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

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15

16 **Abstract** We report on results of a long-term (1978-2015) field study on between-year  
17 variability in annual weight growth of 1-y old individuals of 4 dominant bivalve species on tidal  
18 flats in the western part of the Wadden Sea: 3 filter feeders (*Cerastoderma edule*, *Mytilus edulis*,  
19 and *Mya arenaria*) and 1 filter/deposit feeder (*Macoma balthica*). Relationships between  
20 individual weight gain during the growing season and 2 environmental factors (temperature,  
21 food supply) in the growing season (March – August) were studied. Weight gains varied strongly  
22 from year to year (by an order of magnitude in all species) and showed significant correlations  
23 with water temperatures (negative in *M. balthica*, but positive in the other 3 species).  
24 Chlorophyll concentrations showed a significant (and positive) relationship with growth only in  
25 *M. balthica*. In the other 3 species, year-to-year fluctuations in growth were found to be  
26 synchronized, showing a consistent pattern with elevated values in the years between 1991 and  
27 2005. The abrupt change to faster growth in the early 1990s may have been caused by the  
28 nearly-complete disappearance in the western Wadden Sea of mussel beds for a period of  
29 several years, starting in 1990. The change to declining growth rates in the early 2000s took  
30 place simultaneously with a decline in chlorophyll concentrations and a rapid increase of the  
31 stocks of the invasive bivalve *Ensis directus*. In all 4 studied species, growth rates were  
32 seriously reduced in the 1 year (2012) with exceptionally high numbers of filter-feeding bivalves  
33 on the tidal flats.

34

35

36 **Key words:** seasonal weight gain; long-term data series; water temperature; chlorophyll  
37 concentration; numerical abundance; bivalves; Wadden Sea; *Cerastoderma edule*; *Mytilus*  
38 *edulis*; *Mya arenaria*; *Macoma balthica*.

39

## 40 Introduction

41 An important attribute of a population is the variability of annual weight growth of its  
42 individuals. It contributes to size distribution within the population, to magnitude and  
43 variability of biomass and (somatic and gamete) production of the population and to its  
44 significance as a food source for organisms at higher trophic levels. Mean individual growing-  
45 season weight gains usually vary substantially between years, asking for an analysis of  
46 underlying relationships with variable environmental conditions, such as food supply and  
47 temperature.

48 Examples of long-term studies on growth rates in coastal bivalve populations include a  
49 50-year study in *Mercenaria mercenaria* by Henry and Nixon (2008) and a 30-year study in  
50 *Macoma balthica* by Beukema et al. (2014), both showing significant variability from year to  
51 year in growth. Several factors have been put forward to explain such variability, including (a)  
52 water temperature with either positive (e.g. Jones et al. 1989; Heilmeyer et al. 2005) or  
53 negative (e.g. Jones 1981; Beukema et al. 2009, 2014) effects, (b) positive effects of food supply  
54 (e.g. Carmichael et al. 2012; Beukema et al. 2014), and (c) negative influences of high  
55 abundance of competitors for food (e.g. Peterson and Black 1987; Kamermans et al. 1992;  
56 Weinberg 1998; Beukema and Dekker 2015), which may be executed by (in most studies not  
57 adequately measured) reduction of food supply.

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

72 We hypothesize that annual growth in all species studied will be related positively to  
73 food supply, whereas relationships between temperatures and growth will be species-specific.  
74 As, by local consumption by competitors, local (unknown) food supply values will not have been  
75 identical to values observed at the distant sampling stations for phytoplankton, we add as a

76 hypothesis: growth rates in all species will be negatively related to local abundance of  
77 competitors for food.

78 In view of the present long-term trends in several coastal waters, including the Wadden  
79 Sea, of rising temperatures (Van Aken 2008) and declining eutrophication (Philippart et al.  
80 2007; Henriksen 2009; Loebel et al. 2009), the results will be valuable for understanding of  
81 future developments of growth and productivity as well as for steering management of coastal  
82 areas.

## 83 **Methods**

### 84 1. Study area

85 The data on bivalves were obtained as part of a long-term program involving twice-annual  
86 sampling ever since the 1970s of the macrozoobenthic animals at 15 permanent sampling  
87 stations located on Balgzand, a tidal flat area in the westernmost part of the Wadden Sea (at  
88 about 53° N and 5° E). Further details on the sampling area, the stations, and the methods can  
89 be found in Beukema and Cadée (1997). For the estimates of numerical abundance, data from  
90 all 15 stations were used. For the study of growth rates, we chose a relatively homogeneous  
91 area in the central part of Balgzand including 6 sampling sites (the transects numbered 4, 5, 8,  
92 9, 10, and 11 in Fig. 1). This part of Balgzand covered about one third of the total Balgzand tidal-  
93 flat area of 50 km<sup>2</sup>. In the part of Balgzand to the north of this area (2 sampling sites), data on  
94 growth were scarce due to failing recruitments of the studied species in nearly all years,  
95 probably due to adverse environmental conditions (exposure to strong currents and wave  
96 action, resulting in unstable and coarse sediments). South of the selected area, most (5 out of  
97 7) sampling sites were located at higher intertidal levels (above or around mean-tide level),  
98 where growth rates in bivalves were invariably lower than in the selected area, probably due to  
99 shorter daily immersion times. At the 2 remaining declined sampling sites (numbered 6 and 7 in  
100 Fig. 1) numbers and/or growth rates were consistently reduced in some species for unknown  
101 reasons.

### 102 2. Environmental conditions

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

108 Data on chlorophyll *a* concentrations in surface water were available from a data base of  
109 Rijkswaterstaat ([www.waterbase.nl](http://www.waterbase.nl)). The samples were taken at a frequency of once or twice per

110 month near the temperature station in Marsdiep and in an area called Doove Balg in the central  
111 part of the western Wadden, at about 15 km northeast of Balgzand. We used these concentrations  
112 as a proxy for phytoplankton abundance and available food for suspension feeders. We applied  
113 annual values of mean concentrations for half-y periods (March to August, incl.). For Marsdiep  
114 such chl *a* data were available for all years of the 1978-2015 period, for Doove Balg only for the  
115 21 years 1982-1995 and 2009-2015 (in other years sampling frequency was too low).

116 We did not use a similar long-term series of data on chlorophyll concentrations in the  
117 Marsdiep tidal inlet at the NIOZ jetty (Philippart et al. 2007), because these samples were taken  
118 at the time of high tide, thus characterizing North Sea rather than Wadden Sea water. The applied  
119 Rijkswaterstaat data were from samples taken (mostly) 2 to 3 h before the time of low tide, thus  
120 representing concentrations in water flowing back from the Wadden Sea to the North Sea and  
121 probably being more representative for water masses over tidal flats than high-tide values in  
122 water that did not directly reach tidal flats.

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

123  
124

### 125 3. Bivalve sampling

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

139 Numerical abundance was expressed in  $n\ m^{-2}$ , as means of data from all 15 stations. As an  
140 index of grazing pressure on phytoplankton, we used the sums of numerical densities of the 3  
141 dominant suspension feeding bivalves (*Cerastoderma edule*, *Mya arenaria*, *Mytilus edulis*) at  
142 the start of the growing season in February/March. These densities (particularly when high)  
143 were made up for the greater part by nearly-1-y-olds. Subsequent seasonal weight gain was on  
144 average similar in the individuals of the 3 species (see below: Results, section 2), allowing  
145 addition of their densities for the present purpose. We did not use biomass for this purpose, as  
146 total bivalve biomass was dominated by the contribution of big individuals of *M. arenaria* in  
147 several years, which are expected to filter less per unit of weight than the smaller individuals of  
148 the other species.

149

150

#### 4. Estimates of growth

151 We studied only the growth in the 2<sup>nd</sup> year of life of the bivalves: the growing season that  
152 started at an age of about 0.8 yr. For estimates of growth, we used data of a sampling site only  
153 if the cohort to be studied was represented with at least 3 individuals in the samples taken at  
154 the end of the growing season. For an estimate of mean growth on Balgzand in a particular  
155 year, such numbers should be available at 4 or more of the 6 sampling sites. In practice, this  
156 number usually amounted to 6, as successful year classes tend to arise simultaneously over vast  
157 areas (Beukema et al. 2001). As a consequence of the application of these criteria, growth dates  
158 were lacking for several years. During the 1978-2015 period, sufficient numbers for precise  
159 growth estimates were present in 12 year classes of *C. edule*, 15 of *M. edulis*, 14 of *M. arenaria*  
160 and 32 of *M. balthica*. In 8 years (1980, 1988, 1992, 1997, 2004, 2006, 2009, and 2012), such  
161 estimates were available for all 4 species. In a few additional years, data were available for 2 or  
162 3 species. *Ensis directus* and *Crassostrea gigas* were not included, because there were too few  
163 years with sufficient data on their growth.

164

165

#### 5. Estimates of pumping capacity

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

174

## 6. Statistics

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

$$183 \quad Y_i = \beta_0 + \beta_1(T_i > \tau_1) + \beta_2(T_i > \tau_2) + \epsilon_i$$

184 where  $Y_i$  represents the growth rate in year  $T_i$ ; the  $\beta$ 's are the unknown growth parameters,  
185 the  $\tau$ 's are the unknown time points at which a shift in growth rate occurs, and the  $\epsilon$ 's are  
186 independent and identically distributed normal errors. The three models were fitted (under the  
187 constraint that each period should at least contain two observations) and tested against each  
188 other by the F-test. The F-distribution under the null hypothesis of no change was estimated by  
189 Monte-Carlo simulation (10000 times) in which the time order of the growth rates was  
190 determined by random sampling without replacement from the original data.

191

## 192 Results

193

### 1. Environmental conditions

194 Mean water temperatures for the 6-month growing seasons of the 1979-2015 period (shown in  
195 Fig. 2a) averaged 13.0 °C (SE = 0.15, n = 37) for these half-y periods. They ranged from 11.2 to  
196 14.4 °C and showed a significantly ( $p < 0.01$ ) increasing long-term trend with a mean annual  
197 increase amounting to about 0.04 °C  $y^{-1}$ , which amounts to about 1.5 °C over the entire study  
198 period .

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



205 In the Balgzand area, numbers of filter-feeding bivalves, and thus demand for suspended  
206 food, varied strongly from year to year: from about 20 to about 600 m<sup>-2</sup> (Fig. 2c). These  
207 numerical densities did not show a statistically significant long-term trend.

## 208 2. Between-year variation in seasonal growth rates

209 In all bivalve species studied, the annual estimates of mean individual weight gain in the  
210 growing season varied strongly from year to year, from about 20 or 30 to about 200% of their  
211 long-term averages (Fig. 3). The absolute values of the long-term means of seasonal weight gain  
212 in the 2<sup>nd</sup> growing season amounted to quite similar values in *Cerastoderma edule*, *Mytilus*  
213 *edulis* and *Mya arenaria* of  $0.28 \pm 0.03$ ,  $0.25 \pm 0.04$  and  $0.30 \pm 0.04$  g AFDM ind<sup>-1</sup>, respectively,  
214 and in *M. balthica* to a much lower value of  $0.020 \pm 0.002$  g AFDM ind<sup>-1</sup> (n = 12 to 32: the  
215 numbers of years with sufficient data). Note that most of the SE values shown in Fig. 3  
216 (indicating variability in growth rates between the 6 sampling stations) were relatively small as  
217 compared to the between-year differences in weight gain in the species concerned, showing  
218 that (a) differences between station-estimates in the same year were usually rather small and  
219 (b) a high proportion of the between-year differences in growth rate were, therefore,  
220 statistically significant.

221 At first sight, the distribution of annual values of seasonal weight gain over the entire  
222 1979-2015 period of observation appears to be far from random in the filter-feeding species  
223 (Fig. 3a). Years with peak- and low-values of weight gain tended to occur simultaneously in  
224 these 3 species. For instance, low values in all 3 species were found in 2012, whereas values  
225 were high in all of these species in 1992 and 1997. Indeed, the correlations between the annual  
226 growth rates of these 3 species were positive and statistically significant (Table 1). However, in  
227 the 1 other species *M. balthica* (that takes its food partially by deposit feeding), the pattern of  
228 years with rapid and slow growth (Fig. 3b) deviated from those in the 3 suspension feeders (Fig.  
229 3a). No significant correlations were found between this 1 species and the other 3 species  
230 (Table 1).

231 The similar patterns for the 3 suspension feeding species suggest a breakdown into 3  
232 periods, with the 1991 to about 2005 period showing elevated growth rates (Fig. 3a; Table  
233 2a,b). In all of these 3 species, the differences in mean growth rates between the 1<sup>st</sup> and 2<sup>nd</sup>  
234 and between the 2<sup>nd</sup> and 3<sup>rd</sup> period were statistically significant, whereas not any significant  
235 differences were found between the 1<sup>st</sup> and 3<sup>rd</sup> period (t-tests; Table 2a,b). For *M. arenaria* and  
236 *M. edulis*, the segregated regression model fitted best when tested for 3 periods (as contrasted  
237 to a model with 1 or 2 periods: Table 3 (models 3, 2 and 1, respectively). In *C. edule*, a division  
238 into 2 or 3 periods was less clear-cut (Table 3: no p values of <0.05, i.e. the models did not differ  
239 significantly from each other). The first breakpoint around 1991 was observed in all 3 species,  
240 the second one occurred somewhere around 2006 (Fig. 4), but was not identical in all species.

241 Its timing was between 2004 and 2006 in *M. edulis* (Fig. 4a) and *C. edule* (Fig. 4c) and only  
242 between 2006 and 2009 in *M. arenaria* (Fig. 4b). The last year with elevated growth rates  
243 (means of >1 s.e. above long-term average, see Fig. 3a) occurring simultaneously in all 3 species  
244 was 2004. After that year, such high growth rates did not occur in any year in any of the 3  
245 suspension-feeding bivalve species. In all of these species, growth rates showed a declining  
246 trend over the 2004 to 2015 period, significantly so ( $p < 0.05$ ) in *C. edule* and in *M. arenaria*.

247 In the growth estimates of *M. balthica* no trace of the above 3 periods could be  
248 discerned (Fig. 3b). In this species, not any of the differences in mean growth rates between the  
249 above 3 periods was statistically significant (Table 2a,b). This was the only one of the 4 studied  
250 species in which the estimates suggested a consistent (declining) long-term (1979-2015) trend,  
251 but this trend was statistically non-significant ( $r = -0.22$ ,  $n = 32$ ,  $p = 0.22$ ).

### 252 3. Relationships with environmental factors

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

257 Effects of prevailing water temperatures during the growing season on bivalve growth  
258 rates were substantial. From years with relatively low (11-12 °C) to relatively high (around 14  
259 °C) mean temperatures, weight gains on average roughly doubled in *Mya arenaria* and *Mytilus*  
260 *edulis* (Fig. 5a) and halved in *Macoma balthica* (Fig. 5b). In *Cerastoderma edule* the response of  
261 growth to temperature appeared to be weak (dotted line in Fig. 5a). Growing-season water  
262 temperatures were in the 2<sup>nd</sup> period of elevated growth in suspension-feeding bivalves  
263 significantly higher than in the preceding period (Table 2c). This difference may contribute to an  
264 explanation of the higher growth rates.

265 Annual mean chlorophyll *a* concentrations during March – August periods did not show  
266 significant correlations with seasonal weight gain in any of the 3 suspension feeding bivalve  
267 species (Table 4). However, in *M. balthica* this relationship was significantly positive, both for  
268 the chlorophyll concentrations in the tidal inlet (Marsdiep) and for the concentrations in the  
269 inner part of the western Wadden Sea (Doove Balg). Chlorophyll concentrations were in the 2<sup>nd</sup>  
270 period with elevated growth rates significantly higher than in the subsequent period (Table 2d).  
271 Numerical densities of the 3 main filter-feeding bivalve species together and their filtering  
272 capacity were lower in the 2<sup>nd</sup> period than in the preceding and subsequent period, but not  
273 statistically significantly so (Table 2f and 2e). The quotient of chlorophyll concentrations divided  
274 by numerical density might be used as a proxy for the amount of food available per individual.

275 This quotient was not higher in the 2<sup>nd</sup> as compared to the 1<sup>st</sup> period, but it was significantly  
276 higher in the 2<sup>nd</sup> as compared to the 3<sup>rd</sup> period (Table 2g).

#### 277 4. Relationships with bivalve abundance

278 In most species, relationships between their own abundance and growth rates were weak and  
279 non-significant (“own species” column in Table 4). Only in *Cerastoderma edule*, seasonal weight  
280 gains tended to be lower in years with high numerical densities at the start of the growing  
281 season than in years with low abundance of this species: the Pearson-r value of -0.54 for the  
282 correlation between abundance and growth was statistically significant in this species.

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

292 The statistical significance of the above negative relationships between abundance and  
293 growth completely disappeared if the 6 points for the growth of the 3 species at the 2 highest  
294 densities were omitted:  $r = +0.05$ ,  $n = 35$ ,  $p = 0.8$  (dotted line in Fig. 6a). Thus, growth rates  
295 were reduced only in the 2 years (1988 and particularly 2012, compare Fig. 3a) with the highest  
296 numerical abundance of filter-feeding bivalves at the start of the growing season, when weight  
297 gains in all species studied were well below the long-term average (i.e. 100% in Fig. 6). Even a  
298 mere exclusion of the data for the 1 year (2012) with the highest density (571 m<sup>-2</sup>) turned the  
299 relationship into a non-significant one (dashed line in Fig. 6a), though the slopes of the full and  
300 dashed lines were not very different. Similarly, growth rates in *Macoma balthica* appeared to  
301 be reduced at higher filter-feeding bivalve densities (full line in Fig. 6b:  $r = -0.32$ ,  $n = 32$ ,  $p < 0.05$ ),  
302 but again statistical significance was due only to the inclusion of the 1 year with the highest  
303 total density. Note that the exceptionally low values for weight gain for 2012 appear in Fig. 5a  
304 as a 3-species group of outliers (the 3 lower points at 13.4 °C).

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

310

## 5. Bivalve abundance and food supply

311 High abundance of suspension-feeding bivalves resulted in high volumes of water filtered per  
312 unit of time: a mean increase of  $0.4 \text{ dm}^3 \text{ m}^{-2} \text{ h}^{-1}$  per 1 extra individual bivalve  $\text{m}^{-2}$  ( $r = +0.56$ ,  
313  $p < 0.001$ ,  $n = 37$ : years). For a range of numerical densities of filter feeders up to about  $250 \text{ m}^{-2}$ ,  
314 this increase was steeper:  $0.8 \text{ dm}^3 \text{ m}^{-2} \text{ h}^{-1}$ . At the 2 higher densities, estimated filtering capacity  
315 remained at a level already reached at about  $200 \text{ m}^{-2}$ , as a consequence of the small size of  
316 nearly all bivalve individuals in these 2 years.

317 High abundance of suspension-feeding bivalves resulted in high volumes of water filtered per  
318 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  $250$   
319  $\text{m}^{-2}$ ), the volume of water filtered increased on average by  $0.8 \text{ dm}^3 \text{ m}^{-2} \text{ h}^{-1}$ . At the 2 higher  
320 densities, estimated filtering capacity remained at a level already reached at about  $200 \text{ m}^{-2}$ , as a  
321 consequence of the small size of nearly all bivalve individuals in these 2 years. Over the entire  
322 observed density range, the mean increase per extra individual bivalve  $\text{m}^{-2}$  amounted to  $0.4$   
323  $\text{dm}^3 \text{ m}^{-2} \text{ h}^{-1}$  ( $r = +0.56$ ,  $p < 0.001$ ,  $n = 37$ : years).

324 As shown above (Fig. 6), consistent growth rate reductions occurred only at the highest bivalve  
325 densities, explaining why relationships between filtering capacity and growth were non-  
326 significant in all species.

327 We found no relationship between annual values of bivalve filtering capacity on  
328 Balgzand and chlorophyll concentrations in the growing season in the tidal inlet ( $r$  close to 0.0,  
329  $p > 0.9$ ). The same was the case with the relationship between values of total bivalve abundance  
330 and chlorophyll concentrations.

## 331 Discussion

### 332 a. Species comparison

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

339 We have no unambiguous answer to the question to what extent this lack of  
340 synchronization in this species was due to differences in its way of food gathering and resulting  
341 diet composition. These differences appear to be rather limited: *M. balthica* obtains part of its  
342 food from the water column and, according to observations on Balgzand, its stomach contents

343 showed a better resemblance with the algal species composition of the water than at the  
344 bottom (Kamermans 1994). Unfortunately, not any long-term data are available neither on  
345 composition of stomach contents of the studied bivalves nor on food concentrations on or near  
346 the bottom.

347 The observed differential relationship of water temperature and growth rates in the  
348 various species studied (Fig. 5) offers an alternative explanation. The 3 suspension-feeding  
349 species had in common that they showed a positive relationship of seasonal weight gain with  
350 temperature, whereas this relationship was negative in *M. balthica* (the latter was reported  
351 earlier by Beukema et al. 2009, 2014). This difference in response to high and low temperatures  
352 fits the differential distribution areas of the species: *M. balthica* is a more northern species than  
353 the other 3 bivalves studied. The other (partly) deposit-feeding bivalve species that are living on  
354 tidal flats in the Wadden Sea, *Abra tenuis* and *Tellina tenuis*, are characterized by a more  
355 southern distribution than *M. balthica*. Accordingly, they grow faster in years with relatively  
356 high than low growing-season temperatures (Dekker and Beukema 1993, 1999).

#### 357 b. Growth and food supply

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

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



414 Balgzand, chlorophyll concentrations were significantly lower after 2004 (Table 2d) and this  
415 may have contributed to the significantly lower growth rates in all 3 suspension-feeding bivalve  
416 species observed in the most recent decade. Local filtering activity was relatively high after  
417 2004 (Table 2e), but differences between the 3 periods were non-significant. The 2 years with  
418 peak-abundance of bivalves and high food demands on Balgzand (1988 and 2012, see Fig. 2c),  
419 resulting in growth retardation in these years in all studied species (Fig. 6), were beyond the  
420 1991-2004 period.

421 Two major and relevant changes in the ecosystem of the western Wadden Sea marked the  
422 start and end of the 1991-2004 period with elevated growth rates. A striking event took place in  
423 the summer of 1990, when fishery removed all mussel beds (and almost all cockle beds) from  
424 the tidal flats of Balgzand and surrounding areas (Beukema and Cadée 1996). The dramatic  
425 reduction of the mussel stocks in the entire western Wadden Sea lasted for more than a decade  
426 (Brinkman and Smaal 2003, Dankers et al. 2003). This event might contribute to an  
427 understanding of the higher bivalve growth rates for the 2<sup>nd</sup> period by a diminished food  
428 demand of competitors. According to Philippart et al. (2007), the level of filtering capacity by  
429 mussels in the western Wadden Sea was substantially reduced after 1990. In the early 2000s,  
430 bivalve food demands in the western Wadden Sea will have increased again due to an increase  
431 to high abundance levels (tens of g AFDM m<sup>-2</sup>) of the bivalve *Ensis directus* over extensive areas,  
432 thus becoming the dominant species in the subtidal and low-intertidal part of the western  
433 Wadden Sea (Dekker and Beukema 2012) and along the Dutch mainland coast (Tulp et al.  
434 2010). The increase of this invasive species appears to have contributed to the reduced  
435 chlorophyll concentrations in the 3<sup>rd</sup> (2005-2015) period as measured both in Marsdiep and in  
436 Doove Balg (Fig. 2b; Table 2d).

#### 437 d. Perspectives for the Wadden Sea ecosystem

438 Nowadays, two major changes are in progress in the Wadden Sea and other coastal sea areas:  
439 water temperatures are rising rapidly (Van Aken 2008; Van Oldenborgh et al. 2009) and algal  
440 concentrations and primary production are declining due to de-eutrophication (Philippart et al.  
441 2007; Henriksen 2009). Possible consequences for populations of bivalves appear to be clear in  
442 the case of *Macoma balthica*, which species' growth rates are lower as temperatures are higher  
443 (Beukema et al. 2009; Fig. 4b) and chlorophyll concentrations are lower (Beukema et al. 2014;  
444 Table 4). However, our long-term data for the westernmost part of the Wadden Sea did not  
445 satisfactorily corroborate an expected negative long-term trend in growth rates (Fig. 3b: a non-  
446 significant declining trend).

447 In the other 3 important bivalve species in the Wadden Sea, a prediction of their  
448 prospects is uncertain. Rising temperatures might favour their growth (Fig. 5a), but such  
449 increase in growth rates can proceed only as long as sufficient food is available for increasing

450 costs of maintenance as well as growth. More intense grazing at higher temperature would  
451 deplete food supplies more rapidly.

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

461 Though long-term changes in annual bivalve growth rates may be expected, possible  
462 consequences for the role of bivalves in the Wadden Sea ecosystem may be limited. This is so,  
463 because the observed variability in both annual production as well as biomass is explained for  
464 the greater part by their numerical abundance and in particular by the numbers of their recruits  
465 rather than by their growth rates (Van der Meer et al. 2001; Beukema and Dekker 2006, 2007,  
466 2015; Dekker and Beukema 2007; Beukema et al. 2010). Recruitment success was found to be  
467 lower at high than at low temperatures (Beukema and Dekker 2014). Declining long-term  
468 trends in annual recruitment in Wadden Sea populations were found in *M. balthica*,  
469 *Cerastoderma edule* and *Mytilus edulis* (Beukema and Dekker 2014). On the other hand,  
470 disastrous severe-winter mortalities would become rare events in a warmer climate. So far, a  
471 consistently declining trend in total numbers of suspension-feeding bivalves has not been  
472 observed in the westernmost part of the Wadden Sea (Fig. 2c) and consistent declines in *M.*  
473 *balthica* abundance all over the Dutch Wadden Sea were limited to the last 15 or 20 years  
474 (Beukema et al., in prep.).

475

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590

591 Table 1. Coefficients of between-species Pearson correlations in various years of the 1979-2015  
 592 period of their seasonal weight gains between March and August for their 2<sup>nd</sup> growing season  
 593 (in g AFDM ind<sup>-1</sup>). The numbers of years (n) in each comparison was usually 8 (more only in the  
 594 pair *M. arenaria*/*M. balthica*), being the number of years in which the 2 species involved were  
 595 sufficiently numerous at 4 or more out of the 6 sampling stations.  
 596 Statistical significance indicated by \* (p<0.05) or \*\* (p<0.01).

	<i>Mytilus edulis</i>	<i>Mya arenaria</i>	<i>Macoma balthica</i>
600			
601 <i>Cerastoderma edule</i>	+0.80**	+0.71*	+0.10
602 <i>Mytilus edulis</i>		+0.86**	-0.01
603 <i>Mya arenaria</i>			-0.18
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614			

615 Table 2. Means (with 1 SE) of annual values separately for 3 periods and 4 bivalve species of:  
 616 (a) individual seasonal weight gain in the central part of Balgzand,  
 617 (b) this gain expressed in a relative measure (as in Fig. 3),  
 618 (c) mean water temperatures during the growing seasons (Marsdiep)  
 619 (d) mean chlorophyll concentrations during the growing seasons (Marsdiep and Doove Balg)  
 620 (e) mean filtration capacity of suspension-feeding bivalves on Balgzand  
 621 (f) summed mean numerical densities of 3 species of filter-feeding bivalves on Balgzand  
 622 (g) quotients of chlorophyll concentrations (Marsdiep) divided by filter-feeding bivalve densities  
 623 (Balgzand).

624 Statistical significance of differences between periods by \*, \*\* or \*\*\* for <0.05, <0.01 and  
 625 <0.001, respectively (t-tests). For differences in weight gains between the first and last period,  
 626 no significant differences were found, but for water temperatures and chlorophyll  
 627 concentrations these differences were significant (\*\*).

628 <sup>1)</sup> Data on *M. arenaria* concern the periods 1991-2007 and 2008-2015 (compare Fig. 4).

630	631	1979-1990		1991-2004 <sup>1)</sup>		2005-2015 <sup>1)</sup>
632	a.	Mean weight gain in 2 <sup>nd</sup> growing season in g AFDM ind <sup>-1</sup> ± 1 SE (n = 3 to 10 y)				
633	<i>C. edule</i>	0.25 ± 0.03	*	0.37 ± 0.04	**	0.19 ± 0.03
634	<i>M. edulis</i>	0.15 ± 0.02	***	0.53 ± 0.03	***	0.19 ± 0.02
635	<i>M. arenaria</i>	0.13 ± 0.03	***	0.49 ± 0.05	**	0.15 ± 0.10
636	<i>M. balthica</i>	0.021 ± 0.002		0.018 ± 0.002		0.018 ± 0.003
637	b.	Data of (a) expressed as a % of the long-term mean of the species (n = 3 to 10 y)				
638	<i>C. edule</i>	92 ± 12	*	136 ± 16	**	67 ± 12
639	<i>M. edulis</i>	64 ± 8	***	193 ± 8	**	86 ± 14
640	<i>M. arenaria</i>	43 ± 8	***	161 ± 16	**	48 ± 34
641	<i>M. balthica</i>	111 ± 14		94 ± 9		90 ± 14
642						
643	c.	Mean water temperature March-August in °C (n = 11 to 14)				
644	Marsdiep	12.32 ± 0.24	**	13.35 ± 0.18		13.31 ± 0.24
645						
646	d.	Mean chlorophyll concentration March-August in mg dm <sup>-3</sup>				

647 Doove Balg  $14.2 \pm 1.0$  (10)  $17.7 \pm 2.0$  (5) \*\*  $9.8 \pm 0.4$  (4)

648 Marsdiep  $16.3 \pm 1.2$  (13) \*  $13.2 \pm 0.8$  (13) \*  $10.9 \pm 0.8$  (8)

649 e. Mean bivalve filtration capacity in  $\text{dm}^3 \text{m}^{-2} \text{h}^{-1}$

650 Balgzand  $117 \pm 21$  (12)  $113 \pm 22$  (14)  $145 \pm 17$  (11)

651 f. Mean bivalve densities in  $\text{n m}^{-2}$

652 Balgzand  $104 \pm 25$  (12)  $83 \pm 15$  (14)  $139 \pm 42$  (11)

653

654 g. Index of amount of food available per individual (chlor/density)

655 Quotient of means 0.16 0.16 0.08

656 Mean of quotients  $0.22 \pm 0.03$  (12)  $0.24 \pm 0.07$  (13) \*  $0.14 \pm 0.03$  (11)

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662 Table 3. Residual sum of squares (RSS) for the 3 segmented regression models (1, 2, or 3  
663 periods, respectively), and p-values of the various F-tests. Significant results and finally selected  
664 models in bold.

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

665

666 Table 4. Coefficients of Pearson correlations between seasonal weight gains during the March-  
 667 August growing season and some environmental factors in 4 bivalve species: *Cerastoderma*  
 668 *edule*, *Mytilus edulis*, *Mya arenaria* and *Macoma balthica*. Water temperatures and chlorophyll  
 669 concentrations were measured at high tide in the Marsdiep tidal inlet for March-August  
 670 periods. Chlorophyll concentrations were also available for a station in the inner part of the  
 671 western Wadden Sea (Doove Balg), but for a smaller number of years. Numerical densities (n  
 672 m<sup>-2</sup>) were estimated each year in February/March at the start of the growing season on  
 673 Balgzand. Number (n) of years with sufficient data on weight gain (see Methods) shown in first  
 674 column (with the lower numbers for relationships with chlorophyll in Doove Balg between  
 675 brackets). Statistical significance indicated by \* for p<0.05 and \*\* for p<0.01 (1-sided tests were  
 676 applied for relationships with chlorophyll and density).

677

678	species	n	Water	Chlorophyll		Numerical density of:	
679			temp.	concentration		Own sp.	Σ3 susp.f.
680				Mdiep	Dbalg		
681	<i>C. edule</i>	12 (8)	+0.24	+0.16	+0.40	-0.54*	-0.51*
682	<i>M. edulis</i>	15 (8)	+0.51*	-0.25	+0.08	-0.07	-0.30
683	<i>M. arenaria</i>	14 (8)	+0.56*	-0.24	+0.10	-0.24	-0.35
684	<i>M. balthica</i>	31 (19)	-0.53**	+0.49**	+0.44*	+0.14	-0.32*

685

686



687 Fig. 1. Map of the westernmost part of the Dutch Wadden Sea with the Balgzand tidal-flat  
688 area. The permanent sampling sites for benthic animals are indicated: 12 transects (numbered  
689 1 – 12) and 3 squares (A, B, C). Bivalve growth rates were studied in detail at the 6 transects  
690 numbered 4, 5, 8, 9, 10, and 11 in the central part of Balgzand. The sampling sites for water  
691 temperatures and chlorophyll concentrations are indicated by Marsdiep Noord (main tidal inlet)  
692 and Doove Balg West (inner part of western Wadden Sea).

693 Fig. 2. Long-term data series of estimates of (a) surface water temperatures in Marsdiep, (b)  
694 chlorophyll *a* concentrations as observed in (solid points) the main tidal inlet (Marsdiep) and  
695 (open points) the central part of the westernmost part of the Dutch Wadden Sea (Doove Balg),  
696 and (c) numerical densities of filter-feeding bivalves on Balgzand. The dashed lines show long-  
697 term trends, for Marsdiep and Balgzand data only.

- 698 (a) Mean water temperatures for the March–August growing season (in °C), showing a  
699 significantly increasing trend by  $0.04\text{ °C y}^{-1}$  ( $r = +0.51$ ,  $n = 37$ ,  $p < 0.01$ );  
700 (b) Mean chlorophyll-*a* concentrations (in  $\text{mg m}^{-3}$ ) for the March–August growing season,  
701 showing declining trends by 0.21 and  $0.17\text{ mg m}^{-3}$ , for Marsdiep ( $r = -0.59$ ,  $n = 37$ ,  $p < 0.001$ )  
702 and Doove Balg ( $r = -0.44$ ,  $n = 19$ ,  $p = 0.06$ ), respectively. The outlying point for 1996 was not  
703 used;  
704 (c) Sums of numerical densities (in  $\text{n m}^{-2}$ ) of the 3 main suspension-feeding bivalves  
705 (*Cerastoderma edule*, *Mytilus edulis*, *Mya arenaria*) on Balgzand (means of 15 sampling  
706 sites) at the start of the growing season in February/March. The trend by  $+1.2\text{ y}^{-1}$  ( $r = +0.13$ ,  
707  $n = 40$ ,  $p = 0.4$ ) was non-significant.

708 Fig. 3. Long-term changes in indices for annual growth rates in (a) 3 suspension feeding bivalve  
709 species of bivalves and (b) the bivalve species with a mixed feeding type. Growth rates are  
710 shown as mean seasonal weight gains of individuals in their 2<sup>nd</sup> growing season, expressed as a  
711 percentage of their long-term mean (1979–2015) growth rates (set at 100%). Means are given  
712 with 1 SE with  $n \geq 3$ , but mostly 5 or 6 (the number of Balgzand sampling stations with sufficient  
713 data) and thus represent local variation. The vertical dotted line marks a major change in the  
714 western Wadden Sea: the disappearance of mussel beds in 1990.

- 715 (a) *Cerastoderma edule* (solid squares); *Mytilus edulis* (crosses); *Mya arenaria* (open  
716 circles);  
717 (b) *Macoma balthica* (solid squares).

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

722 Fig. 5. Relationships between seasonal water temperatures (T) in the tidal inlet (in °C) and  
723 indices for annual growth rates in (a) 3 suspension feeding species of bivalves and (b) the  
724 species with a mixed feeding type. Growth rates are expressed in relative weight gains (%), as in  
725 Fig. 3.

726 (a) *Cerastoderma edule* (solid squares); *Mytilus edulis* (crosses); *Mya arenaria* (open  
727 circles);  
728 (b) *Macoma balthica* (solid squares).

729 Best linear fits:

730 *C. edule*: % = -96 + 15.1 T (r = +0.24, n=12, p=0.5)

731 *M. edulis*: % = -339 + 33.8 T (r = +0.51, n=15, p=0.05)

732 *M. arenaria*: % = -378 + 37.0 T (r = +0.56, n=14, p<0.05)

733 *M. balthica*: % = 402 - 23.4 T (r = -0.53, n=32, p<0.01).

734 Fig. 6. Relationship between numerical abundance (D) of bivalve suspension feeders (data from  
735 Fig. 2c) and a measure of seasonal bivalve growth (as in Fig. 3: percentages of their long-term  
736 mean seasonal weight gain: %) in (A) values found in the 3 suspension feeders: either (■)  
737 *Cerastoderma edule*, (x) *Mytilus edulis*, or (o) *Mya arenaria* and (B) the mixed feeder *Macoma*  
738 *balthica*. The relationships shown by full lines include all species and all years with sufficient  
739 growth observations, for the dashed lines the 1 year with highest density (571 m<sup>-2</sup>) was  
740 excluded, for the dotted line also the year with the one but highest density (376 m<sup>-2</sup>) was  
741 excluded. Only the slopes of the full lines significantly differed from 0 (A: r = -0.39, n=41, p <  
742 0.01; B: r = -0.32, n=32, p<0.05; 2-sided tests). See Fig. 3 for standard errors of the separate  
743 values. Separate best fits for the 3 species in (A) for all densities:

744 *C. edule*: % = 118 - 0.14 D, r = -0.51, n = 12, p = 0.09;

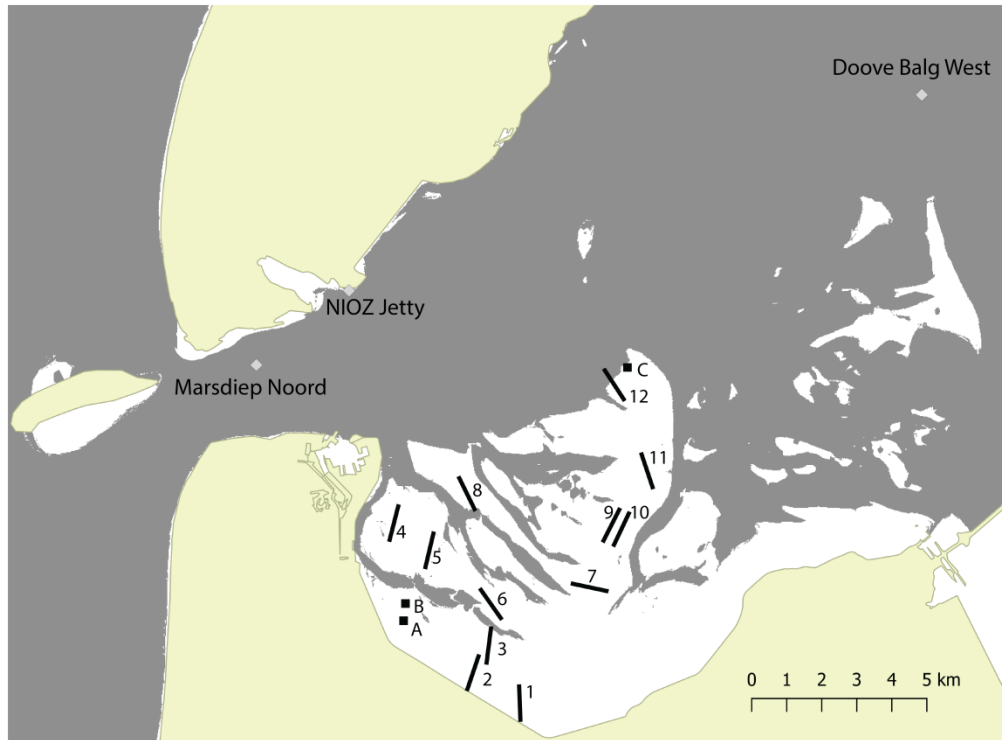
745 *M. edulis*: % = 119 - 0.12 D, r = -0.30, n = 15, p = 0.27;

746 *M. arenaria*: % = 124 - 0.19 D, r = -0.43, n = 14, p = 0.12.

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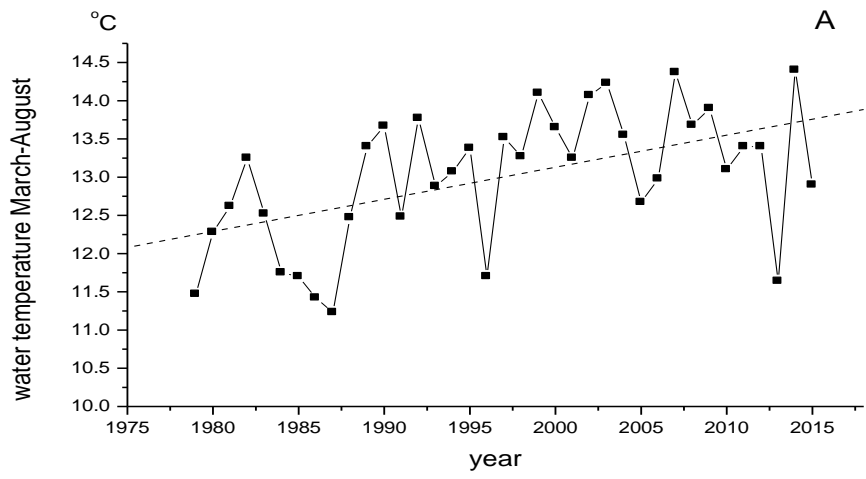
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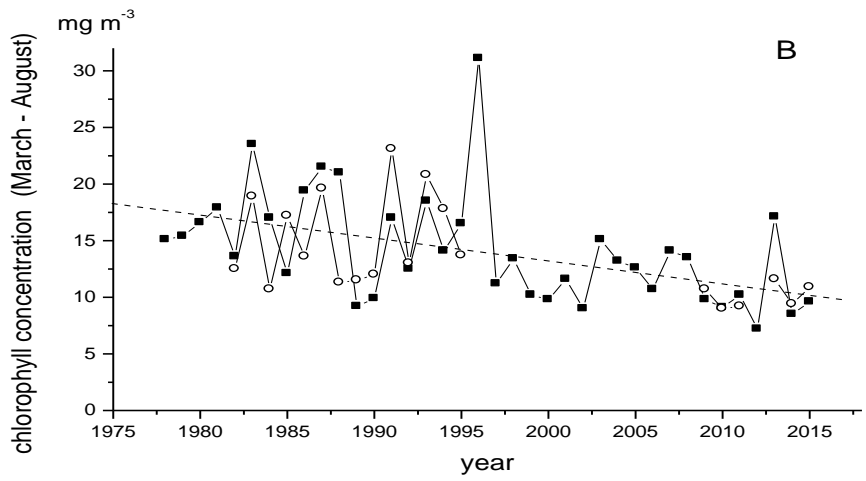
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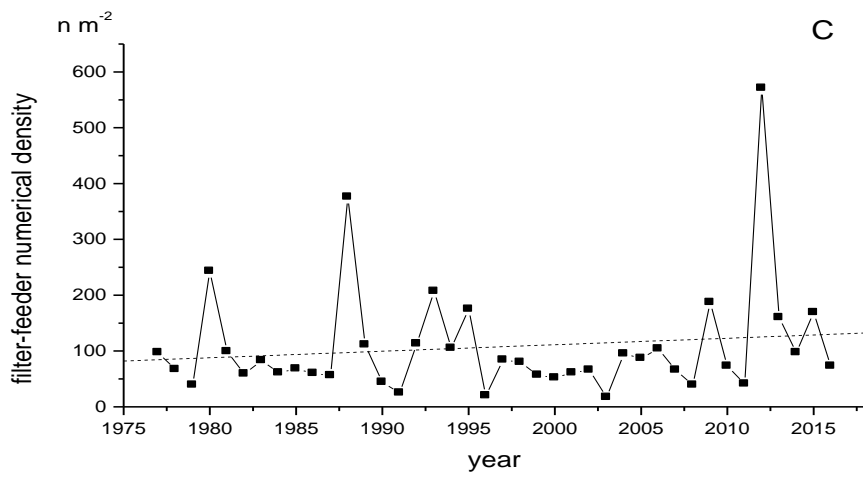
752 Fig. 1



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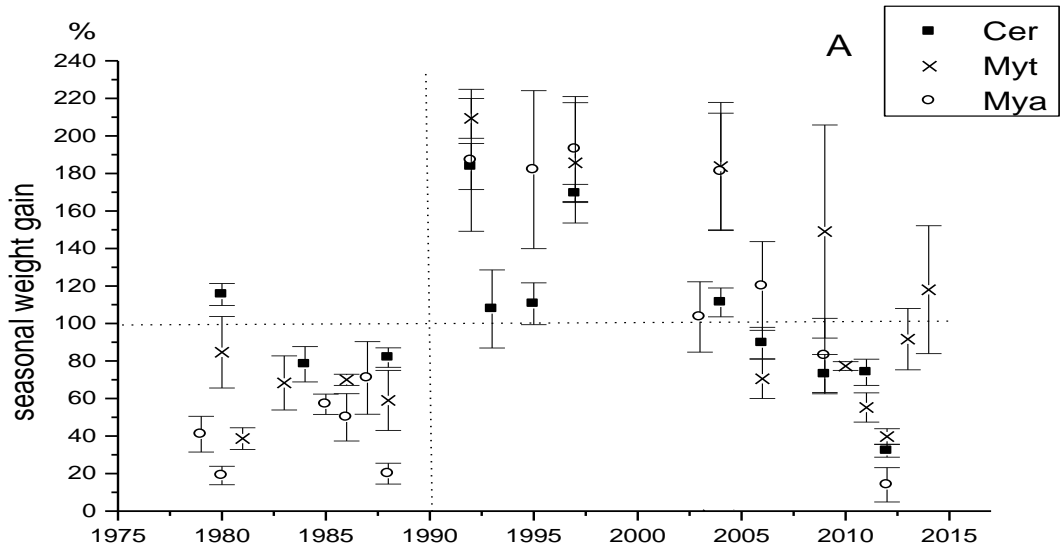


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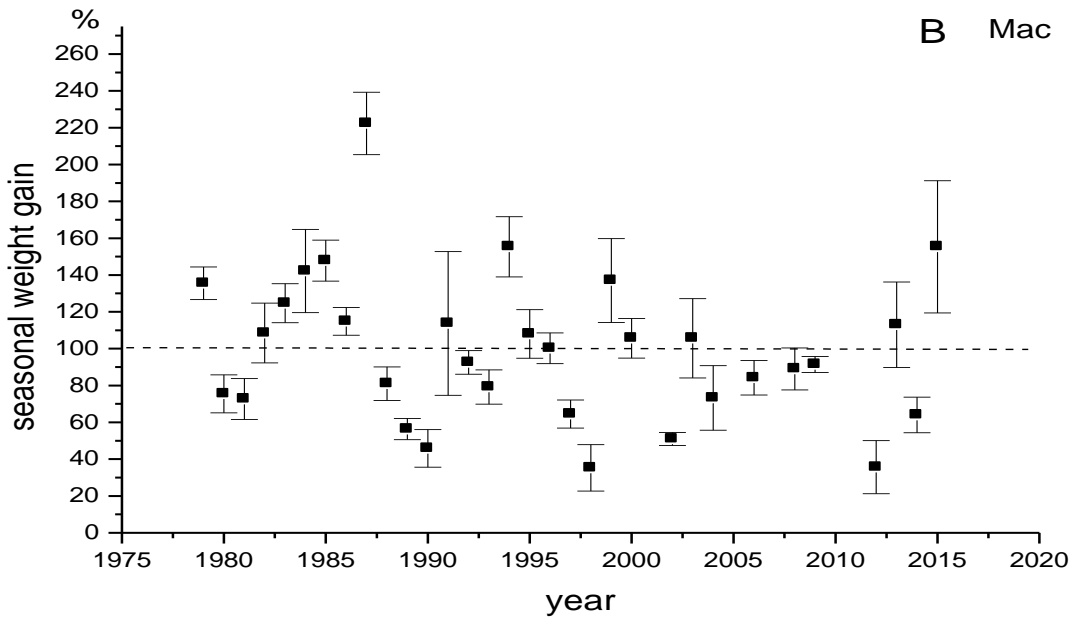


755 Fig. 2

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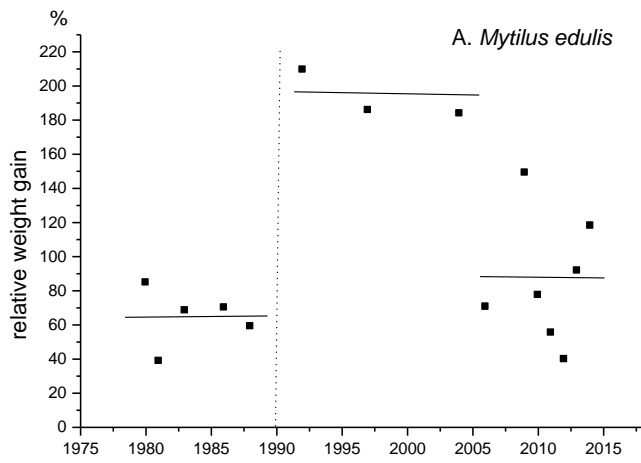
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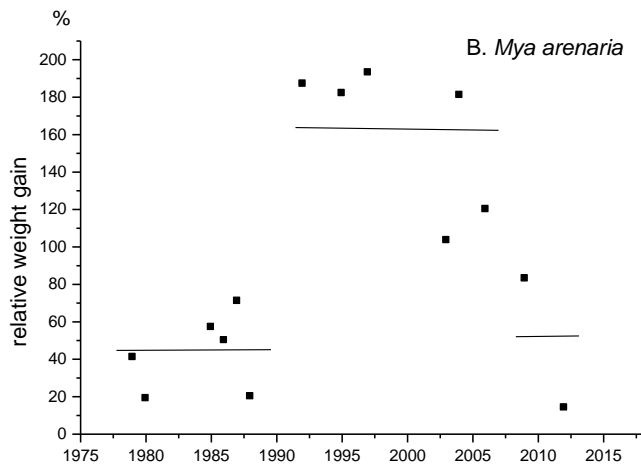
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759 Fig. 3

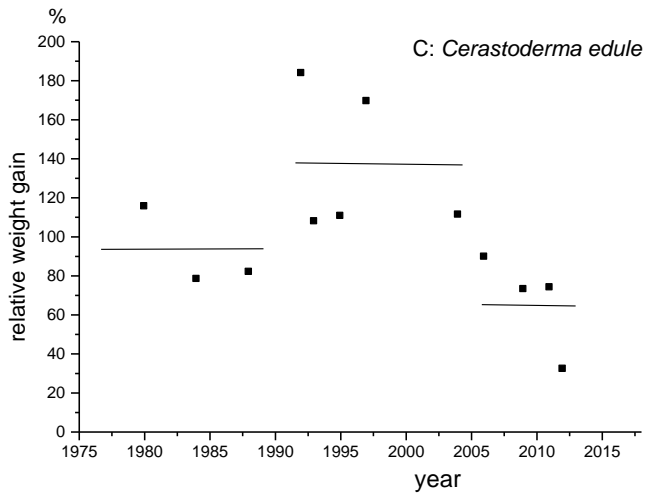
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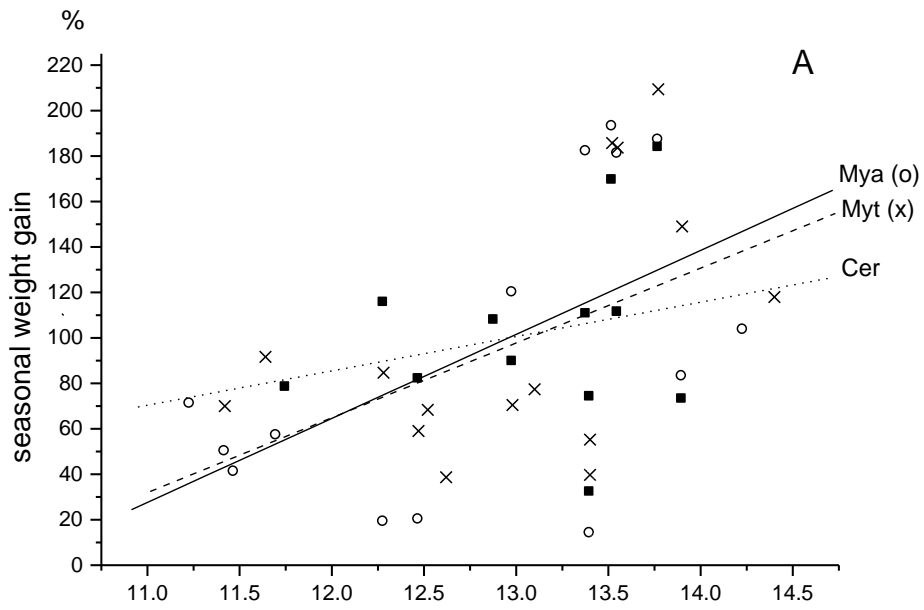
763 Fig. 4

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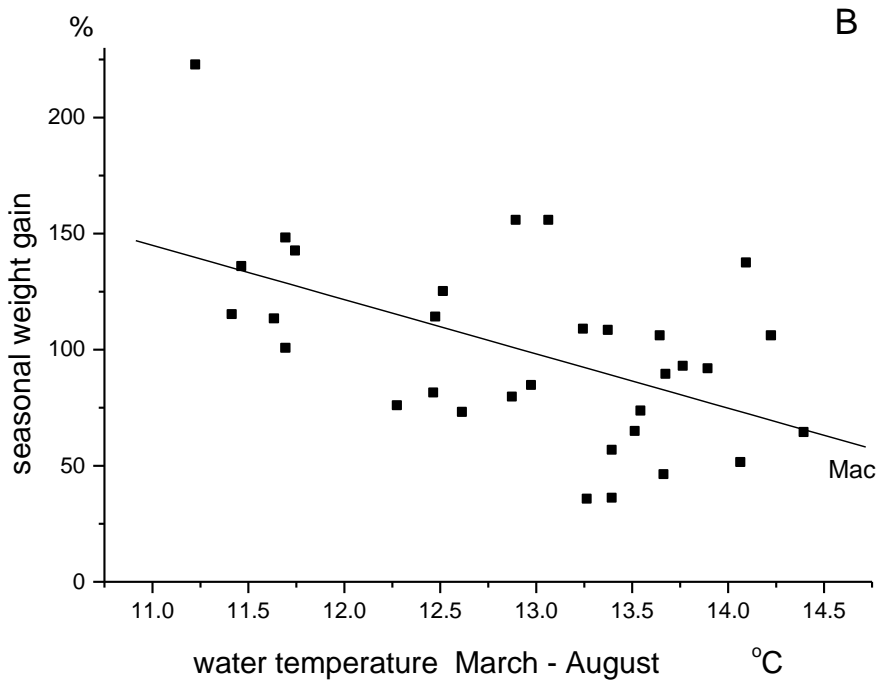
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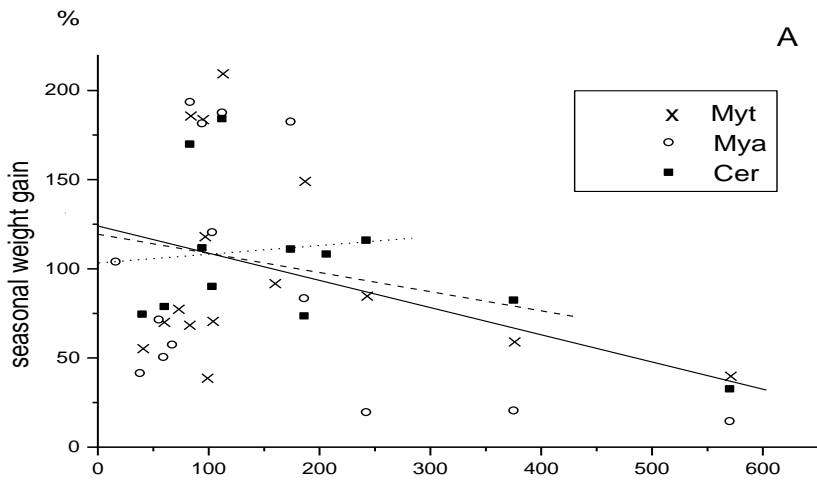


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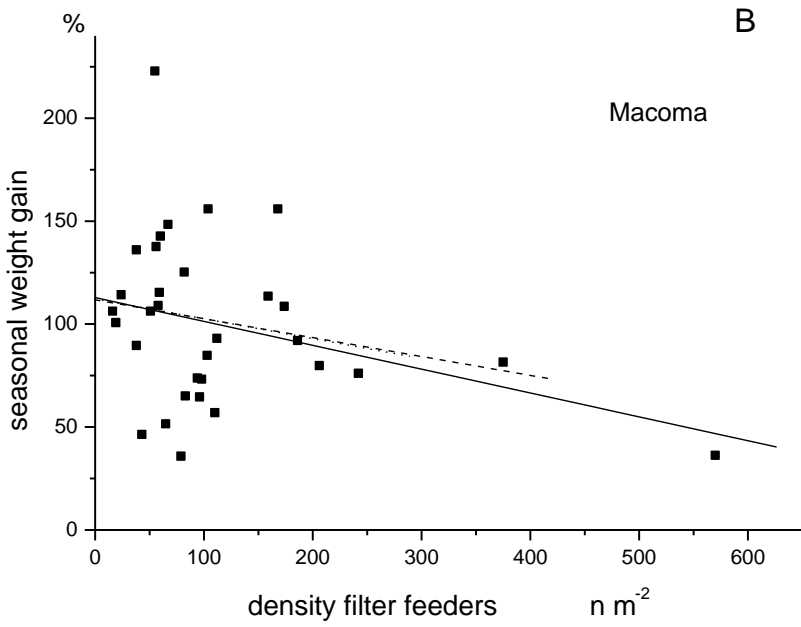


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769 Fig. 5



770



771

772 Fig. 6