

The carrying capacity of a tidal flat area for suspension-feeding bivalves

J. J. Beukema*, R. Dekker

NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, and Utrecht University, PO Box 59, 1790AB Den Burg, Texel, The Netherlands

ABSTRACT: To investigate the relationship between stock size and production of an entire feeding guild, and in particular to find out whether this relationship is dome-shaped (showing an optimal abundance for production), we used a 40 yr data set of the 3 most important suspension-feeding bivalves (*Cerastoderma edule*, *Mytilus edulis*, and *Mya arenaria*) in a Wadden Sea tidal flat area (about 20 km²). The data set contained data on numerical density of individuals, annual rates of weight growth, recruitment, survival, and secondary production. At higher densities (>400 ind. m⁻²), we found reductions of growth rate and recruitment. At the highest densities, the reduction in weight growth was so strong that production was lower than its maximal values at intermediate densities. This optimal density of around 400 ind. m⁻² was considered to represent the carrying capacity of the system for suspension-feeding bivalves. High densities resulting in reduced production, however, rarely (in only 5 % of the years) occurred over the 40 yr monitoring period. Clear bottom-up limitation of bivalve production was thus very unusual in the studied area. Year-to-year variation in growth and production of suspension-feeding bivalves were not related to chlorophyll concentrations in the main tidal stream and did not follow the declining long-term trends of primary production and chlorophyll concentrations. The main conclusion of the paper is that production increases with stock size, but only to a certain threshold value that is rarely reached as a consequence of recruitment being curtailed by a top-down process (predation on young stages).

KEY WORDS: Bivalves · Tidal flats · Wadden Sea · Weight growth · Secondary production · *Cerastoderma edule* · *Mytilus edulis* · *Mya arenaria*

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

In ecosystem studies, the term carrying capacity is used in a variety of ways (Chapman & Byron 2018). Smaal et al. (1998) discussed the history of the concept and Smaal et al. (2013) concluded that it has yet to be clearly defined. Rather than choosing one of the numerous published definitions of carrying capacity, we prefer a population-dynamic approach, using the outcome of a study of relationships between abundance of members of a feeding guild in an ecosystem (in the present case: suspension-feeding bivalves in the Wadden Sea) with their annual rates of somatic growth, recruitment, survival, and particularly secondary production.

At high numbers of suspension-feeding bivalves, we expect to see a decline of one or more of these rates, ultimately resulting in a decline of production. We then operationally define the carrying capacity of an ecosystem as the abundance level (stock size) at which production reaches its maximal value. Our definition of carrying capacity as the optimal stock size for production is in accordance with that of Bacher et al. (1997), Carver & Mallet (1990), and Duarte et al. (2003). This dome-shaped curve of the relationship between stock density and production also resulted from ecosystem models by Bacher et al. (1997), Duarte et al. (2003), and Ferreira et al. (2007). In practice, Heral (1993), however, found an asymptotic increase of cultured oyster production at higher

*Corresponding author: jan.beukema@nioz.nl

stock sizes, without a clear sign of an optimal value. For natural marine populations, reports of relationships between density and production appear to be non-existent.

From our long-term (>40 yr) monitoring of the benthic fauna of an extensive tidal-flat area, we know that the stock of bivalves on Wadden Sea tidal flats varies strongly between years. Levels of density have been found to range from <10 to >500 ind. m⁻² and biomass from <2 to >20 g ash-free dry mass (AFDM) m⁻² (Beukema et al. 2010, 2017). Bivalves usually represented a substantial portion of the total biomass of benthic animals on the tidal flats of the Dutch Wadden Sea, viz. 50–60% (Beukema 1976, Compton et al. 2013, Christianen et al. 2017). They are thus dominant species of the Wadden Sea ecosystem, contributing significantly to both grazing pressure on phytoplankton and as a food supply for shellfish-eating fishes and birds.

The studied suspension-feeding bivalves (*Cerastoderma edule*, *Mytilus edulis*, and *Mya arenaria*) are known to compete for food: the stomach contents of simultaneously collected members of these species were highly similar (Kamermans 1994); isotope analysis data also indicate that pelagic algae dominate their diets (Herman et al. 2000, Christianen et al. 2017). These 3 species thus constitute a feeding guild. The high year-to-year variability in their total densities enables a study of the relationship between their abundance and production.

Earlier work on the Wadden Sea tidal-flat ecosystem pointed to (1) reduced growth and production at (rarely occurring) very high numerical densities in *C. edule* (Beukema & Dekker 2015), (2) reduced growth in all 3 species of suspension-feeding bivalves at (rarely occurring) very high densities (Beukema et al. 2017), (3) a strong positive influence of recruitment success on subsequent year-class production (*C. edule*: Beukema & Dekker 2006; *M. edulis*: Beukema & Dekker 2007), and (4) a positive influence of preceding recruitment and survival on biomass in the latter 2 species (Beukema et al. 2010). So far, however, we have not reported on production of the total feeding guild, which provides a clue to the carrying capacity of the system for such a guild. The present study integrates several results reported in the above papers. In particular, it follows Beukema et al. (2017). However, in the present paper we adapted all of these data to refer to the 20 km² area for which we had estimated growth rates (in all age classes instead of 1 yr olds only).

We are not aware of any other similar study in a natural marine benthic ecosystem of a (necessary)

comparable length. The length of the data series on macrozoobenthos used in this study appears to be unique and allows for a meaningful and novel study on the relationship between density and production. To date, such studies have been performed not by drawing conclusions from real observations, but only by modelling underlying processes (for instance Bacher et al. 1997, Duarte et al. 2003, Ferreira et al. 2007). The only exception we found was the study by Heral (1993) on oyster production, but that study appears to be flawed: part of the biomass data were calculated from production (actually not total production, but yield only).

The objectives of the present study were (1) to find out whether or not the curve depicting the relationship between stock size and production of an entire feeding guild is dome-shaped, (2) to estimate (stock size at) maximal production, and (3) to explore which processes might underlie the shape of the curve.

2. MATERIALS AND METHODS

2.1. Study area

The data on bivalves were obtained as part of a long-term program that has been running since the 1970s, involving twice-annual sampling of the macrozoobenthic fauna at 15 permanent sampling stations on Balgzand, a tidal flat area in the westernmost part of the Wadden Sea (53° N, 5° E). Further details on the sampling area, stations, and methods can be found in Beukema & Cadée (1997). In the present paper, for estimates of density, growth rate and production data from 6 stations in the central part of Balgzand (transects 4, 5, 8, 9, 10, and 11 in Fig. 1) were used. This part of Balgzand covers about one-third of the total Balgzand tidal-flat area of 50 km². We chose this 20 km² area because almost all suspension-feeding bivalve production was realized within this area (*Mytilus edulis*: 99%, Beukema & Dekker 2007; *Cerastoderma edule*: 85%, Beukema & Dekker 2006). Environmental conditions in the area are relatively homogeneous, with intertidal levels of between -4 and -6 dm from mean tide level and silt contents of the sediment of 1–5%. In the part of Balgzand north of this area, data on growth are scarce due to failing recruitments of the studied species in nearly all years; this is probably due to adverse environmental conditions (exposure to strong currents and wave action, resulting in unstable and coarse sediments). South of the selected area, growth rates were invariably lower, probably due to higher inter-

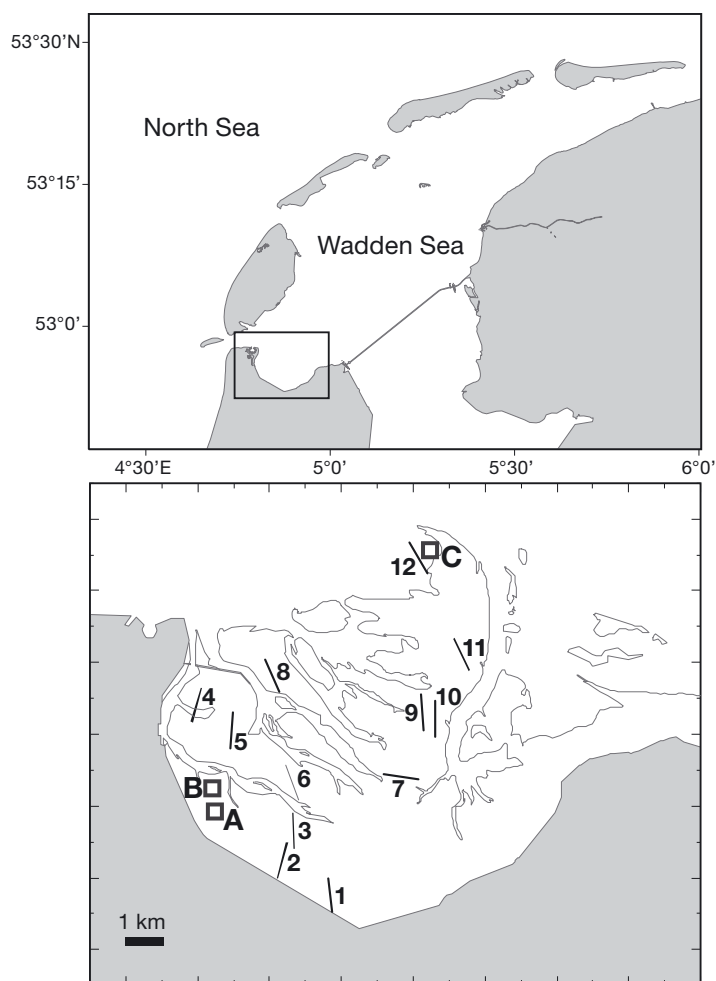


Fig. 1. (Top) Westernmost part of the Wadden Sea and (bottom) the tidal-flat area called Balgzand. Permanent sampling sites are indicated: 12 transects (numbered 1–12) and 3 squares (A, B, and C). Our study area was limited to the central part of Balgzand: transects 4, 5, 8, 9, 10, and 11. Based on Fig. 1 of Beukema & Dekker (2015)

tidal levels (shorter daily immersion times). Moreover, densities of suspension-feeding bivalves are frequently low there.

2.2. Environmental conditions

Temperature values were derived from daily observations of surface water temperatures from the Royal Netherlands Institute for Sea Research (NIOZ) jetty at the shore of the Marsdiep tidal inlet (the main tidal inlet of the westernmost part of the Dutch Wadden Sea), about 5–10 km from the Balgzand sampling stations. Monthly data were available for all years of the study period and are summarized in Van Aken (2008).

Chlorophyll *a* (chl *a*) concentrations in surface water are available from the databases of NIOZ (P. Jacobs et al. unpubl. data) and Rijkswaterstaat (www.waterbase.nl). The samples were taken at a frequency of at least once or twice mo^{-1} near the temperature station in the Marsdiep tidal inlet, around high tide by NIOZ and 2–3 h before low tide by Rijkswaterstaat. We used these concentrations as a proxy for phytoplankton abundance and available food for suspension feeders. We applied annual values of the mean concentrations observed for 6 mo (March–August, inclusive). Such chl *a* data were available for (nearly) all years of the 1978–2015 period. The 2 data series were positively correlated ($r = 0.34$, $n = 37$, $p < 0.05$; without an outlying point for 1996: $r = 0.52$, $n = 36$, $p = 0.001$), and therefore we used their averages. Unfortunately, no data on temperature or chl *a* were available for the tidal flat areas studied. The data used were proxies. We are aware of the much higher variability of the actual values at the tidal flats. From data gathered over 2 yr, Kamermans (1994) found a close similarity in monthly means of chl *a* concentrations measured above tidal flats and in the Marsdiep tidal inlet. They were higher above the tidal flats than in the inlet at high tide by resuspension and lower at low tide by consumer filtration.

2.3. 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 March, when cores of nearly 0.02 m^2 were used, the sampled area covered a total of $0.95 \text{ m}^2 \text{ transect}^{-1}$. In August (when numbers of ind. m^{-2} are much higher) we used smaller cores of nearly 0.01 m^2 , thus covering $0.45 \text{ m}^2 \text{ transect}^{-1}$. Bivalves were sorted from the sieved (1 mm mesh) samples, assigned to age classes (cohorts indicated by year of birth), counted (numerical density expressed in no. m^{-2}), sorted to mm shell length classes, their soft parts dried to constant weight for several days at 60°C , weighed per mm length class, incinerated (2 h at $500\text{--}600^\circ\text{C}$) and again weighed to obtain, by subtraction, ash-free dry mass (AFDM).

As a bivalve abundance index, we used 6 station means of March and August estimates for each year for animals older than 0.5 yr, expressed in $\text{no. of ind. m}^{-2}$. Recruitment was defined as the 6 station mean no. m^{-2} of 0-group individuals (<0.5 yr old) of each species found in August. Survival between March and August was the percentage of individuals (6 station mean of each species) still present in August.

A few more species living on Balgzand belong to the group of suspension-feeding bivalves, but they have occurred only in recent years and usually in low numbers: *Ensis leei (directus)* and *Magellana (Crassostrea) gigas*. They were not included in the present study because too few data on their growth in the studied area were available.

2.4. Bivalve growth and production

For each species and at each sampling station, estimates of weight gain per individual (g AFDM ind.⁻¹) in the 2nd and following growing seasons were obtained by subtracting mean weight in March from mean weight in the subsequent August of the individuals born in the same year. We considered the March–August period as the season for annual somatic growth (Beukema & Dekker 2006, Dekker & Beukema 2007). For estimates of growth, we used data of a sampling site only if the cohort to be studied was represented with 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 be available at 4 or more of the 6 sampling sites. In practice, this number amounted to 6 in more than half of the years, as successful year classes tended to arise simultaneously over vast areas (Beukema et al. 2001). All growth data were expressed as a percentage of the long-term mean growth of the group (species/age class), as explained in Beukema et al. (2017). The percentages for the various age classes of a species found every year were averaged to obtain a year-index for the species.

As growth in the studied species is (positively) related to water temperature during the growing season, all annual-growth index values were corrected to apply to a mean water temperature of 13°C. For this correction, we used the relationship shown in Beukema et al. (2017), indicating increases in relative growth per 1°C higher water temperature to amount to averages of 24% in *C. edule*, 21% in *M. edulis*, and 27% in *M. arenaria*. Thus, if a relative growth rate of 100% was observed in *C. edule* in a certain year with a mean water temperature of 12°C, then the corrected value for 13°C would have been 100 + 24 = 124%. In this way, all observed relative growth rates were corrected for a possible temperature effect. From hereon, these temperature-corrected data were generally used.

Secondary production was calculated according to the weight-increase-summation method (Van der

Meer et al. 2005) for the half-year periods March–August: $P = \sum(N \times \Delta g)$, where N = mean numerical density (mean of March and August estimate) and Δg = mean (uncorrected and non-averaged) individual weight change between March and August. Estimates for all age classes (except recruits) and all 3 species were summed to an estimate of total suspension-feeding bivalve production, expressed in g AFDM m⁻² per 0.5 yr. This estimate differs from those presented for *C. edule* and *M. edulis* in Beukema & Dekker (2006) and Beukema & Dekker (2007), respectively. The present estimates show only the positive production values for the growing seasons, omitting the (mostly negative) contributions for the autumn/winter seasons, when the animals generally lose weight.

2.5. Statistical methods

For evaluation of statistical significance, we used the Spearman rank correlation test. This is a simple test, making no demands as to a normal distribution of the data used. For the relationship between density and production, we tried some models, but none gave a better description than a quadratic function.

3. RESULTS

3.1. Environmental conditions

Annual means of water temperatures as measured in the main tidal inlet during the March–August growing seasons from 1979–2015 are shown in Fig. 2a of Beukema et al. (2017). The annual mean water temperatures during the growing seasons varied from 11.2 to 14.4°C. The values showed a rising trend for the 1979–2015 observation period of 0.04°C yr⁻¹ ($r = 0.51$, $n = 37$, $p < 0.01$).

Annual means of chl *a* concentrations in the main tidal inlet during the March–August growing seasons of 1975–2015 are shown in Fig. 2b of Beukema et al. (2017). These concentrations showed significantly declining trends for the 1978–2017 observation periods. The NIOZ data series showed a decline of 0.23 mg m⁻³ yr⁻¹ ($r = -0.61$, $n = 39$, $p < 0.001$) from about 20 to about 12 mg m⁻³ yr⁻¹, and in the Rijkswaterstaat series (1978–2015), a decline of 0.21 mg m⁻³ yr⁻¹ ($r = -0.48$, $n = 38$, $p = 0.002$) from about 17 to about 10 mg m⁻³ yr⁻¹. Long-term averages for the 38 yr of the 1978–2015 period amounted to 14.6 and 14.3 mg m⁻³, respectively, for the NIOZ and Rijkswaterstaat data.

3.2. Annual densities of individuals

Total numerical densities of suspension-feeding bivalves in the central part of Balgzand varied from year to year over a wide range, from 5 to 1016 m⁻², with an average of 138 m⁻² (Fig. 2A). In nearly all years, total densities were <250 m⁻². Only in 1980, 1988, and 2012 were the densities of individuals substantially higher. These high densities resulted from exceptionally successful recruitments in nearly all species in the summers of 1979, 1987, and 2011 (Beukema et al. 2001, Beukema & Dekker 2014). For the greater part (55%), these bivalves were cockles *Cerastoderma edule*, whereas mussels *Mytilus edulis* and gaper clams *Mya arenaria* each accounted for about 22% of the long-term total. As the dominant species, densities of *C. edule* largely determined total densities. The significantly positive correlations between densities of *C. edule* and those of *M. edulis* and *M. arenaria* ($r = 0.37$ and 0.73 , $n = 40$ and 40 , $p < 0.02$ and < 0.001 , respectively) contributed to the high year-to-year variability in total densities. Peaks and lows in total density often resulted from simultaneous peaks or lows in density of 2 or 3 species.

Long-term trends in the densities shown in Fig. 2A were non-significant in *C. edule* ($r = +0.04$), *M. edulis* ($r = -0.20$), and in total densities ($r = +0.09$), but significantly positive in *M. arenaria* ($r = +0.34$, $n = 40$, $p < 0.05$).

3.3. Annual weight growth

During the March–August growing season, AFDW increased by about 0.3 g ind.⁻¹ in the second growing season of the life of all 3 species, by about the same values in the subsequent growing seasons in *C. edule* and *M. edulis*, but by much higher values in the scarce, older individuals of *M. arenaria* (Table 1).

The growth estimates were corrected and combined (as explained in Section 2.4) to obtain estimates of relative growth in a certain year for a certain species. The data are shown in Fig. 2B as a growth index for each species for as many years as sufficient data were available. Growth rates were significantly higher in the 1990s than in the preceding and following period (Beukema et al. 2017). Standard errors of annual growth rates of all 3 species were shown in Fig. 3 of Beukema et al. (2017). The standard errors observed in the year with the highest bivalve abundance (2012) did

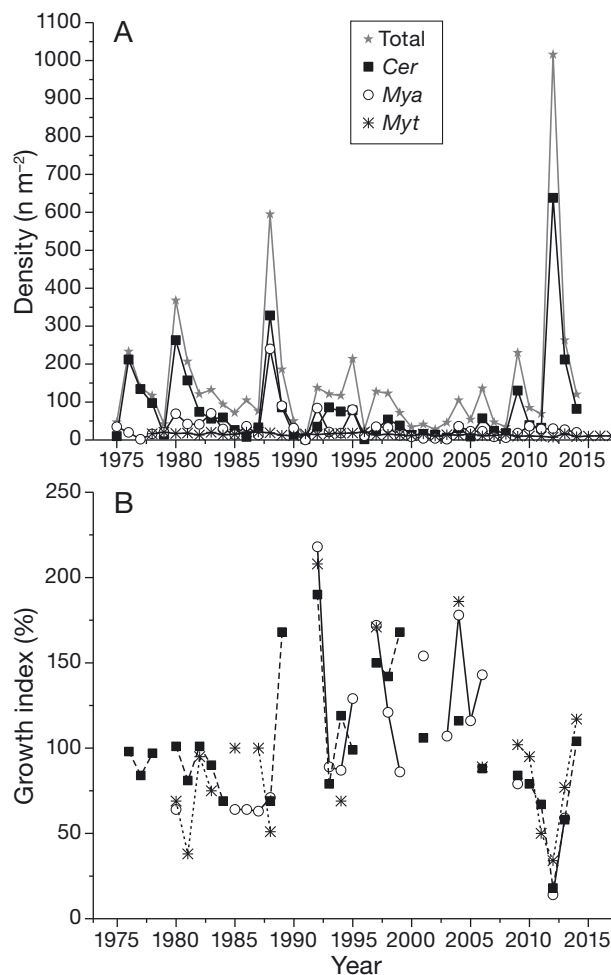


Fig. 2. Long-term (1975–2015) changes in (A) densities (no. ind. m⁻²) during the growing season (means of observations in March and August) of *Cerastoderma edule* (*Cer*), *Mytilus edulis* (*Myt*), and *Mya arenaria* (*Mya*). Totals shown by filled stars. Means of densities observed at 6 Balgzand transects. (B) Indices for annual growth in *Cerastoderma edule*, *Mytilus edulis*, and *Mya arenaria*. Growth rates are shown as mean (temperature-corrected) seasonal weight gains, expressed as a percentage of their long-term mean (1979–2015) growth rates (set at 100%), as explained in Section 2.4. In none of the species did growth show a significant long-term trend

Table 1. Long-term means (± 1 SE) of weight increments during successive growing seasons in the 3 main species of suspension-feeding bivalves on Balgzand, expressed in g ash-free dry mass (AFDM) ind.⁻¹. Number of years with sufficient observations are shown in parentheses. A value for a year was included only if an estimate was available from at least 4 sites, each with at least 3 individual observations

Species	Growing season		
	Second	Third	Fourth
<i>Cerastoderma edule</i>	0.30 \pm 0.02 (20)	0.23 \pm 0.03 (11)	0.28 \pm 0.04 (6)
<i>Mytilus edulis</i>	0.25 \pm 0.03 (15)	0.32 \pm 0.06 (7)	No data
<i>Mya arenaria</i>	0.30 \pm 0.02 (15)	0.86 \pm 0.09 (11)	1.37 \pm 0.08 (4)

not (or rarely) overlap with those of other years with lower bivalve densities. Note that the variability in numbers (Fig. 2A) was much higher than that in growth rates (Fig. 2B).

3.4. Abundance relationships

In all 3 species, growth rates appeared to show declining trends with increasing totals of suspension-feeding bivalve densities (Fig. 3). The negative relationships, however, were all weak and statistically non-significant (Spearman test). Without the one low point at the highest density in each graph, the correlation coefficients even dropped to values between 0.18 and 0.23, with p-values well above 0.1. For standard errors and statistical treatment of such relationships, see Beukema et al. (2017). For the present discussion, the relevant point is that any negative dependence of growth on numerical density was based only on growth estimates at the rarely occurring very high densities.

Within the range of densities between 0 and 200 to 400 m^{-2} , little (if any) relationship was observed between density and growth (Fig. 3); values of r were close to 0 in all 3 species. Densities were within this range in by far the majority of observation years. Growth rates in these years showed a great deal of (unexplained) variation from year to year. Consistently low growth values (well below 100% of the long-term average) at high densities occurred at suspension-feeding bivalve densities of $>500 \text{ m}^{-2}$ in *C. edule* and *M. edulis*, and $>300 \text{ m}^{-2}$ in *M. arenaria*. The numbers of years with such consistently reduced growth at high abundance amounted to 2 in *C. edule*, 2 in *M. edulis*, and 3 in *M. arenaria*. Years with growth observations at lower bivalve densities were much more numerous. Severely reduced growth rates (of $<50\%$ of the long-term average) at high densities occurred in only 1 year (2012, the year with the highest bivalve abundance) in all 3 species, i.e. in only about 3% of the years of observation.

In the 3 yr with the highest bivalve abundance, recruitment was relatively low in all 3 bivalve species, amounting on average to 29, 15, and 1% of the long-term average in *C. edule*, *M. edulis*, and *M. arenaria*, respectively. In an earlier paper (Beukema & Dekker 2018), we showed the negative dependence of recruitment of 3 bivalve species on the densities of adult *C. edule*. As these densities were closely correlated with total adult bivalve densities (see above), very similar relationships were observed between total bivalve densities and recruitment success of bi-

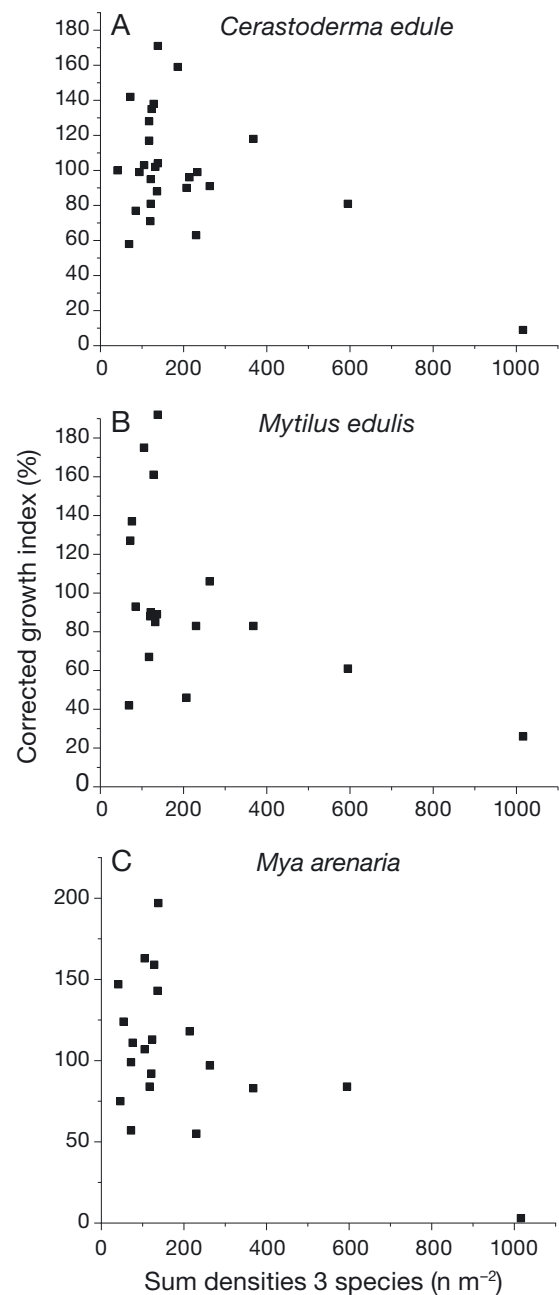


Fig. 3. Relationships between the sums of density (no. ind. m^{-2}) of 3 species of suspension-feeding bivalves (from Fig. 2A) and indices of relative weight growth (from Fig. 2B) in (A) *Cerastoderma edule*, (B) *Mytilus edulis*, and (C) *Mya arenaria*. Spearman r -values for the correlations amounted to 0.2, 0.3, and 0.3, respectively (all $p > 0.1$)

valve species. Thus, the above low recruitments in the 3 yr with high bivalve abundance fit with the general relationship, i.e. these low recruitments were expected.

Survival between March and August was not significantly related to annual total bivalve abundance

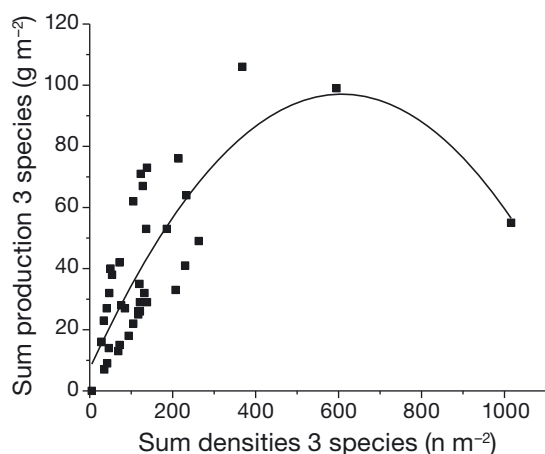


Fig. 4. Relationship between the sums of density (N ; no. m^{-2}) of 3 species of suspension-feeding bivalves (from Fig. 2A) and the somatic production (P ; g ash-free dry mass [AFDM] m^{-2}) of the 3 species together in the March–August periods over 39 yr (1976–2014; one point for each year of observation). Best fit: $P = 7.3 + 0.30N - 0.00024N^2$ ($r^2 = 0.62$)

in any of the 3 species. Spearman r -values were non-significant ($r = 0.01, 0.04$ and 0.02 in *C. edule*, *M. edulis*, and *M. arenaria*, respectively). In the year with the highest total bivalve abundance (2012), survival percentages were above the long-term average in all 3 species.

Bivalve production (P) strongly depended on bivalve abundance (N) (Fig. 4). P increased linearly with N up to about $400 \text{ ind. } m^{-2}$, according to $P = 1.4 + 0.22N$ ($r = 0.80, n = 37, p < 0.001$). The rightmost 2 points in Fig. 4 at $N = 600$ and 1000 m^{-2} show values of P well below the extrapolated linear increase suggested by the P values observed at lower densities. The maximal value of P was reached at $N \approx 400 \text{ ind. } m^{-2}$. Thus, at densities higher than about 400 m^{-2} (this occurred only twice in the period of about 40 yr), P was lower than expected from the above linear increase. In these 2 years, the increased abundance to extremely high densities could no longer compensate for the larger decline in growth rates, resulting in a reduction of P . As a result, the best fitting relationship between density and P is a dome-shaped quadratic function (with a high r^2 value).

3.5. Relationships with chlorophyll concentrations

The steady decline of the chl a concentrations by $0.22 \text{ mg } m^{-3} \text{ yr}^{-1}$ resulted in a total decline over the period of observation of about $8 \text{ mg } m^{-3}$, representing about half of the values found in the initial years.

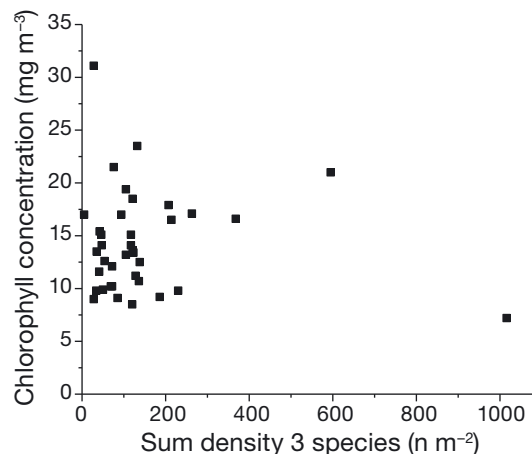


Fig. 5. Relationship between the sums of density (no. $\text{ind. } m^{-2}$) of 3 species of suspension-feeding bivalves (from Fig. 2A) and the chlorophyll concentrations in the main tidal inlet (means of Rijkswaterstaat and Royal Netherlands Institute for Sea Research data). Each point represents the March–August period of 1 yr. The relationship was not significant ($r = -0.16, n = 37, p = 0.4$)

This substantial long-term decline in food supply, however, did not result in significantly declining long-term trends in the growth rates of the studied bivalves (Fig. 2B). Moreover, we did not find significant relationships between growing-season chl a concentrations and growth index values in any of the 3 studied species. The Pearson- r values found for this relationship varied from -0.12 to $+0.15$ (with p -values of 0.6 to 0.7).

Only the coincidence (in 2012) of the lowest chl a concentration ($7.2 \text{ mg } m^{-3}$) with the lowest growth index values of the entire period of observation in all 3 species (Fig. 2B) appears to point to a possible positive relationship between food concentration and bivalve growth rate. In the other 2 high-density years (1980 and 1988, the years with P -values of around the maximum, i.e. at carrying capacity), the chl a concentrations in the main tidal stream of about 14 and $17 \text{ mg } m^{-3} \text{ yr}^{-1}$, respectively, were around or above the long-term average of $14.4 \text{ mg } m^{-3} \text{ yr}^{-1}$. Thus, our estimates of maximal secondary production were at chl a concentrations that were representative for the area.

Chl a concentrations in the tidal inlet were not significantly related to bivalve abundance on Balgzand (Fig. 5: $r = -0.16, p = 0.4$). Thus, these concentrations were apparently not affected by bivalve grazing pressure on the tidal flats. The position of the low point (in 2012) for chl a concentration in Fig. 5 is, however, remarkable: it was observed at the highest bivalve density on Balgzand.

4. DISCUSSION

4.1. Carrying capacity

We found a dome-shaped curve for the relationship between numerical density and secondary production of suspension-feeding bivalves (Fig. 4), i.e. there was an optimal density of suspension-feeding bivalves at which their production was maximal. This meets the expectation from the models of Bacher et al. (1997) and Ferreira et al. (2007), but differs from the relationship found by Heral (1993). The dome-shaped curve allows for an estimate of maximal production per growing season of suspension-feeding bivalves ($P \approx 100 \text{ g AFDM m}^{-2}$) and the optimal density at which this maximum is realized (around 400 ind. m^{-2}). We propose that these values represent the carrying capacity of the studied ecosystem for suspension-feeding bivalves. At higher densities, growth rates were reduced to an extent that production declined in spite of the higher numbers of producing animals.

Rather than for separate species, we defined carrying capacity for a (substantial) part of the Wadden Sea ecosystem, namely the group of suspension-feeding bivalves (representing more than half of the zoobenthic biomass at the tidal flats). These animals have similar needs: all of them graze on phytoplankton in the water layer just above the bottom and thus compete for food. If food becomes a limiting resource, these species will all be affected at the same time. Indeed, all 3 studied species simultaneously showed seriously reduced growth rates at the highest bivalve density (Figs. 2 & 3). Thus, it is logical to define carrying capacity not for separate species, but for the total group of species within the same feeding guild: the suspension-feeding bivalves.

Our estimates of maximal production and density at carrying capacity refer to an area of about 20 km^2 . More locally, densities of over 400 m^{-2} are frequently reached in small tidal-flat areas of $<1 \text{ km}^2$, such as mussel or oyster beds and aggregates of cockles. For such small areas, reductions in growth rate hardly occur, though Kamermans (1993) and Dekker & Beukema (2012) found some indications. At larger scales (10 to several to 10s of km^2), mean bivalve densities exceeding about 400 m^{-2} appear to be extremely rare. They occurred on Balgzand only twice (1988 and 2012; see Fig. 2A) during a 40 yr monitoring period. Jensen (1992, 1993) once observed such high densities in the Danish Wadden Sea.

Survival rates were not reduced at these high densities (at least within the range of densities studied, which did not exceed 1000 m^{-2}), a result also re-

ported for the bivalves *Limecola balthica* and *Cerastoderma edule* (Van der Meer et al. 2001b). In young *Mytilus edulis* (mussel seed), Capelle et al. (2016) observed negative density-dependent survival, affecting production in mussel cultures. Recruitment, on the other hand, was reduced at the highest bivalve densities, as also reported for *C. edule* in Beukema & Dekker (2018). As a consequence of the small size of the recruits, this reduction hardly affected (the high) production in the year of their birth, but it did reduce total densities and production in subsequent years. This may explain why the durations of the peaks in numbers (Fig. 2A) were so short (only 1 yr).

In 95% (37 out of 39) of the years of the study period, bivalve production increased linearly with numerical density, with growth rates being independent of density in all 3 species in the vast majority of years. A similar conclusion was reached for *L. balthica* populations on Balgzand (Van der Meer et al. 2001a) and the *C. edule* population on Balgzand (Beukema & Dekker 2015). This means that processes other than bottom-up ones (by competition for food) must have limited bivalve numbers, keeping their densities (far) below the carrying capacity level in almost all years. Among such processes we identified a top-down one: the serious and decisive predation by shrimps and shore crabs on young benthic stages of bivalves (Beukema & Dekker 2014). Reise (1985) came to a similar conclusion for tidal-flat ecosystems.

4.2. Primary and secondary production

Heip et al. (1995) summarized reports of total macrozoobenthos production across various estuaries, showing a wide range of values which were usually not higher than some 10s of $\text{g AFDM m}^{-2} \text{ yr}^{-1}$. The maximal bivalve production values (around $100 \text{ g AFDM m}^{-2}$ in 6 mo) we found (Fig. 4) are high but not unique. Hibbert (1976) reported total bivalve production of $38\text{--}92 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$ at 3 sites in a 0.6 km^2 tidal flat area in southern England. Möller & Rosenberg (1983) found extremely high production values of $>300 \text{ g AFDM m}^{-2}$ in an exceptionally strong year class of *Mya arenaria* (and even $>400 \text{ g}$ for this species and *C. edule* together). These values were observed in small (about 0.01 km^2), shallow subtidal bays along the Swedish west coast. Our values refer to a much larger area of about 20 km^2 , i.e. about 3% of the total area of the Marsdiep basin.

The observed high bivalve production of around $100 \text{ g AFDM m}^{-2}$ would have used up a substantial

portion of the local primary production, all the more as these animals also need (an unknown amount of) food for their maintenance and reproduction. According to conversion factors suggested by Herman et al. (1999), viz. 0.5 for AFDW to gC and 1.8 for respiration to production, a food intake by bivalves at this production level may be calculated at 140 gC m⁻². Rates of primary production in the main tidal stream of the western Wadden Sea were estimated at about 200 gC m⁻² yr⁻¹ (Philippart et al. 2007, P. Jacobs et al. unpubl. data) and at a similar amount above and on the tidal flats (Cadée & Hegeman 1974). For the half-year periods of the growing seasons, this would equal about 150 gC m⁻². This amount has to provide food for not only the zooplankton, but all other benthic and pelagic organisms as well, thus it may have been (too) tight for the bivalves. In fact, it is doubtful whether the bivalves could maintain these high densities on the local primary production.

In practice, however, bivalves and other filtering benthic animals do not depend strictly on local primary production, as they obtain their food largely from continually renewed water passing by tidal currents. Above tidal flats, phytoplankton concentrations in flood water are seriously reduced by bivalve aggregations (Peterson & Black 1987, 1991, Kamermans 1993, 1994, Jonsson et al. 2005). Nevertheless, we found no decline of chl *a* concentrations in the major tidal stream with increasing bivalve numbers up to about 600 m⁻²; only at the highest bivalve abundance (in 2012) did we find a serious reduction of chl *a* concentrations (the lowest value in almost 40 yr; Fig. 5). In that one year, bivalve densities were extremely high all over the western Wadden Sea (Kamermans & Van Asch 2018).

The explanation of the above lack of response at almost all grazing levels may be 3-fold: (1) about half of the diet of the suspension-feeding bivalves on the tidal flats consists of benthic rather than pelagic algae (Kamermans 1994); (2) algae in fresh water drained from Lake IJssel also contribute significantly to bivalve food supply (Jung et al. 2019); and (3) the volume of the water present above tidal flats is only about 5% of the total basin volume and the residence and turnover times of the Balgzand area amount to only a few tides (Zimmerman 1976), which excludes a serious reduction of the chl *a* concentrations at the tidal inlet by bivalve grazing on Balgzand tidal flats. Indeed, long-term mean chl *a* concentrations as estimated by the Rijkswaterstaat were hardly lower than those by NIOZ, though NIOZ data were gathered at high tide and Rijkswaterstaat data a few hours before low tide. Apparently, water exchange between the

North Sea and Wadden Sea is so rapid that Wadden Sea bivalve populations could not substantially deplete the phytoplankton population.

In turn, tidal-stream chl *a* concentrations were not found to influence growth rates of suspension-feeding bivalves on the Balgzand tidal flats (with the possible exception of 2012). However, the strong year-to-year variation in growth rates cannot be explained as long as chl *a* concentrations are not actually measured exactly in the area where the bivalves lived. It is unfortunate that no relevant long-term observations on food concentrations above tidal flats are available.

4.3. Bottom-up regulation

In the Balgzand data series, we found little evidence for consistent bottom-up regulation of growth and production of suspension-feeding bivalves. We found growth rates that were reduced at the highest densities in only 2 or 3 of about 20 yr of observation in the various species (Fig. 3). Total suspension-feeding bivalve production was reduced in only 2 out of 39 yr (Fig. 4).

At first sight, this result appears contradictory to the conclusions of Heip et al. (1995) and Herman et al. (1999), who stated that primary production and food availability are decisive for biomass and secondary production of zoobenthos. However, their conclusions came from geographic comparisons between a number of estuarine and coastal ecosystems. Such area-to-area comparisons appear to be the only solid evidence for strong bottom-up regulation of zoobenthic biomass and production. In contrast, the present study dealt with between-year differences within a single system. Within this system, between-year fluctuations in growth appeared to be only rarely affected by bivalve stock size or by (distantly estimated) chl *a* concentrations. However, observations all over 2 extensive tidal basins in the western Wadden Sea did show negative relationships between stock sizes and growth rates in *C. edule* (Kamermans & Van Asch 2018), suggesting a bottom-up process over a wide range of densities of this species. Unfortunately, these results are reported only in the 'grey' literature and need confirmation. On the other hand, the long-term decline of chl *a* concentrations in the Wadden Sea ever since the mid-1990s (Beukema et al. 2017) did not result in a decline of total bivalve biomass in Balgzand (rather, an increase was observed by Beukema & Dekker 2019) nor of total zoobenthic biomass (Dekker 2012, authors' unpubl. obs.). These findings are contrary to the expectation

expressed by Beukema et al. (2002), who described an (at that time) existing positive relationship between chl *a* concentrations and zoobenthic biomass.

5. CONCLUSIONS

Over a wide range of numerical densities of suspension-feeding bivalves, growth rates were unrelated to density. Growth rates in all 3 studied species only declined to rates below their long-term averages at densities over about 400 ind. m⁻². These declines were strong enough to reverse the relationship between numbers and production. Production was optimal at bivalve numbers around 400 m⁻². This abundance level may be designated as the carrying capacity of vast Wadden Sea tidal-flat areas for the group of suspension-feeding bivalves.

The declining trends in primary production (Philippart et al. 2007, P. Jacobs et al. unpubl. data) and chl *a* concentrations may cause a decline of this carrying capacity in the future. Our 2 highest estimates of secondary production were in the 1980s, in years with chl *a* concentrations around the long-term average; currently, these concentrations are about 30 % lower. So far, no declining trends in growth rates of bivalves have been observed (our Fig. 2B; Kamermans & Van Asch 2018). Rising temperatures (Van Aken 2008), on the other hand, might cause future increases in bivalve growth rates (Beukema et al. 2017).

The lack of clear-cut bottom-up effects in the studied ecosystem may be due to the infrequent occurrence of high bivalve densities. Typically, these densities are regulated by top-down processes and kept down to levels far below the carrying capacity of the system. This effective top-down regulation of bivalve numbers by epibenthic predators would have prevented an overloading of the system in all but 5 % of the 40 yr of observations, making bottom-up limitation of growth and production of suspension-feeding bivalves a rare phenomenon on the studied tidal flats.

Acknowledgements. We thank Henk van der Veer (NIOZ, Texel), Jaap van der Meer (WUR, Wageningen), and Pauline Kamermans (WUR, Wageningen) for useful comments on earlier versions of this paper. We are grateful to Pascalle Jacobs (NIOZ) for making available the chlorophyll concentration data of the NIOZ monitoring program.

LITERATURE CITED

- ecosystem models. *Aquat Ecol* 31:379–394
- ✦ Beukema JJ (1976) Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. *Neth J Sea Res* 10:236–261
 - ✦ Beukema JJ, Cadée GC (1997) Local differences in macrozoobenthic response to enhanced food supply caused by mild eutrophication in a Wadden Sea area: food is only locally a limiting factor. *Limnol Oceanogr* 42:1424–1435
 - ✦ Beukema JJ, Dekker R (2006) Annual cockle *Cerastoderma edule* production in the Wadden Sea usually fails to sustain both wintering birds and a commercial fishery. *Mar Ecol Prog Ser* 309:189–204
 - ✦ Beukema JJ, Dekker R (2007) Variability in annual recruitment success as a determinant of long-term and large-scale variation in annual production of intertidal Wadden Sea mussels (*Mytilus edulis*). *Helgol Mar Res* 61:71–86
 - ✦ Beukema JJ, Dekker R (2014) Variability in predator abundance links winter temperatures and bivalve recruitment: correlative evidence from long-term data in a tidal flat. *Mar Ecol Prog Ser* 513:1–15
 - ✦ Beukema JJ, Dekker R (2015) Density dependence of growth and production in a Wadden Sea population of the cockle *Cerastoderma edule*. *Mar Ecol Prog Ser* 538:157–167
 - ✦ Beukema JJ, Dekker R (2018) Effects of cockle abundance and cockle fishery on bivalve recruitment. *J Sea Res* 140:81–86
 - Beukema JJ, Dekker R (2019) Is food supply for shellfish eating birds in the Wadden Sea affected by the between-species synchrony in year-to-year fluctuations of bivalve population parameters? *Helgol Mar Res* 73:8
 - ✦ Beukema JJ, Dekker R, Essink K, Michaelis H (2001) Synchronized reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. *Mar Ecol Prog Ser* 211:143–155
 - ✦ Beukema JJ, Cadée GC, Dekker R (2002) Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. *J Sea Res* 48:111–125
 - ✦ Beukema JJ, Dekker R, Philippart CJM (2010) Long-term variability in bivalve recruitment, mortality, and growth and their contribution to fluctuations in food stocks of shellfish-eating birds. *Mar Ecol Prog Ser* 414:117–130
 - ✦ Beukema JJ, Dekker R, Drent J, van der Meer J (2017) Long-term changes in annual growth of bivalves in the Wadden Sea: influences of temperature, food, and abundance. *Mar Ecol Prog Ser* 573:143–156
 - ✦ Cadée GC, Hegeman J (1974) Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. *Neth J Sea Res* 8:260–291
 - ✦ Capelle JJ, Wijsman JWM, van Stralen MR, Herman PMJ, Smaal AC (2016) Effect of seeding density on biomass production in mussel bottom culture. *J Sea Res* 110:8–15
 - ✦ Carver CEA, Mallet AL (1990) Estimating the carrying capacity of a coastal inlet for mussel culture. *Aquaculture* 88:39–53
 - ✦ Chapman EJ, Byron CJ (2018) The flexible application of carrying capacity in ecology. *Glob Ecol Conserv* 13:e00365
 - ✦ Christianen MJA, Middelburg JJ, Holthuijsen SJ, Jouta J and others (2017) Benthic primary producers are key to sustain the Wadden Sea food web: stable carbon isotope analysis at landscape scale. *Ecology* 98:1498–1512
 - ✦ Compton TJ, Holthuijsen S, Koolhaas A, Dekinga A and others (2013) Distinctly variable mudscapes: distribution gradients of intertidal macrofauna across the Dutch
- ✦ Bacher C, Duarte P, Ferreira JG, Raillard O (1997) Assessment and comparison of the Marennes-Oléron Bay (France) and Carlingford Lough (Ireland) carrying capacity with

- Wadden Sea. *J Sea Res* 82:103–116
- Dekker R (2012) Macrozoobenthosonderzoek MWTL, voor- en najaar 2010, Waterlichaam: Waddenzee (Balgzand en sublitorale westelijke Waddenzee). Rapportnummer BM10.11, NIOZ, Texel
- ✦ Dekker R, Beukema JJ (2007) Long-term and large-scale variability in productivity of the tellinid bivalve *Macoma balthica* on Wadden Sea tidal flats. *Mar Ecol Prog Ser* 337:117–134
- ✦ Dekker R, Beukema JJ (2012) Long-term dynamics and productivity of a successful invader: The first three decades of the bivalve *Ensis directus* in the western Wadden Sea. *J Sea Res* 71:31–40
- ✦ Duarte P, Meneses R, Hawkins AJS, Zhu M, Fang J, Grant J (2003) Mathematical modelling to assess the carrying capacity for multi-species culture within coastal waters. *Ecol Modell* 168:109–143
- ✦ Ferreira JG, Hawkins AJS, Bricker SB (2007) Management of productivity, environmental effects and profitability of shellfish aquaculture—the Farm Aquaculture Resource Management (FARM) model. *Aquaculture* 264:160–174
- Heip CHR, Goosen NK, Herman PMJ, Kromkamp J, Middelburg JJ, Soetaert K (1995) Production and consumption of biological particles in temperate tidal estuaries. *Oceanogr Mar Biol Annu Rev* 33:1–149
- Heral M (1993) Why carrying capacity models are useful tools for management of bivalve molluscs culture. In: RF Dame (ed) *Bivalve filter feeders in estuarine and coastal ecosystem processes*. Springer-Verlag, Berlin, p 455–477
- ✦ Herman PMJ, Middelburg JJ, Van de Koppel J, Heip CHR (1999) Ecology of estuarine macrobenthos. *Adv Ecol Res* 29:195–240
- ✦ Herman PMJ, Middelburg JJ, Widdows J, Lucas CH, Heip CHR (2000) Stable isotopes as trophic tracers: combining field sampling and manipulative labelling of food resources for macrobenthos. *Mar Ecol Prog Ser* 204:79–92
- ✦ Hibbert CJ (1976) Biomass and production of a bivalve community on an intertidal mud-flat. *J Exp Mar Biol Ecol* 25:249–261
- ✦ Jensen KT (1992) Dynamics and growth of the cockle, *Cerastoderma edule*, on an intertidal mud-flat in the Danish Wadden Sea: effects of submersion time and density. *Neth J Sea Res* 28:335–345
- ✦ Jensen KT (1993) Density-dependent growth in cockles (*Cerastoderma edule*): evidence from interannual comparisons. *J Mar Biol Assoc UK* 73:333–342
- ✦ Jonsson R, Petersen JK, Karlsson O, Loo LO, Nilsson S (2005) Particle depletion above experimental bivalve beds: in situ measurements and numerical modeling of bivalve filtration in the boundary layer. *Limnol Oceanogr* 50:1989–1998
- ✦ Jung AS, Van der Veer HW, Van der Meer MTJ, Philippart CJM (2019) Seasonal variation in the diet of estuarine bivalves. *PLOS ONE* 14:e0217003
- ✦ Kamermans P (1993) Food limitation in cockles (*Cerastoderma edule* (L.)): influences of location on tidal flat and of nearby presence of mussel beds. *Neth J Sea Res* 31:71–81
- ✦ Kamermans P (1994) Similarity in food source and timing of feeding in deposit- and suspension-feeding bivalves. *Mar Ecol Prog Ser* 104:63–75
- Kamermans P, Van Asch M (2018) Monitoring draagkracht voor schelpdieren in relatie tot opschaling MZIs in de Waddenzee en Oosterschelde. Rapport C043/18. Wageningen Marine Research, Wageningen
- ✦ Möller P, Rosenberg R (1983) Recruitment, abundance and production of *Mya arenaria* and *Cardium edule* in marine shallow waters, western Sweden. *Ophelia* 22:33–55
- ✦ Peterson CH, Black R (1987) Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. *Limnol Oceanogr* 32:143–166
- ✦ Peterson CH, Black R (1991) Preliminary evidence for progressive sestonic food depletion in incoming tide over a broad tidal sand flat. *Estuar Coast Shelf Sci* 32:405–413
- ✦ Philippart CJM, Beukema JJ, Cadée GC, Dekker R and others (2007) Impacts of nutrient reduction on coastal communities. *Ecosystems* 10:95–118
- Reise K (1985) *Tidal flat ecology. An experimental approach to species interactions*. Springer Verlag, Berlin
- ✦ Smaal AC, Prins TC, Dankers N, Ball B (1998) Minimum requirements for modelling bivalve carrying capacity. *Aquat Ecol* 31:423–428
- ✦ Smaal AC, Schellekens T, van Stralen MR, Kromkamp JC (2013) Decrease of the carrying capacity of the Oosterschelde estuary (SW Delta, NL) for bivalve filter feeders due to overgrazing? *Aquaculture* 404-405:28–34
- ✦ Van Aken HM (2008) Variability of the water temperature in the western Wadden Sea on tidal to centennial scales. *J Sea Res* 60:227–234
- ✦ Van der Meer J, Beukema JJ, Dekker R (2001a) Long-term variability in secondary production of an intertidal bivalve population is primarily a matter of recruitment variability. *J Anim Ecol* 70:159–169
- Van der Meer J, Piersma T, Beukema JJ (2001b) Population dynamics of benthic species on tidal flats: the possible roles of shorebird predation. In: Reise K (ed) *Ecological comparisons of sedimentary shores. Ecological Studies Vol 151*, Springer-Verlag, Berlin, p 317–335
- Van der Meer J, Heip CH, Herman PJM, Moens T, Van Oevelen D (2005) Measuring the flow of energy and matter in marine benthic animal populations. In: Eleftheriou A, McIntyre A (eds) *Methods for the study of marine benthos*. Blackwell Science, Oxford, p 326–407
- ✦ Zimmerman JTF (1976) Mixing and flushing of tidal embayments in the western Dutch Wadden Sea. I. Distribution of salinity and calculations of mixing time scales. *Neth J Sea Res* 10:149–191

Editorial responsibility: Omar Defeo,
Montevideo, Uruguay

Submitted: January 25, 2019; Accepted: August 7, 2019
Proofs received from author(s): October 10, 2019