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

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Abstract

To investigate the relationship between stock size and production of an entire feeding guild, and in particular to find out whether it is dome-shaped (showing an optimal abundance for production), we used a 40-year data set of the 3 most important suspension-feeding bivalves (*Cerastoderma edule, Mytilus edulis,* and *Mya arenaria*) in a Wadden Sea tidal flat area of about 20 km^2. The data set contained data on numerical density of individuals, annual rates of weight growth, recruitment, survival, and secondary production. At higher densities (> 400 individuals 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 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 during the 40-y 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 insufficient recruitment by a top-down process (predation on young stages).

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 is not 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 a decline of one or more of these rates, finally resulting in a decline of production. We then operationally define carrying capacity of an ecosystem as the abundance level (stock size) at which production in this system reaches its maximal value. Our definition of carrying capacity as the optimal stock size for production is in accordance with the ones of Bacher et al. (1998), of Carver & Mallet (1990) and of Duarte et al. (2003). Such a dome-shaped curve of the relationship between stock density and production also resulted from ecosystem models by Bacher et al. (1998), Duarte et al. (2003), and Ferreira et al. (2007). In practice, Héral (1993), however, found an asymptotic increase of cultured oyster production at higher 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 years) 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 of individuals were found to range from <10 to >500 m^{-2} and biomass from <2 to >20 g AFDM m^{-2} (Beukema et al. 2010, 2017). Usually, bivalves represented a substantial share in 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 as well as on 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 content of simultaneously collected members of these species were highly similar (Kamermans 1994). Isotope analysis data also indicate that pelagic algae dominate the diets of the 3 studied bivalve species (Herman et al. 2000, Christianen et al. 2017). The 3 species included in the present study 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 did not report 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-km^2 area were we had estimated growth rates (in all age classes instead of 1-y 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 the present study appears to be unique and allows a meaningful and novel study on the relationship between density and production. So far, such studies have been performed not by drawing conclusions from real observations but only by modelling underlying processes, for instance Bacher et al. (1998), Duarte et al. (2003), Ferreira et al. (2007). The only exception we found was the study by Héral (1993) on oyster production, but this 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 are (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. Methods

2.1. Study area

The data on bivalves were obtained as part of a long-term program involving twice-annual sampling ever since the 1970s of the macrozoobenthic fauna at 15 permanent sampling stations located on Balgzand, a tidal flat area in the westernmost part of the Wadden Sea (at about 53° N and 5° E). Further details on the sampling area, the stations, and the methods can be found in Beukema & Cadée (1997). In the present paper, we used for the estimates of density of individuals, growth rate and production only data from 6 stations in the central part of Balgzand (the transects numbered 4, 5, 8, 9, 10, and 11 in Fig. 1). This part of Balgzand covered about one third of the total Balgzand tidal-flat area of 50 km^2. We chose this 20-km^2 area because almost the total 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 mostly -4 to -6 dm from mean tide level and silt contents of the sediment of mostly 1 to 5%. In the part of Balgzand to the north of this area, data on growth were scarce due to failing recruitments of the studied species in nearly all years, probably due to adverse environmental conditions (exposure to strong currents and wave action, resulting in unstable and coarse sediments). South of the selected area, growth rates were invariably lower than in the selected area, probably due to higher intertidal levels (shorter daily immersion times). Moreover, densities of suspension-feeding bivalves were frequently low there.

2.2. Environmental conditions

Temperature values were derived from daily observations of surface water temperatures from the NIOZ jetty at the shore of the Marsdiep tidal inlet (the main tidal inlet of the westernmost part of the Dutch Wadden Sea) at about 5 to 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* concentrations in surface water were available from databases of NIOZ (see Jacobs et al. unpubl.) and of Rijkswaterstaat (www.waterbase.nl). The samples were taken at a frequency of at least once or twice per month near the temperature station in the Marsdiep tidal inlet, around high tide by NIOZ and 2 to 3 hours before the time of 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 the 6 months March to August, incl. Such chlorophyll *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 the outlying point for 1996: $r = 0.52$, $n = 36$, $p = 0.001$) and we, therefore, used their averages. Unfortunately, no data on temperature nor on chlorophyll are 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 in 2 years, Kamermans (1994) found a close similarity in monthly means of chlorophyll 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 per transect covered a total of 0.95 m^2. In August (when numbers of individuals m^{-2} are much higher) we used smaller cores of nearly 0.01 m^2, thus covering 0.45 m^2 per transect. Bivalves were sorted from the sieved (1-mm mesh size) samples, assigned to age classes (cohorts indicated by the year of birth), counted (numerical density was expressed in n m^{-2}), sorted to mm shell length classes, their soft parts dried to constant weight for several days at 60^0 C, weighed per mm length class, incinerated (2 hours at 500-600^0 C) and again weighed to obtain by subtraction AFDM (ash-free dry mass).

As bivalve abundance index we used 6-station means of March and August estimates for each year of animals older than 0.5 year, expressed in numbers of individuals m^{-2}. Recruitment was defined as the 6-station mean number m^{-2} of 0-group individuals (less than 0.5 y 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 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 (in g AFDM ind^{-1}) in the 2nd and following growing seasons were obtained by subtracting mean weight in March from mean weight in 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 tend to arise simultaneously over vast areas (Beukema et al. 2001). All growth data were expressed in 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 for every year were averaged to 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^{o} C. For this correction we used the relationship shown in Beukema et al. (2017), indicating increases in relative growth per 1 ^{o}C higher water temperature to amount to averages of 24% in *C. edule*, to 21% in *M. edulis* and to 27% in *M. arenaria*. Thus, if in *C. edule* a relative growth rate of 100% was observed 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. In the following, generally these temperature-corrected data are 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: $P = \Sigma (n \cdot \Delta g)$, with 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. It is expressed in g AFDM m^{-2} per 0.5 y. 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 animal generally lose weight.

2.5. Statistical methods

For evaluation of statistical significance, we generally 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 1979-2015 are shown in figure 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 by 0.04 °C y^{-1} ($r = 0.51$, $n = 37$, $p<0.01$).

Annual means of chlorophyll *a* concentrations in the main tidal inlet during the March - August growing seasons 1975-2015 are shown in figure 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 by 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 the Rijkswaterstaat series (1978-2015) a decline by 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 years 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 the densities of individuals were 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 *C. edule*, whereas mussels *M. edulis* and gaper clams *M. arenaria* each accounted for about 22% of the long-term total. As a 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* ($r = +0.04$), in *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, ash-free dry weights 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 Methods to obtain estimates of relative growth in a certain year in 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 figure 3 of Beukema et al. (2017). The standard errors observed in the year with the highest bivalve abundance (2012) did 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 appear 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 r 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 is 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 in all 3 species close to 0. Densities in by far the majority of observation years were within this range. Growth rates in these years showed a lot 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 m^{-2} in *C. edule* and in *M. edulis*, and of >300 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 years 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 bivalve species. Thus the above low recruitments in the 3 years 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 in any of the 3 species. Spearman-r values amounted to non-significant values of 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 happened to be above the long-term average in all 3 species.

Bivalve production P strongly depended on bivalve abundance N (Fig. 4). Up to about 400 individuals m^{-2}, P increased linearly with N, 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 P values well below the extrapolated linear increase suggested by the P values observed at lower densities. The maximal value of P was reached at N = about 400 individuals m^{-2}. Thus at higher densities than about 400 m^{-2} (anyway this occurred only twice in the period of about 40 year), P became 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 production is a dome-shaped quadratic one (with a high r^2 value).

3.5. Relationships with chlorophyll concentrations

The steady decline of the chlorophyll concentrations by 0.22 mg m^{-3} y^{-1} resulted in a total decline over the period of observation of about 8 mg m^{-3}, representing about half of the values found in the initial years. 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 chlorophyll concentrations and growth index values in any of the 3 species studied. 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 chlorophyll concentration (7.2 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 production values of around the maximum, i.e. at carrying capacity), the chlorophyll concentrations in the main tidal stream of about 14 and 17 mg m^{-3} y^{-1}, respectively, were around or above the long-term average of 14.4 mg m^{-3} y^{-1}. Thus, our estimates of maximal secondary production were at chlorophyll concentrations that were representative for the area.

Chlorophyll 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 2012-point for chlorophyll 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. (1998) and Ferreira et al. (2007), but differs from the relationship found by Héral (1993). The dome-shaped curve allows an estimate of the maximal production per growing season of the suspension-feeding bivalves (of around 100 gAFDM m^{-2}) and the optimal density at which this maximum is realized (around 400 individuals 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 such 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, all of these species will be affected at the same time. Indeed, all 3 studied species simultaneously showed seriously reduced growth rates at the highest bivalve density (Figs 2 and 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 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, some 10 to several to tens 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-year 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 reported 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 a negatively 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 year).

In 95% (37 out of 39) of the years of the study period, bivalve production increased linearly with numerical density; growth rates being independent of density in all 3 species in the vast majority of years. A similar conclusion was reached for *Limecola balthica* populations on Balgzand (Van der Meer et al. 2001a) and the cockle *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) expressed a similar conclusion for tidal-flat ecosystems.

4.2. Primary and secondary production

Heip et al. (1995) summarized reports of total-macrozoobenthos production of various estuaries, showing a wide range of values which were usually not higher than some tens of g AFDM m^{-2} y^{-1}. The maximal bivalve production values of around 100 g AFDM m^{-2} in half a year we found (Fig. 4) are high but not unique. Hibbert (1976) found a total-bivalve production of 38 to 92 g AFDM m^{-2} y^{-1} at 3 sites in a 0.6-km^2 tidal flat area in southern England. Mőller & Rosenberg (1983) found extremely high production values of >300 g AFDM m^{-2} in an exceptionally strong year class of *Mya arenaria* (and even >400 g for this species and *Cerastoderma edule* together). These values were observed in small (about 0.01 km^2) and 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 g AFDM m^{-2}, would have used up a substantial share 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 of 140 gC m^{-2}. Rates of primary production in the main tidal stream of the western Wadden Sea were estimated to amount to about 200 gC m^{-2} y^{-1} (Philippart et al. 2007, Jacobs et al. unpubl.) and to 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 the zooplankton and 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 at these high densities could maintain on the local primary production.

In practice, however, bivalves and other filtering benthic animals do not depend on strictly 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 chlorophyll concentrations in the major tidal stream with increasing bivalve numbers up to about 600 m^{-2}; only at the highest bivalve abundance (in 2012) we found a serious reduction of chlorophyll concentrations (Fig. 5: to the lowest value in almost 40 years). 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 consisted 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 turn over times of the Balgzand area amount to only a few tides (Zimmerman 1976), excluding a serious reduction of the chlorophyll concentrations at the tidal inlet by bivalve grazing on Balgzand tidal flats. Indeed, long-term mean chlorophyll concentrations by the Rijkswaterstaat estimates 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 North Sea and Wadden Sea is so rapid that Wadden Sea bivalve populations could generally not substantially deplete the phytoplankton population.

In turn, tidal-stream chlorophyll 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 chlorophyll concentrations are not actually measured exactly in the area where the bivalves lived. It is unfortunate that not any 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. In only 2 or 3 out of about 20 years of observation in the various species, we found growth rates that were reduced at the highest densities (Fig. 3). Total suspension-feeding bivalve production was reduced in only 2 out of 39 years (Fig. 4).

At first sight, this result appears contradictory to conclusions of Heip et al. (1995) and Herman et al. (1999), who state that primary production and food availability are decisive for biomass and secondary production of zoobenthos. However, they conclude this 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. The present study, however, deals 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) chlorophyll 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 chlorophyll concentrations in the Wadden Sea ever since the mid-1990s (Beukema et al. 2017) did not result in a decline on Balgzand of total bivalve biomass (rather an increase was observed by Beukema & Dekker 2019) nor of total zoobenthic biomass (Dekker 2012 and own unpublished observations). These findings are contrary to the expectation expressed by Beukema et al. (2002), who described an at that time existing positive relationship between chlorophyll concentrations and zoobenthic biomass.

5. Conclusions

Over a wide range of numerical densities of suspension-feeding bivalves, growth rates were unrelated to their density. Only at densities of over about 400 individuals m^{-2}, growth rates in all 3 studied species declined to rates below their long-term averages. 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, Jacobs et al., unpubl.) and chlorophyll 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 chlorophyll concentrations of around the long-term average, but nowadays these concentrations are lower by about 30%. So far, no declining trends in growth rates of bivalves have been observed (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 rarity of observations of clear-cut bottom-up effects in the studied ecosystem may be due to the infrequent occurrence of high bivalve densities. Usually, 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 will have prevented an overloading of the system in all but 5% of the 40 years of observation, making bottom-up limitation of growth and production of suspension-feeding bivalves a rare phenomenon on the studied tidal flats.

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Table 1. Long-term means of weight increments (+ 1 standard error) during successive growing seasons in the 3 main species of suspension-feeding bivalves on Balgzand, expressed in g AFDM ind^{-1}. Number of years with sufficient observations mentioned between brackets. A value for a year was included only if an estimate was available from at least 4 sites with each at least 3 individual observations.

Growing season:	2nd	3rd	4th
C. edule	0.30 + 0.02 (20)	0.23 + 0.03 (11)	0.28 + 0.04 (6)
M. edulis	0.25 + 0.03 (15)	0.32 + 0.06 (7)	
M. arenaria	0.30 + 0.02 (15)	0.86 + 0.09 (11)	1.37 + 0.08 (4)

Legends

Fig. 1. Map of (top) the westernmost part of the Wadden Sea and (bottom) the tidal-flat area called Balgzand. The permanent sampling sites are indicated: 12 transects (numbered 1-12) and 3 squares (A, B, and C). Our present study area is limited to the central part of Balgzand: the 6 transects 4, 5, 8, 9, 10, and 11. Based on Fig. 1 of Beukema & Dekker (2015).

Fig. 2. Long-term (1975-2015) changes in:
(A) Densities (n m^{-2}) during the growing season (means of observations in March and August) of the 3 species (solid squares) *Cerastoderma edule,* (crosses), *Mytilus edulis* and (open circles) *Mya arenaria.* Totals shown by solid stars. Means of densities observed at 6 Balgzand transects.
(B) Indices for annual growth in (solid squares) *Cerastoderma edule*, (crosses) *Mytilus edulis*, and (open circles) *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 the text. In none of the species growth showed a significant long-term trend.

Fig. 3. Relationships between the sums of density (n 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-values around of over 0.1).

Fig. 4. Relationship between the sums of density (N: n m^{-2}) of 3 species of suspension-feeding bivalves (from Fig. 2A) and the somatic production (P in g AFDM m^{-2}) of the 3 species together in the March-August periods of 39 years (1976 – 2014). One point for each year of observation. Best fit: $P = 7.3 + 0.30 N - 0.00024 N^2$ ($r^2 = 0.62$).

Fig. 5. Relationship between the sums of density (n m^{-2}) of 3 species of suspension-feeding bivalves (from Fig. 2A) and the chlorophyll concentrations in the main tidal inlet (means of RW

and NIOZ data). Each point represents the March-August period of 1 year. The relationship was far from significant ($r = -0.16$, $n = 37$, $p = 0.4$).

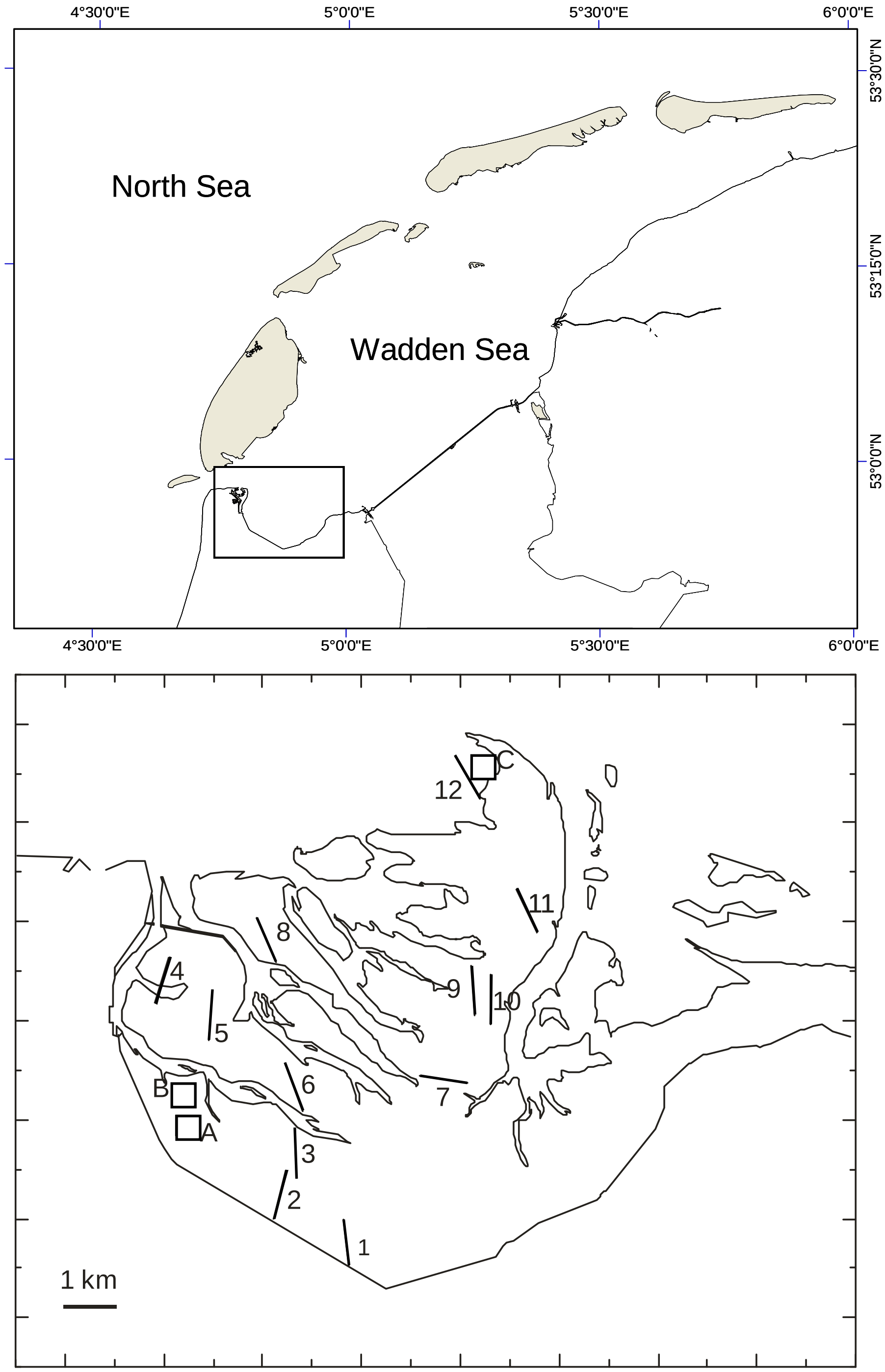
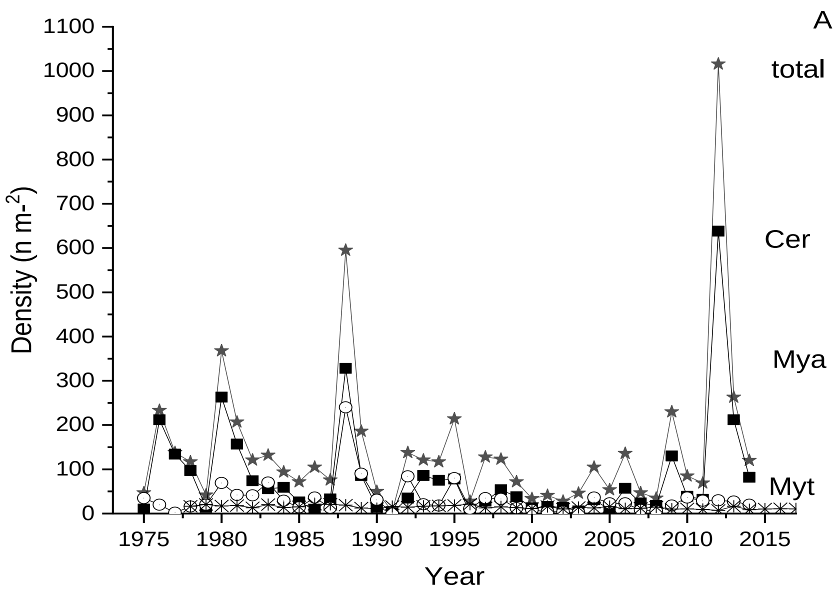

4°30'0"E
5°0'0"E
5°30'0"E
6°0'0"E
53°30'0"N
53°15'0"N
53°0'0"N
North Sea
Wadden Sea
C
12
11
8
4
9
10
5
6
B
7
A
3
2
1
1 km

Fig. 1


A
total
Cer
Mya
Myt
Density (n m-2)
Year

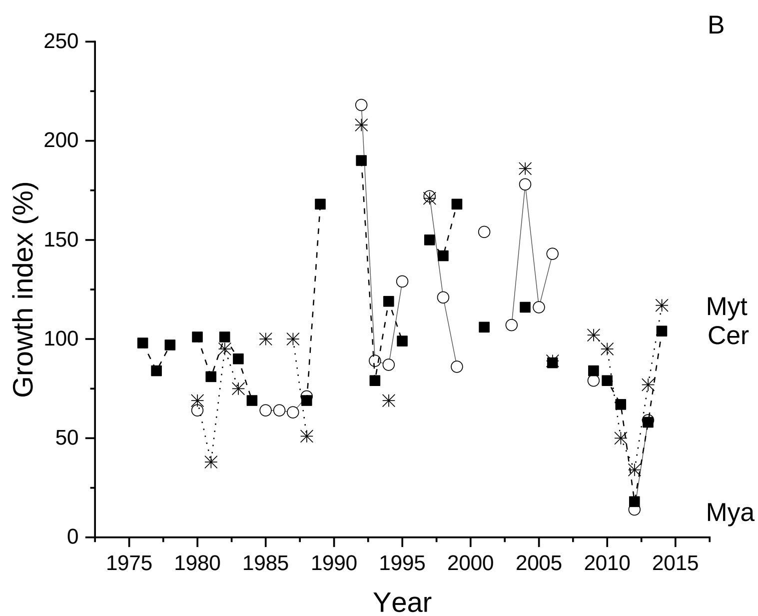
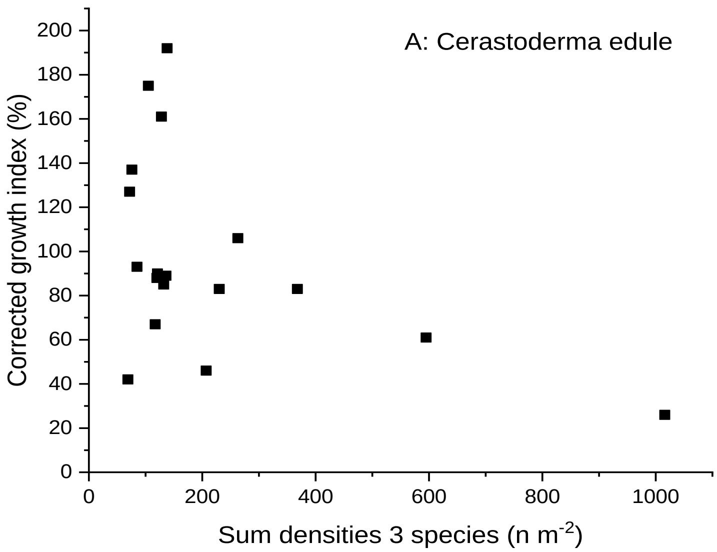
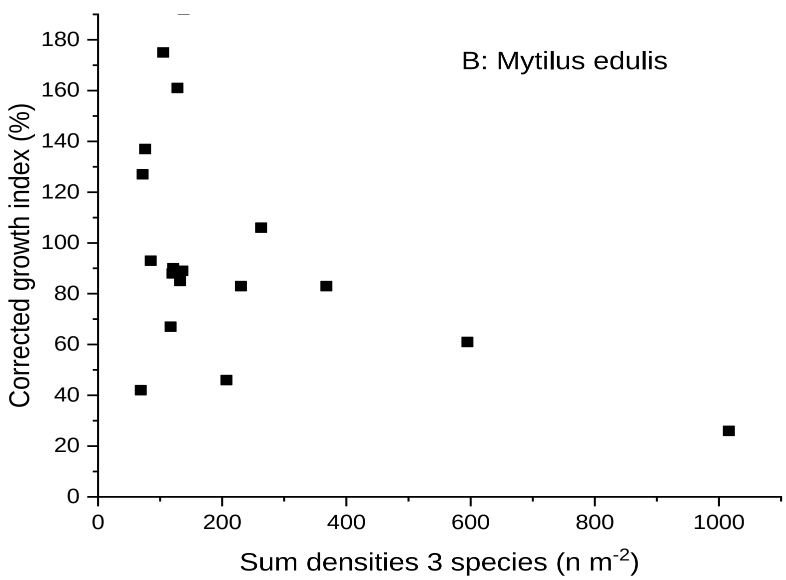

B
Myt
Cer
Mya
Growth index (%)
Year

Fig. 2


A: Cerastoderma edule
Corrected growth index (%)
Sum densities 3 species (n m-2)
0
20
40
60
80
100
120
140
160
180
200
0
200
400
600
800
1000


B: Mytilus edulis
Corrected growth index (%)
Sum densities 3 species (n m-2)
0
20
40
60
80
100
120
140
160
180
0
200
400
600
800
1000

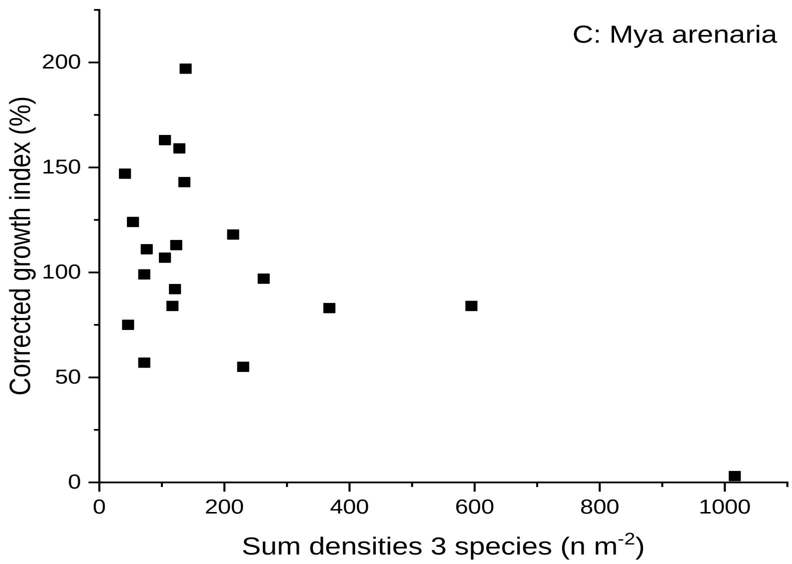

C: Mya arenaria
Corrected growth index (%)
0
50
100
150
200
0
200
400
600
800
1000
Sum densities 3 species (n m-2)

Fig. 3

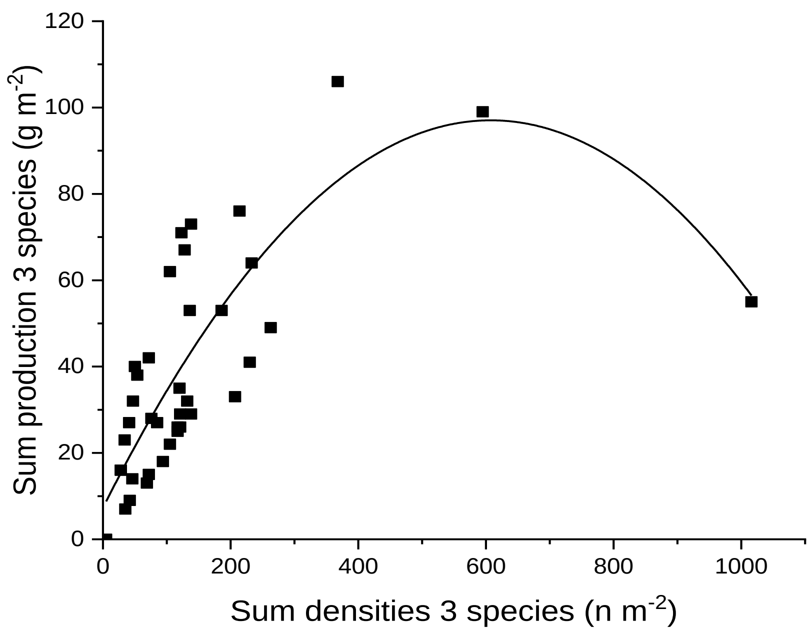
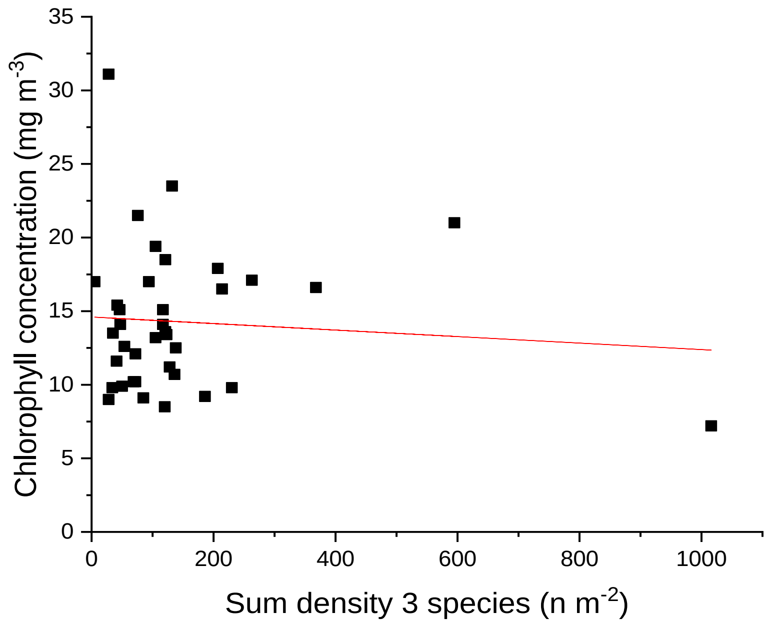

Sum production 3 species (g m-2)
0
20
40
60
80
100
120
0
200
400
600
800
1000
Sum densities 3 species (n m-2)

Fig. 4



Chlorophyll concentration (mg m-3)
35
30
25
20
15
10
5
0
0
200
400
600
800
1000
Sum density 3 species (n m-2)

1 Fig. 5