

# Long-term changes in annual growth of bivalves in the Wadden Sea: influences of temperature, food, and abundance

J. J. Beukema<sup>1,\*</sup>, R. Dekker<sup>1,2</sup>, J. Drent<sup>1,2</sup>, J. van der Meer<sup>1,2</sup>

<sup>1</sup>NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands

<sup>2</sup>Utrecht University, 3508 TC Utrecht, The Netherlands

**ABSTRACT:** We report on results of a long-term (1978–2015) field study on between-year variability in annual weight growth of 1 yr old individuals of 4 dominant bivalve species on tidal flats in the western part of the Wadden Sea: 3 filter-feeders (*Cerastoderma edule*, *Mytilus edulis*, and *Mya arenaria*) and 1 filter/deposit-feeder (*Macoma balthica*). Relationships between individual weight gain during the growing season and 2 environmental factors (temperature, food supply) in the growing season (March to August) were studied. Weight gains varied strongly from year to year (by an order of magnitude in all species) and showed significant correlations with water temperatures (negative in *M. balthica*, positive in the other 3 species). Chlorophyll concentrations in the water showed a significant positive relationship with growth only in *M. balthica*. In the other 3 species, year-to-year fluctuations in growth were synchronized, showing a consistent pattern with elevated values between 1991 and 2005. The abrupt change to faster growth in the early 1990s may have been caused by the nearly complete disappearance in the western Wadden Sea of mussel beds for a period of several years, starting in 1990. The change to declining growth rates in the early 2000s took place simultaneously with a decline in chlorophyll concentrations and a rapid increase in stocks of the invasive bivalve *Ensis directus*. In all 4 studied species, growth rates were strongly reduced in 2012, a year with exceptionally high numbers of filter-feeding bivalves on the tidal flats.

**KEY WORDS:** Seasonal weight gain · Long-term data series · Chlorophyll concentration · *Cerastoderma edule* · *Mytilus edulis* · *Mya arenaria* · *Macoma balthica*

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## INTRODUCTION

An important attribute of a population is the variability in the annual weight growth of its individuals. This variability contributes to size distribution within the population, to magnitude and variability of biomass and (somatic and gamete) production of the population, and to its significance as a food source for organisms at higher trophic levels. Mean individual growing-season weight gains usually vary substantially between years, requiring an analysis of under-

lying relationships with variable environmental conditions, such as food supply and temperature.

Examples of long-term studies on growth rates in coastal bivalve populations include a 50 yr study of *Mercenaria mercenaria* (Henry & Nixon 2008) and a 30 yr study of *Macoma balthica* (Beukema et al. 2014), both showing significant variability from year to year in growth. Several factors have been proposed to explain such variability, including (1) water temperature, with either positive (e.g. Jones et al. 1989, Heilmayer et al. 2005) or negative (e.g. Jones

\*Corresponding author: jan.beukema@nioz.nl

1981, Beukema et al. 2009, 2014) effects, (2) positive effects of food supply (e.g. Carmichael et al. 2012, Beukema et al. 2014), and (3) negative influences of a high abundance of competitors for food (e.g. Peterson & Black 1987, Kamermans et al. 1992, Weinberg 1998, Beukema & Dekker 2015), which have been caused by (in most studies not adequately measured) reduction in food supply.

Here we used a long series (starting in the 1970s) of monitoring data on abundance and growth of 4 dominant bivalve species. The data were collected twice annually in an extensive tidal-flat area (Balgzand) in the westernmost part of the Wadden Sea. Detailed long-term data were available on water temperature and chlorophyll *a* (chl *a*) concentration in the nearby tidal inlet. We present correlative relationships between these long data series to find evidence for possible effects of water temperature, food supply, and food competition on annual body weight gains in bivalve individuals. Moreover, we assess the degree to which years with rapid or slow growth coincided in the 4 species. The studied species include 3 true suspension-feeders that take their food from the overlying water (the common cockle *Cerastoderma edule*, the blue mussel *Mytilus edulis*, and the gaper clam *Mya arenaria*) and 1 mixed-type feeder that feeds at the interface between the water column and the bottom by suspension- and deposit-feeding (Baltic tellin *Macoma balthica*). In the Wadden Sea, these bivalves are dominant species, making up together a large share of the total macrozoobenthic biomass, amounting to about 60% on the intertidal (Beukema 1976) and about 70% in the subtidal (Dekker 1989).

We hypothesized that annual growth in all species studied would be positively related to food supply, whereas relationships between temperature and growth would be species-specific. As a result of local consumption by competitors, local (unknown) food supply values will not have been identical to values observed at distant sampling stations for phytoplankton; therefore, we also hypothesized that growth rates in all species would be negatively related to local abundances of competitors for food.

In view of the present long-term trends in several coastal waters, including the Wadden Sea, of rising temperatures (Van Aken 2008) and declin-

ing eutrophication (Philippart et al. 2007, Henriksen 2009, Loebl et al. 2009), the results of this study will be valuable for understanding future developments of growth and productivity as well as for steering management of coastal areas.

## MATERIALS AND METHODS

### Study area

The data on bivalves were obtained as part of a long-term program, begun in the 1970s, involving twice-annual sampling of macrozoobenthic animals at 15 permanent sampling stations located on Balgzand, a tidal flat area in the westernmost part of the Wadden Sea (ca. 53°N, 5°E). Further details on the sampling area, stations, and methods can be found in Beukema & Cadée (1997). For the estimates of numerical abundance, data from all 15 stations were used. For the study of growth rates, we chose a relatively homogeneous area in the central part of Balgzand including 6 sampling sites (transects numbered 4, 5, 8, 9, 10, and 11 in Fig. 1). This part of Balgzand covers about one-third of the total Balgzand tidal-flat area of 50 km<sup>2</sup>. In the part of Balgzand to the north of this area (2 sampling sites), data on growth were

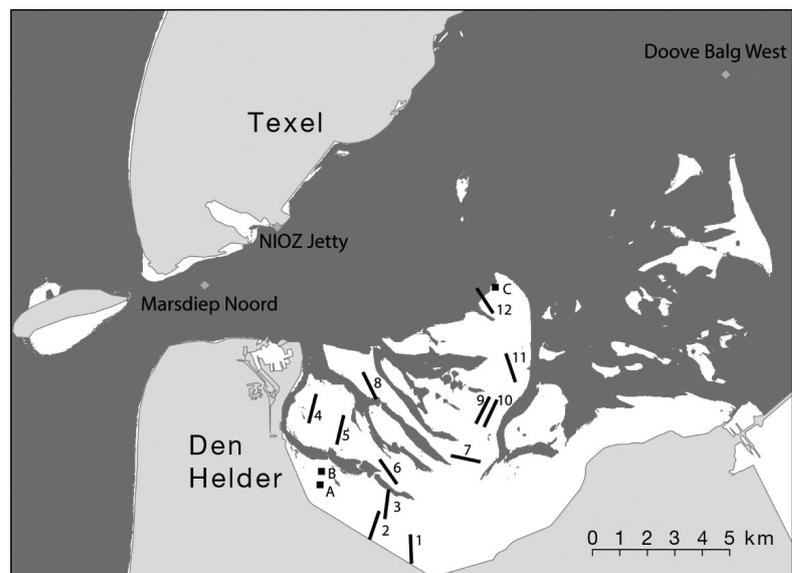


Fig. 1. Westernmost part of the Dutch Wadden Sea, showing the Balgzand tidal-flat area. The white areas are tidal flats, the light grey areas are land, and the dark grey areas are subtidal. The permanent sampling sites for benthic animals are indicated: 12 transects (1–12) and 3 squares (A–C). Bivalve growth rates were studied in detail at the 6 transects numbered 4, 5, 8, 9, 10, and 11 in the central part of Balgzand. The sampling sites for water temperatures and chlorophyll concentrations are indicated by Marsdiep Noord (main tidal inlet) and Doove Balg West (inner part of western Wadden Sea)

scarce due to failing recruitments of the studied species in nearly all years, probably due to adverse environmental conditions (exposure to strong currents and wave action, resulting in unstable and coarse sediments). South of the selected area, most (5 out of 7) sampling sites were located at higher intertidal levels (above or around mean-tide level), where growth rates in bivalves were invariably lower than in the selected area, probably due to shorter daily immersion times. At the 2 remaining sampling sites (numbered 6 and 7 in Fig. 1), numbers and/or growth rates were consistently reduced in some species for unknown reasons.

### Environmental conditions

Temperature values were derived from daily observations of surface water temperatures from the NIOZ jetty at the northern shore of the Marsdiep tidal inlet (the main tidal inlet of the westernmost part of the Dutch Wadden Sea) at about 10 km from the Balgzand sampling stations (Fig. 1). Monthly data were available for all years of the study period and were summarized by Van Aken (2008) and completed for recent years (courtesy of J. Nauw).

Data on chl *a* concentrations in surface water were available from a database of Rijkswaterstaat (<http://live.waterbase.nl>). The samples were taken at a frequency of once or twice per month near the temperature station in Marsdiep and in an area called Doove Balg in the central part of the western Wadden Sea, ca. 15 km northeast of Balgzand. We used these concentrations as a proxy for phytoplankton abundance and available food for suspension-feeders. We applied annual values of mean concentrations for half-year periods (March through August). For Marsdiep, chl *a* data were available for all years from 1978 to 2015, whereas for Doove Balg they were available only for the 21 years including 1982 to 1995 and 2009 to 2015 (in other years, sampling frequency was too low).

These chlorophyll data were from samples taken (mostly) 2 to 3 h before the time of low tide, thus representing concentrations in water flowing back from the Wadden Sea to the North Sea. Unfortunately, no data were available for water flooding the tidal flats, nor for concentrations of microphytobenthos. Another long-term series of data on chlorophyll concentrations in the water of the Marsdiep tidal inlet (Philippart et al. 2007) was even less adequate, because these samples were taken at the time of high tide, thus characterizing North Sea rather than Wadden Sea water. Although the annual means of this

data set were strongly positively correlated with those of the Rijkswaterstaat set, we did not use it.

### Bivalve sampling

Along each of the 1 km transects on Balgzand (Fig. 1), 50 cores were taken twice annually at equal intervals to a depth of about 25 cm. In February and March, when cores of nearly 0.02 m<sup>2</sup> were used, the sampled area per transect covered a total of 0.95 m<sup>2</sup>. In August and September, using cores of nearly 0.01 m<sup>2</sup>, we covered 0.45 m<sup>2</sup> per transect. At the 3 square sampling sites, samples of about 1 m<sup>2</sup> were collected in the same months. Bivalves were sorted from the sieved (1 mm mesh size) samples, assigned to age classes (cohorts indicated by the year of birth), counted (numerical density, expressed in n m<sup>-2</sup>), sorted to mm shell length classes, their soft parts dried to constant weight, weighed per mm length class, incinerated, and again weighed to obtain, by subtraction, the ash-free dry mass (AFDM). For each species and at each sampling station, estimates of weight gain per individual (in g AFDM ind.<sup>-1</sup>) in the second growing season were obtained by subtracting mean weight in March from mean weight in the subsequent August of the individuals born in the preceding year. The annual means presented are averages of estimates assessed at 4 to 6 transects.

Numerical abundance was expressed in n m<sup>-2</sup>, as means of data from all 15 stations. As an index of grazing pressure on phytoplankton, we used the sums of numerical densities of the 3 dominant suspension-feeding bivalves (*Cerastoderma edule*, *Mya arenaria*, *Mytilus edulis*) at the start of the growing season in February/March. These densities (particularly when high) were made up largely of nearly 1 yr old individuals. Subsequent seasonal weight gain was on average similar in the 3 species (see 'Results'), allowing addition of their densities for the present purpose. We did not use biomass for this purpose, as total bivalve biomass was dominated by the contribution of large individuals of *M. arenaria* in several years, which are expected to filter less per unit of weight than smaller individuals of the other species.

### Estimates of growth

We studied only the growth in the second year of life of the bivalves: the growing season that started at an age of about 0.8 yr. For estimates of growth, we used data of a sampling site only if the cohort to be

studied was represented by at least 3 individuals in the samples taken at the end of the growing season. For an estimate of mean growth on Balgzand in a particular year, such numbers should have been available at 4 or more of the 6 sampling sites. In practice, this number usually amounted to 6, as successful year classes tend to arise simultaneously over vast areas (Beukema et al. 2001). As a consequence of the application of these criteria, growth dates were lacking for several years. During the period 1978–2015, sufficient numbers for precise growth estimates were present in 12 year classes of *C. edule*, 15 of *M. edulis*, 14 of *M. arenaria*, and 32 of *M. balthica*. In 8 years (1980, 1988, 1992, 1997, 2004, 2006, 2009, and 2012), such estimates were available for all 4 species. In a few additional years, data were available for 2 or 3 species. *Ensis directus* and *Crassostrea gigas* were not included, because too few years provided sufficient data on their growth.

### Estimates of pumping capacity

Total filtering capacity of filter-feeding bivalves on Balgzand was calculated for each year as the sum of water volumes pumped by the individual species (*C. edule*, *M. edulis*, *M. arenaria*, *E. directus*, and *C. gigas*)  $\text{m}^{-2} \text{h}^{-1}$ . For the species-specific estimates, their numerical densities, size distributions, and submersion times of the sampling sites were taken into account. Relationships between length and filtration rates were taken from Møhlenberg & Riisgård (1979) for *C. edule*, Bougrier et al. (1995) for *C. gigas*, Riisgård & Seerup (2003) for *M. arenaria*, Kamermans et al. (2013) for *E. directus*, and Riisgård et al. (2014) for *M. edulis*.

### Statistics

Statistical significance of differences between averages was tested by *t*-tests. Strengths of correlations (and of trends: correlations with year number) were expressed in Pearson *r*-values with 2-sided *p*-values. To define periods of successive years with similar growth rates, segmented regression models were fitted to the time series data of the growth rates of *C. edule*, *M. arenaria*, and *M. edulis*. We assumed that the variability in growth rate could be described by either 1, 2, or 3 periods in each of which the growth was constant, apart from an independent and identically distributed random error  $\epsilon$ . So, for example, the 3-period model is given by

$$Y_i = \beta_0 + \beta_1(T_i > \tau_1) + \beta_2(T_i > \tau_2) + \epsilon_i \quad (1)$$

where  $Y_i$  represents the growth rate in year  $T_i$ , the  $\beta$ 's are the unknown growth parameters, the  $\tau$ 's are the unknown time points at which a shift in growth rate occurs, and the  $\epsilon$ 's are independent and identically distributed normal errors. The 3 models were fitted (under the constraint that each period should contain at least 2 observations) and tested against each other with an *F*-test. The *F*-distribution under the null hypothesis of no change was estimated by Monte-Carlo simulation (10 000 times) in which the time order of the growth rates was determined by random sampling without replacement from the original data.

## RESULTS

### Environmental conditions

Mean water temperatures for the 6 mo growing seasons of the period 1979–2015 (Fig. 2a) averaged 13.0°C (SE = 0.15,  $n = 37$ ) for these half-year periods. They ranged from 11.2 to 14.4°C and showed a significantly ( $p < 0.01$ ) increasing long-term trend with a mean annual increase of ca. 0.04°C  $\text{yr}^{-1}$ , which amounts to about 1.5°C over the entire study period.

At both sampling stations, the estimates of mean chl *a* concentrations for the March to August half-year periods fluctuated by a factor of 2 to 3 and showed a declining trend, significantly so in the longest series in the main tidal inlet (Fig. 2b). The estimates at the 2 stations were positively correlated ( $r = 0.60$ ,  $n = 21$ ,  $p < 0.01$ ) and showed similar long-term averages:  $13.8 \pm 0.7$  ( $n = 36$ ) and  $13.7 \pm 0.9$   $\text{mg m}^{-3}$  ( $n = 21$ ) for the Marsdiep and Doove Balg, respectively. The declining long-term trends amounted to about  $-0.2 \text{ mg m}^{-3} \text{ yr}^{-1}$  or to about 8  $\text{mg m}^{-3}$  over the entire study period.

In the Balgzand area, numbers of filter-feeding bivalves, and thus demand for suspended food, varied strongly from year to year, from about 20 to about 600  $\text{m}^{-2}$  (Fig. 2c). These numerical densities did not show a statistically significant long-term trend.

### Between-year variation in seasonal growth rates

In all bivalve species studied, the annual estimates of mean individual weight gain in the growing season varied strongly from year to year, from about 20 or 30% to about 200% of their long-term averages (Fig. 3). The absolute values of the long-term means

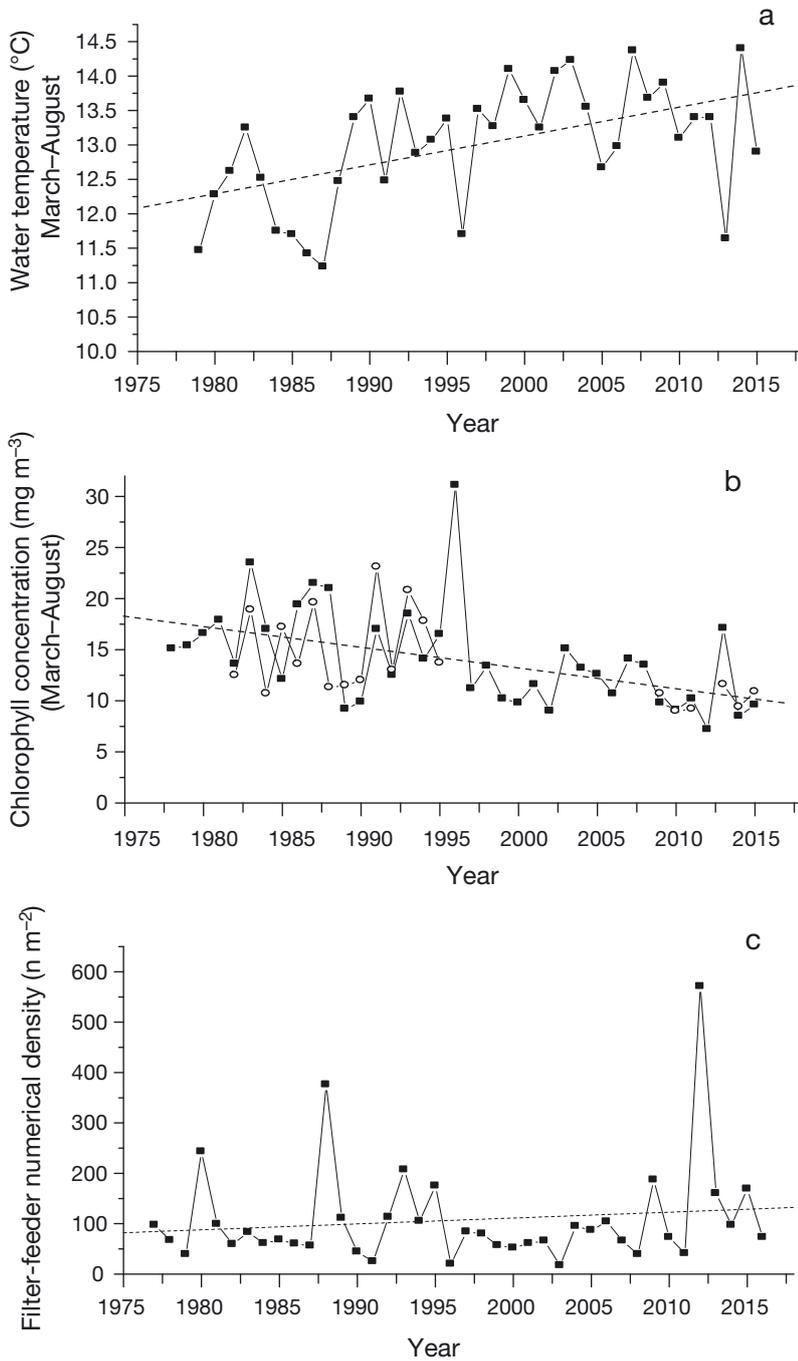


Fig. 2. Long-term data series of estimates of (a) mean surface water temperatures in Marsdiep for the growing season (March–August), showing a significantly increasing trend by  $0.04^{\circ}\text{C yr}^{-1}$  ( $r = 0.51$ ,  $n = 37$ ,  $p < 0.01$ ); (b) mean chlorophyll a concentrations for the growing season, as observed in the main tidal inlet (Marsdiep, ■, showing declining trends by  $0.21$  and  $0.17 \text{ mg m}^{-3}$ ;  $r = -0.59$ ,  $n = 37$ ,  $p < 0.001$ ) and the central part of the westernmost part of the Dutch Wadden Sea (Doove Balg, ○,  $r = -0.44$ ,  $n = 19$ ,  $p = 0.06$ ), respectively (the outlying point for 1996 was not used) and (c) sums of numerical densities of the 3 main suspension-feeding bivalves (*Cerastoderma edule*, *Mytilus edulis*, *Mya arenaria*) on Balgzand (means of 15 sampling sites) at the start of the growing season in February/March. The trend by  $+1.2 \text{ yr}^{-1}$  ( $r = 0.13$ ,  $n = 40$ ,  $p = 0.4$ ) was non-significant. The dashed lines show long-term trends for Marsdiep and Balgzand data only

of seasonal weight gain in the second growing season amounted to similar values in *Cerastoderma edule*, *Mytilus edulis*, and *Mya arenaria* of  $0.28 \pm 0.03$ ,  $0.25 \pm 0.04$ , and  $0.30 \pm 0.04 \text{ g AFDM ind.}^{-1}$ , respectively, and in *Macoma balthica* to a much lower value of  $0.020 \pm 0.002 \text{ g AFDM ind.}^{-1}$  ( $n = 12$  to  $32$ : the numbers of years with sufficient data). Note that most of the SE values shown in Fig. 3 (indicating variability in growth rates between the 6 sampling stations) were relatively small compared to the between-year differences in weight gain in the species concerned, showing that (1) differences in between-station estimates in the same year were usually rather small and (2) a high proportion of the between-year differences in growth rate were therefore statistically significant.

The distribution of annual values of seasonal weight gain over the entire period of observation (1979–2015) appears to be far from random in the filter-feeding species (Fig. 3a). Years with peak and low values of weight gain tended to occur simultaneously in these 3 species. For instance, low values in all 3 species were found in 2012, whereas values were high in all 3 species in 1992 and 1997. Indeed, the correlations between the annual growth rates of these 3 species were positive and statistically significant (Table 1). However, in the other species (*M. balthica*), which ingests food partially by deposit-feeding, the pattern of years with rapid and slow growth (Fig. 3b) deviated from those in the 3 suspension-feeders (Fig. 3a). No significant correlations were found between *M. balthica* and the other 3 species (Table 1).

The similar patterns for the 3 suspension-feeders suggest a breakdown into 3 periods, with the period 1991 to about 2005 showing elevated growth rates (Fig. 3a, Table 2a,b). In all 3 species, the differences in mean growth rates between the first and second and between the second and third period

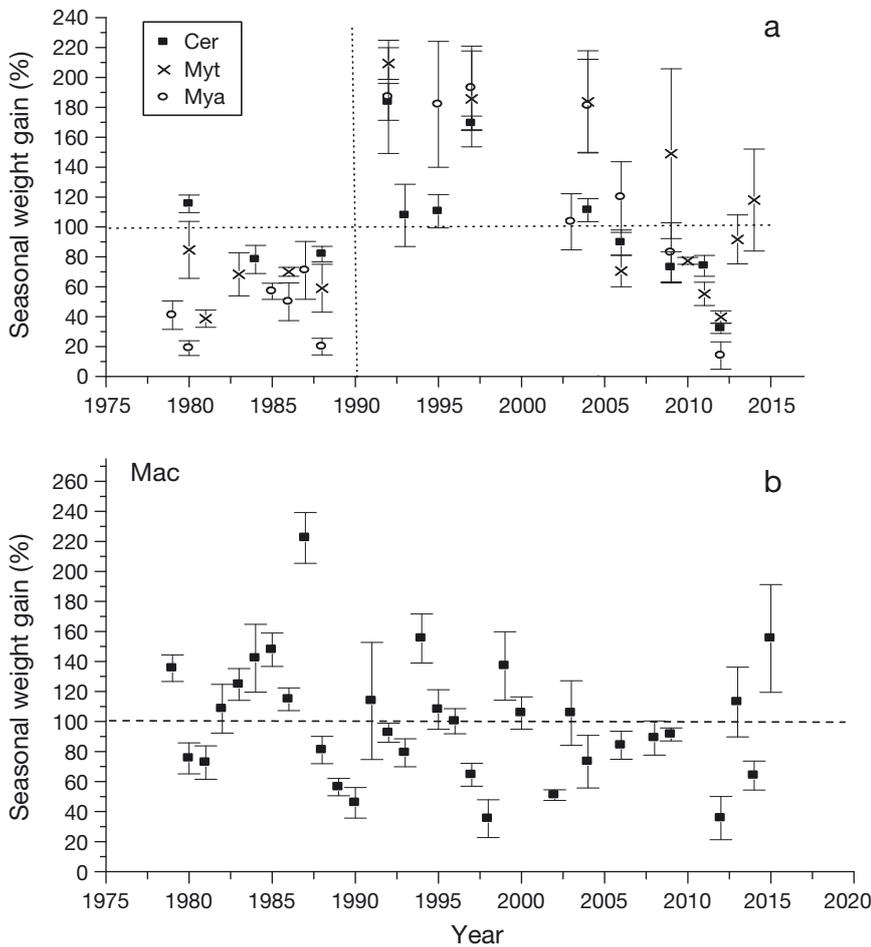


Fig. 3. Long-term changes in indices for annual growth rates in (a) 3 suspension-feeding bivalve species (■: *Cerastoderma edule*, x: *Mytilus edulis*, o: *Mya arenaria*) and (b) the mixed-feeder *Macoma balthica*. Growth rates are shown as mean seasonal weight gains of individuals in their second growing season, expressed as a percentage of their long-term mean (1979–2015) growth rates (set at 100%; horizontal dashed line). Means are given with 1 SE with  $n \geq 3$ , but mostly 5 or 6 (the number of Balgzand sampling stations with sufficient data) and thus represent local variation. The vertical dotted line marks a major change in the western Wadden Sea, viz. the disappearance of mussel beds in 1990

Table 1. Coefficients of between-species Pearson correlations in various years of the period 1979–2015 of seasonal weight gains of bivalves between March and August for their second growing season. The number of years in each comparison was usually 8 (more only in the pair *Mya arenaria*/*Macoma balthica*); this includes the number of years in which the 2 species involved were sufficiently numerous at 4 or more of the 6 sampling stations; \* $p < 0.05$ , \*\* $p < 0.01$

	<i>Mytilus edulis</i>	<i>Mya arenaria</i>	<i>Macoma balthica</i>
<i>Cerastoderma edule</i>	0.80**	0.71*	0.10
<i>Mytilus edulis</i>		0.86**	-0.01
<i>Mya arenaria</i>			-0.18

were statistically significant, whereas no significant differences were found between the first and third periods (*t*-tests; Table 2a,b). For *M. arenaria* and *M. edulis*, the segregated regression model fitted best when tested for 3 periods (better than the model with 2 periods, and much better than the one with 1 period [Table 3]). In *C. edule*, a division into 2 or 3 periods was less clear-cut (Table 3: no *p*-values of  $< 0.05$ , i.e., the models did not differ significantly from each other). The first breakpoint around 1991 was observed in all 3 species; the second occurred somewhere around 2006 (Fig. 4), but was not identical in all species. Its timing was between 2004 and 2006 in *M. edulis* (Fig. 4a) and *C. edule* (Fig. 4c) and between 2006 and 2009 in *M. arenaria* (Fig. 4b). The last year with elevated growth rates (means of  $> 1$  SE above the long-term average, see Fig. 3a) occurring simultaneously in all 3 species was 2004. After that year, such high growth rates did not occur in any year in any of the 3 suspension-feeding bivalve species. In all 3 species, growth rates showed a declining trend over the period 2004–2015, significantly so ( $p < 0.05$ ) in *C. edule* and in *M. arenaria*.

In the growth estimates of *M. balthica*, no indication of the above 3 periods could be discerned (Fig. 3b). In this species, none of the differences in mean growth rates between the above 3 periods was statistically significant (Table 2a,b). This was the only one of

the 4 studied species in which the estimates suggested a consistent (declining) long-term (1979–2015) trend, although this trend was not significant ( $r = -0.22$ ,  $n = 32$ ,  $p = 0.22$ ).

### Relationships with environmental factors

Water temperatures during the growing season showed correlative relationships with weight gains that were statistically significant in 3 out of the 4 studied species (first column of Table 4). Note that the correlations were positive in the 3 suspension-feeders (Fig. 5a), but negative in *M. balthica* (Fig. 5b).

Table 2. Means ( $\pm 1$  SE) of annual values for 3 periods and 4 bivalve species for (a) individual seasonal weight gain in the central part of Balgzand, (b) this gain expressed as a relative measure (as in Fig. 3), (c) mean water temperatures during the growing season (Marsdiep), (d) mean chlorophyll concentrations during the growing season (Marsdiep and Doove Balg), (e) mean filtration capacity of suspension-feeding bivalves on Balgzand, (f) summed mean numerical densities of 3 species of filter-feeding bivalves on Balgzand, and (g) quotients of chlorophyll concentrations (Marsdiep) divided by filter-feeding bivalve densities (Balgzand). Significant differences between periods are indicated by \* $p < 0.05$ , \*\* $p < 0.01$ , and \*\*\* $p < 0.001$  ( $t$ -tests). No significant differences were found in weight gains between the first and last period (a,b), but for water temperatures and chlorophyll concentrations (c,d), these differences were significant (\*\*). Numbers in parentheses in (d–g) are numbers of observations

	1979–1990		1991–2004 <sup>a</sup>		2005–2015 <sup>a</sup>
(a) Mean weight gain in 2nd growing season in g ash-free dry matter ind. <sup>-1</sup> (n = 3–10 yr)					
<i>Cerastoderma edule</i>	0.25 $\pm$ 0.03	*	0.37 $\pm$ 0.04	**	0.19 $\pm$ 0.03
<i>Mytilus edulis</i>	0.15 $\pm$ 0.02	***	0.53 $\pm$ 0.03	***	0.19 $\pm$ 0.02
<i>Mya arenaria</i>	0.13 $\pm$ 0.03	***	0.49 $\pm$ 0.05	**	0.15 $\pm$ 0.10
<i>Macoma balthica</i>	0.021 $\pm$ 0.002		0.018 $\pm$ 0.002		0.018 $\pm$ 0.003
(b) Data from (a) expressed as % of the long-term mean of the species (n = 3–10 yr)					
<i>C. edule</i>	92 $\pm$ 12	*	136 $\pm$ 16	**	67 $\pm$ 12
<i>M. edulis</i>	64 $\pm$ 8	***	193 $\pm$ 8	**	86 $\pm$ 14
<i>M. arenaria</i>	43 $\pm$ 8	***	161 $\pm$ 16	**	48 $\pm$ 34
<i>M. balthica</i>	111 $\pm$ 14		94 $\pm$ 9		90 $\pm$ 14
(c) Mean water temperature March–August in °C (n = 11 to 14)					
Marsdiep	12.32 $\pm$ 0.24	**	13.35 $\pm$ 0.18		13.31 $\pm$ 0.24
(d) Mean chlorophyll concentration in March to August in mg dm <sup>-3</sup>					
Doove Balg	14.2 $\pm$ 1.0 (10)		17.7 $\pm$ 2.0 (5)	**	9.8 $\pm$ 0.4 (4)
Marsdiep	16.3 $\pm$ 1.2 (13)	*	13.2 $\pm$ 0.8 (13)	*	10.9 $\pm$ 0.8 (8)
(e) Mean bivalve filtration capacity in dm <sup>3</sup> m <sup>-2</sup> h <sup>-1</sup>					
Balgzand	117 $\pm$ 21 (12)		113 $\pm$ 22 (14)		145 $\pm$ 17 (11)
(f) Mean bivalve densities in n m <sup>-2</sup>					
Balgzand	104 $\pm$ 25 (12)		83 $\pm$ 15 (14)		139 $\pm$ 42 (11)
(g) Index of amount of food available per individual (chl/density)					
Quotient of means	0.16		0.16		0.08
Mean of quotients	0.22 $\pm$ 0.03 (12)		0.24 $\pm$ 0.07 (13)	*	0.14 $\pm$ 0.03 (11)

<sup>a</sup>Data on *M. arenaria* are from the periods 1991–2007 and 2008–2015 (cf. Fig. 4)

Table 3. Residual sum of squares (RSS) for the 3 segmented regression models (1, 2, or 3 periods, respectively), and p-values of the various  $F$ -tests. See 'Results' for details. Significant results and selected models in **bold**

Species	Model	RSS	p (test versus model 1)	p (test versus model 2)
<i>Cerastoderma edule</i>	<b>1</b>	<b>19234</b>		
	2	11884	0.130	
	3	8188	0.211	0.349
<i>Mya arenaria</i>	1	58801		
	2	31030	0.062	
	<b>3</b>	<b>11989</b>	<b>0.017</b>	0.075
<i>Mytilus edulis</i>	1	43727		
	2	34079	0.367	
	<b>3</b>	<b>9972</b>	<b>0.017</b>	<b>0.008</b>

Effects of prevailing water temperatures during the growing season on bivalve growth rates were substantial. From years with relatively low (11–12°C) to relatively high (around 14°C) mean temperatures,

weight gains on average roughly doubled in *M. arenaria* and *M. edulis* (Fig. 5a) and halved in *M. balthica* (Fig. 5b). In *C. edule*, the response of growth to temperature appeared to be weak (Fig. 5a). In the second period of elevated growth in suspension-feeding bivalves, growing-season water temperatures were significantly higher than in the preceding period (Table 2c). This difference may partly explain the higher growth rates.

Annual mean chl *a* concentrations during March to August did not show significant correlations with seasonal weight gain in any of the 3 suspension-feeding bivalves (Table 4). However, in *M. balthica*, this relationship was significantly positive, both for the chlorophyll concentrations in the tidal inlet (Marsdiep) and for the concentrations in the inner part of the western Wadden Sea (Doove Balg). Chlorophyll concentrations were significantly higher in the second period with elevated growth rates than in the subsequent period (Table 2d). Numerical densities of the 3 main filter-feeding bivalve species

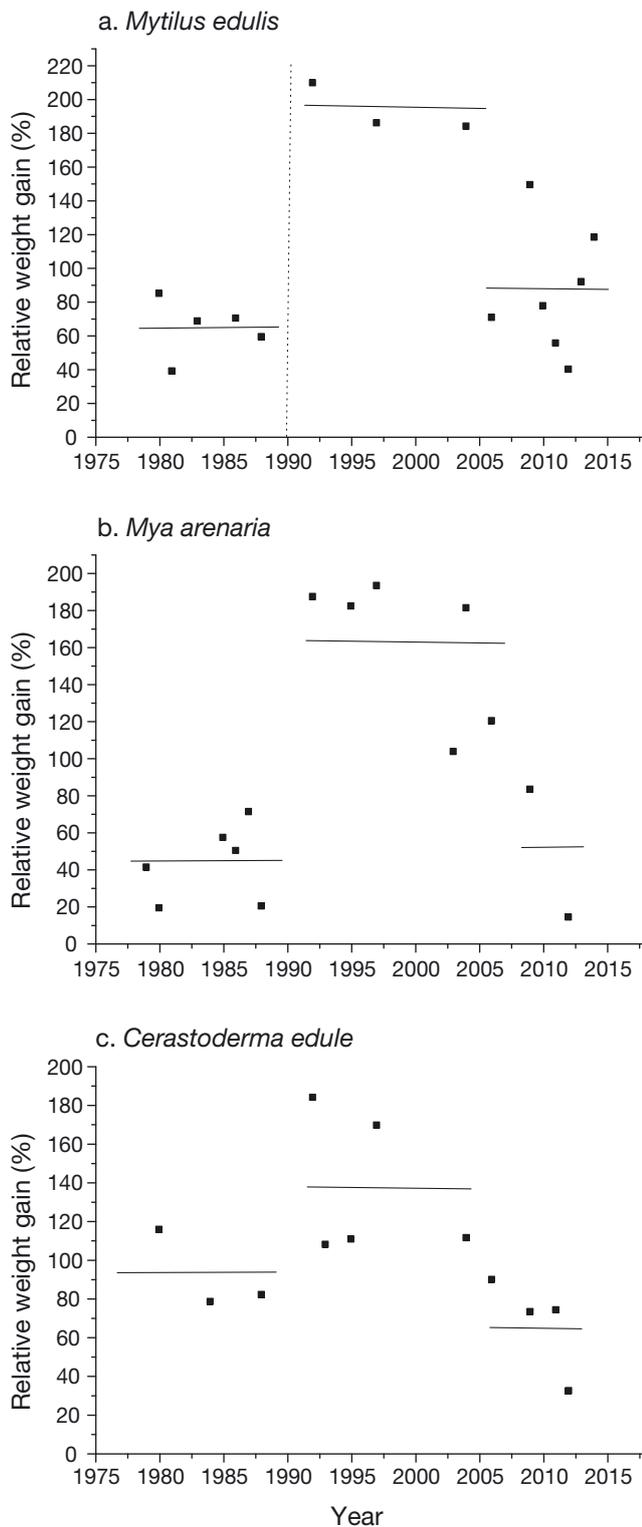


Fig. 4. Long-term changes in relative growth rates (expressed as in Fig. 3; data from Fig. 3a) on Balgzand in 3 species of suspension-feeding bivalves: (a) *Mytilus edulis*, (b) *Mya arenaria*, and (c) *Cerastoderma edule*. The horizontal lines show the 3 periods as revealed by the segmented regression model (Table 3)

together and their filtering capacity were lower in the second period than in the preceding and subsequent period, though not significantly so (Table 2e,f). The quotient of chlorophyll concentrations divided by numerical density could be used as a proxy for the amount of food available per individual. This quotient was not higher in the second than in the first period, but it was significantly higher in the second as compared to the third period (Table 2g).

### Relationships with bivalve abundance

In most species, relationships between their own abundance and growth rates were weak and non-significant ('own species' column in Table 4). Only in *C. edule* did seasonal weight gains tend to be lower in years with high numerical densities at the start of the growing season than in years with low abundance of this species (Pearson  $r = -0.54$  for the correlation between abundance and growth, was statistically significant,  $p < 0.05$ ).

As total densities of all 3 suspension-feeding bivalve species together may be more relevant for the total food demand of suspended food than the density of only 1 species, we also studied relationships between summed densities of these species against their seasonal weight growth (Fig. 6a). When the data of all 3 species were taken together, the observed negative relationship proved to be highly significant (Pearson  $r = -0.39$ ,  $n = 41$ ,  $p < 0.01$ ; Fig. 6a). Separate correlations for the species were also all negative, but significantly so only in *C. edule* and *M. balthica* (Table 4 and Fig. 6b, respectively). Note in Fig. 3 that in all 4 species, the growth rates observed in 2012 (the year with the highest total density of filter-feeders) were lower than in any other year.

The statistical significance of the above negative relationships between abundance and growth completely disappeared when the 6 points for the growth of the 3 species at the 2 highest densities were omitted ( $r = 0.05$ ,  $n = 35$ ,  $p = 0.8$ ; Fig. 6a). Thus, growth rates were reduced only in the 2 years (1988 and particularly 2012, compare Fig. 3a) with the highest numerical abundance of filter-feeding bivalves at the start of the growing season, when weight gains in all species studied were well below the long-term average (i.e., 100% in Fig. 6). Even a mere exclusion of the data for the year with the highest density (2012:  $571 \text{ m}^{-2}$ ) turned the relationship into a non-significant one (dashed line in Fig. 6a), although the slopes of the solid and dashed lines were not very different. Similarly, growth rates in *M. balthica*

Table 4. Coefficients of Pearson correlations between seasonal weight gains in 4 bivalve species during the March to August growing season and some environmental factors. Water temperatures and chlorophyll concentrations were measured at high tide in the Marsdiep tidal inlet. Chlorophyll data were also available for a station in the inner part of the western Wadden Sea (Doove Balg), but for fewer years. Numerical densities were estimated each year in February/March at the start of the growing season on Balgzand. Number (n) of years with sufficient data on weight gain (see 'Materials and methods') is shown in first column (with numbers for relationships with chlorophyll in Doove Balg in parentheses); \*  $p < 0.05$ , \*\*  $p < 0.01$  (1-sided tests were applied for relationships with chlorophyll and density). Relationships between each species' own abundance and growth rates were weak ('own sp.' column).  $\Sigma 3$  susp. f.: data of all 3 suspension-feeders species taken together

Species	n	Water temp.	Chlorophyll concentration		Numerical density	
			Marsdiep	Doove Balg	Own sp.	$\Sigma 3$ susp.f.
<i>Cerastoderma edule</i>	12 (8)	0.24	0.16	0.40	-0.54*	-0.51*
<i>Mytilus edulis</i>	15 (8)	0.51*	-0.25	0.08	-0.07	-0.30
<i>Mya arenaria</i>	14 (8)	0.56*	-0.24	0.10	-0.24	-0.35
<i>Macoma balthica</i>	31 (19)	-0.53**	0.49**	0.44*	0.14	-0.32*

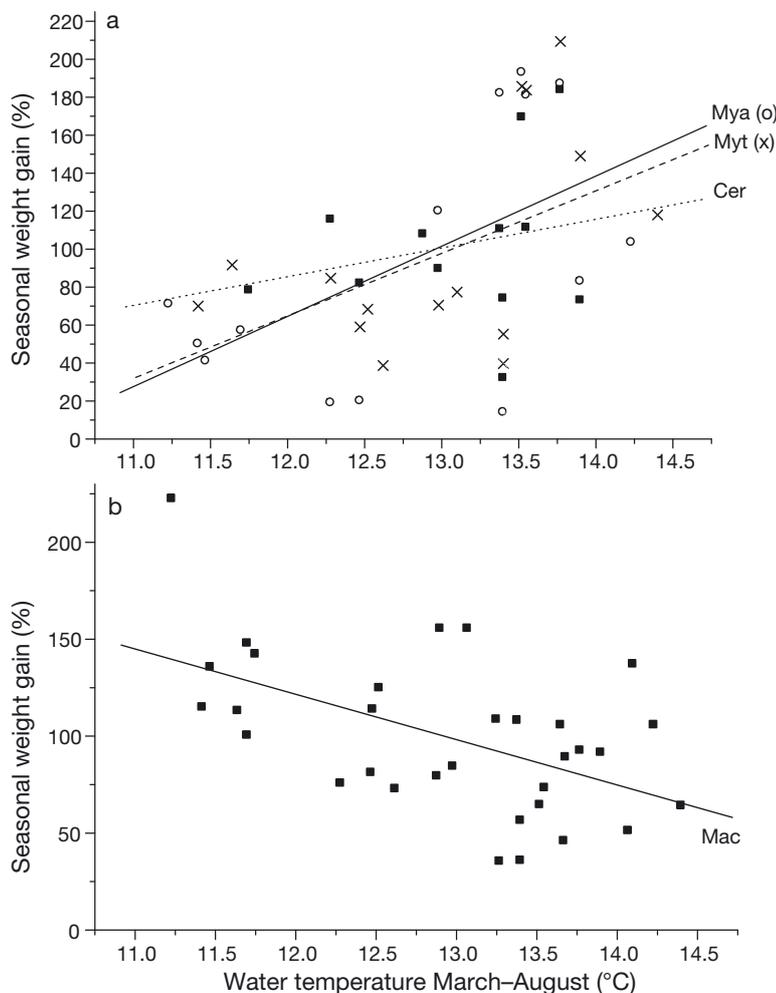


Fig. 5. Relationships between seasonal water temperatures ( $T$ , °C) in the tidal inlet and indices of annual growth rates in (a) 3 suspension-feeding bivalves ( $\blacksquare$ : *Cerastoderma edule*,  $\times$ : *Mytilus edulis*,  $\circ$ : *Mya arenaria*) and (b) the mixed-feeder *Macoma balthica*. Growth rates are expressed in relative weight gains (%), as in Fig. 3. Best linear fits for the 4 species were: *C. edule*: % =  $-96 + 15.1 T$  ( $r = 0.24$ ,  $n = 12$ ,  $p = 0.5$ ); *M. edulis*: % =  $-339 + 33.8 T$  ( $r = 0.51$ ,  $n = 15$ ,  $p = 0.05$ ); *M. arenaria*: % =  $-378 + 37.0 T$  ( $r = 0.56$ ,  $n = 14$ ,  $p < 0.05$ ); *M. balthica*: % =  $402 - 23.4 T$  ( $r = -0.53$ ,  $n = 32$ ,  $p < 0.01$ )

appeared to be reduced at higher filter-feeder densities (solid line in Fig. 6b:  $r = -0.32$ ,  $n = 32$ ,  $p < 0.05$ ), but again statistical significance was due only to the inclusion of the year with the highest total density. Note that the exceptionally low values for weight gain for 2012 appear in Fig. 5a as a 3-species group of outliers (the 3 lower points at 13.4°C).

Omitting the severely reduced 2012 growth rate data from the relationships between water temperature and seasonal weight gain (Fig. 5) enhanced the statistical significance of these correlations (becoming  $p < 0.05$  in 3 out of the 4 species). In the case of relationships with chlorophyll concentrations (Table 4), all non-significant correlations remained so, as did the significant ones in *M. balthica*.

### Bivalve abundance and food supply

High abundance of suspension-feeding bivalves resulted in high volumes of water filtered per unit of time, up to about  $200 \text{ dm}^3 \text{ m}^{-2} \text{ h}^{-1}$ . For each extra individual bivalve  $\text{m}^{-2}$  (up to about  $250 \text{ m}^{-2}$ ), the volume of water filtered increased on average by  $0.8 \text{ dm}^3 \text{ m}^{-2} \text{ h}^{-1}$ . At the 2 higher densities, estimated filtering capacity remained at a level already reached at about  $200 \text{ m}^{-2}$ , as a consequence of the small size of nearly all bivalve individuals in these 2 years. Over the entire observed density range, the mean increase per extra ind.  $\text{m}^{-2}$  amounted to  $0.4 \text{ dm}^3 \text{ m}^{-2} \text{ h}^{-1}$  ( $r = 0.56$ ,  $p <$

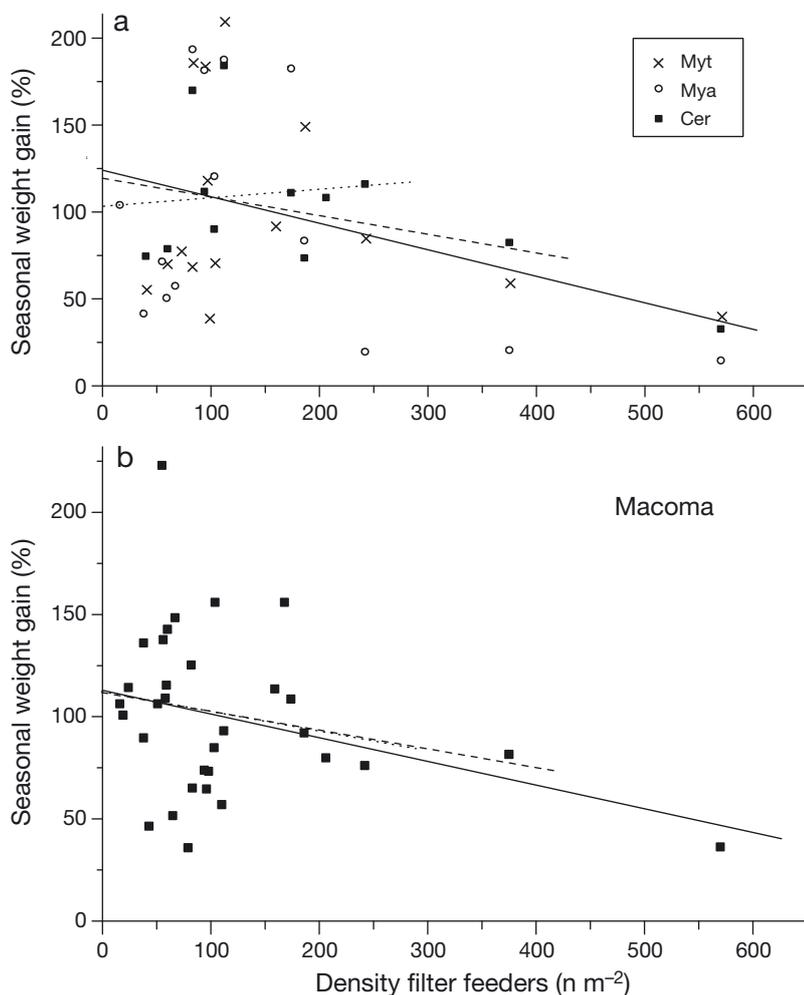


Fig. 6. Relationship between numerical abundance ( $D$ ) of bivalve suspension-feeders (data from Fig. 2c) and a measure of seasonal bivalve growth (as in Fig. 3: % of their long-term mean seasonal weight gain) in (a) values found in the 3 suspension-feeders (■: *Cerastoderma edule*, ×: *Mytilus edulis*, ○: *Mya arenaria*) and (b) the mixed-feeder *Macoma balthica*. The relationships shown by solid lines include all species and all years with sufficient growth observations. For the dashed lines, the year with the highest density ( $571 \text{ m}^{-2}$ ) was excluded, and for the dotted line, the year with the second highest density ( $376 \text{ m}^{-2}$ ) was also excluded. Only the slopes of the solid lines significantly differed from 0 (a:  $r = -0.39$ ,  $n = 41$ ,  $p < 0.01$ ; b:  $r = -0.32$ ,  $n = 32$ ,  $p < 0.05$ ; 2-sided tests). See Fig. 3 for standard errors of the separate values. Separate best fits for the 3 species in (a) for all densities: *C. edule*: % =  $118 - 0.14D$  ( $r = -0.51$ ,  $n = 12$ ,  $p = 0.09$ ); *M. edulis*: % =  $119 - 0.12D$  ( $r = -0.30$ ,  $n = 15$ ,  $p = 0.27$ ); *M. arenaria*: % =  $124 - 0.19D$  ( $r = -0.43$ ,  $n = 14$ ,  $p = 0.12$ )

0.001,  $n = 37$  years). As shown above (Fig. 6), consistent growth rate reductions occurred only at the highest bivalve densities, explaining why relationships between filtering capacity and growth were non-significant in all species.

We found no relationship between annual values of bivalve filtering capacity on Balgzand and chlorophyll concentrations in the growing season in the tidal inlet ( $r$  close to 0.0,  $p > 0.9$ ). This was also the

case with the relationship between values of total bivalve abundance and chlorophyll concentrations.

## DISCUSSION

### Species comparison

In all 4 studied bivalve species, the estimates of seasonal weight gains of the individuals revealed substantial between-year variability, by a factor of about 10. In the 3 suspension-feeding species (*Cerastoderma edule*, *Mya arenaria*, and *Mytilus edulis*), this variability showed a similar long-term pattern: years characterized by either rapid or slow growth largely coincided. However, the partly deposit-feeding species *Macoma balthica* did not share this synchronized fluctuation pattern.

We have no unambiguous answer to the question to what extent this lack of synchronization in this species was due to differences in its method of food acquisition and the resulting diet composition. These differences appear to be rather limited: *M. balthica* obtains part of its food from the water column, and observations on Balgzand indicated that its stomach contents showed a better resemblance with the algal species composition of the water than of that at the bottom (Kamermans 1994). Unfortunately, no long-term data are available on the composition of stomach contents of the studied bivalves or on food concentrations on or near the bottom.

The observed differential relationship of water temperature and growth rates in the species studied (Fig. 5) offers an alternative explanation. The 3 suspension-feeders showed a positive relationship of seasonal weight gain with temperature, whereas this relationship was negative in *M. balthica* (the latter was reported earlier by Beukema et al. 2009, 2014). This difference in response to high and low temperatures fits the differential distribution areas of the species: *M. balthica* is a more northern species than the other 3 bivalves studied. The other

(partly) deposit-feeding bivalve species that inhabit tidal flats in the Wadden Sea, viz. *Abra tenuis* and *Tellina tenuis*, are characterized by a more southern distribution than *M. balthica*. Accordingly, they grow faster in years with relatively higher growing-season temperatures (Dekker & Beukema 1993, 1999).

### Growth and food supply

Our results on *M. balthica* growth differed in another way from those of the other 3 species: only this bivalve showed a significant (positive) relationship between growth and chlorophyll concentration. Against our expectation, we found no such positive relationships in any of the 3 suspension-feeders (Table 4). We see no obvious explanation.

An analysis of possible relationships between growth rates and food supply was seriously hampered by a lack of data on chlorophyll concentrations at sites within the area where the growth data were obtained. The sampling stations for chlorophyll in the westernmost part of the Wadden Sea (Marsdiep and Doove Balg) were at distances of about 10 and 30 km, respectively, from Balgzand. It is questionable whether the available chlorophyll data can be used as indices of actual local food supply on the tidal flats, as these data were assessed in deep water masses that had not flowed over the tidal flats where we assessed growth rates. On the one hand, the strong positive correlation between the observed concentrations at the 2 distant sampling stations points to some overall representativeness of these values for the entire western Wadden Sea. On the other hand, chlorophyll concentrations are bound to be affected by local processes such as primary production (causing increases) and intensive grazing by benthos and zooplankton (causing reductions). Particularly when grazing pressure is high in shallow water, food supply can be strongly reduced locally and temporarily (Peterson & Black 1987, 1991), warranting a study on a local scale of relationships between competitor abundance and growth rates. We found negative relationships between competitor abundance on Balgzand and growth rate and think that this may be indicative of local and temporal food limitation at least at the highest levels of food demand. Apparently, the filtering activity of competitors affected only local food supplies, as we did not find any relationship between bivalve filtering activity on Balgzand and chlorophyll concentrations in the tidal inlet, at a distance of almost 10 km.

The negative relationships between competitor abundance and growth rates (Table 4) were significant only in *C. edule* (as also reported by Beukema & Dekker 2015) and in *M. balthica*. Serious reductions, to <50% of the long-term average, that occurred in all 4 species simultaneously, were observed only in the year (2012) with the highest abundance of filter-feeding bivalves in the study area (Fig. 6). Such substantial growth reduction in bivalves as a consequence of food shortage by competition appears to be a rare phenomenon in the Wadden Sea. Apart from the present finding that occurred in only 1 year out of a monitoring period of about 40 yr, it has been reported once for cockles in the Danish Wadden Sea, when their densities exceeded 1000 m<sup>-2</sup> for a short period (Jensen 1993). Some further relevant evidence is available for bivalves in coastal areas. Dekker & Beukema (2012) reported a significantly negative relationship between biomass and growth in the suspension-feeding bivalve *Ensis directus* in the western Wadden Sea. The observation on Balgzand by Kamermans (1993) of reduced growth of cockles in areas close to mussel beds follows this pattern. In the Oosterschelde, a tidal basin in the southwestern Netherlands, Smaal et al. (2013) found a positive correlation between chlorophyll concentrations and flesh content of mussels (which is positively related to preceding growth rate) and a negative relationship between mussel flesh content and total bivalve stock size.

In conclusion, we have no reason to suspect that annual weight gains in bivalve individuals are not positively influenced by high food supply *in situ*. Unfortunately, the data we had available on food concentrations were inadequate: a meaningful relationship can be found only if food supply is assessed with satisfactory frequency in the local area where the bivalves live.

### Long-term pattern

The long-term pattern of growth in the 3 filter-feeding species (Fig. 3a) revealed a conspicuous feature: the growth data could be divided into 3 periods (Fig. 4), with consistently elevated growth rates for the second period that started abruptly in 1991 and ended around 2005. What conditions made this period special?

Water temperatures in the area were significantly lower before than after 1991 (Table 2c), and this difference may have contributed to the higher growth rates of *M. edulis* and *M. arenaria* for the period

1991–2004 (Table 4, Fig. 5a). It is more difficult to evaluate the possible contributions of differences in food supply. As discussed above, no actual data are available for food supply on Balgzand itself. In the western Wadden Sea and probably also on Balgzand, chlorophyll concentrations were significantly lower after 2004 (Table 2d), and this may have contributed to the significantly lower growth rates in all 3 suspension-feeding bivalve species observed in the most recent decade. Local filtering activity was relatively high after 2004 (Table 2e), but differences between the 3 periods were non-significant. The 2 years (1988 and 2012) with peak abundance of bivalves and high food demands on Balgzand (see Fig. 2c), resulting in growth retardation in these years in all studied species (Fig. 6), were outside the period 1991–2004.

Two major and relevant changes in the ecosystem of the western Wadden Sea marked the start and end of the period 1991–2004 with elevated growth rates. A striking event took place in the summer of 1990, when a combination of storms and extraordinarily intensive fishery removed all mussel beds (and almost all cockle beds) from the tidal flats of Balgzand and surrounding areas (Beukema & Cadée 1996). The dramatic reduction of the mussel stocks in the entire western Wadden Sea lasted for more than a decade (Brinkman & Smaal 2003, Dankers et al. 2003). This event might contribute to an understanding of the higher bivalve growth rates for the second period as a result of diminished food demand of competitors. According to Philippart et al. (2007), the level of filtering capacity by mussels in the western Wadden Sea was substantially reduced after 1990. In the early 2000s, bivalve food demands in the western Wadden Sea will have increased again due to an increase to high abundance levels (tens of g AFDM m<sup>-2</sup>) of the bivalve *Ensis directus* over extensive areas, which has thus become the dominant species in the subtidal and low-intertidal part of the western Wadden Sea (Dekker & Beukema 2012) and along the Dutch mainland coast (Tulp et al. 2010). The increase of this invasive species appears to have contributed to the reduced chlorophyll concentrations in the third period (2005–2015) as measured both in Marsdiep and in Doove Balg (Fig. 2b, Table 2d).

### Perspectives for the Wadden Sea ecosystem

At present, 2 major changes are in progress in the Wadden Sea and other coastal sea areas: water temperatures are rising rapidly (Van Aken 2008, Van Oldenborgh et al. 2009), and algal concentrations

and primary production are declining due to de-eutrophication (Philippart et al. 2007, Henriksen 2009). Possible consequences for populations of bivalves appear to be clear in the case of *M. balthica*, whose growth rates decline as temperatures increase (Beukema et al. 2009; Fig. 4b) and chlorophyll concentrations decrease (Beukema et al. 2014; Table 4). However, our long-term data for the westernmost part of the Wadden Sea did not satisfactorily corroborate an expected negative long-term trend in growth rates (Fig. 3b: non-significant declining trend).

For the other 3 important bivalve species in the Wadden Sea, a prediction of their prospects is uncertain. Rising temperatures might favor their growth (Fig. 5a), but such increases in growth rates can proceed only as long as sufficient food is available for increasing costs of maintenance as well as growth. More intense grazing at higher temperature would deplete food supplies more rapidly. The declining growth rates in *C. edule* and *M. arenaria* observed for the last decade, a period with rising temperatures, might reflect the declining trend in chlorophyll concentrations.

Two recently introduced suspension-feeding bivalve species are now becoming dominant species in Dutch coastal waters: *Crassostrea gigas* (Troost 2010) and *E. directus* (Tulp et al. 2010, Dekker & Beukema 2012, Witbaard et al. 2015) and add to the demands for suspended algal food. In the present paper (Fig. 6), we report first signs that bivalve food demands can surpass food supplies, resulting in growth retardation in filter-feeding bivalves at high abundance. When declining trends in primary production and chlorophyll concentrations continue, years characterized by such growth retardation might become more frequent, the more so if food demands increase as a result of higher temperatures and increasing stocks of invasive species.

Although long-term changes in annual bivalve growth rates may be expected, possible consequences for the role of bivalves in the Wadden Sea ecosystem may be limited. This is because the observed variability in both annual production as well as biomass is explained in large part by their numerical abundance and in particular by the numbers of recruits rather than by their growth rates (Van der Meer et al. 2001, Beukema & Dekker 2006, 2007, 2015, Dekker & Beukema 2007, Beukema et al. 2010). Recruitment success is lower at high than at low temperatures (Beukema & Dekker 2014). Declining long-term trends in annual recruitment in Wadden Sea populations were found in *M. balthica*, *C. edule*, and *M. edulis* (Beukema & Dekker 2014).

On the other hand, disastrous severe winter mortalities would become rare events in a warmer climate. To date, a consistently declining trend in total numbers of suspension-feeding bivalves has not been observed in the westernmost part of the Wadden Sea (Fig. 2c).

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