Phenology of abundance of bivalve spat and of their epibenthic predators: limited evidence for mismatches after cold winters

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ABSTRACT: Annual recruitment of bivalves in the Wadden Sea is usually more successful in summers after cold than after mild winters. The new generation (0-group) of the main predators (shrimps and shore crabs) of early benthic stages of bivalves appear later in spring on tidal flats after colder winters. If these predators were more retarded by low water temperatures than their prey, the bivalve post-larvae would profit from a head start, enabling them to outgrow most predators and generate a strong new year-class. To test this hypothesis, we present a data series on bivalve post-larval density and 0-group shrimp and shore crab biomass in April to July of 10 to 30 yr in a tidal flat of the western Wadden Sea. With lower preceding winter water temperature, post-larvae of the bivalves *Macoma balthica, Cerastoderma edule*, and *Mya arenaria* and members of 0-group shrimp *Crangon crangon* and shore crab *Carcinus maenas* arrived later in spring, but only crabs responded much stronger to water temperatures than their prey did. Among the bivalves, post-larvae of *M. balthica* were the first to arrive and *C. edule* the last. Among the 0-group predators, shrimps arrived in April/May and shore crabs in June/July. Shrimp were present simultaneously with tiny just-settled bivalve post-larvae after cold and mild winters, whereas juvenile crabs were usually too late to seriously affect the abundance of the earliest bivalve prey. For most of spring, predation by crabs was limited to prey consumption by older crabs. Late-summer recruit numbers could be predicted within 1 or 2 mo after the start of their settlement, indicating that critical interactions occurred when they were very small. We conclude that there is limited evidence for possible mismatches in timing of interactions between just-settled bivalve post-larvae and their epibenthic predators as an explanation for the generally higher recruitment success in bivalves after severe winters.

KEY WORDS: Seasonal timing · Water temperature · Tidal flats · Wadden Sea · *Macoma balthica* · *Cerastoderma edule* · *Mya arenaria* · *Crangon crangon* · *Carcinus maenas*

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INTRODUCTION

Annual recruitment in bivalve species is notoriously variable, from complete failures to highly successful years with spat densities in summer amounting to thousands per m^2. In the Wadden Sea, recruitment is a key process in the functioning of the ecosystem, as it largely determines subsequent magnitudes of biomass and annual production of the benthic system (Van der Meer et al. 2001, Beukema et al. 2010). Therefore, the functioning of the Wadden Sea ecosystem can be understood only with a better under-

standing of the processes behind recruitment variation, including an identification of the main causes of recruitment failure or success in bivalves.

Among the processes that have been put forward to explain year-to-year variability in bivalve recruitment, predation in spring on early post-settlement stages plays a dominant role (Reise 1985, Beukema et al. 1998, Philippart et al. 2003, Beukema & Dekker 2005, Andresen & Van der Meer 2010, Andresen et al. 2013). In the Wadden Sea, predation pressure in spring is strongly related to temperatures in the preceding months, as 2 of the most important predators

of newly settled bivalves appear later in spring and are initially less abundant on tidal flats after a cold than after a mild winter: the brown shrimp *Crangon crangon* (L.) (Beukema 1992) and the shore crab *Carcinus maenas* (L.) (Beukema 1991). It is therefore well imaginable that the frequently noticed positive influence of cold winters on subsequent bivalve recruitment (Beukema et al. 1998, Strasser et al. 2003, and references therein) is exerted via a lower predation pressure on early benthic stages of the bivalves after such winters. Such a winter-temperature effect would explain the observed synchrony of recruitment success over the entire Wadden Sea (Beukema et al. 2001), pointing to causal factors underlying recruitment variability that are common to several bivalve species and are effective over extensive areas.

The precise mechanism of how winter temperature affects bivalve recruitment success via differential survival of early benthic stages is still insufficiently known. It could involve (1) a lower predation pressure after colder winters by an overall lower predator abundance over most of the period of post-larvae presence (Beukema et al. 2001, Beukema & Dekker 2005), and/or (2) a temporal mismatch in the abundances of predators and their prey after cold winters (Strasser & Günther 2001, Philippart et al. 2003, Andresen 2013, Durant et al. 2013). According to the latter hypothesis, the new generations of shrimps and crabs might arrive too late in the springs after cold winters to coincide with the peak abundances of the earliest bottom stages of bivalves. The latter then have the opportunity to outgrow their predators (Reise 1985, Strasser 2002, Andresen et al. 2013). It has even been argued (Strasser & Günther 2001, Philippart et al. 2003, Andresen 2013) that the timing of prey presence relative to predator arrival (i.e. whether there is a temporal match or mismatch) may offer a better explanation for the effects of epibenthic predators on bivalve recruitment success than merely variation in overall predator abundance. We discuss the first hypothesis (effects of overall predator abundance variation) in a companion publication (Beukema & Dekker 2014, this volume).

In the present paper, we deal in particular with the second of the above hypotheses (concerning a temporal mismatch of predators and prey) by studying long-term data series gathered over several decades in spring on changes in the abundance of juveniles of 2 predator species and spat of 3 bivalve species in the same tidal flat, and relating these abundance estimates to preceding winter water temperatures. The bivalves studied were *Macoma balthica* (L.), *Cerastoderma edule* (L.), and *Mya arenaria* L.

MATERIALS AND METHODS

Study area

Around 1970, we started a long-term monitoring program involving twice-annual sampling of macrozoobenthos at 15 permanent sampling stations located on Balgzand, a 50 km^2 tidal flat area in the westernmost part of the Wadden Sea (at about 53° N, 5° E). The locations of the sampling stations are shown in Fig. 1. At these 15 stations, numerical densities of bivalve recruits were assessed each year in August as a measure of annual recruitment success. More detailed data on abundance of bivalve spat and their predators were collected by frequent sampling at 3 sites near the station indicated by B in Fig. 1. Further details on the sampling area, the sampling stations, and the methods can be found in Beukema & Cadée (1997).
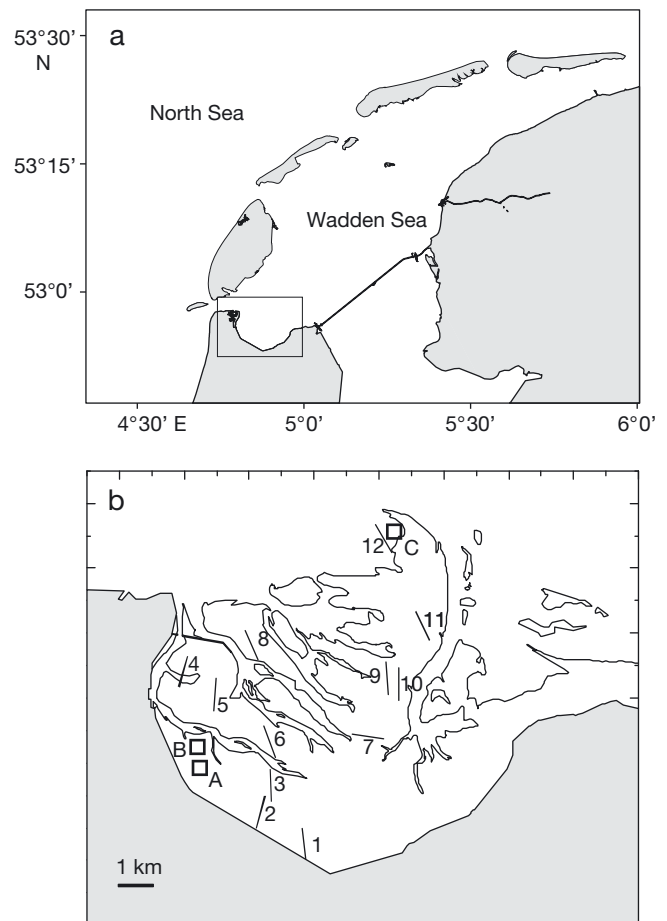

Fig. 1. (a) Westernmost part of the Wadden Sea and (b) the Balgzand tidal-flat area, showing locations of the 15 fixed sampling stations (12 line transects of 1 km and 3 squares of 900 m^2) for twice-annual monitoring of macrozoobenthos. More frequent data on abundances in spring periods of shrimps, shore crabs, and bivalve spat were collected near Stn B

Water temperatures

Temperature values were derived from daily observations of surface water temperatures from a jetty at the shore of the Marsdiep tidal inlet (the main tidal inlet of the westernmost part of the Dutch Wadden Sea) at <10 km from the Balgzand study area. Monthly data were available for all years of the study period and were summarized by Van Aken (2008). We show these data as averages for 2 mo periods in winters and springs of the study period (Fig. 2).

Predators

Since 1983, we have run a special sampling program for shrimps and shore crabs, involving about twice monthly sampling from late April to late July at low tides at 3 intertidal sites, located around sampling Stn B in Fig. 1. Small shrimps (up to a length of 2 or 2.5 cm), and probably also small crabs (of <2 cm carapace width), do not migrate with the tide, being equally abundant on the tidal flats at low and high tide (J. J. Beukema unpubl. data). Therefore, sampling can be performed at low tide, when precise samples can easily be taken by corers. Abundance of these epibenthic predator species is expressed in g ash-free dry mass (AFDM) m^{-2}. For further details on location of sampling sites and methods, see Beukema (1991, 1992).

Larger (>2 cm) 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). Although some of the 1-group shore crabs have a carapace width of <2 cm, they are ignored in the present paper, which deals only with 0-group crabs. Because of the low numbers on tidal flats of the 1-group crabs (a few individuals m^{-2}, declining in the course of spring and summer to nearly 0), it was impossible to study their phenology. They already arrive on tidal flats in late winter or early spring, long before the arrival of bivalve spat.

Bivalves

Annual recruitment is defined as numerical density (n m^{-2}) of 0-group bivalves in August, i.e. a few months after their settlement as post-larvae on the tidal flats. The 1 mm sieves that we used retained spat of a shell length of more than about 1.5 mm.

To obtain more detailed records on the course of numerical densities of spat between their initial settlement as post-larvae (at a size of ~250 µm shell length, cf. Drent 2002) in spring and Balgzand-wide recruitment assessments in August, bivalve spat populations were sampled 3 to 10 times in the May to August periods of each of 10 years (1986, 1987, 1988, 1991, 1994, 1995, 1996, 1997, 1998, 2000) around Balgzand Stn B (Fig. 1). This site is located within the area where shrimps and shore crabs were frequently sampled. The 300 µm sieves that we used retained post-larvae of a shell length of ≥0.5 mm. In some years, sampling for post-larvae began too late to obtain a proper estimate of the start of mass settlement in 1 or 2 species (i.e. high spat numbers were already observed on the first sampling occasion of that year). For this reason, we decided not to estimate the onset of settlement in 3 years (1994, 1995, 1997) for *Macoma balthica* and in 2 years (1991, 1994) for *Mya arenaria*.
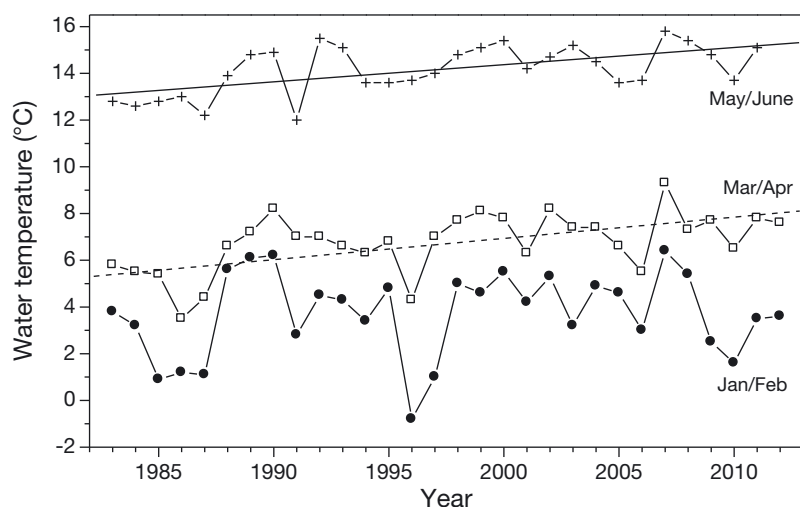

Fig. 2. Changes over a 30 yr (y) period (1983–2012) in 2 mo means of water temperatures (T, °C) in the Marsdiep tidal inlet (courtesy H. van Aken, NIOZ) in May/June (crosses), March/April (open symbols), and winter (2 coldest months: January and February; solid symbols). Significant long-term trends are indicated by best-fit lines: May/June: $T = -123 + 0.069\ y$, r = 0.56, p < 0.01; solid line) and March/April: $T = -144 + 0.075\ y$, r = 0.52, p < 0.01; dashed line)

Data analysis

To estimate the biomass values (predators) or the numerical densities (bivalve spat) at fixed dates or to estimate dates at which abundance of predators or their prey reached a cer-

tain threshold value, we applied linear interpolation from assessments on neighboring dates. If only data from 1 neighboring date were available, we either excluded that year or we made estimations by extrapolation (only if the sampling date was very close to the desired date).
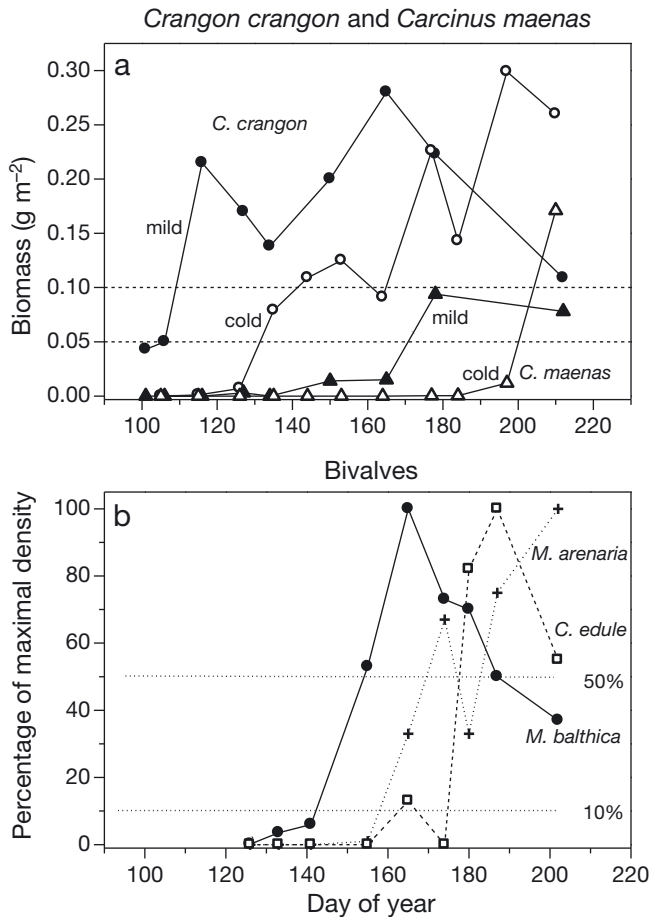

Fig. 3. Examples of how we assessed dates (day of year) at which the abundance of predators and their bivalve prey reached a certain level. (a) Biomass values of small shrimp *Crangon crangon* (circles) and 0-group shore crab *Carcinus maenas* (triangles) in spring/summer after the mildest (2007: solid symbols) and coldest (1996: open symbols) winter of the 30 yr period of observation. The date at which shrimp biomass surpassed 0.05 g m^{-2} (lower dotted horizontal line) is used as an index for the time of arrival of shrimps on the tidal flat. For 0-group shore crabs, a lower level of 0.01 g m^{-2} was used to estimate arrival time. (b) Numerical spat densities of 3 bivalve species on successive sampling dates between early May and late July 1987, expressed as a precentage of their maximal density observed in 1987. The date at which densities surpassed 10% of the maximal density (lower dotted horizontal line) is used as an index for the time of arrival of post-larvae of the species on the tidal flat. A higher criterion (e.g. 50%, upper dotted horizontal line) would allow inclusion of more years in the overall dataset, but the estimated day of year would be up to 10 to 20 d later than the actual start of settlement, which is undesirable

Examples of such a procedure are shown in Fig. 3. For instance, in shrimps *Crangon crangon*, a biomass level of 0.05 g m^{-2} was reached on day of year 106 and 132 after the mildest and coldest winter, respectively (Fig. 3a). An illustration of interpolation procedures for the timing of bivalve spat is shown in Fig. 3b. Because between-year variability in the numerical densities of spat covered a wide range in all bivalve species (from close to 0 to >1000 m^{-2}), we could not use absolute figures as fixed threshold values for between-year variability in timing of spat appearance on the tidal flat. Instead, we chose to use the dates on which the spat densities reached 10% of their maximal value in the year concerned.

The patterns of change in abundance over the course of spring shown in Fig. 3 for a few single years were typical for all years. They resemble earlier described patterns for numerical densities and biomass values after cold and mild winters in shrimps (Beukema 1992) as well as in shore crabs (Beukema 1991) and for predator densities in 1 year by Van der Veer et al. (1998). Note the common pattern of low initial values early in the season followed by steep increases until a high level is reached only a few weeks after the start of the steeply increasing phase. As an index for arrival time at the tidal flat, we chose the time when a certain low abundance level was reached to obtain a time early in the phase of steep increase (the lower horizontal lines in Fig. 3a,b). These chosen abundance levels amounted to 10% of maximal annual values in numerical densities of bivalve spat and low biomass values in the predators (0.01, 0.05, or 0.1 g AFDM m^{-2} in shrimps and 0.01 g AFDM m^{-2} in 0-group shore crabs).

For statistical tests and regressions with numerical densities of spat (which usually showed strongly skewed distributions) we used log$_{10}$-transformed data.

RESULTS

Water temperatures

In the Wadden Sea area, winters differ widely in character, resulting in substantial between-year variability in winter water temperatures. In the rare severe winters, water temperatures remain well below 0°C for prolonged periods, resulting in mean water temperatures during the 2 coldest month (January/February) of around 0°C, whereas in most winters, these mean temperatures exceed +2 or +3°C (Fig. 2). Over a >140 yr study period, Van Aken

(2008) found a particularly strong between-season correlation between water temperatures in winter and in the subsequent spring. Within the 30 yr period (1983 to 2012) of our studies, there were significantly positive relationships between water temperatures in January/February and those in March ($r = 0.75$, $p < 0.0001$), April ($r = 0.50$, $p < 0.01$), May ($r = 0.73$, $p < 0.0001$), and June ($r = 0.42$, $p < 0.05$). Thus, extreme winter temperatures were still tangible in water temperatures throughout the following spring.

In our 30 yr study period, spring (March to June) water temperatures significantly rose at a mean rate of $0.07 \pm 0.02°C$ (SE, n = 30) per year (Fig. 2). However, no statistically significant long-term trend was observed for this period in the more irregular water temperatures in winter.

Time of arrival of predators

As a criterion for the annual time of arrival of shrimps *Crangon crangon*, we chose (by interpolation, see Fig. 3a) the date at which their increasing biomass surpassed the threshold value of 0.05 g AFDM m^{-2} (being <20% of the biomass of ~0.3 g m^{-2} they would usually reach in late spring or early summer, cf. Beukema 1992). The thus estimated arrival dates varied (Fig. 4a) from Day 96 (i.e. in early April) to Day 151 (1 June), with a long-term mean of Day 122 ± 2 (early May). After cold winters, arrivals were significantly later than after mild winters: arrival times were delayed by 4.1 ± 1.1 d for each °C that the water temperature in winter (January/February) had been lower (solid symbols and line in Fig. 4a). For comparison, we added in Fig. 4a (open symbols and dashed line) the days at which shrimp biomass values surpassed a higher level of 0.10 g m^{-2} (still <35% of usual maximal amounts). This took place on average on Day 136 (mid-May), which was 3.8 ± 1.3 d later for each °C that the water temperature in winter had been lower. These 2 mean values of 4.1 and 3.8 d per °C did not significantly differ. Thus, the arbitrary choice of the criterion for arrival (0.05 g AFDM m^{-2} instead of a higher threshold) only marginally affected the outcome.

In 0-group shore crabs *Carcinus maenas*, the estimated arrival dates (for a 0.01 g AFDM m^{-2} threshold) varied strongly (Fig. 4b) from Day 127 (early May) to Day 211 (late July), with a long-term mean of Day 173 ± 3 (late June). After cold winters, arrivals were later than after mild winters: the index of arrival time was significantly delayed by 7.6 ± 1.2 d for each °C that the water temperature in winter (January/

February) had been lower (Fig. 4b). In shore crabs, responses to winter temperatures were significantly stronger (7.6 ± 1.2 versus 4.1 ± 1.1 d per °C, n = 30, $p < 0.01$, *t*-test) than in shrimps.

Time of arrival of bivalve post-larvae

The mean day of year for the index of arrival dates that we used (i.e. 10% of the maximal spat density observed in the year concerned, see Fig. 3b for procedure) amounted to Day 131 ± 4 (n = 7, early May) in
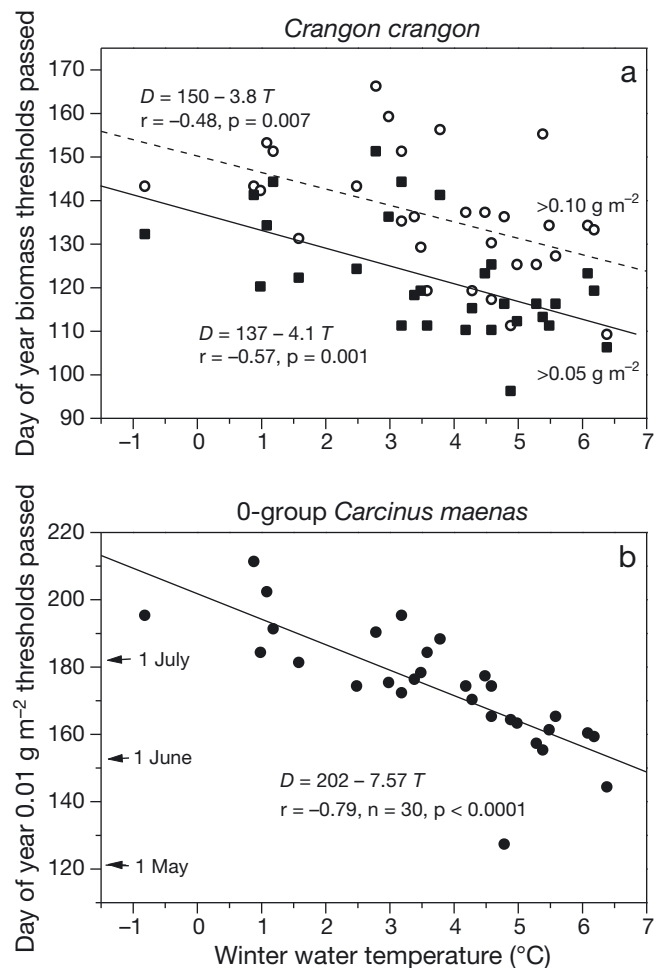

Fig. 4. Relationships between water temperatures (T, °C) in the tidal inlet in winter (means of daily values for January/February periods) and subsequent dates (as day of year, D, where $D = 1$ on 1 January) on which (a) juvenile shrimps *Crangon crangon* and (b) 0-group shore crabs *Carcinus maenas* arrived in substantial numbers at a Balgzand tidal flat. As the estimated arrival date, we used the date on which biomass of the predator reached a certain biomass level: 0.05 g ash-free dry mass (AFDM) m^{-2} (solid symbols and line in a) or 0.10 g AFDM m^{-2} (open symbols and dashed line in a) in *C. crangon* and 0.01 g AFDM m^{-2} in *C. maenas*

Macoma balthica, Day 138 ± 6 (n = 8, mid-May) in *Mya arenaria*, and Day 149 ± 5 (n = 10, late May) in *Cerastoderma edule*. In nearly all years, the post-larvae arrived on the tidal flat in the order *M. balthica / M. arenaria / C. edule*. This order is in accordance with the relatively early spawning time in *M. balthica* and late time in *C. edule* (Honkoop & Van der Meer 1998).

The above index (using 10 % of maximal abundance) was chosen arbitrarily as being sufficiently close to the date of settlement initiation. Because the 300 μm sieve used did not retain the smallest of the just-settled post-larvae, actual numbers m^{-2} at the time of sampling will have been higher than 10 % of maximal density and may be close to the date at which mass (>10 %) settlement started. The choice of a higher (e.g. 50 %, cf. Fig. 3b) criterion would have allowed inclusion of more years (i.e. fewer years when sampling began too late would have to be removed from the dataset), but the estimated day of year would be an undesirable 10 to 20 d further from the actual start of settlement (compare solid and dashed lines in Fig. 5a).

In all 3 species, the indices for arrival time indicated earlier settlement after mild than after cold winters, significantly so in *C. edule* and in 1-sided tests also in *M. arenaria* and nearly so in *M. balthica* (Fig. 5b). The use of 1-sided tests is considered sound, because any acceleration (rather than the expected retardation) of spawning or larval development after colder winters is not to be expected. Rates of retardation amounted to 4.4 ± 1.6 d (n = 10) per °C in *C. edule*, to 4.4 ± 2.2 d (n = 8) per °C in *M. arenaria* and to 2.7 ± 1.5 d (n = 7) per °C in *M. balthica.* The differences between the values for the 3 species were non-significant.

In *M. balthica* (but unfortunately not in the other bivalves), we were also able to estimate spawning time for every year, following the method described by Philippart et al. (2003), on the basis of water temperatures in early spring (see Drent 2004). The estimated day of year of the middle of the

spawning season (i.e. when water temperature reaches 8.3°C) in the 29 yr period 1983 to 2011 varied from Day 82 (i.e. in late March) to Day 120 (late April), with a long-term mean of Day 102 ± 2 (mid-April). After cold winters, spawning took place later than after mild winters: spawning occurred earlier by
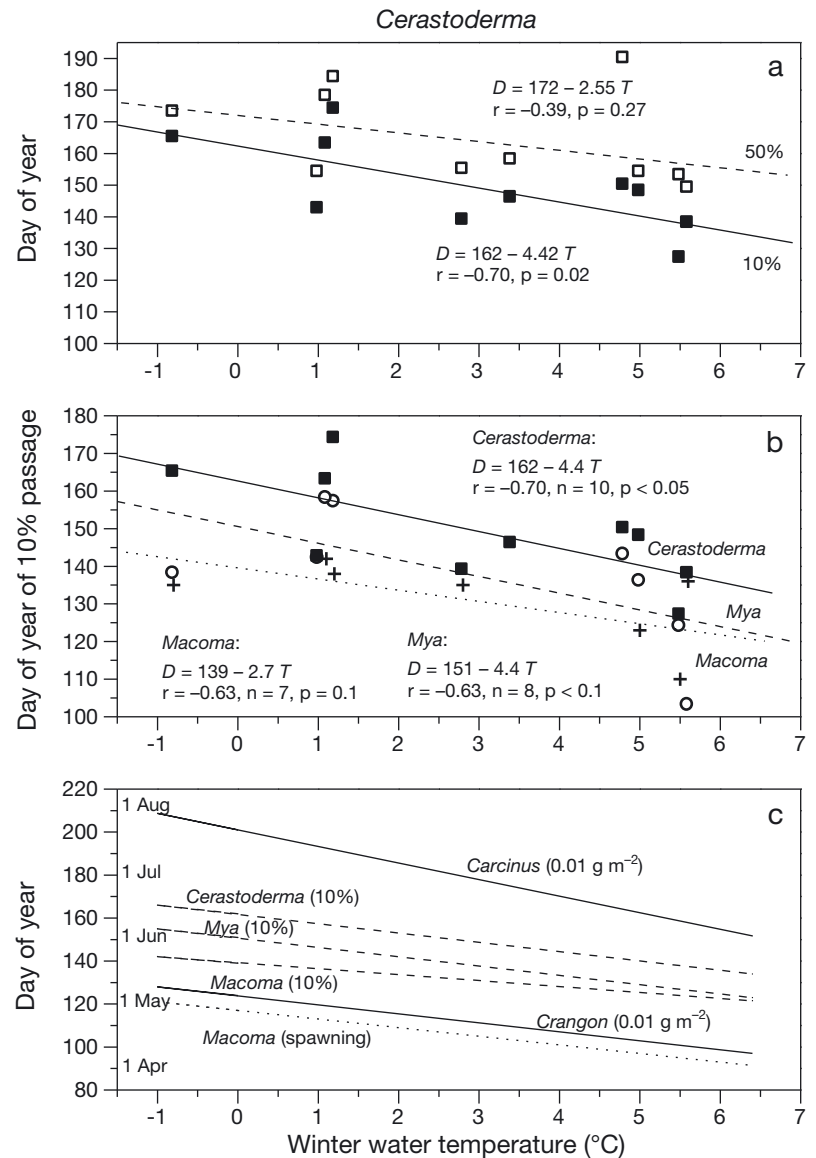

Fig. 5. Relationships between water temperatures (*T*, °C) in the tidal inlet in winter (means of daily values for January/February periods) and subsequent dates (as day of year, *D*) on which early stages of various species reached a certain abundance level. (a) Spat of *Cerastoderma edule* surpassing a level of 50 % (open symbols, dashed line) or 10 % (solid symbols and line) of their maximal numerical density in 10 yr. (b) Spat of 3 bivalve species surpassing a level of 10 % of their maximal density in 7 to 10 yr: *C. edule* (solid symbols and line, n = 10), *Mya arenaria* (open symbols, dashed line, n = 8), and *Macoma balthica* (crosses and dotted line, n = 7). (c) Summary of best fits of these relationships in epibenthic predators (solid lines) and bivalve prey (dashed and dotted lines). Only the slope for the relationship in 0-group *Carcinus* differed significantly from the other 5 slopes

4.0 ± 0.7 d for each °C that the water temperature in winter (January/February) had been higher. In comparison with the above rates of decline of settlement time with winter water temperature of 4.4 d per °C observed in the 2 other bivalve species, the value of 4.0 for *M. balthica* spawning time acceleration shows a better match than the above value of 2.7 for their index of post-larvae arrival.

The assembled estimates of decline rates (Table 1, Fig. 5c) indicate that the 3 bivalves and 1 of their predators (*C. crangon*: 4.1 ± 1.1 d per °C) showed similar responses of around 4 d per °C to differences in water temperatures in the preceding winter. Only 0-group *C. maenas* with 7.6 ± 1.2 d per °C responded significantly stronger than any of the bivalves.

Timing of establishment of bivalve cohort strength

It is to be expected that recruitment success of a species in a certain year will already reveal itself at some date before its annual assessment in August as part of our long-term sampling program. This early signal can be noted from the date in spring/early summer after which the numbers of post-larvae of a species on the tidal flats no longer change substantially, indicating that the critical (decisive) processes that determine success or failure of a cohort are over. We studied correlative relationships between (log-transformed) final recruit densities in samples taken in August of 10 years and numerical densities of post-larvae observed in these years on 15 May, 1 June,

Table 1. Summary of best fits for the relationships between water temperatures in winter (*T*, °C, January/February means) and timing of arrival on the tidal flat of epibenthic predators and their small bivalve prey (day of year, *D*: days after 1 January). Criteria for arrival: reaching a biomass level of 0.05 and 0.01 g ash-free dry mass (AFDM) m^{-2} in *Crangon crangon* and *Carcinus maenas*, respectively, and a spat density of 10% of the maximal value for the year for each of the 3 bivalve species: *Macoma balthica, Mya arenaria*, and *Cerastoderma edule.* The last column enumerates the long-term means of arrival time (day of year ± 1 SE)

	Relationship	Mean *D*
Predators		
C. crangon (all)	$D = 137 - 4.1 (\pm 1.1)\ T$	122 ± 2
C. maenas (0-group)	$D = 202 - 7.6 (\pm 1.2)\ T$	173 ± 3
Bivalves		
M. balthica (eggs)	$D = 117 - 4.0 (\pm 0.7)\ T$	102 ± 2
M. balthica (spat)	$D = 139 - 2.7 (\pm 1.5)\ T$	131 ± 4
M. arenaria (spat)	$D = 151 - 4.4 (\pm 2.2)\ T$	138 ± 4
C. edule (spat)	$D = 162 - 4.4 (\pm 1.6)\ T$	149 ± 5

15 June, 1 July, and 15 July (obtained by interpolation, cf. Fig. 3b). In *M. balthica*, we could also relate recruit densities to egg densities (kindly made available by J. Drent, who used a formula developed by Honkoop & Van der Meer 1997). We used 2 sets of August recruit densities: (1) from 1 station (B) that was situated close to the sites for post-larvae sampling (Fig. 6a) and (2) from the entire Balgzand (means of densities observed at 15 permanent stations; Fig. 6b).

In all 3 bivalve species, the Spearman coefficients (r) of such correlations indicated closer relationships as the sampling date for post-larvae densities more
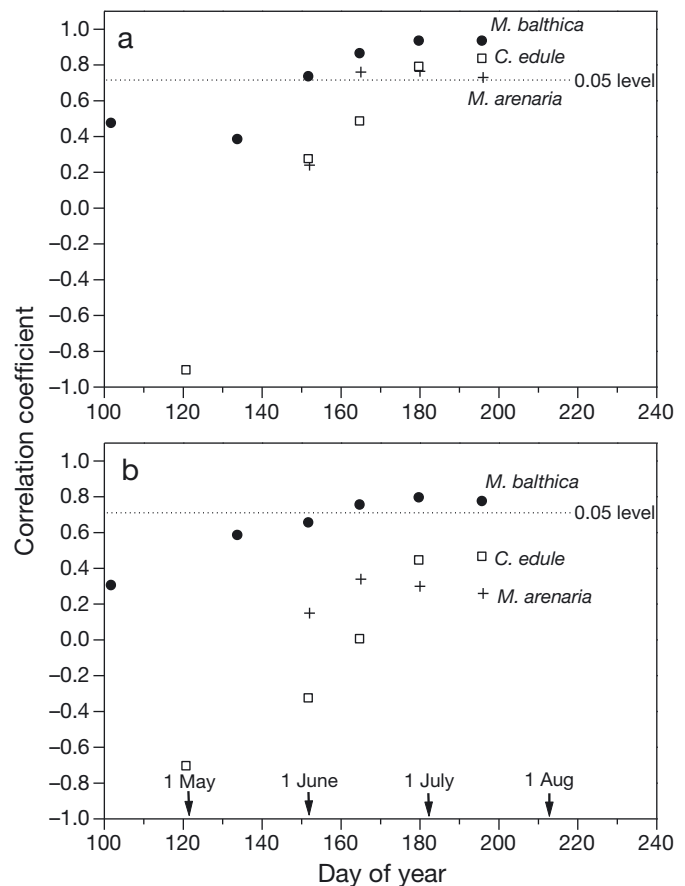

Fig. 6. Strength of relationships between log$_{10}$-transformed numerical densities of post-larvae at various dates in May/June/July periods of 10 years and ultimate log$_{10}$-transformed recruit densities in August of these years, expressed in Pearson-r values for 3 bivalve species: *Macoma balthica* (solid symbols), *Cerastoderma edule* (open symbols), and *Mya arenaria* (crosses). Values above the dotted horizontal line indicate statistically significant relationships. Correlation coefficients for relationships between recruit densities and egg densities in April (points on Days 102 and 121) were also added for *M. balthica* and *C. edule*. Correlation coefficients were calculated for data from (a) 1 station (B) close to the sampling sites for post-larvae and (b) the entire Balgzand area (means of estimates from 15 sampling stations)

closely approached the time of recruitment assessment in August (Fig. 6). Higher r values (compare Fig. 6a to Fig. 6b) were found for correlations with recruit densities at the 1 nearby station (B) than with the averages for 15 stations (which were 0 to 9 km, on average 4.6 km, away from the sampling sites for post-larvae).

In *M. balthica*, numerical densities of post-larvae were already indicative of final recruitment success around 1 June, and such predictions scarcely improved after 15 June (Fig. 6a). Early June will have been no more than about 1 mo after the start of mass settlement of post-larvae in this species, as mass spawning takes place on average in mid-April, the pelagic larval stage will last 3 to 4 wk (Drent 2002), and already in mid-May of most years, high numbers of spat could be collected with a 300 µm sieve (Fig. 5b).

Reliable predictions of final recruitment success were already possible starting from 15 June for *M. arenaria*, and from 1 July for *C. edule* (Fig. 6a). These species spawn a few weeks later than *M. balthica* and also start mass settlement a few weeks later (Fig. 5b). Note that the above species order of timing of establishment of cohort strength was identical to the order of timing of appearance of post-larvae on the tidal flat shown in Fig. 5b.

Thus, in all 3 species studied, significant correlations between the numerical densities of their post-larvae in spring and those of their recruits in August already arose within 1 or at most 1.5 mo after their mass settlements. Apparently, critical processes governing recruitment success were still in full operation during May (but only weakly so after this month) in *M. balthica*, but operated up to and including the first half of June in *M. arenaria*, and during all of June in *C. edule*.

DISCUSSION

Match/mismatch hypothesis

With the present climate change, the match/mismatch hypothesis about the timing of interactions between consumers and their food resources deserves particular attention (Durant et al. 2007, 2013). Recent rates of increase in sea surface temperatures were particularly high in the western part of Europe, amounting to about 0.05°C yr⁻¹ (Belkin 2009). According to Van Aken (2010), Wadden Sea water temperatures in all seasons reflected the recent trend of a warming climate. Differential effects of rising temperatures on phenology of predators and their

prey will not only change the match of predator requirements with resource availability, but will also be relevant for the question to what extent a resource is heavily preyed upon and whether it can maintain a high abundance (Durant et al. 2013). In the present paper, we present some relevant evidence with regard to the match/mismatch hypothesis. This hypothesis states that predators (in this case: shrimps and shore crabs) show a stronger response to elevated temperatures early in the year than their prey (early benthic stages of bivalves), resulting in early appearance on the tidal flats relative to their prey in years starting with a mild winter. Such relatively early starts of predation pressure would increase risk for tiny spat, allowing only minor proportions of the bivalve post-larvae to outgrow their predators and thus resulting in failures of bivalve recruitment.

Both in bivalve spat (Fig. 5) as well as in their main predators (Fig. 4), low temperatures in winter (and subsequent spring) retarded the time of the start of their benthic life by several days per 1°C that the preceding winter had been colder. For a mismatch to occur, it is essential that the number of delay days per 1°C lower temperatures is higher in predators than in their prey. At the Wadden Sea tidal flat, we did not observe such a difference in retardation rate between juvenile shrimps and bivalves (Table 1 and Fig. 5c: the best-fit line for *Crangon crangon* runs almost parallel to those for the various bivalve species). In contrast, the response for 0-group *Carcinus maenas* was significantly steeper than for any of the bivalves.

The stronger response of 0-group *C. maenas*, however, would not necessarily mean that resulting mismatches with the timing of their prey could play an important role in the causation of variability of recruitment success of the studied bivalve species. Members of the new generation of shore crabs arrived on the tidal flat 1 to 2 mo later than the early benthic stages of *Macoma balthica* and *Mya arenaria* did (Table 1), i.e. when these post-larvae will already have outgrown the small shore crabs and recruitment success in these 2 species is already fixed (Fig. 6). Only for the survival of the fraction of the post-larvae of these bivalves that arrive relatively late (as compared to early settlers), might 0-group shore crabs have played a role, but it was not a decisive one: the correlation coefficients shown in Fig. 6 for these 2 species hardly changed after mid-June. The situation might be different for post-larvae of *Cerastoderma edule*, whose mass arrivals generally took place only about 1 mo before those of 0-group shore crabs, and high proportions of *C. edule* post-larvae (particularly the last to arrive on the tidal flats) may have been

vulnerable to shore crabs. However, *C. edule* spat are rapid growers, and the earlier arrivers will escape predation by 0-group crabs. Predation on bivalve spat by shore crabs is not limited to prey consumption by members of the new crab generation. Low numbers of members of older age groups are present on tidal flats throughout the spring period and may cause significant mortality in bivalve post-larvae (Beukema & Dekker 2014).

The situation may be different in other areas. In the Danish Wadden Sea, Jensen & Jensen (1985) observed in July (of 1 year) more or less simultaneous peak numbers of *Cerastoderma* and *Carcinus* and substantial elimination of juvenile cockles by juvenile shore crabs. In the Dutch Wadden Sea, maximal predation pressure by 0-group shore crabs was estimated to be exerted as late as in August (Philippart et al. 2003), when most *Cerastoderma* spat will already be too big to be a suitable prey for small crabs. At that time, we found recruitment success of this bivalve in the western Dutch Wadden Sea to be already fixed (cf. Fig. 6).

We found delays in appearance after cold winters to be similar in shrimps and bivalve post-larvae (Table 1, Fig. 5c). The annual time of spawning in bivalves appears to be triggered by a temperature threshold (Drent 2004), i.e. the annual process of interaction of new bivalve generations with shrimps starts at different dates but at similar temperatures and thus similar feeding rates of the individual predators. Therefore, it will be the between-year variability in shrimp (and crab) abundance rather than timing and temperature conditions that will be decisive for the outcome of the predation process; i.e. success or failure of bivalve recruitment in any year. During the critical spring periods (roughly before Day 180, see Fig. 6), abundances of epibenthic predators tend to be higher after mild than after cold winters (shrimps: see Figs. 5 & 7 of Beukema 1992; shore crabs: see Figs. 3 & 5 of Beukema 1991). This might explain the frequently observed winter-temperature-related variability in bivalve recruitment. We report detailed data on the relationship between shrimp and shore crab abundance in spring and subsequent bivalve recruitment success in summer in a companion paper (Beukema & Dekker 2014).

Two earlier studies executed in the Wadden Sea area presented evidence in favor of an important role of mismatches in synchronic presence of bivalve spat and their epibenthic predators after cold winters. Strasser & Günther (2001) studied the abundance of larvae of shore crabs and of 5 bivalves in the spring periods of 3 years in the northern Wadden Sea. After

a cold winter (1996), they found a substantially longer delay (as compared to a moderate and a mild winter) in shore crab larvae than in bivalve larvae. Based on this finding, they stressed the importance of temporal mismatches for recruitment success in bivalves. However, these data refer to only 3 years and to pelagic stages well before the time of interactions between early benthic stages. In the 3 bivalves we studied, the delays in the larvae observed by Strasser & Günther (2001) correspond with the delays that we found in the same years in terms of time of arrival of bivalve spat on a tidal flat. In contrast, for shore crabs, we found delays that were only half as long as the 6 to 8 wk that Strasser & Günther (2001) observed in larval concentrations.

Andresen (2013) compared the timing of peak settlements on tidal flats in 6 years between shrimps, 0-group crabs, and 3 species of bivalves, using largely the same set of rough data as we did. Unfortunately, the choice in that paper (p. 69) of 'the periods of steepest abundance increase of juveniles before the maximum abundance' as the relevant period of peak settlement may have introduced a bias when used to identify the period when predator–prey interaction is most crucial. By ignoring in some years earlier peaks of predator abundance that happened to be somewhat lower than the final maximal density reached in the same year, early periods of strong interactions may have been missed in these years. For example (open circles in our Fig. 3a), the timing of maximal settlement of shrimps in 1996 was as late as Day 197 (mid-July) and this was the timing chosen by Andresen (2013). However, an earlier peak already occurred on Day 153 (early June), and the time at which shrimp biomass surpassed the 0.05 g m^{-2} level (our criterion) in that year was even earlier, around Day 132, i.e. by mid-May. Similar differences between timing estimates by Andresen (2013) and in our paper occurred in 1995, both in shrimps and shore crabs. Thus, we think that the conclusion of Andresen (2013) that in some years predators arrived much later on the tidal flats than their bivalve prey is wrong and that mismatches supposed on this basis cannot be used as evidence for a match/mismatch hypothesis to explain variability in bivalve recruitment success. We think that our definition of predator timing (viz. when their increasing abundance in spring exceeds a certain level) is less ambiguous and, particularly, more relevant than an index of maximal predator settlement. As the most intense predation occurs on the very small just-settled post-larvae (Andresen 2013, Andresen et al. 2013), substantial predator presence early in the settlement season is

more relevant than the occurrence of possible later abundance peaks. For the same reason, we think that the annual period of maximal predation pressure by 0-group shore crabs as assessed to be no earlier than August (Philippart et al. 2003) appears to provide little evidence with respect to an evaluation of the match/mismatch hypothesis.

Time of establishment of cohort strength

For a further study of the causation of variability in annual bivalve recruitment, it is crucial to know when exactly the processes take place that decisively affect whether recruitment in certain years becomes a failure or a success. We found that recruitment success in a certain year could reliably be predicted within 1 or 1.5 mo after the annual start of mass settlement of their post-larvae in spring: i.e. already around 1 June in *M. balthica*, around 15 June in *M. arenaria*, and around 1 July in *C. edule* (Fig. 6a). Processes taking place after these dates will have had only a minor influence on final recruit abundance. Decisive processes for recruitment success took place before these dates, i.e. during the stages of egg production and/or larval or early post-larval development. Because increases in the correlation coefficients for the relationships with final recruit densities were substantial exclusively in the first 1 to 1.5 mo after the start of mass settlement, the decisive process for determination of recruitment success appears to take place only during this limited period.

In *M. balthica*, egg densities in early spring were not significantly related to summer recruit densities (Fig. 6a,b: data point near Day 100). In this species, egg production is higher after cold than after mild winters (Honkoop & Van der Meer 1997, 1998). However, this did not result in substantially higher concentrations of larvae after a cold winter (Strasser & Günther 2001). Moreover, Honkoop et al. (1998) showed that for the period 1973 to 1996, only a minor part of the year-to-year variation in *M. balthica* recruitment on Balgzand could be explained by variation in estimated egg production of the population. The negative relationship found in *C. edule* between the index of egg production and recruit density (Fig. 6a,b: data point near Day 120) is in accordance with the low concentrations of larvae of this species that were found after a cold winter by Strasser & Günther (2001) and with the stock-recruitment relationship found to be negative over a wide range of annual stock sizes of this species, as already revealed long ago by Hancock (1973).

Regarding the larval stage, it is questionable whether environmental conditions for bivalve larvae are consistently better after cold than after mild winters. Water temperatures during the larval life stage will be similar in different years if spawning time is governed by temperature thresholds. Feeding conditions may be slightly better after colder winters, as chlorophyll *a* (chl *a*) concentrations in spring tend to be slightly higher after cold than after mild winters (Beukema et al. 2014). Bos et al. (2006) argued that growth of bivalve larvae in north-west European waters is often food limited. However, in laboratory experiments with *M. balthica*, Bos et al. (2007) did not observe consistent effects of food concentration on larval mortality. Moreover, chl *a* concentrations in spring (kindly made available by C. J. M. Philippart, NIOZ, Texel) did not show a significant relationship with subsequent recruit densities in summer (J. J. Beukema pers. obs.).

We conclude that it is uncertain whether any pre-settlement process 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. For a study of the influence of epibenthic predator abundance on bivalve recruitment success, the results reported in the present paper are highly relevant. Our findings suggest that for recruitment success in the 'early' species *M. balthica* and *M. arenaria*, shrimp abundance would be of particular importance, whereas 0-group shore crab abundance might play a significant role in recruitment success of *C. edule* that settle later in the season. Thus, further studies on bivalve recruitment variability may be most fruitful if the emphasis is on interactions between post-larvae of *M. balthica* and *M. arenaria* as prey and shrimp as the predator in May/June, whereas for post-larvae of *C. edule* the most relevant period is later in the season (in June/July) and both shrimps as well as 0-group shore crabs should be included.

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