^{-2} , as assessed in August of the same year on Balgzand (means of 15 sites) for 40 yr (1973–2012) in 4 bivalve species. The lines depict best linear fits with $n = 40$. Statistical tests are on Pearson r values with $n = 40$. (a) *Macoma balthica*, (b) *Cerastoderma edule*, (c) *Mytilus edulis*, (d) *Mya arenaria*

ponderance of 0 or near-0 values among their biomass values in May and June (cf. Fig. 4b). The Pearson correlation coefficients shown in Fig. 6 were in all 4 cases similar to the Spearman r values shown in Table 3 and were all highly significant (at the 0.01 level or better).

In *M. balthica*, the 4 (out of a total of 30) years with the most successful recruitments ($>400 \text{ m}^{-2}$) were characterized by well below average shrimp biomass values observed in May, i.e. at most about $0.05 \text{ g AFDM m}^{-2}$ (Fig. 6a). Failing recruitments, on the other hand, occurred over a wide range of shrimp abundance. There were some outlying data points with failing recruitments at low shrimp abundance (and after relatively low winter temperatures, cf. Fig. 5a). As all of these outliers referred to years with very low adult stocks, they may have been caused by insufficient egg production (resulting in recruitment limitation) in these years. A discussion of stock-recruitment relationships, however, is outside the scope of the present paper.

In *C. edule*, recruitment success was on average >10 times higher at the lowest than at the highest epibenthic predator biomass values found in June (Fig. 6b). All successful recruitments ($>100 \text{ m}^{-2}$) were observed in years with below-average (i.e. $<0.43 \pm 0.04 \text{ g AFDM m}^{-2}$) predator abundance. The most successful recruitment ($>1000 \text{ m}^{-2}$) coincided with a 0-value for shore crab biomass in June (and a low total predator biomass, as shown in Fig. 6b). Recruitment failures (recruit densities of around 10 m^{-2}) occurred over a wide range of (mostly well above average) predator biomass.

In *M. edulis*, recruit densities were on average 2 orders of magnitude higher at the lowest than at the highest predator biomass in June (Fig. 6c). Recruitment failures as well as successes were observed over a wide range of predator abundance. Nevertheless, the best linear fit of the negative relationship shown in Fig. 6c was steep and highly significant.

In *M. arenaria*, recruit densities were significantly negatively related to shrimp biomass in June, with on

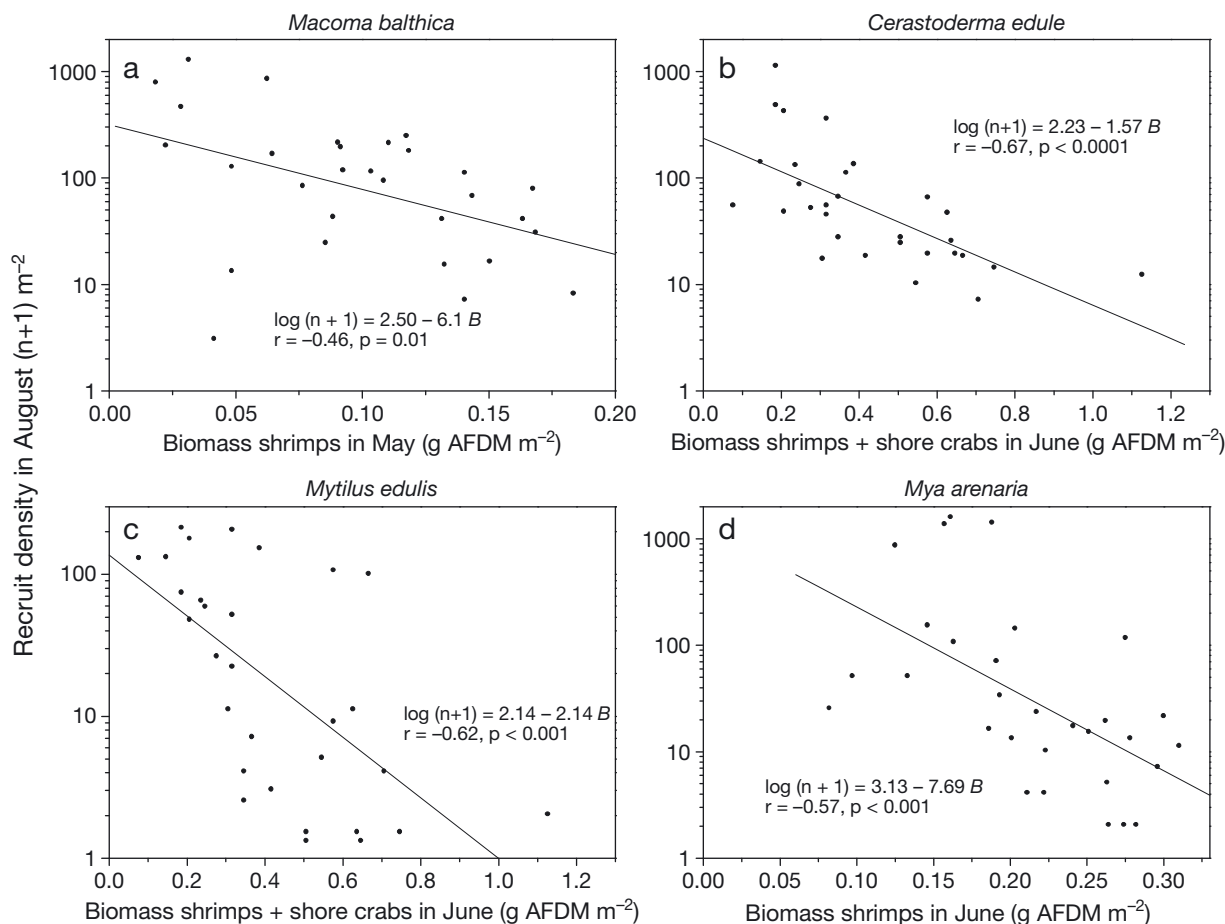


Fig. 6. Selection of relationships between biomass (B , in g ash-free dry mass [AFDM] m^{-2}) of epibenthic predators in a spring month and subsequent recruitment success (n m^{-2} , expressed as $\log_{10} [n+1]$) in 4 bivalve species in August. The solid lines depict best linear fits. Statistical tests are on Pearson r values with $n = 30$ (the years 1983 to 2012). For further statistical evaluation, cf. Table 3 for Spearman r values for the same relationships. (a) *Macoma balthica* recruitment in August and shrimp biomass in May, (b) *Cerastoderma edule* recruitment in August and total predator biomass in June, (c) *Mytilus edulis* recruitment in August and total predator biomass in June, (d) *Mya arenaria* recruitment in August and shrimp biomass in June

average about 10 times higher densities at the lowest than at the highest shrimp biomass values (Fig. 6d). Highly successful recruitments (around $1000 m^{-2}$) were restricted to years with below-average abundance of shrimps, whereas real failures ($<10 m^{-2}$) occurred only in years with above-average shrimp biomass in June.

DISCUSSION

Importance of epibenthic predation on tidal flats

The results presented in the present paper are of a correlative nature. This raises the question whether the negative relationships observed between epibenthic predator abundance and subsequent bivalve spat numbers were of a causative nature. We think

that the abundant evidence (see below) that is available from experimental studies points to the existence of a generally effective process of consumption by epibenthic predators decisively reducing bivalve spat densities, leading to recruitment failures in most years.

Decades ago, conclusive exclusion-cage experiments executed on tidal flats by Reise (1978, 1985a) provided strong arguments for the suspicion that epibenthic predators regularly reduce bivalve recruit numbers to low levels. Within cages with sufficiently small mesh to prevent the entrance of crabs and shrimps, bivalve recruit densities rose to high levels, often exceeding those of surrounding areas by no less than 1 or 2 orders of magnitude. However, when predators were allowed entrance or when they were deliberately introduced to such cages, this enhancement of densities of juvenile bivalves did not occur.

Review papers by Peterson (1979) and Reise (1985b) include numerous examples of early experiments with essentially similar results. Several more recent studies showed strong effects of predator exclusion on bivalve recruitment success as well (Mattila et al. 1990, Fernandes et al. 1999, Richards et al. 1999, Beal et al. 2001, Hiddink et al. 2002, Hunt & Mullineaux 2002, Strasser 2002, Flach 2003, Van der Heide et al. 2014), all suggesting that substantial reduction of bivalve recruitment by epibenthic predation is a generally occurring phenomenon. Results from detailed laboratory experiments (Andresen & Van der Meer 2010) strengthen the interpretation of results from cage experiments.

The most numerous epibenthic predators on Wadden Sea tidal flats are shore crabs *Carcinus maenas* and shrimps *Crangon crangon* (Jensen & Jensen 1985, Strasser 2002). These predators consume substantial numbers of bivalve spat, as revealed by immunoassays of gut contents (Van der Veer et al. 1998), by visual identification of stomach contents (Pihl & Rosenberg 1984, Pihl 1985, Hiddink et al. 2002), and by direct observations in the laboratory (Andresen & Van der Meer 2010, Whitton et al. 2012). All of the above authors judged that consumption rates and abundance of epibenthic predators could be sufficiently high to account for severe reductions in numbers of early benthic stages of bivalves in the field. However, to date, only few studies have been published that directly connect year-to-year variations in epibenthic predator abundance in the field with resulting variability in spat numbers and cohort strength in bivalves. We began using this approach in 2 of our earlier publications that deal with shrimp-abundance/bivalve-recruitment relationships (Beukema et al. 1998, Beukema & Dekker 2005).

Winter temperatures and recruitment success

Several authors noticed that bivalve recruit densities found in coastal areas in summer vary strongly from year to year and that recruitment success may be related to the temperature of the preceding winter, with the most successful recruitments occurring after the coldest winters (Möller & Rosenberg 1983, Jensen & Jensen 1985, Beukema 1992a, Beukema et al. 2001, 2009, Strasser et al. 2001a, 2003, Strasser 2002). Results of the present study corroborated the negative relationship between winter temperatures and recruit densities in the following summer for all 4 bivalve species studied, in 3 of them significantly so (Table 1). In all 4 bivalves, the 2 coldest (out of 40)

winters were invariably followed by successful recruitments of >100 spat m^{-2} in August, whereas the 3 mildest winters were followed in 3 species by failing recruitments of only about 10 spat m^{-2} (Fig. 5). These similar relationships between recruitment and winter temperature in the 4 studied species may explain why between-year variation in magnitude of recruitment was synchronized in the most important bivalve species (Table 2), pointing to a common process behind the variability in recruitment success. We hypothesize that this common process was differential predation pressure exerted on early post-larval stages of these bivalves: significantly lower abundances (and later appearances) in spring after cold than after mild winters were observed both in shrimps (Table 1, Fig. 4a; Beukema 1992b) as well as in shore crabs (Table 1, Fig. 4b,c; Beukema 1991).

Recruitment success at low and high predator abundances

In all 4 bivalve species studied, we found at least 1 (but in 2 species, several; Table 3) negative relationship between August recruit densities and predator abundance in spring that were of high statistical significance ($p < 0.01$ or 0.001). Because so many (28) correlation coefficients were calculated (Table 3) and these coefficients were not mutually independent, not much importance should be attached to correlations with a lower significance level, and in any bivalve species only 1 correlation should be considered as independent. All 3 groups of predators (shrimps and 0- and 1-group shore crabs) were involved in the strongest correlations observed.

In *Macoma balthica*, only the correlation with shrimp abundance in May was highly significant (Table 3; cf. Fig. 6a). In the other bivalve species, strong relationships were primarily observed with predator abundance in June. This difference between the bivalve species in timing of the critical period may have to do with the early seasonal maximal post-larval settlement on the tidal flats in *M. balthica*: in all years, occurring in May as compared to between late-May and late-June in the other 3 bivalve species (Dekker & Beukema 2014). The most relevant season for a study of interactions between bivalve post-larvae and their epibenthic predators will be the first month after bivalve settlement, when they are still small enough (Andresen et al. 2013) to be eaten in high numbers by all of the relatively small 0-group shrimps and shore crabs which have to be about 10 times longer than their prey (Hiddink et al. 2002). The 1-

group shore crabs also present are able to consume a wider range of prey sizes and will exert their predatory influence throughout spring and early summer.

In *Cerastoderma edule* and *Mytilus edulis*, the strongest negative relationships were found with abundance of shore crabs, both the 0- and 1-groups (Table 3). Timing of settlement in various years was studied in *C. edule* (not in *M. edulis*), and their post-larvae frequently settled so late in the season (in the course of June) that even the 0-group shore crabs may have played a role as important predators (Dekker & Beukema 2014). In *Mya arenaria*, timing of settlement was found to be intermediate (Dekker & Beukema 2014). In accordance with these differences in timing, the strongest correlation observed was with shrimp abundance in June (rather than in May as in the earlier settling *M. balthica*), whereas the role of 0-group shore crabs appeared to be smaller in *M. balthica* than in *C. edule* and *M. edulis* (Table 3).

Together, the positive relationships between winter temperatures and predator (both shrimp and shore crab) abundance in spring (Fig. 4) and the invariably negative relationships between predator abundance and bivalve recruitment success (Table 3, Fig. 6) would offer an explanation for (1) the frequently reported relationships between winter temperatures and recruitment success in these bivalves (which were corroborated in the present study: Fig. 5), (2) the synchronization of successful and failing recruitments in the 4 bivalve species (subjected to the same predators) in the same area (Table 2), and (3) the weaker (but statistically significant) synchronization of recruitment success in different parts of the Wadden Sea (Beukema et al. 2001, Strasser et al. 2003) which share winters of similar character.

Other possible processes

Some other processes may have contributed to the observed relationships between winter temperatures and bivalve recruitment success:

(1) Seasonal weight loss in Wadden Sea bivalves is generally lower in cold than in mild winters (Honkoop & Beukema 1997), and accordingly, body weight and egg production per female in spring are higher when the preceding winter has been colder (Honkoop & Van der Meer 1997, 1998). However, Strasser & Günther (2001) did not observe higher concentrations of larvae of most bivalve species in the German Wadden Sea after a cold winter, as compared to 2 milder winters. Moreover, Honkoop et al. (1998) showed that for the period 1973 to 1996, only a minor part of

the between-year variation in *M. balthica* recruitment on Balgzand could be explained by variation in egg production of the population.

(2) Larval survival from egg to metamorphosis might be higher at lower temperatures, as observed experimentally in *M. balthica* (Drent 2002). However, in any year, the mass of larvae of this species will experience similar water temperatures because the timing of their mass spawning appears to be triggered by temperature (Drent 2004).

(3) Feeding conditions for bivalve larvae might be better after cold than after mild winters. Although neither chlorophyll concentrations in spring months (made available by C. J. M. Philippart, NIOZ, Texel) nor timing of the peak of food availability were significantly correlated with water temperatures in winter (Philippart et al. 2003), food supply might nevertheless differentially affect larval growth and survival after cold and mild winters. The period during which larvae are present in the water in high numbers differs from year to year: after cold winters they appear later than after mild winters (Strasser & Günther 2001) and as a consequence, *M. balthica* larvae then feed mostly in May rather than in April. Chlorophyll *a* (chl *a*) concentrations in May after a cold winter were on average (6 years with lowest winter temperatures) slightly higher (29 ± 7 mg chl *a* m⁻³) than in April after milder winters (20 ± 2 mg). Larvae of other bivalve species that would feed more in June than in May after such cold winters, would encounter slightly lower food concentrations in June: on average 17.5 ± 3 mg compared to 23 ± 3 mg chl *a* m⁻³. Thus, after cold as compared to mild winters, there was no evidence for a consistently better match of larval presence in the water with high levels of food availability. Moreover, results of experiments showed that the effects of food limitation on survival and growth of post-larvae were inconsistent (Bos et al. 2007). Indeed, between-year variation in chl *a* concentrations in spring did not suggest any relationship with subsequent recruit densities in summer (J. J. Beukema unpubl.).

(4) Negative adult–juvenile interactions might be weaker after cold than after mild winters. In the Wadden Sea, severe winters reduce stocks of adult cockles to very low levels (Beukema 1985, Jensen 1992, Beukema et al. 1993, Strasser et al. 2001b). In these years, larval mortality as a consequence of inhalation by adults will be reduced (André et al. 1993) and settlement of post-larvae enhanced (André & Rosenberg 1991). However, André & Rosenberg (1991) found only limited effects of adult abundance on subsequent recruitment success.

Thus far, it is uncertain whether any of the above pre-settlement processes contributes decisively to recruitment variability in the studied tidal-flat bivalves. For the moment, we tend to agree with the conclusion of Ólafsson et al. (1994) that post-settlement processes (such as epibenthic predation) generally play a more important role in the regulation of bivalve populations than larval availability or quality.

Long-term trends in recruitment success

Concerns about declining benthic populations in the Wadden Sea refer in particular to species that are important as food supply for birds. In some bivalve species, declining trends have been reported for recent decades: in *M. edulis* by Nehls et al. (2006) and in *M. balthica* by Beukema et al. (2009). In the latter species, we found a highly significant declining trend in annual recruitment (Table 1, Fig. 1a) and in the former, a marginally significant negative trend (Table 1, Fig. 1c). The question arises whether these declines in stock size can rightly be ascribed to the warming climate and whether these declines were due to increasing epibenthic predation.

In the subtidal of the western Wadden Sea, both shrimps as well as shore crabs showed strongly increasing trends over the period 1970 to 2010 (Tulp et al. 2012). On the studied tidal flat, an increasing long-term trend among predators was significant only in shrimp biomass in May (Fig. 2a). Negative correlations of shrimp abundance in May with subsequent bivalve recruitment was most significant (as compared to the 2 other bivalve species) for *M. balthica* and *M. edulis* (Table 3). Moreover, these correlations were stronger than those with 1-group shore crabs (both in May and June) and those with June abundance of shrimps. Thus, shrimp abundance in May appeared to be of particular importance for summer recruitment in these 2 bivalve species, and its positive (climate-related) long-term trend may have contributed to the negative long-term trends in *M. balthica* and *M. edulis* recruitment and stock sizes.

This does not imply that effects of climate change (mediated through temperature-induced variability in epibenthic predation pressure) would be the exclusive explanation for the stock declines in the above 2 species. In *M. edulis*, fishing removed virtually all intertidal mussel banks in the western part of the Wadden Sea in 1990, and subsequent recovery in this area was very slow and incomplete, probably due to a lack of suitable substrate after the destruction of the mussel beds (Beukema & Dekker 2007,

Van der Heide et al. 2014). In *M. balthica*, adult mortality was extraordinarily high in the 7 yr from 1999 to 2006 (Beukema et al. 2009), leading to small adult stocks and probably to insufficient production of eggs and larvae to maintain the usual level of recruitment.

As the variable annual recruitment appears to be the main factor that determines subsequent biomass in bivalve populations on Wadden Sea tidal flats (Beukema et al. 2010), any consistently negative trend in recruitment success might seriously reduce production and stock size in bivalves (*M. balthica*: Van der Meer et al. 2001, Dekker & Beukema 2007; *C. edule*: Beukema & Dekker 2006; *M. edulis*: Beukema & Dekker 2007; *Ensis directus*: Dekker & Beukema 2012). A succession of a number of years with failing bivalve recruitment resulted in a period of low bivalve biomass, causing interrelated problems for fisheries and birds (Beukema & Cadée 1996). Thus, negative trends in bivalve recruitment will have far-reaching consequences.

The present global warming is manifest in sea surface temperatures, in particular in western Europe (Belkin 2009). Our results on the relationship between water temperature and abundance of shrimps and shore crabs (Fig. 4) would predict increasing levels of epibenthic predation pressure with ongoing warming of the Wadden Sea ecosystem. This might result in further long-term declines in bivalve stock sizes and annual recruitment success. The latter declines are already more or less significant in 3 out of the 4 important bivalve species we studied (Table 1, Fig. 1), warranting continuation of the present monitoring project of the macrozoobenthos in the western Wadden Sea.

Concluding remarks

In our opinion, Reise (1985a) was right in stating that the tidal-flat ecosystem and similar benthic systems are functioning in most years well below their carrying capacity (i.e. the asymptote of population size that the ecosystem can support) for bivalves as a consequence of severe predation pressure in most years on small bivalve spat by epibenthic predators. Only in exceptional conditions, when such predators are unusually scarce (for instance after a severe winter or locally within enclosures), can high proportions of early benthic stages survive and can bivalve biomass reach high levels. Under such conditions, growth rates are reduced (Jensen 1992, 1993), a clear sign that the carrying capacity of the area is approached.

Because reaching the upper limit of zoobenthic biomass appears to be a rare event and, moreover, only a weak correlation between nutrient concentrations (and primary production) and macrozoobenthic biomass was found (Philippart et al. 2007), we conclude that the results of the present paper may indicate a stronger top-down than bottom-up regulation of the benthic ecosystem of the Wadden Sea.

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