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Bottom-up as well as top-down processes govern zoobenthic secondary production in a tidal-flat ecosystem

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Abstract

For decades, we monitored numbers and weights of the macrozoobenthos in a vast tidal-flat area in the Dutch Wadden Sea. We used data collected since 1992 to estimate annual secondary production. Data on chlorophyll concentrations and primary production were available for a nearby tidal inlet, showing rapid increases in the late 1970s and gradual declines since the late 1980s. The benthos responded with a doubling of biomass around 1980 and gradual declines of summer biomass, annual production as well as seasonal biomass gain for the 1992–2019 de-eutrophication period. In nearly all years, production of bivalves (on average 25.5 gAFDM m^{-2} yr^{-1}) accounted for more than half of the total zoobenthic production (averaging 42.7 gAFDM m^{-2} yr^{-1}). Production values for individual years were not correlated with chlorophyll concentrations or primary production of that year, but did show a significantly positive relationship with bivalve recruitment success in the preceding year. As recruitment was governed by predation pressure on early bivalve bottom stages, it is a top-down process. Bottom-up processes were expressed in the gradually declining long-term trend of bivalve growth rates and secondary production during the de-eutrophication period and also in a few years when bivalve numbers were so high that growth rates were reduced by food competition. In by far most years, numbers of bottom animals were too low to fully exploit the carrying capacity of the system and production increased linearly with preceding recruitment.

Heip et al. (1995) argue that system-wide biomass and production of macrobenthic suspension feeders are limited by the planktonic primary production of the system. If biomass and production of macrozoobenthos (which is mostly dominated by suspension feeders and most of it thus directly dependent on phytoplankton for their food) are indeed regulated primarily bottom-up, positive relationships may be expected between primary production/algal food supply (chlorophyll concentrations) and biomass/secondary production of their consumers (by far the greater part of the bottom fauna). Such positive relationships were indeed observed by comparison of different ecosystems with different productivity (Herman et al. 1999). However, an equally interesting question is, whether such relationships can be found also when estimates for different years are compared within one single ecosystem.

For the westernmost part of the Wadden Sea, now decennia-long data series are available for estimates of biomass and production of the tidal-flat macrozoobenthos (Beukema and Dekker 2020) as well as for phytoplankton concentrations and primary production in a nearby tidal inlet (Philippart et al. 2007). These data enabled a detailed study on relationships of levels and of year-to-year changes in primary and secondary production.

In earlier papers (Beukema et al. 2002; Philippart et al. 2007), we showed that zoobenthic biomass strongly and rapidly increased around 1980 on Wadden Sea tidal flats within a few years after a doubling of chlorophyll concentrations (as a consequence of increased nutrient concentrations and primary production) in the main tidal inlet. The subsequent de-eutrophication started after the mid-1980s, with declining nutrient concentrations, chlorophyll concentrations and primary production (Philippart et al. 2007). It resulted in declines of annual biomass increases in the growing season (Beukema and Dekker 2020) and in declines of annual growth rates in the main bivalves (Beukema et al. 2017). Such changes point to a declining trend in secondary production.

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Author Contribution Statement: J.J.B. developed the line of thought and wrote most of the paper. R.D. collected most of the data and prepared the figures.

In this paper, we give evidence that the secondary production of the macrozoobenthos declined during the de-eutrophication period. In this way, we show a close connection between levels of primary production/algal food supply with those of zoobenthic production/biomass. We think that production estimates are more relevant and meaningful than estimates of biomass, because the bottom fauna is composed for a varying part of big individuals (particularly of the long-living bivalve *Mya arenaria*) that contribute a lot to biomass but little to production. The relationship between primary production/algal food supply with secondary production is more interesting than that with exclusively animal biomass, because it gives more insight in the functioning of the system. Moreover, we investigate in this paper what other processes governed magnitude and variability of annual secondary production.

Measurements of secondary production contribute to a better understanding of the functioning of an ecosystem (Dolbeth et al. 2012). Generally, such estimates were found to vary a lot from year to year (Möller et al. 1985; Maurer et al. 1992; Dolbeth et al. 2005; Beukema and Dekker 2019, 2022). However, to our knowledge, really long-term data series on secondary production in marine benthic systems have never been published. Representative estimates of ecosystem productivity ask for data for a period of at least some 4 or 5 yr (Beukema and Dekker 2006; Dekker and Beukema 2007). For a determination of long-term trends, even much longer data series are indispensable (Beukema and Dekker 2020). As far as we are aware, no other studies have been published on the effects of temporal variation in algal food supply or primary production on variation in biomass or production of communities of marine bottom animals. Frank et al. (2006) studied the dependence of fishery yields on primary production and found in several areas evidence for bottom-up control: positive relationships between an index of phytoplankton concentrations and fishery yield.

We tested the following hypotheses: (1) long-term trends in the level of secondary production of the bottom fauna follow those of primary production and chlorophyll concentrations and are thus regulated bottom-up; (2) short-term, year-to-year, fluctuations in secondary production may not be affected primarily by simultaneous short-term fluctuations in primary production or chlorophyll concentrations, but by other processes.

Methods

The data we used on annual chlorophyll concentrations were generally the mean values of observations from data bases of NIOZ and RW (Rijkswaterstaat), but 1974 and 1975 from NIOZ only and 1976 and 1977 from RW only. Data for 2011–2017 were friendly communicated by P. Jacobs (pers. comm.). Data used on primary production for the 1970s and 1980s were from Cadée and Hegeman (2002), but partly (1973, 1985) recalculated to match later data, for 1974, 1975, 1986 and 1990–2003 from Philippart et al. (2007), and for 2012–2014 from Jacobs et al. (2020).

The macrozoobenthos on Balgzand (a 50-km^2 tidal flat area in the westernmost part of the Wadden Sea) was sampled in a consistent way from 1970 to 2019 two times per year at each of 15 sites, using cores and 1-mm sieves. Sampling took place at the time of the year, March and August, when macrozoobenthic biomass was at its annual minimum and maximum, respectively (Beukema 1974). Further details on the Balgzand area and on sampling the macrozoobenthos can be found in Beukema and Cadée (1997) and in Beukema and Dekker (2019). March cores were taken to a depth of 25–30 cm, August cores were taken to this depth only starting from around 1990. Before that time, most deep-living animals (large *Mya arenaria* and *Arenicola marina*) were not sampled in summer. Precise biomass and production data from summer samples and annual means of winter and summer samples are thus available only for the 1992–2019 period.

For the bivalves, we obtained direct estimates on annual production by the weight-increment summation method (Van der Meer et al. 2005), using twice-annual sampling data on numerical densities (n m^{-2}) and biomass (g AFDM m^{-2}, ash-free dry mass). Details are published in a number of earlier papers on bivalve production measurements: *Cerastoderma edule* (Beukema and Dekker 2006), *Mytilus edulis* (Beukema and Dekker 2007), *Macoma balthica* (Dekker and Beukema 2007; Beukema and Dekker 2013), and *Ensis leei* (Dekker and Beukema 2012). So far, results on similar research on *Mya arenaria* are unpublished.

Annual production values in other benthic species were estimated by applying the Brey model (Brey 1990, 2001). This method proved to be unsuitable for estimating production in the dominating bivalves in the studied system, as it seriously underestimated real production in all large bivalves (Beukema and Dekker 2022). The other species included all polychaetes (except for the predators *Nephtys* species) and crustaceans (except for the predators *Crangon crangon* and *Carcinus maenas*). The snail *Peringia ulvae* was not considered, because it feeds predominantly on algae attached to sand grains. We included only secondary producers that depend (more or less) on phytoplankton, as we had no estimates available on abundance and production of other algae such as benthic microalgae. Typical suspension feeders (such as *C. edule*, *Mytilus edule*, and *Mya arenaria*, all dominating in the bottom fauna of tidal flats) almost fully depend on phytoplankton, whereas most deposit (most worms) and mixed feeders (such as *Mac. balthica*) depend on both (Herman et al. 2000).

For evaluation of statistical significance of correlations, we generally used the Spearman rank test and sometimes the Wilcoxon test. These are simple tests, making no demands as to a normal distribution of the data used.

Results

Changes in chlorophyll concentration and primary production

Annual estimates of Chlorophyll *a* concentrations for the March–August growing season, when by far most of the secondary production is realized, increased strongly in the 1970s

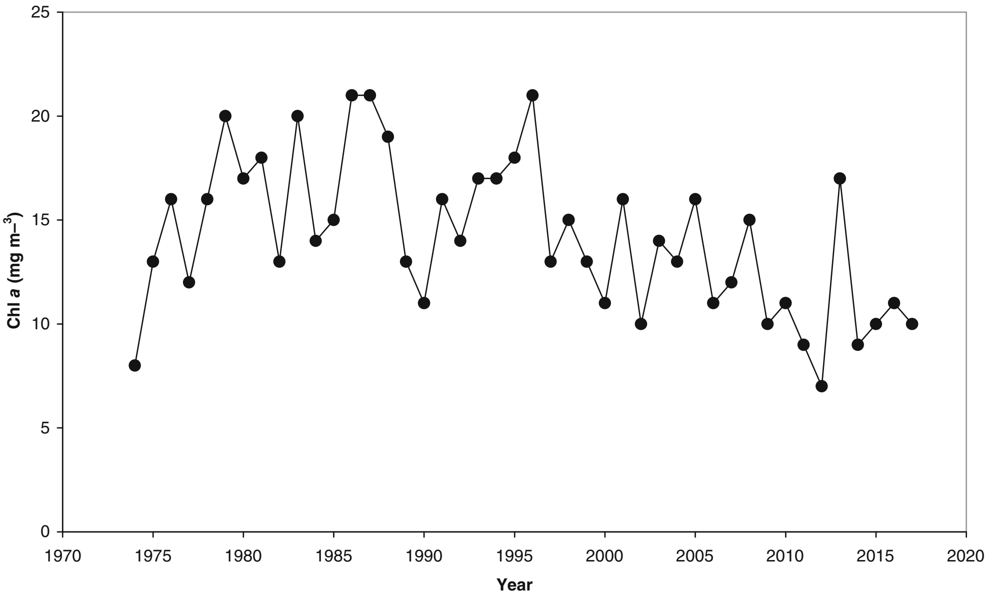

Fig. 1. Long-term changes in mean chlorophyll *a* concentrations (mg m^{-3}) for the growing seasons (March–August, incl.) of 1974–2017 as observed in the Marsdiep tidal inlet, at about 5 km from Balgzand. The negative trend for the 1992–2017 period is statistically significant ($r = -0.66$, $n = 26$, $p < 0.001$).

to reach maximal values in the 1980s and early 1990s and subsequently showed a declining trend (Fig. 1). Annual estimates for the entire year (Cadée and Hegeman 2002; Philippart et al. 2007) showed similar trends, at a level of about 60% of the seasonal values shown in Fig. 1. The declining trend shown in Fig. 1 was highly significant for the 26-yr period 1992–2017 during which we studied secondary production: $r = -0.66$, $n = 26$, $p < 0.001$. Around 2019, the level of the concentration amounted to about 65% of that around 1992.

For primary production, fewer estimates are available (Fig. 2). These annual estimates by Cadée and Hegeman (2002), Philippart et al. (2007) and Jacobs et al. (2020) showed a picture that is similar to the one for Chl *a* concentrations (Fig. 1): a strong increase from the 1970s to the 1980s, followed by a declining trend since the mid-1980s. This trend

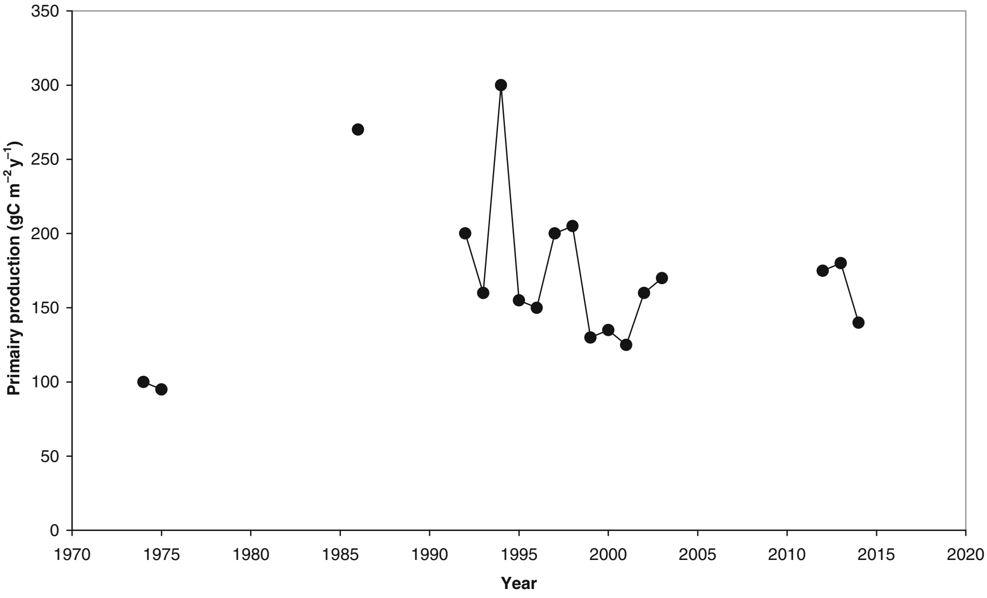

Fig. 2. Long-term observations on annual primary production (gC m^{-2} yr^{-1}) in the Marsdiep tidal inlet. Most data from Philippart et al. (2007).

was non-significant for the limited data available for the period starting in 1992 ($r = -0.28$). Around 2019, the level of the primary production amounted to about 70% of that around 1992. The mean annual primary production for the 1992–2019 period amounted to 172 gC m^{-2} yr^{-1}.

Changes in zoobenthic biomass

Late-winter biomass of all macrozoobenthic secondary producers (except *P. ulvae*) suddenly increased from about 20 gAFDM m^{-2} in the 1970s to around 30 gAFDM m^{-2} in the 1980s (Fig. 3). Further details on this increase and its possible cause can be found in Beukema and Cadée (1997) and Beukema et al. (2002). Subsequent years showed strong fluctuations and no significant trend. The extremely high values in 1999–2000, 2005–2006, and 2016–2019 were caused particularly by a high abundance of the big adults of *Mya arenaria* with biomass values of around 20 gAFDM m^{-2}.

Reliable late-summer observations are available for the data series starting in 1992 (open points in Fig. 3). For the 28 yr of the 1992–2019 period, the summer biomass values showed a significantly declining trend: $r = -0.41$, $n = 28$, $p < 0.05$. As a consequence of this trend (and the absence of a clear trend in winter values), the difference deltaB between the summer and winter values of the same year declined significantly in the course of the study period (open points in Fig. 4): $r = -0.60$, $n = 28$, $p < 0.01$. This decline was strong: less than half of the level in the 1990s was left in the 2010s.

Changes in zoobenthic secondary production

During the 28-yr period, 1992–2019, the mean total secondary production of the macrobenthic animals that are for their food (largely) dependent on phytoplankton amounted to 42.7 gAFDM m^{-2} yr^{-1}. The values showed a significantly declining trend (solid points in Fig. 4): $r = -0.38$, $n = 28$, $p < 0.05$. The most recent production values amounted to about 70% of the initial ones, a less strong decline than the one found in deltaB, but similar to those observed in chlorophyll concentrations and primary production. Annual values of secondary production were not significantly correlated with values for the same year for chlorophyll concentrations or primary production.

The mean total secondary production of the bottom animals of 42.7 gAFDM m^{-2} yr^{-1} or about 20 gC m^{-2} yr^{-1} amounted to an average of about 12% of the mean pelagic primary production of 172 gC m^{-2} yr^{-1}. This percentage strongly varied from 6% to 21%, without a clear trend.

In most (21 out of 28) years, bivalves produced more than polychaetes, on average 25.6 and 16.5 gAFDM m^{-2} yr^{-1}, respectively (Fig. 5). Only during the 5 yr, 1999–2003, polychaete production was consistently higher than bivalve production. This was a consequence of the bloom of the worm species *Marenzelleria viridis* around the year 2000 (Jung et al. 2020). This newly introduced species reached production values of around 10 gAFDM m^{-2} yr^{-1} during this period, a substantial part of the total polychaete production. Top values in bivalve production were found in 2005, 1992, and 1995.

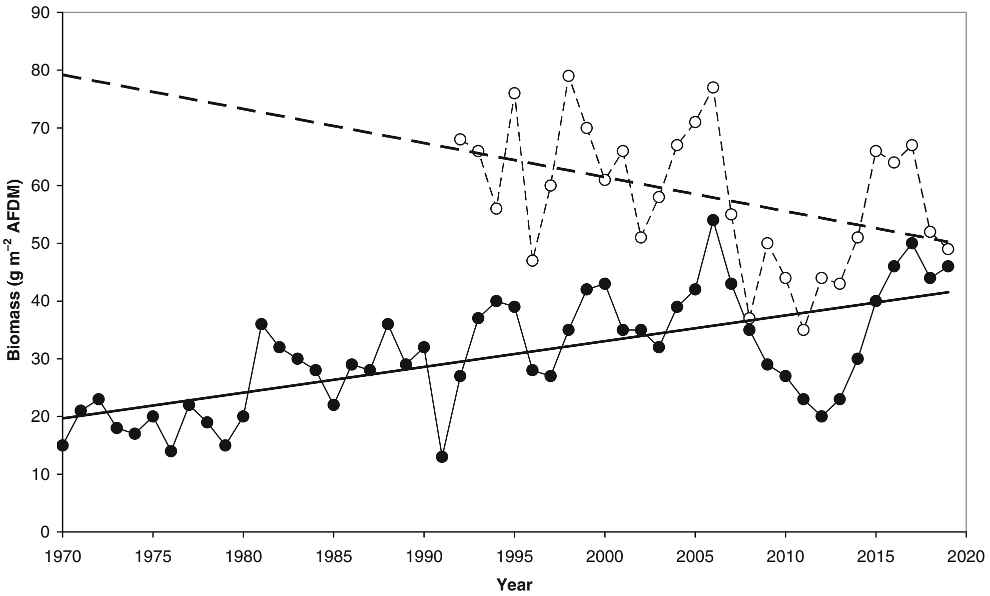

Fig. 3. Long-term changes in mean biomass (gAFDM m^{-2}) of macrobenthic secondary producers (except *Peringia ulvae*) as observed in late winter (solid points, 1970–2019) and late summer (open points, 1992–2019) on Balgzand (means of 15 sampling stations). Best linear fit of winter-biomass change: $B = 0.446\ y - 861$. The increase in late-winter biomass over the entire 1970–2019 period was highly significant ($r = +0.68$, $n = 50$, $p < 0{,}001$). The change in winter biomass over the 28-yr period 1992–2019 was nonsignificant ($r = +0.20$). Best linear fit of summer biomass change (open points): $\mathrm{B} = -0.59\ y + 1243$. The negative trend in late-summer biomass over the 28-yr period 1992–2019 was significant (Spearman $r = -0.41$, $n = 28$, $p < 0.05$).

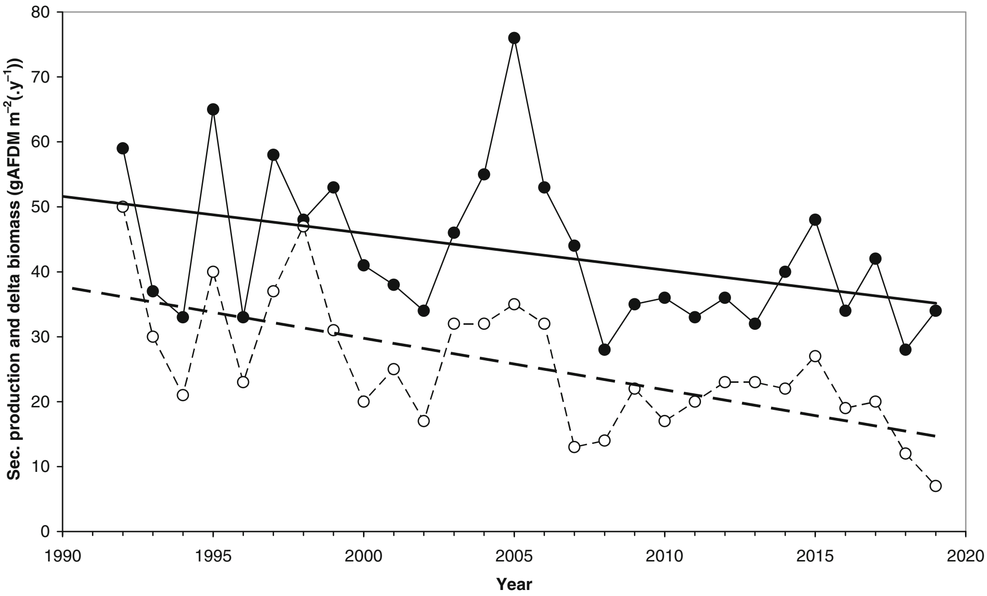

Fig. 4. Long-term (28 yr of the 1992–2019 period) changes in seasonal (March–August) biomass increase (open points, deltaB: summer minus preceding winter biomass) of benthic secondary producers (*Peringia ulvae* excluded) (in gAFDM m^{-2}) and macrozoobenthic secondary production (solid points, *P* in gAFDM m^{-2} yr^{-1}). Best linear fits: deltaB $= -0.795\ y + 1620$ and $P = -0.57\ y + 1180$. Both negative trends are statistically significant. deltaB: $r = -0.56$, $n = 28$, $p < 0.01$ and *P*: $r = -0.38$, $n = 28$, $p < 0.05$.

The value of 52 g m^{-2} yr^{-1} in 2005 was caused by an extremely high production of 23 g m^{-2} yr^{-1} by *E. leei*, an invasive species like *Mar. viridis*. It reached a peak biomass around 2006 (Jung et al. 2020). The other high bivalve production values in 1992 (44 g m^{-2} yr^{-1}) and 1995 (48 g m^{-2} yr^{-1}) were caused by *Myt. edulis* (15 g m^{-2} y^{-1}) and *Mya arenaria* (21 g m^{-2} yr^{-1}), respectively.

The declining trend in polychaete production during the 28-yr period had borderline significance: $r = -0.37$, $n = 28$, $p = 0.05$. The simultaneous decline in bivalve production was non-significant ($r = -0.20$), the sum of both was ($r = -0.38$, *see* Fig. 4).

The similar patterns in values of annual secondary production P and those of annual seasonal biomass increase deltaB

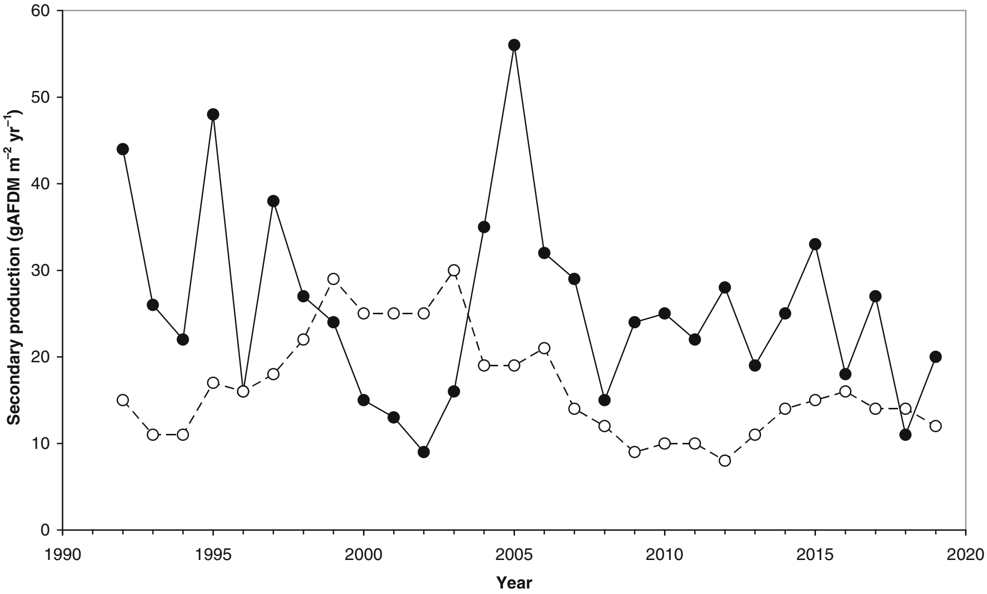

Fig. 5. Long-term changes in macrozoobenthic secondary production (in gAFDM m^{-2} yr^{-1}), separately for bivalves (solid points) and polychaetes (open points). The trend for bivalves is nonsignificant ($r = -0.20$), that for polychaetes has borderline significance ($r = -0.37$, $n = 28$, $p = 0.05$).

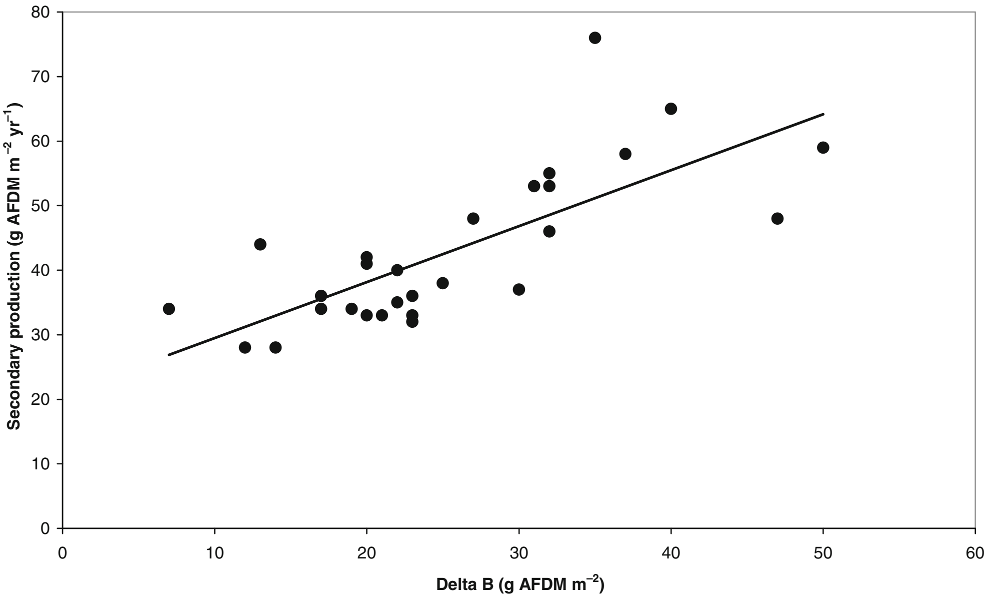

Fig. 6. The relationship between annual estimates of seasonal biomass increase (deltaB in gAFDM m^{-2}) and secondary production (P in gAFDM m^{-2} yr^{-1}) of benthic secondary producers (except *Peringia ulvae*). Best linear fit: $P = 21 + 0.87 \text{delta}B$, Spearman rank test: $r = 0.77$, $n = 28$, $p < 0.001$.

(Fig. 4) point to a strong correlation between these two variables. Indeed, P increased with increasing deltaB: Spearman $r = 0.77$, $n = 28$, $p < 0.001$ (Fig. 6). Production was invariably higher than biomass increase during the growing season, because not all producers survived to the summer samplings and could contribute to summer biomass.

Changes in growth rates

In several years of the 1992–2019 period, estimates of mean individual growth of bivalves could be made. Nearly all of the available data have been published in fig. 3 of Beukema et al. (2017) and fig. 2 of Beukema and Dekker (2019). For the 1992–2019 study period, negative trends in growth rates were found in the most important bivalve species: *C. edule* $r = -0.97$ ($n = 10$, $p < 0.001$), *Myt. edulis* $r = -0.63$ ($n = 9$, $p < 0.1$), *Mya arenaria* $r = -0.59$ ($n = 10$, $p < 0.1$), and *E. leei* $r = -1.00$ ($n = 5$, $p < 0.05$). In these species, growth rates were consistently higher in the 1990s than in later years (*see* fig. 4 in Beukema et al. 2017). *Mac. balthica* growth showed no trend (fig. 3b in Beukema et al. 2017). Combining the relative growth estimates of the four species that showed a negative trend, the means of the species estimates showed a significantly declining trend: $r = -0.73$ ($n = 18$, $p < 0.01$). On average, the growth rates of the big bivalves roughly halved from around 1992 to around 2019.

Recruitment and production

In an earlier paper (Beukema and Dekker 2019), we showed that total bivalve production (sum of three most important species: *C. edule*, *Myt. edulis*, and *Mya arenaria*) showed a strong and highly significant positive correlation with spat density at the start of the second growing season, when spat individuals are 9 or 10 months old. This correlation was present over a wide range of spat densities. Only in the few years with very high spat densities (causing reduced growth rates), production was lower than expected on the base of the strong relationship found for the great majority of years with lower densities. Therefore, the actual relationship was curvilinear (*see* fig. 4 of Beukema and Dekker 2019): a long ascending part over almost the total range of densities, followed by a descending part covering only a few years with very high spat densities.

Such a curvilinear relationship between bivalve spat density and subsequent bivalve production proved to be true also for the (much higher) spat densities as estimated already in summer, at a spat age of 3 or 4 months (open points in Fig. 7). In this figure, we included summed data of five bivalve species: *C. edule, Myt. edulis, Mya arenaria, Mac. balthica*, and *E. leei*. For the calculation of the correlations, numbers of *Mac. balthica* recruits were divided by 10, because annual growth of individuals of this small sized species was only about one-tenth of that in the other bivalve species. Therefore, Fig. 7 does not show real sums of densities of all bivalves, but an index: real sums of spat densities of all bivalve species except for those of *Mac. balthica* (which were reduced to 10%).

Despite the production reduction at the highest spat densities (caused by growth reduction by food competition, *see* Beukema and Dekker 2019), the positive correlation between total (sum of five most important species) bivalve production and the sum of their spat densities was highly significant: $r = 0.70$, $n = 28$, $p < 0.001$ (Fig. 7, open points, dashed line).

As bivalves accounted in nearly all years for the greater part of total secondary production, total secondary production (including polychaetes and non-predatory crustaceans) also

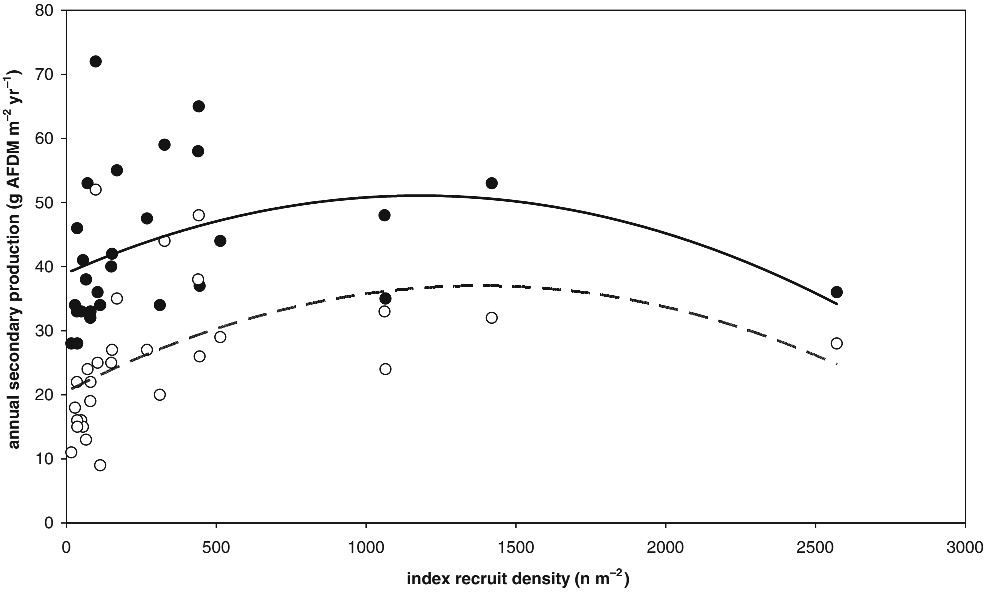

Fig. 7. Second-order polynomial fits of relationships between (an index of) bivalve recruit abundance in the preceding summer (R in n m^{-2}) and annual estimates of total secondary production (P-total, solid points, solid line) and bivalve production (P-bivalves, open points, dashed line) (in gAFDM m^{-2} yr^{-1}). P-total $= 39.0 + 0.021\ R - 0.000009\ R^2$ and P-bivalves $= 20.5 + 0.025\ R - 0.000009\ R^2$. The r^2 values amounted to 0.12 and 0.20, respectively.

showed a significantly positive relationship with the bivalve spat densities in the preceding summer: $r = 0.48$, $n = 28$, $p < 0.02$ (Fig. 7, solid points, solid line). Such positive correlations were absent for production values assessed 2 yr after recruitment. Apparently, recruitment influence on production is short term.

Top-down vs. bottom-up control of secondary production

To compare the relative contributions to the between-year variation in secondary production of the two factors recruitment and eutrophication state, we plotted the relationship between preceding recruitment and subsequent (next year) production separately for two equal groups of years: those

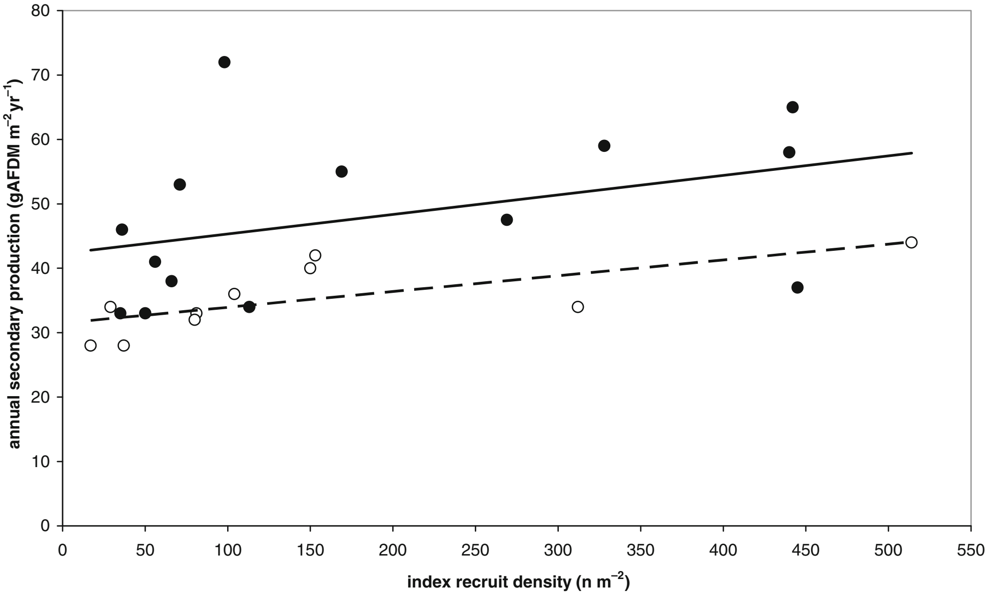

Fig. 8. Relationships between (an index of) bivalve recruit abundance in the preceding summer (R in n m^{-2}) and annual estimates of total secondary production P for two periods: the 14 yr 1992–2005 (the 14 solid points) and 10 yr out of the 14 yr 2006–2019 (the 10 open points). First period: $P = 42 + 0.0303\ R$ and second period: $P = 32 + 0.0245\ R$. For the second period, four points were omitted, because their R values were outside the range of R values in the first period.

with high primary production (1992–2005: solid points and solid line in Fig. 8) and those with low primary production (2006–2019: open points and dashed line). We restricted the comparison to the 24 yr with an overlapping range of recruitment values (0–520 m^{-2}), thus excluding the production in the 4 yr (2006, 2009, 2012, 2015) with extremely high foregoing recruitment values.

For each of the two groups of years, the relationship was significantly positive (Spearman test, $r = 0.39$ and 0.69, both $p < 0.05$) and nearly parallel. The slopes did not differ significantly. The level of the points for the first (high eutrophication) group was significantly higher than that for the low-eutrophication group of years, on average 48 ± 3.4 and 35 ± 1.7 g m^{-2} yr^{-1} ($n = 14$ and 10, respectively; $p < 0.01$, Wilcoxon test). Mean recruitment values in the 2 groups of 14 and 10 yr did not differ significantly (Wilcoxon test). A comparison of recruitment indices between the two groups of 14 yr (1991–2004 vs. 2005–2018) showed an on average significantly higher recruitment ($p < 0.05$, Wilcoxon test) in the second period. Thus, despite the lower eutrophication state, recruitment was on average more successful. There was no negative effect of de-eutrophication on bivalve recruitment.

Discussion

The parallel declines in on the one hand chlorophyll concentrations/primary production and on the other hand zoobenthic summer biomass/seasonal biomass increases/secondary production for the 1992–2019 period point to a general influence of a bottom-up process governing productivity of the benthic fauna. All above data series showed a decrease by about 30% from around 1992 to around 2019. Another parallel change was observed in the late 1970s/early 1980s, when chlorophyll concentrations/primary production as well as zoobenthic biomass roughly doubled (Beukema et al. 2002). These similar changes at the levels of primary production and primary consumers strengthen a causal relation.

The decline of production during the de-eutrophication period occurred in bivalves as well as in polychaetes. The declining trends in production values and the underlying seasonal biomass increase during the 1992–2019 period may be explained by declining growth rates. Such declines were indeed observed in all important bivalve species (Beukema et al. 2017). This indicates a declining trend in the availability of food and therefore directly points to a bottom-up process. The observed changes in eutrophication stage, we observed in this one ecosystem are in accordance with the relationships which were found by comparing ecosystems by Herman et al. (1999). We now show that this relationship is not limited to differences in zoobenthic biomass but is valid also for differences in zoobenthic production.

In contrast to summer values, late-winter macrozoobenthic biomass did not show a decline during the 1992–2019 period. There are two possible causes for the difference in trends of summer and winter biomass. In the first place, after 1990, there were hardly any severe winters causing mass mortalities in sensitive species and thereby low values of total late-winter biomass (*see* fig. 2 in Beukema and Dekker 2020). Second, successful recent recruitments in *Mya arenaria* resulted in high biomass values in this species with big adults with relatively low weight gain in the growing season.

The above results have important implications for interpreting long-term trends in zoobenthos dynamics. Short-term year-to-year changes appear to be governed mainly by another process than the bottom-up one, because short-term fluctuations in chlorophyll concentrations were not found to be correlated with those of macrozoobenthos biomass and production. The repeatedly observed strong dependence on preceding recruitment success of macrozoobenthic biomass (Beukema et al. 2010) as well as production (Van der Meer et al. 2001; Beukema and Dekker 2006, 2007, 2019; Dekker and Beukema 2007, 2012) indicates the nature of the underlying process. Recruitment success was found to be largely determined by predation pressure exerted by shore crabs and shrimps on early bottom stages of bivalves (Reise 1985; Strasser 2002; Beukema and Dekker 2014). It is thus a top-down process. The high variability in annual recruitment success of bivalves (Beukema and Dekker 2019) will have been the main cause of the high variability in annual secondary production of bivalves (Fig. 5, solid points). The two processes, bottom-up and top-down, appear to have affected secondary production independently, as bivalve recruitment success did not decline with decreasing eutrophication.

Bivalve species experienced many more years with recruitment failure than success (Beukema and Dekker 2014, 2019). In the years 1992–2019, secondary production (of bivalves as well as the total of secondary producers) was strongly correlated with bivalve spat numbers in the preceding summer and these numbers were in most years too low to reach high production values in the subsequent year (Beukema and Dekker 2019). Only in a few exceptional years (especially in 2012 after a record-high bivalve recruitment success in 2011), bivalve recruitment was so high that growth and production were reduced in the following year (the rightmost point in Fig. 7). The year 2012 was the only year with a reduced chlorophyll concentration that could be linked with high bivalve abundance and grazing (Beukema and Dekker 2019). In all other years, there would have been sufficient primary production and food supply to enable a higher secondary production. A lack of sufficient numbers of consuming and growing secondary producers prevented in nearly all years that the ceiling for secondary production was reached. This was a consequence of the top-down governed variation in recruitment success.

In some years, invasive species (*Mar. viridis*, *E. leei*) accounted for a substantial part of the secondary production. During a number of years these species bloomed and reached high values for biomass (Jung et al. 2020) and production.

Apparently, for such species there was an open niche with sufficient food available.

The lack of correlation between the annual values of chlorophyll concentrations and secondary production might have been caused by two opposing processes: an enhancement of secondary production by higher chlorophyll concentrations but at the same time an increased demand of food to fuel the higher production resulting in lower chlorophyll concentrations. None of these relationships was statistically significant, nor was the one between recruitment in the preceding year and chlorophyll concentration.

A mean secondary production of the macrozoobenthos community of 42.7 gAFDM m^{-2} yr^{-1} is relatively high on a global scale, but it is in line with the mean estimate of 40 gAFDM m^{-2} yr^{-1} for coastal areas published by Whittaker (1975). With this value, it is the most productive type of ecosystem distinguished by Whittaker, 5 times richer than the global average or the average for marine areas. Similarly high secondary production values for benthic communities in coastal areas in Portugal and a part of the German Wadden Sea were reported by Sprung et al. (2001).

The food chain efficiency we found was highly variable from year to year (6–21%). Such variability was not unexpected in view of the lack of correlation between annual values of secondary production and those of chlorophyll concentration/primary production. Moreover, not all necessary data were available to calculate the efficiency precisely. Use of a 0.5-mm sieve, instead of the 1-mm sieve we used, would certainly have resulted in (slightly) higher estimates of secondary production. Furthermore, not all primary food sources were included, as no estimates were available for annual production by microphytobenthic algae, nor was a quantification available for suspended particulate organic matter imported from elsewhere and probably an important food source (Jung et al. 2019). Most probably, our estimate of 6–21% is a serious overestimate. To our knowledge, an effort to estimate fully and precisely the ratio between secondary and primary production may never have been made for any marine ecosystem.

Model calculations (Brinkman and Smaal 2003) predicted the decline by de-eutrophication of primary as well as secondary production. Unfortunately, this model was never published in any reviewed periodical, nor was it ever calibrated or validated. The most relevant explanation in the present context can be found in Ens et al. (2004). The results shown in the present paper might serve as a partial validation. The correspondence between the model outcomes and real observations is certainly not disappointing: both the declining trend and the degree of reduction were rightly predicted. Further comparisons between model calculations and observations are certainly necessary.

Data availability statement

The data are stored in a file at NIOZ.

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Conflict of Interest

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