Recruitment variation in *Macoma balthica*: a laboratory examination of the match/mismatch hypothesis

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ABSTRACT: Long-term observation (1973 to 2001) of recruitment in the intertidal bivalve *Macoma balthica* (L.) in the western Wadden Sea has revealed that interannual variation in recruitment may be possibly governed by match/mismatch mechanisms. Mismatch occurs when spawning takes place before or at the beginning of the spring phytoplankton bloom, whereas matching occurs when spawning takes place during the spring bloom. To test the match/mismatch hypothesis, a laboratory experiment was conducted in which 6 batches of *M. balthica* larvae were reared at different starting times during a phytoplankton spring bloom (April to May 2002). Larvae were reared in Wadden Sea seawater with the natural phytoplankton assemblage at 2 larval concentrations. As controls, larvae of the same batches were reared in filtered seawater with *Isochrysis galbana*. A clear effect of fertilisation date on larval growth and development rates was observed, which however could not be explained by phytoplankton concentration differences. In addition, no effects of fertilisation date or food level on mortality were detected. Hence, in this experiment, larval performance was affected by the timing of spawning, although the underlying mechanisms remain unclear.

KEY WORDS: Bivalve larvae · Food limitation · Development · Phytoplankton

INTRODUCTION

The match/mismatch hypothesis of Cushing (1975) states that variability in fish recruitment is caused by annual variation in temporal and/or spatial overlap between fish larvae and prey. The underlying assumptions are: (1) that spawning occurs at a fixed time with little annual variation and (2) that prey reproduction is coupled to primary production, which varies on a yearly basis due to environmental stochasticity. Therefore, a match or mismatch of the larvae with primary production would result in varying levels of starvation and subsequent survival (Cushing 1990).

The existence of such a match/mismatch of larvae and their prey has predominantly been investigated and demonstrated for commercial fish species, usually by correlating field data on prey concentrations with recruit densities (review in Cushing 1990, Fortier et al.

1995, Platt et al. 2003), or by subjecting larvae to different feeding conditions (e.g. Gotceitas et al. 1996). In contrast, little is known about the relation between larval food availability and recruitment in bivalves (review in Olson & Olson 1989), although Phillips (2002) provides evidence for negative effects of low larval food availability on age and size at metamorphosis and post-settlement growth.

Philippart et al. (2003) have shown in a correlation study that the variation in recruitment of the intertidal bivalve *Macoma balthica* in the Wadden Sea may be partly due to a match/mismatch of larvae and phytoplankton. A mismatch may occur when temperature-induced spawning (Lammens 1967) takes place before or at the start of the light-induced phytoplankton bloom (Cadée 1986), while a match occurs when spawning is induced after the start of the phytoplankton bloom.

The aim of the present study was to investigate the existence of a match/mismatch of *Macoma balthica* larvae and the phytoplankton on which they feed in the Wadden Sea, as suggested by Philippart et al. (2003). For this purpose a 2-factor experiment was used in which fertilisation date and food level were varied. The fertilisation date was varied by fertilising *M. balthica* eggs at different dates within the spawning season of the bivalve. The food level was varied by rearing the larvae in seawater taken directly from the Wadden Sea (2 levels of phytoplankton) or in filtered seawater enriched with *Isochrysis galbana* (control level). Effects on growth, development rate, and mortality of larvae were estimated. It was hypothesised that a mismatch would occur early in the season, when phytoplankton concentrations were low, while a match would occur later in the season, when algal concentrations were high. A mismatch was predicted to result in increased larval mortality, low growth rates and a restricted development.

MATERIALS AND METHODS

General methods. Mature adult *Macoma balthica* were collected from the Mok Bay (Texel, The Netherlands, 53° 00' N, 4° 45' E) in March 2002 and stored at 5°C in aerated basins (50 × 40 × 10 cm) prefilled with sandy sediment. Each basin contained about 100 individuals. To keep them in good condition, the animals were fed 3 times wk^{-1} with a mixture of concentrated algae (*Isochrysis galbana* and *Tetraselmis* sp.; Reed Mariculture). To prepare food for the *M. balthica* larvae, a continuous culture of *I. galbana* was set up in the laboratory at 15°C.

Production and maintenance of larvae. Individual *Macoma balthica* were induced to spawn in April and May 2002, and the procedure followed was that of Honkoop et al. (1999). On average, about 40% of the adults spawned. Fertilisation was carried out by pipetting eggs of several females into a beaker and adding 1 to 3 ml of sperm suspension derived from 1 or more males. The resultant mixture was left undisturbed overnight at 15°C. Fertilised eggs (diameter approximately 100 μm) were then separated from all other matter by rinsing them over stacked sieves of 120 and 50 μm. Subsequently, they were transferred into 1 l glass bottles containing filtered (1 μm) and UV-irradiated seawater (UVFS) dosed with 1.5×10^{-5} g l^{-1} Penicillin G potassium salt and 2.5×10^{-5} g l^{-1} streptomycin sulphate (Drent 2002). The bottles were placed on a roller-table (2 to 3 rpm) and maintained at 15°C. At Day 3 the majority of larvae had reached the D-stage.

Experimental set-up. The experiment consisted of 2 treatments examining: (1) the fertilisation date and (2) the food level (Table 1). The fertilisation date was varied by rearing 6 batches of larvae (A, B, C, D, E and F) at different moments in the natural spawning season of *Macoma balthica* (April to May) (Table 1). Three food levels were applied to the D-larvae (6 replicates per food level). The first food level (SW1) consisted of 50 μm filtered natural seawater, which was collected at high tide (53° 01' N, 4° 48' E). The concentration of larvae in SW1 was set at 1 larva ml^{-1}. The second food level (SW5) was identical to that of SW1, but the concentration of larvae was set at 5 larvae ml^{-1}, i.e. per capita food levels were 20% of those in SW1. The third food level (control) consisted of UVSF enriched with 5.0×10^4 cells ml^{-1} of *Isochrysis galbana*. The concentration of larvae was set at 1 larva ml^{-1}. In total, 18 different combinations of fertilisation date and food level were obtained (Table 1). To keep the larvae in suspension, the replicates (300 ml glass bottles) were placed on a roller-table (4 to 5 rpm). During the experiment, the seawater was changed 3 times wk^{-1}. Replicates were taken out of the experiment to perform growth and development measurements, after which they were preserved with 5 to 10% formalin to determine larval concentrations (see below). The temperature was kept constant at 15°C.

Larval food availability. A 20 ml sample of natural seawater was taken for phytoplankton analysis (details in Cadée 1986), each time the water was refreshed. Phytoplankton taxa with a maximum length of 20 μm were selected for further analysis, since the average larval shell length in this experiment was 192 ± 0.7 μm (mean ± SE, n = 2392) and *Macoma balthica* larvae probably only ingest food particles up to the diameter of their mouth, i.e. up to 20.5 ± 0.4 (mean ± SE, n = 15) for larvae of 184.9 ± 9.2 μm (n = 15) (J. van Iperen pers. comm.). Food availability for each batch was calculated by determining the average number of palatable phytoplankton cells ml^{-1} for the 21 d rearing period.

Table 1. Experimental set-up. For each of the 18 combinations (6 fertilisation dates × 3 food levels), the number of replicates is indicated. SW1: natural seawater, 1 larva ml^{-1}; SW5: natural seawater, 5 larvae ml^{-1}; control: filtered seawater enriched with *Isochrysis galbana* (50 000 cells ml^{-1})

Treatment 1: fertilisation date		Treatment 2: food level		
Code	Date 2002	SW1	SW5	Control
A	4 Apr	5	5	5
B	8 Apr	6	5	6
C	15 Apr	6	5	6
D	22 Apr	6	3	6
E	29 Apr	6	6	6
F	9 May	6	6	6

Growth. To obtain a time series for the determination of larval growth, shell length (15 to 25 individuals) was measured at Days 7, 10, 14, 17, 21 and 24. The growth rate ($\mu m\ d^{-1}$) was calculated from the 6 replicates with the linear model: $SL = a + b(Age - 3)$, where SL is the shell length (μm), a is the initial shell length (μm) at Day 3, b is the growth rate ($\mu m\ d^{-1}$) and Age is the age of the larvae (d).

Development. The absence or presence of a foot was scored to determine larval development status. Development was expressed as the average percentage of larvae that had developed a foot (pediveliger and competent larvae), i.e. the average percentage of all replicates per food level. When possible, average values for age and shell length of larvae that had developed a foot were calculated with the logistic regressions: $\ln[p(1-p)^{-1}] = \alpha + b\,Age$ and $\ln[p(1-p)^{-1}] = \alpha + b\,SL$, respectively.

Mortality. Larval concentrations were measured at Days 3, 7, 10, 14, 17, 21 and 24. The concentration at Day 3 was considered as the initial concentration. Estimates of mortality were obtained by fitting a regression line through the natural logarithms of the concentrations against time, according to: $\ln(N_t) = \ln(N_0) - rt$, where N_t is the larval concentration at time t (larvae ml^{-1}), N_0 is the initial concentration (larvae ml^{-1}), r is the mortality (d^{-1}) and t is the age of the larvae (d).

Data analysis. Data on larval growth, development and mortality were normalised to correct for the effect of initial larval quality, which may vary among batches due to storage effects on the adults. For this purpose, data of the control treatment were set at 100% and the data of the SW1 and SW5 treatments were expressed relative to the control treatment (%). Two-factor analysis of variance without replication (Zar 1996), referred to as 'analysis of variance' in the following sections, was used to determine the effect of fertilisation date and food level on larval growth, development and mortality.

RESULTS

Larval food availability

Analysis of the 53 phytoplankton taxa revealed only 5 taxa that were considered suitable for larval consumption: small flagellates (<10 μm), *Phaeocystis* spp. single cells (probably all *P. globosa*), large flagellates (>10 μm), *Rhodomonas* spp. and *Katodinium rotundatum*. Cells from the other taxa were not considered suitable, since they were either too large (>20 μm) or formed chains or colonies.

The concentration of small flagellates varied between 420 and 2080 cells ml^{-1} from the beginning of April until the first week of May (Fig. 1). Subsequently, an increase of up to almost 5000 cells ml^{-1} was observed, decreasing to a level of 800 cells ml^{-1} in the third week of May. The number of small flagellates accounted for 89% of the concentration of the suitable phytoplankton species in the study period, whilst *Phaeocystis* spp. single cells made up 3%, *Rhodomonas* spp. 4% and large flagellates 4% (Fig. 1).

The food availability per batch was similar for Batches A, B, C and D, ranging between 1701 and 1790 cells ml^{-1} and then increased by approximately 25% to a level of ca. 2304 cells ml^{-1} for Batches E and F
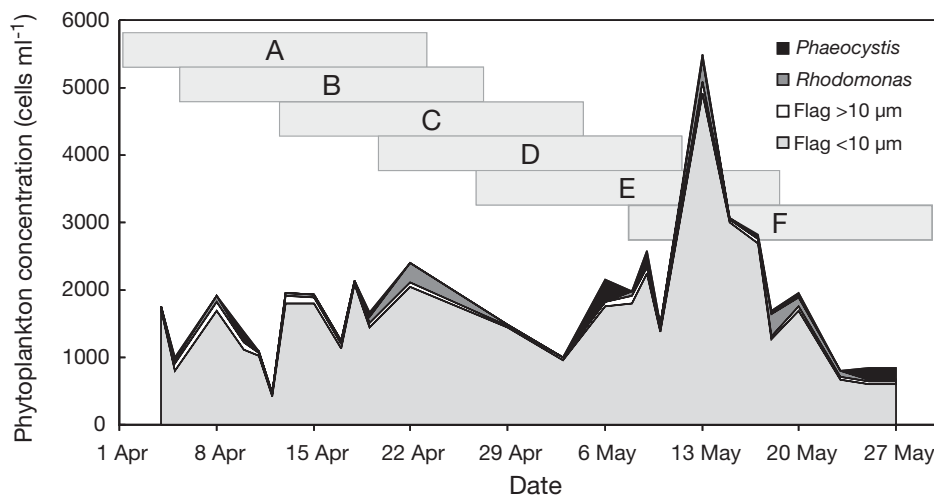

Fig. 1. Concentration of palatable phytoplankton taxa during the experimental period in the seawater used for the SW1 and SW5 food levels, including small flagellates (<10 µm), large flagellates (>10 µm), *Rhodomonas* spp. and *Phaeocystis* spp. single cells. The duration of the rearing period for each batch (A to F) of *Macoma balthica* larvae is indicated by blocks

(Fig. 2). Small flagellates dominated the total food availability. Small flagellate availability for Batches A, B, C and D ranged between 1491 and 1631 cells ml^{-1} and then increased by approximately 25% to a level of ca. 2070 cells ml^{-1} for Batches E and F. *Phaeocystis* spp. single cell concentration increased from 8 cells ml^{-1} in Batch A to 86 cells ml^{-1} in Batch F. *Rhodomonas* spp. cell concentration did not show a temporal trend, and

varied between 57 and 129 cells ml^{-1}. Large flagellates did not show a trend in concentration either, and varied between 56 and 78 cells ml^{-1} (Fig. 2).

Larval growth

The initial shell length (mean ± SE) of the D-larvae at Day 3 varied between 149 ± 1 and 159 ± 1 µm (Fig. 3). At Day 24, the shell length of larvae in the control food level varied between 221 ± 6 and 253 ± 6 µm, in the SW1 food level between 188 ± 4 and 219 ± 4 µm and in the SW5 food level between 186 ± 2 and 231 ± 5 µm (Fig. 3). On average, larvae in the control food level grew 4.8 ± 0.4 µm d^{-1}, in the SW1 food level 2.7 ± 0.4 µm d^{-1} and in the SW5 food level 2.4 ± 0.4 µm d^{-1} (Table 2, Fig. 4).

Larvae subjected to food level SW1 in early April grew at a rate of 34% of those in the control food level, while in late May, they grew at a rate of about 70% (Fig. 4). Larvae subjected to food level SW5 grew more slowly than those in SW1 (Fig. 4). Analysis of variance of the normalised growth rates revealed a strongly significant effect of the timing of fertilisation and a significant effect of food level (Table 3). When the normalised growth rates were compared with the average phytoplankton availability, no correlation could be detected (SW1: p = 0.092, r^2 = 0.43; SW5: p = 0.25, r^2 = 0.12).
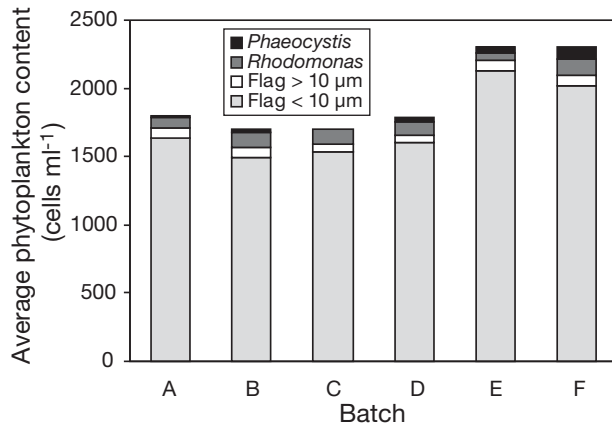

Fig. 2. Average food concentration (cells ml^{-1}) for *Macoma balthica* larvae reared in natural seawater (food levels SW1 and SW5) during the 3 wk rearing period for each of the batches (A to F), which were initiated at different times during the season. Phytoplankton species codes are the same as in Fig. 1
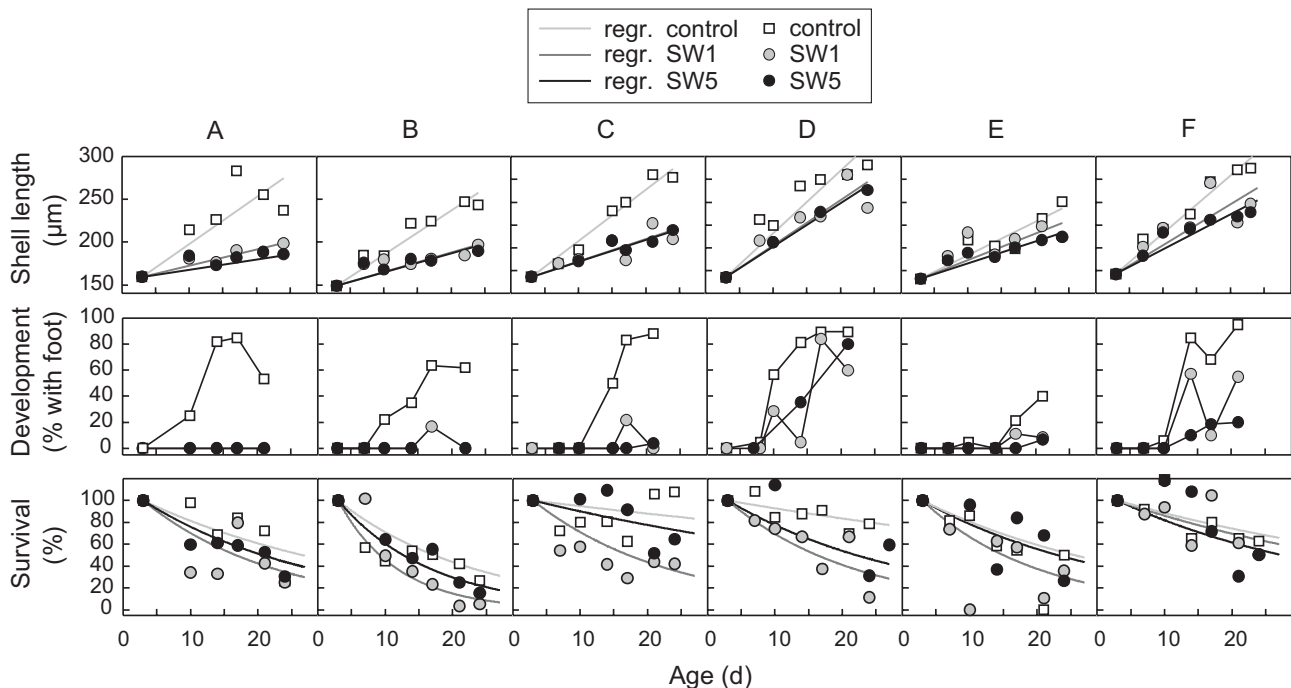

Fig. 3. *Macoma balthica* larvae. Shell length (µm; average of 15 to 25 individual larvae replicate^{-1}), development (% of larvae replicate^{-1} that have developed a foot) and survival (% of initial number of larvae replicate^{-1} that have survived), with regression lines showing growth (µm d^{-1}) and mortality (d^{-1}) for larval Batches A to F, which were initiated at different times during the season

Table 2. *Macoma balthica* larvae. Growth rate (µm d^{-1}), development, expressed as average percentage of larvae that have developed a foot (%), and mortality (d^{-1}). Normalised data expressed as percentage of control treatment. **Bold** values: means ± SE

| Code	Batch Start	End	Growth (µm d^{-1}) SW1	SW5	Control	Development (%) SW1	SW5	Control	Mortality (d^{-1}) SW1	SW5	Control
Original data											
A	4 Apr	25 Apr	1.9	1.5	5.5	0.00	0.00	40.86	0.050	0.039	0.029
B	8 Apr	29 Apr	2.3	2.2	5.2	2.38	0.00	26.11	0.112	0.071	0.049
C	15 Apr	6 May	2.0	1.9	4.5	3.11	0.64	31.62	0.049	0.015	0.008
D	22 Apr	13 May	4.0	3.8	5.5	25.30	28.82	45.89	0.052	0.036	0.011
E	29 Apr	20 May	2.3	1.9	3.0	2.78	0.95	9.42	0.058	0.035	0.031
F	9 May	30 May	3.6	3.1	5.1	17.45	6.93	36.29	0.021	0.028	0.017
Mean			**2.7**	**2.4**	**4.8**	**8.5**	**6.2**	**31.7**	**0.057**	**0.037**	**0.024**
SE			**0.4**	**0.4**	**0.4**	**4.2**	**4.6**	**5.3**	**0.012**	**0.008**	**0.006**
Normalized data											
A	4 Apr	25 Apr	34	28	100	0	0	100	172	134	100
B	8 Apr	29 Apr	44	43	100	9	0	100	230	147	100
C	15 Apr	6 May	43	43	100	10	2	100	649	198	100
D	22 Apr	13 May	73	70	100	55	63	100	495	343	100
E	29 Apr	20 May	79	65	100	29	10	100	188	113	100
F	9 May	30 May	71	61	100	48	19	100	122	163	100
Mean			**56**	**51**	**100**	**27**	**20**	**100**	**237**	**156**	**100**
SE			**8**	**7**	**–**	**13**	**15**	**–**	**50**	**32**	**–**
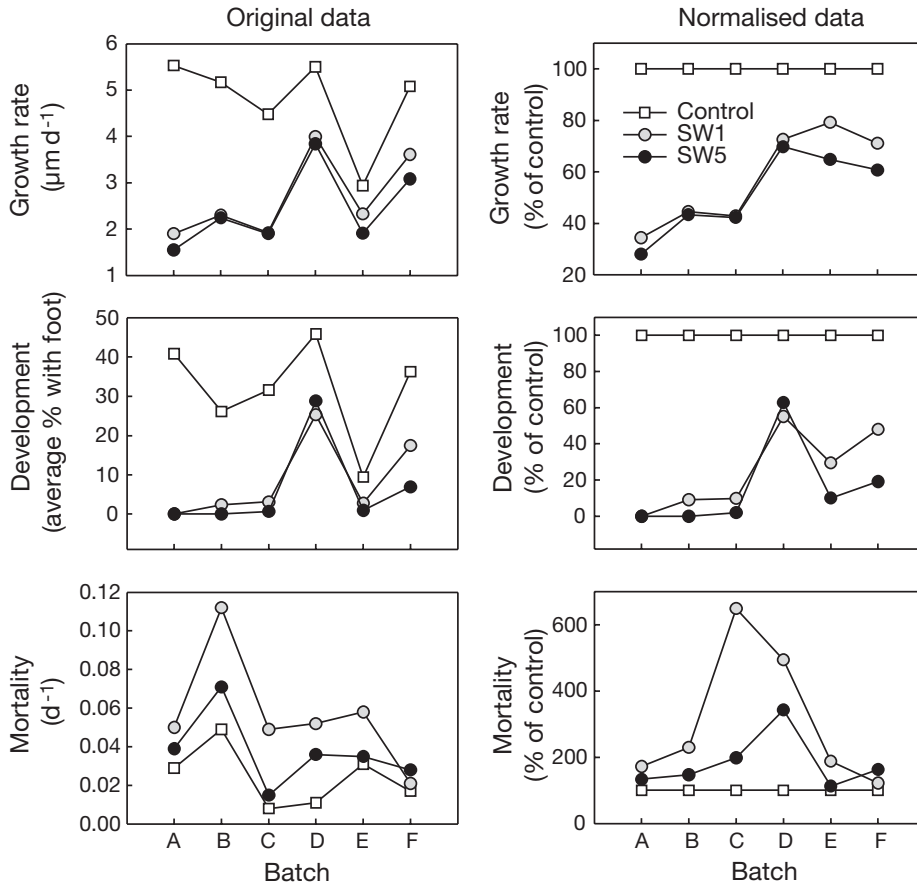
Fig. 4. *Macoma balthica* larvae. Growth, development and mortality of larvae reared on natural phytoplankton assemblages at 6 different times during the reproductive season. Left panels: growth rate (µm d^{-1}), development rate (% of larvae that have developed a foot; average of 5 replicates) and mortality (d^{-1}) per treatment. Right panels: normalised growth rate (% of control group), normalised development rate (% of control group) and normalised mortality rate (% of control group); normalised rates serve to correct for differences in the initial larval quality

Table 3. *Macoma balthica* larvae. Testing (2-factor analysis of variance without replication) for differences in normalised growth rate (%), normalised development rate (%) and normalised mortality (%) of larvae among manipulations of fertilisation date and food level. **Bold** values: p < 0.05

Analysis of variance	Variable	SS	df	MS	F	p
Normalised growth rate	Fertilisation date	3044.18	5	608.84	40.11	**<0.001**
(n = 12, r² = 0.98)	Food level	106.41	1	106.41	7.01	**0.046**
	Error	75.89	5	15.18		
Normalised development rate	Fertilisation date	5076.53	5	1015.31	11.74	**0.008**
(n = 12, r² = 0.93)	Food level	276.37	1	276.37	3.19	0.134
	Error	432.46	5	86.49		
Normalised mortality	Fertilisation date	1.87×10^{-5}	5	3.73×10^{-4}	2.56	0.163
(n = 12, r² = 0.76)	Food level	4.78×10^{-5}	1	4.78×10^{-4}	3.28	0.130
	Error	7.30×10^{-5}	5	1.46×10^{-5}		

Larval development

In general, larvae in the control food levels were able to develop faster than in the SW1 and SW5 food levels (Figs. 3 & 4). The percentage of larvae that had developed a foot (including pediveliger larvae) at Day 24 in the control food levels varied between 40 and 95%. The logistic regression showed that the larvae in the control food level developed a foot, on average, in 18.8 ± 1.5 d (mean ± SE), at a length of 231 ± 3.3 µm. Most larvae that were offered natural seawater (food levels SW1 and SW5) in April (Batches A, B and C) did not develop into pediveligers at all, while a considerable fraction did develop a foot in the beginning of May (notably Batches D and F) (Fig. 3). In general, the percentage of larvae that had developed a foot at Day 24 in the SW1 food levels varied between 0 and 60%, and in the SW5 food levels, between 0 and 80% (Table 2).

An analysis of variance of the normalised data on development of treatments SW1 and SW5 demonstrated a significant effect of the fertilisation date (Fig. 4, Table 3), but no effect of food level. When the normalised development rates were compared with the average phytoplankton availability, no correlation could be detected (SW1: p = 0.31, r² = 0.06; SW5: p = 0.94, r² = 0.00).

Larval mortality

At Day 24, the concentration of larvae in the control food level varied between 79 and 26% (sensu Batch C: 108%) of the initial concentration at Day 3, while the concentrations in the SW1 food levels varied between 42 and 5%, and in the SW5 food levels, between 69 and 15% of the initial concentrations (Fig. 3). Average (±SE) mortality rates of larvae in the control food level were 0.024 ± 0.006 d⁻¹; in the SW1 food level, 0.057 ± 0.012 d⁻¹; and in the SW5 food level, 0.037 ± 0.008 d⁻¹ (Table 2, Fig. 4).

An analysis of variance of the normalised data of Treatments SW1 and SW5 on mortality demonstrated no significant effects of fertilisation date or of food level (Table 3). When the normalised mortality rates were compared with the average phytoplankton availability, no correlation could be detected (SW1: p = 0.21, r² = 0.19; SW5: p = 0.47, r² = 0.00).

DISCUSSION

Philippart et al. (2003) hypothesised that a match/mismatch mechanism of *Macoma balthica* larvae and their phytoplankton, at least partly, determines *M. balthica* recruitment. The current results show indeed that the timing of spawning affects the growth and development of *M. balthica* larvae. For example, in early April (Batch A), larvae in a concentration of 1 larva ml⁻¹ in natural seawater (SW1) grew very slowly (1.9 µm d⁻¹) and did not develop a foot (0%), which points to a mismatch between larvae and their food source. Some weeks later, in the beginning of May (Batch D), larvae in SW1 had doubled their growth rates (4.0 µm d⁻¹). Also, a relatively high percentage of larvae in SW1 had developed a foot (25%) (Table 2). This increase indicates a match between larvae and their food source. Towards the end of May, both growth and development rates decreased to intermediate levels (Fig. 4), pointing to a mismatch again. In the experiment the temperature was kept constant at 15°C.

The control food level served to correct for the effect of initial larval quality (normalisation). The results showed that the quality of the larvae in the controls was stable (Fig. 4), although some variation in growth, development and mortality of larvae was present, notably in Batch E (Fig. 4). Such variation may have been caused by differences in adult condition due to storage effects (Lannan 1980) or due to the outbreak of bacterial or viral infections (review in Elston 1993).

Alternatively, it may have been caused by the differences in genetic constitution of the parents and, hence, of the larvae (e.g. Hilbish et al. 1999), although this is less probable since larvae in each batch originated from a random group of parents that all originated from the same population. Whatever the cause of variation, from Fig. 4 it is clear that the same variation applied to the SW1 and SW5 food levels, i.e. the data for the SW1 and SW5 food levels co-varied with the data for the control food level.

Normalised growth and development rates were clearly affected by fertilisation date (Table 3), while normalised mortality was not. This demonstrates that the timing of spawning is of great importance for bivalve larvae and that the differences in growth and development rates must have been caused by the differences in the food content of the seawater. Furthermore, the normalised growth rate was affected by food level, while the normalised development and mortality rates were not (Table 3). This suggests that resource or interference competition (Keddy 1989) reduced the intake rate of the larvae at the SW5 food levels as compared to the SW1 food levels.

The recorded growth rates of 3.0 to 5.5 µm d^{-1} for *Macoma balthica* larvae in the control food level compare well to larval growth rates observed by Drent (2002) of 5.2 µm d^{-1}. The recorded average age (18.8 d) and size (231 µm) at the moment of the appearance of a foot were slightly lower than the values of 20.6 d and 254 µm, respectively, as observed by Drent (2002). The average growth rates in the SW1 (2.7 µm d^{-1}) and SW5 (2.4 µm d^{-1}) food levels were very low compared to those in the control level, but compared well to growth rates of 1.0 to 3.1 µm d^{-1} of *Mytilus edulis* larvae at food levels of 1 to 3×10^4 cells *Isochrysis* ml^{-1} (Pechenik et al. 1990). Finally, the recorded mortality rates of 0.037 to 0.057 d^{-1} were in line with those observed by Drent (2002), but lower than the natural daily mortality rates of meroplanktonic larvae of 0.13 to 0.28 d^{-1} (review in Rumrill 1990). This is probably due to absence of predators and diseases under *in vitro* conditions.

The observed time effects on growth, development and mortality of *Macoma balthica* larvae reared in natural seawater (SW1 and SW5) could not be explained by phytoplankton abundance, since the average phytoplankton cell concentration only slightly increased through time (Fig. 2). Based on long-term phytoplankton observations (>30 yr), it was expected to observe a change from low cell numbers (2×10^3 cells ml^{-1}) at the start of the bloom to high numbers (2×10^5 cells ml^{-1}) some weeks later (Cadée 1986). Instead, phytoplankton cell concentrations remained relatively low during the entire experimental period. Chlorophyll *a* (chl *a*) data for the same period confirmed the results

(G. C. Cadée unpubl. data). A phytoplankton bloom came after all, but only in June 2002 when the chl *a* content amounted to 178% of the long-term average (G. C. Cadée unpubl. data). Although the results do not support the original match/mismatch hypothesis that is defined in terms of quantities of prey and predators (Cushing 1975), it is clear that there is a time effect, probably caused by a change in the food content of the seawater during the experimental period.

One explanation for the observed effects is that the species composition and, hence, the nutritional quality of the small flagellates may have changed over time, while total phytoplankton cell numbers remained more or less constant, which is in line with the results of Beaugrand et al. (2003). Previous studies have demonstrated that growth rates often cannot be explained by variation in phytoplankton concentrations or phytoplankton consumption alone (Pechenik & Fisher 1979). The biochemical composition of the phytoplankton also has a large impact on the growth and development rates of plankton (Wacker et al. 2002, Klein Breteler et al. 2005). In addition, larvae may selectively feed on phytoplankton according to growth rate and chemical content (Baldwin 1995).

Macoma balthica may be more sensitive to a match/mismatch with phytoplankton in spring than other bivalve species in the Wadden Sea that spawn later in the season (Honkoop & Van der Meer 1998). For example, *Mytilus edulis* spawns in response to phytoplankton blooms (Starr et al. 1990), and therefore the larvae will probably be subjected to starvation less frequently. Since *M. balthica* juveniles may be consumed by predators such as size-selective shrimp and shore-crabs (Beukema 1992, Hiddink et al. 2002), the strategy of *M. balthica* to spawn early at the cost of a possible mismatch between larvae and phytoplankton may have been developed to avoid predators and reduce juvenile mortality (Philippart et al. 2003). This suggests that *M. balthica* is an 'early strategist' (Fortier et al. 1995). Due to the rising seawater temperatures in the Wadden Sea, a mismatch between *M. balthica* larvae and their food is likely to occur more frequently in the future, since the spawning period of *M. balthica* is moved to an earlier time in the year, while the onset of the phytoplankton bloom is not affected (Philippart et al. 2003). In addition, mild winters decrease the reproductive output of *M. balthica* and advance shrimp predation (Philippart et al. 2003). Together these factors may result in a decline of the *M. balthica* population and, possibly, long term, in a selection for later-breeding *M. balthica*. Besides climate-related changes, other factors such as pollutants and discharged pharmaceuticals from sewage treatment plants may affect the timing of spawning of bivalves in the Wadden Sea by delaying or speeding up the

spawning time (e.g. Honkoop et al. 1999). In our study area, however, neither concentrations of pharmaceuticals nor their effects on aquatic organisms have been determined yet (Schrap et al. 2003).

In conclusion, a clear effect of the timing of spawning of adult *Macoma balthica* on the growth and development of their offspring was detected in the current experiment. However, these differences could not be attributed to temporal changes in phytoplankton concentrations. This suggests that food quality may have changed over time. To determine the nutritional value of different phytoplankton species for *M. balthica* larvae, laboratory experiments may be used (Volkman et al. 1989, Jonsson et al. 1999). In addition, diet choice experiments could be performed to estimate ingestion rates of different species of phytoplankton by *M. balthica* larvae. To gain insight into feeding preferences in the field, larval stomach contents could be determined (Raby et al. 1997).

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