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Decrease of the carrying capacity of the Oosterschelde estuary (SW Delta, NL) for bivalve filter feeders due to overgrazing?

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ABSTRACT

In the Oosterschelde estuary, primary production has decreased by 50% in the last 15 years. Nutrient concentrations are low but primary production is nutrient limited only for short periods during the growing season. Dominant bivalve filter feeder stocks consist of mussels (*Mytilus edulis*), cockles (*Cerastoderma edule*) and the introduced Pacific oysters (*Crassostrea gigas*). The mussel stock, which is under control of the mussel farmers, has decreased due to shortage of mussel seed, cockle stocks have maintained and oysters have expanded. Total filtration capacity has increased, also due to the invasion of *Ensis americanus.*

Bivalve growth and condition are food limited, as shown by a negative correlation between average mussel meat content and bivalve filter feeder stock size in a certain year. The annual growth of cockles has decreased, and the fraction picoplankton is now up to 30% of total phytoplankton. Food limitation, high filtration capacity, picoplankton abundance, and only short-term bottom-up control of primary production by nutrient limitation, point to overgrazing as a cause of primary production decline. Further expansion of shellfish stocks may induce the risk of overexploitation.

1. Introduction

Bivalve filter feeders, such as mussels (*Mytilus edulis*), cockles (*Cerastoderma edule*) and oysters (*Crassostrea gigas*) play a dominant role in many estuarine and coastal waters, owing to their great abundance, large filtration capacity and their role as prey for higher trophic levels (Dame, 2012). The commercial exploitation of bivalves has led to an increased biomass in many coastal waters, thereby raising questions about the impact on the culture itself and on the ecosystem (McKindsey et al., 2006). In many studies, the impact analysis is based on a carrying capacity evaluation, but this concept is not clearly defined. Smaal et al. (1998) argued that a distinction should be made between the original ecological carrying capacity concept, being the asymptote of the natural population size supported for a given time in a given ecosystem (Krebs, 1972) and the exploitation carrying capacity, as the stock size that gives maximum harvest. The fundamental difference is that maximum harvest is obtained at a population size that is typically not at its asymptote level. Inglis et al. (2000) proposed a distinction in physical, production, ecological and social carrying capacity. Physical carrying capacity defines the total area of farms that can be accommodated in a given space; the production capacity is defined as the standing stock at which the annual production of the marketable cohort is maximised; this is similar to the exploitation carrying capacity. The ecological carrying capacity is the stocking or farm density of the exploited population which causes unacceptable environmental impacts, and the social capacity is the level of farm development that causes unacceptable social impacts. This definition of ecological carrying capacity has little to do with the original ecological concept and raises the—societal—question on what is (un) acceptable. As pointed out by Gibbs (2009), this approach to ecological capacity is a social construct, encapsulated by the social carrying capacity. Gibbs defines carrying capacity as (i) production capacity: the absolute long-term yield that can be produced within a region, (ii) ecological capacity: the yield that can be produced without leading to significant changes to ecological processes, species, populations or communities, (iii) economic capacity: the biomass that investors are willing to establish and maintain, and (iv) social carrying capacity: the biomass/water space of culture that the community is willing to allow. In this definition of ecological carrying capacity, there still is an overlap with social capacity, as the level of changes that are considered significant is a societal parameter, and it is unrealistic to consider aquaculture with no ecological changes. Gibbs acknowledges the difficulties with the concept and he considers that analysing impacts of aquaculture on the various types of carrying capacity is a moving target, that is due to changes as a result of unpredictable external factors, technological innovations and changing stakeholder appreciations.

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Despite criticism on the carrying capacity concepts in the context of aquaculture and nature management, the impact of bivalve shellfish culture on production capacity can be demonstrated relatively easy by analysing data of bivalve stock size and annual averaged bivalve growth and production that are generally registered by farmers and authorities. For the Oosterschelde, Smaal and van Stralen (1990) and Smaal et al. (2001) showed a negative correlation between stock size and growth of mussels on the basis of data from farmers. A positive correlation between shellfish growth and food availability was shown for the Oosterschelde (van Stralen and Dijkema, 1994) and for the Ria de Arosa (Blanton et al., 1987). It shows that food availability can be considered as the main driver for production capacity, and this is the basis of predictive modelling of production carrying capacity (Grant and Filgueira, 2011).

Studies addressing unacceptable (Inglis et al., 2000) or significant (Gibbs, 2009) impacts on the ecological carrying capacity can either be numerous, if all types of impacts on the environment are addressed, or rather restricted, if the impact on food availability for other filter feeders is the focus.

In this paper we address effects on the production and the ecological carrying capacity, as defined in Smaal et al., 1998, through an analysis of effects of shellfish on food availability for suspension feeders in the ecosystem.

Our study is based on time series of stock size, individual growth, shellfish production, primary production and chlorophyll concentration from the Oosterschelde estuary (SW Netherlands; Fig. 1). Shellfish production comes from bottom culture of mussels (*M. edulis*) and oysters (*C. gigas*), and fisheries of wild cockles (*C. edule*). Mussel spat and half-grown mussels are imported from the Wadden Sea and further cultivated on lease sites, mainly in the western and central parts of the estuary.

Cockle fishery depends entirely on wild stocks mainly living on the tidal flats. Due to the *Bonamia ostreae* disease, flat oysters had decimated and culture activities are now based on the introduced Pacific oyster that is carried out on a limited scale on sublitoral culture plots in the eastern part of the estuary (Fig. 1). The introduction of the Pacific oysters has resulted in an unprecedented expansion of the species over north-western Europe (Smaal et al., 2005; Troost, 2010). In the Oosterschelde it is now the dominant filter feeding stock, and at least 700 ha of the tidal flats, so outside the cultivation areas, has been colonised by the oysters (Smaal et al., 2009).

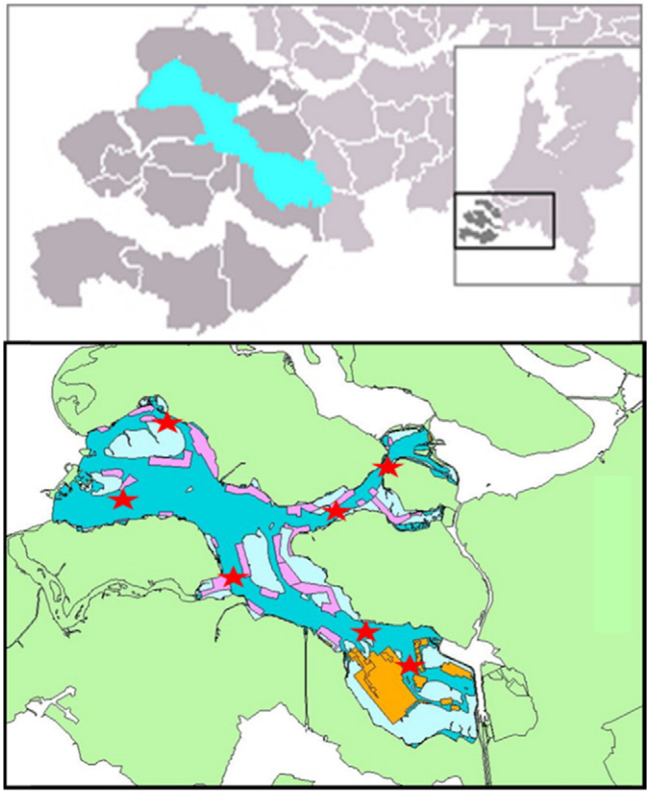

Fig. 1. The Oosterschelde estuary (SW Netherlands) with sampling stations for chlorophyll, suspended matter and primary production measurements (★) and mussel culture plots in the western and central parts (purple), and oyster culture plots in East (orange).

Food availability in the Oosterschelde is mainly based on local primary production (Herman and Scholten, 1990), limited by nutrient availability in summer and light in winter, but there are also indications of top-down control through grazing (Geurts van Kessel, 2004; Prins et al., 2012). The Oosterschelde case has shown that bottom-up control through nutrients is less relevant than generally assumed for nutrient limited coastal waters (Philippart et al., 2007) because of the regulating role of filter feeders (Dame, 2012; Dame and Prins, 1998; Prins and Smaal, 1994). The relation between filter feeder stock size, nutrient concentration and primary production time series will be nonlinear, because at an increasing stock size, filtration and nutrient regeneration will have a stimulating effect on primary production and phytoplankton turnover, while at a stock size above a certain value, primary production will decrease due to overgrazing of phytoplankton. Eventually a new equilibrium may be reached, but in exploited areas this is unlikely because of the activities of the farmers. As a consequence of overgrazing, non-filtered primary producers like picoplankton may profit from regenerated nutrients (Cranford et al., 2009). In this study we test the hypothesis that under the current conditions in the Oosterschelde, the shellfish stock size is now limiting primary production due to overgrazing.

2. Material and methods

2.1. Study area

The Oosterschelde estuary is a macrotidal system with an average depth of 9 m, a tidal range of 3.25 m and a surface of 350 km^2, of which 30% consist of tidal flats (Fig. 1). Owing to a large-scale coastal engineering project finalised in 1987, the estuary has changed considerably, resulting in reduced water exchange with the North Sea and reduced fresh inflow (Nienhuis and Smaal, 1994). Water residence time has doubled on average, hence the system became more dominated by the internal processes rather than exchange with the North Sea. The estuary changed into a tidal bay, characterised by a relatively high salinity, high water transparency, long water residence time and low inorganic nutrient concentrations (Table 1). The Oosterschelde can be divided in 4 subareas (west, central, north and east). Sampling stations for primary production, total particulate matter (TPM), chlorophyll, inorganic nutrients as well as for shellfish stocks were distributed over the subareas. In our data analysis we pooled the data for the subareas as the outcomes of the analysis were not different for the various subareas.

Table 1
Main characteristics of the Oosterschelde estuary (Nienhuis and Smaal, 1994); nutrient concentrations are maximum winter values (see Kromkamp and Ihnken, 2011).

Total surface, km^2	351
Tidal flats, km^2	114
Average depth, m	9.01
Volume, m^3 10^6	2741
Mean tidal range, cm	325
Residence time, d	10/150
Freshwater load m^3 s^{-1}	25
Nitrate/nitrite, µmol l^{-1}	30
Ammonia, µmol l^{-1}	10
Phosphate (SRP), µmol l^{-1}	1.5
Silicate, µmol l^{-1}	25

2.2. Primary production, nutrient, TPM and chlorophyll data

Annual primary production data are based on biweekly C14 incubations and extrapolations by using irradiance, secchi disc, TPM and chlorophyll data, and modelled and validated as tidal basin production data (Malkin et al., 2010). Nutrient, TPM and chlorophyll-a data are based on routine monitoring programmes of NIOZ and analysed by autoanalyser, gravimetric and high-performance liquid chromatography methods, respectively. For TPM, chlorophyll sampling and primary production measurements, 0.45 μm Whatman GFC and nitrocellulose filters were used, respectively. Sampling stations used in this study are shown in Fig. 1: stations phytoplankton programme.

2.3. Filter feeder stock size and filtration capacity

In the period 1995–2009, the filter feeders were dominated by mussels (*M. edulis*), cockles (*Ceratoderma edule*) and Pacific oysters (*C. gigas*). The sum of the biomass of Baltic tellin (*Macoma balthica*), slipper limpet (*Crepidula fornicata*), tunicates and sponges stayed in total below 10% of total biomass (Imares data). Recently considerable densities of invasive razor clams (*Ensis americanus*) have been detected locally in the subtidal areas of the OS (NIOZ survey data) but there are no bay wide data. In our study we therefore focused on the main filter feeder stocks of mussels, cockles and oysters. Data on standing stocks of mussels and cockles are based on annual area-wide assessments. It should be noticed that >90% of the mussels are from cultivated stocks. Mussel surveys are done in spring with a Van Veen grab on 100 subtidal culture plots in the Oosterschelde. On each culture plot, 5 Van Veen grab replicate samples are taken and mussels are counted as small (seed <15 mm), medium (half-grown 15–45 mm) and large (consumption size > 45 mm) specimen and weighted. A conversion is used for total wet weight (including the shell) (TWW) to ash-free dry weight (AFDW) = 20 (Imares protocol). Survey accuracy was estimated at a coefficient of variance = 15% (De Mesel and Wijsman, 2011).

Surveys for cockles are carried out in spring on 400 intertidal sampling stations based on a fixed grid. Samples are taken with a specific device covering 0.1 m^2 surface. Cockle density is estimated per year class and total wet weight is measured. Conversion of total wet weight to ash-free dry weight is done on the basis of subsamples, with an average value: TWW/AFDW = 30 (Imares protocol). Accuracy of the cockle stock assessment was tested for 2000–2003 data and had a coefficient of variance of 20% (Kamermans et al., 2003).

Stock assessments of the introduced Pacific oyster have started in 1998 and were done in 2003 and 2005. These data were used as ground truth for a reconstruction of the oyster stock by using aerial photographs (Kater and Baars, 2004; Smaal et al., 2009). Field data are based on contour mapping and random subsampling of 0.5 m^2 (nr of samples varied with bed size, on average 1 per ha) and weighing total amount of oysters, and counting and weighting the number of live oysters. Live oyster biomass was converted into ash-free dry weight by an empirical established factor for wild oysters: TWW/AFDW = 100 (Smaal et al., 2009). Biomass estimation of cultivated oysters is based on harvest data and a mean cultivation period per cohort of 3 years. Hence annual harvest is multiplied by 3 for the stock estimation of cultured oysters.

The filtration capacity of the main stocks was calculated on the basis of assumptions of standard clearance rates of animals of 1 g AFDW. For mussel = 48 L/g AFDW/day, cockle = 24 L/g AFDW/day, oyster = 100 L/g AFDW/day (based on Cranford et al., 2011) and for the razor clam 36 L/g AFDW/day (Kamermans and Dedert, 2012).

2.4. Harvest data

The annual net mussel yield for a certain year is based on the accumulated yield of the auction deliveries throughout the harvesting season from July until December. The yield is registered separately for different cultivation areas. Mussel data collection is quite extensive as it is registered per party at the auction. As there is no auction for the oysters, harvest data were derived from the Fish Board and these are based on annual reports by the farmers.

2.5. Bivalve growth estimations

All harvested mussels are traded through the auction in Yerseke, where registration is done for total gross and net yield and condition (% flesh). We made use of condition data from this database as an index for annual growth of mussels in different culture areas. The condition of mussels is estimated as the amount of flesh, weighed after 5 min cooking, relative to the total weight, and expressed as %. It was shown that this condition parameter significantly correlated with the growth rate of mussels normalised for 45 mm length (van Stralen and Dijkema, 1994). Auction data of mussel condition were averaged per area for the period July–October as in this period on average 66% of the landings occurs and the mussel condition is relatively stable over the season.

Average annual growth of cockles for a particular year was derived from the annual stock assessments by distracting mean total wet weight of year class 1 in the previous year from class 2. Growth data of cultivated oysters were derived from registration by an individual farmer (per comm. A. Cornelisse).

2.6. Statistical analysis

All data series were tested for trends in time. To identify possible causes for trends in time multiple regression analyses were performed. No significant interactions between explanatory variables were found. Therefore, only linear regressions are shown. Trends and correlations were not different for the various subareas, hence data were pooled for the different subareas for final analysis. All numerical analyses were performed within the environment R 2.12.2 (R Development Core Team, 2011).

3. Results

3.1. Primary production, chlorophyll and nutrient concentrations

Primary production has shown a significant decrease ($p < 0.001$) over the period 1995–2009 from 319 to 155 gC/m2/year (Fig. 2). The average annual chlorophyll-a concentrations varied around 4 μg/l, with a slight decrease over time (Fig. 3, $p = 0.043$, slope $= -0.1212$). Annual average total particulate matter (TPM) concentrations have increased

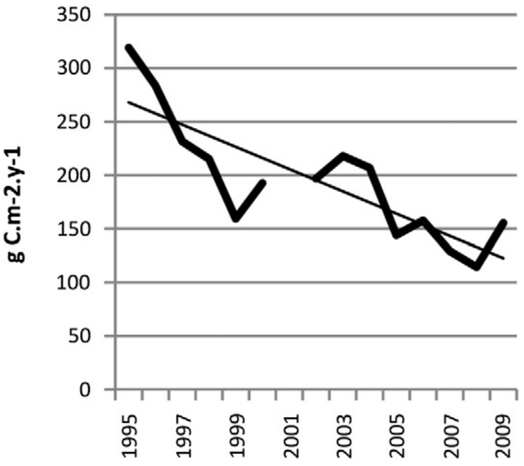

Fig. 2. Trend in stochastically modelled annual basin primary production ($p = 0.0002120$, adj. $R^2 = 0.67$; Spearman's rank correlation coefficient = 0.81) over the period 1995–2009.

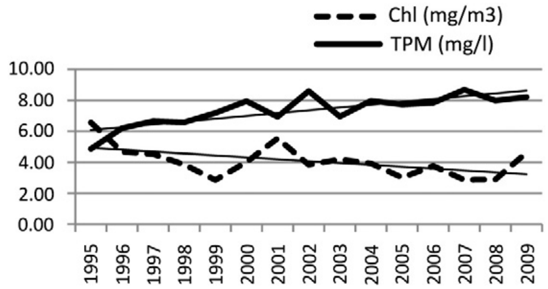

Fig. 3. Annual average chlorophyll (Chl) and total particulate matter (TPM) $p = 0.00034$, adj $R^2 = 0.64$) concentrations over the period 1995–2009.

slightly from 6 to 8 mg/L ($p = 0.00034$, slope = 0.182); changes are very limited in quantitative terms. Concentrations of the macronutrients N, P and Si showed seasonal variation with higher concentrations in winter and low concentrations in spring and summer, corresponding with the seasonality in phytoplankton growth (Prins et al., 2012). Average winter concentrations are shown in Table 1. A statistical analysis by Kromkamp and Ihnken (2011) showed that there was a slight but significant decrease of phosphate, silicate and ammonia concentrations over the period 1995–2009, and no trend in nitrate and nitrite concentrations. In spring both phosphate and silicate decreased rapidly to limiting concentrations, but phosphate concentrations recovered relatively quickly from June onwards, causing a short period of potential P limitation for non-Si requiring phytoplankton and P–Si co-limitation for diatoms, while over summer Si concentrations may become limiting for diatoms.

A field survey in 2010 showed that chlorophyll-a of phytoplankton consisted for up to 30% of picoplankton (NIOZ data). No trend analysis can be performed as this analysis started only in 2010.

3.2. Bivalve stock size and filtration

Total stock of dominant bivalve species in the Oosterschelde remained rather stable over the period 1995–2009 (Fig. 4). Total stock varied between 3.5 and 6 mln kg afdw, which corresponds to 10–17 g afdw/m2.

The mussel stock showed a significant decrease over the period 1995–2009 ($n = 15$, $p < 0.001$), from around 3 to 1.5 mln kg afdw. The mussel stock is controlled by the mussel farmers. Stocking of the Oosterschelde culture plots is based on fishery of wild seed, predominantly in the Dutch Wadden Sea. Due to protective measures and recruitment failures, total seed harvest has declined since the 1990s (Smaal et al., 2010).

The cockle stocks varied between 0.46 and 1.93 mln kg afdw in 1997 and 2006 respectively. There is a variable stock size with very low values after the severe winters of 1996 and 1997 and recovery afterwards (Fig. 4).

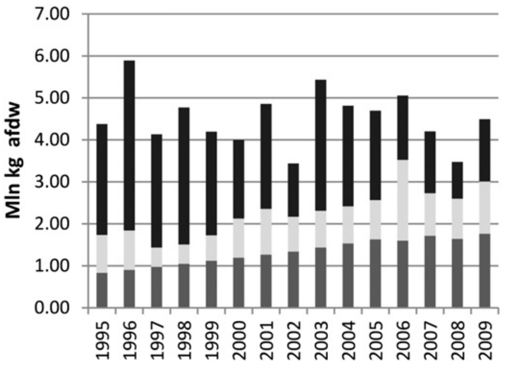

Fig. 4. Standing stocks of cockles (green), mussels (red) and oysters (blue) in mln kg afdw over the period 1995–2009.

The biomass of the introduced Pacific oyster was reconstructed on the basis of aerial photographs and ground truth in recent years (Smaal et al., 2009). It showed doubling of the stock from 0.8 to 1.6 mln kg afdw over the period 1995–2009. There was an experimental fishery in 2006–2008 to reduce the expansion of the wild stock; in total ca 0.2 mln kg afdw was removed from the central and eastern Oosterschelde (Wijsman et al., 2008). The culture stock is relatively small and amounts ca 0.1 mln kg afdw. The Pacific oyster is still expanding on wild beds, despite removal through fishery in 2006–2008, resulting in maintenance of the total filter feeder stock. However, the filtration activity of oysters is much higher than for cockles and mussels, hence total filtration has shown an increase. We calculated an increase of total clearance rates of 240 million m3 per day in 1995, that is 8.7% of total volume, to 310 million m3 per day in 2009 (11.3% per day). This calculation includes the filtration capacity of *E. americanus*. Based on extrapolated data of NIOZ surveys on permanent quadrats in the west and the east, the stock size in the Oosterschelde is estimated as 0.9 million kg afdw; this results in an estimated filtration capacity of 33 million m3 per day.

3.3. Bivalve landings

Total harvest of cultured mussels has decreased significantly ($p < 0.001$, $n = 15$) from ca 40 to 20 mln kg fresh weight per year, corresponding with a decrease in stock size (Fig. 5). Fishery on wild cockle beds has decreased dramatically due to measures for maintaining food stock for birds since 1999; cockle landings from mechanical harvesting only occurred in 2006 and amounted 2 mln kg cooked meat weight (data Fish Board). Oyster harvest occurs throughout the year with average values of 3 mln kg fresh weight per year (data Fish Board).

3.4. Growth indications

The condition of the harvested mussels is used as an index for growth. Values fluctuate between 21.3 and 25.8%. The very low value of 18.2% was recorded in 2006, a year with relatively high summer temperatures. There is no temporal trend (Fig. 6). It shows that growth rates of the mussels have maintained, while stock and harvest sizes have decreased (Fig. 5). In contrast, cockle growth, measured as the increase in average individual weight for year-class 1 to 2 has shown a significant decrease over time, from 8 g per year in 1995 to ca 5 g/year in the recent period (Fig. 7). Average growth rates of cultivated oysters have declined from 10 to 3 g wet weight per month in 2002 and 2009 respectively (pers comm A. Cornelisse).

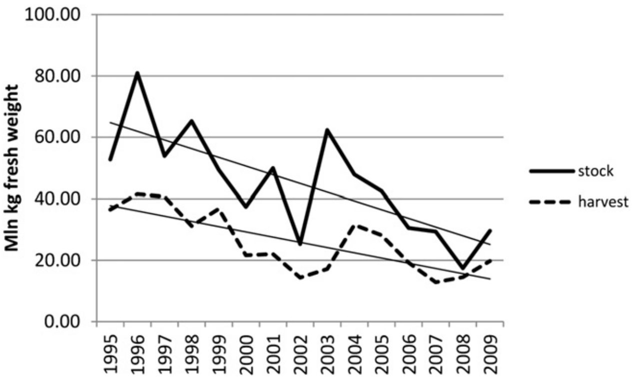

Fig. 5. Trend in total stock size ($p = 0.0016$, adj. $R^2 = 0.51$, Spearman's rank correlation coefficient = 0.65) and annual harvest of mussels ($p = 0.00085$, adj. $R^2 = 0.56$, Spearman's rank correlation coefficient = 0.76) in the period 1995–2009.

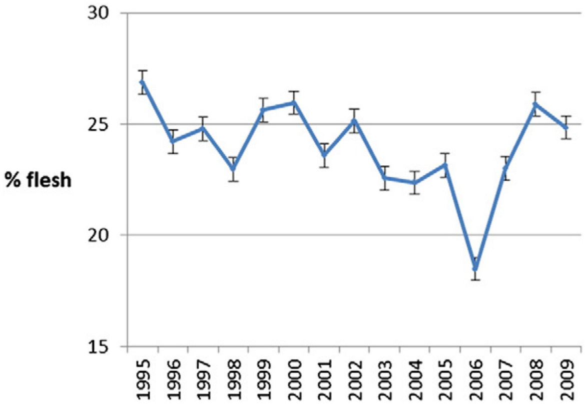

Fig. 6. Average annual flesh content and standard error ($n = 680$/yr) of harvested mussels according to auction data over the landing season July–October for the period 1995–2009.

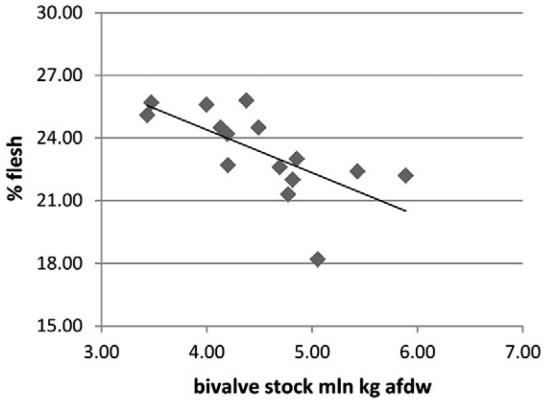

Fig. 8. Relation between the condition of harvested mussels (as % flesh) and the size of the bivalve stock per year over the period 1995–2009 ($y = -2.0569x + 32.644$, $p = 0.0038$, adj. $R^2 = 0.45$, Spearman's rank correlation coefficient = 0.36).

3.5. Mussel growth and bivalve stock size

Although there is no relation between mussel condition (flesh content) and mussel stock and harvest sizes, there is a significant negative correlation between the flesh content of landed mussels and total annual bivalve stock size over the period 1995–2009 (Fig. 8). It shows that lower mussel growth (as indicated by flesh content of harvested mussels) corresponds with larger bivalve stocks, and vice versa, while this does not hold for the mussel stocks per se, that are under control of the mussel farmers.

4. Discussion

4.1. Primary production

Primary production has halved in the study period. Nutrient concentrations are relatively low and P, Si and NH4 concentrations have shown a slight decreasing trend. However, this is not sufficient to explain the primary production decrease (Kromkamp and Ihnken, 2011; Prins et al., 2012). In fact, nutrient concentrations have decreased already since 1987, when the large scale coastal engineering Delta project resulted in a sudden decrease of freshwater input after completion of the compartment dams and the storm surge barrier (Nienhuis and Smaal, 1994). Due to the constructions, tidal exchange and current velocities have reduced and the system turned into a nutrient rather than light limited system. Despite these dramatic changes, the primary production has maintained at an average level of 400 gC/m2/year until the period 1992–1995 (Bakker et al., 1994; Geurts van Kessel, 2004; Wetsteijn and Kromkamp, 1994). It was postulated that primary production in the post-barrier, nutrient limited period was maintained due to the positive feedbacks by the dominant filter feeders through nutrient regeneration (Prins and Smaal, 1994; Smaal et al., 2001). The fact that nutrient concentrations can still be measured during the growth season is largely due the rapid rates of phytoplankton turnover (2–0.5 days in summer, Kromkamp unpublished), and these high regeneration rates are due to the high grazing rates. In the preceding period, this mechanism was less prominent as the system was more turbid and more open to the North Sea and to the river inflow (Nienhuis and Smaal, 1994), although the Oosterschelde has been a self-sustaining system, also prior to the Delta project (Herman and Scholten, 1990). After the introduction and further expansion since 1964 (Drinkwaard, 1999; Smaal et al., 2009), the filter feeder stocks became dominated by the Pacific oyster. Nutrient regeneration induced by the increased grazing rates will not stimulate primary production anymore and the balance between stimulation of production by nutrient regeneration and loss rates of biomass due to grazing seems to be shifting towards higher loss rates. Hence, we hypothesise that primary production is now decreasing due to overgrazing. This is in contrast to the preceding periods when there was nutrient limitation and grazing induced nutrient regeneration (1987–1995), while prior to the Delta project (before 1987), primary production in the Oosterschelde estuary was mainly light limited.

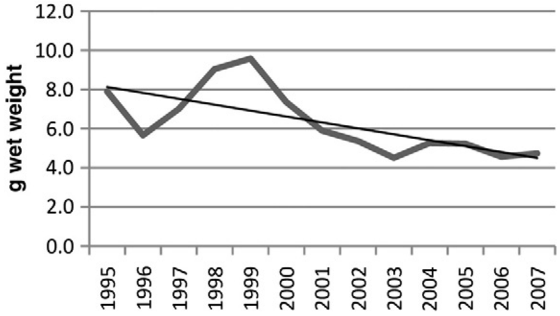

Fig. 7. Trend in annual growth rate of cockles ($p = 0.0088$, adj. $R^2 = 0.43$, Spearman's rank correlation coefficient =0.69) over the period 1995–2007.

4.2. Bivalve stocks

Bivalve stocks in the Oosterschelde have been dominated by human exploitation. The mussel stocks are for more than 90% controlled by mussel farmers and are located on subtidal bottom culture plots. Seed supply through natural recruitment has decreased since the 1990s (Smaal et al., 2010) and this is the main cause of the decrease in the standing stock of mussels, from 4.1 to 0.8 mln kg AFDW in 1996 and 2008 respectively.

The cockle stock is determined by natural recruitment, survival and growth. Fishery mortality is low in comparison to natural mortality. In the period 1995–2009 there is a small increase in the stock size but longer time series do not show a trend (Kamermans et al., 2004). Cockle stocks usually show large fluctuations, due to variations in recruitment success and mass mortality in cold winters. Winter temperatures play a major role, as cold winters cause high mortality as well as high recruitment success (Beukema, 1985). This explains the low values in 1996 and 1997 (severe winters) and recovery afterwards. Average values vary between 5 and 20 g afdw/m^2 intertidal area but local densities are much higher due to the patchy distribution. These values are comparable to other areas like the Wadden Sea (Ens et al., 2004).

After the first experimental introduction in the Oosterschelde of the Pacific oyster in 1964, it has lasted several years before the species was cultivated at a larger scale. Once this had started, expansion also started, as in contrast to the expectation, the species was able to reproduce in the Oosterschelde, particularly during warm summers (Drinkwaard, 1999). On the basis of aerial photographs and ground truthing, littoral stock development was reconstructed from 1981–2003 (Kater and Baars, 2004). Various surveys have been carried out since 1998, both in littoral and sublittoral areas. The stock size from these surveys is probably an underestimation as no quantitative information is available of the sublittoral stock (Smaal et al., 2009). It is clear that the oysters have expanded dramatically and are now the dominant bivalve species in the Oosterschelde. In terms of filtration capacity oysters are even more important than on the basis of biomass. If we include the recently established stocks of the invasive razor clam, total filtration capacity has increased by 30% in 2009 compared to 1995.

It is concluded that total filtration capacity due to the oysters and the razor clams has shown considerable increase and the question is what impact this may have on the production and the ecological carrying capacity.

4.3. Growth

As an indicator of individual growth we use data of the meat content of the mussels as registered at the mussel auction; this delivers an extensive database as all harvested parties are registered by the auction. There is a significant correlation between meat content of mussels and mussel growth in the preceding period, as shown by Smaal and van Stralen (1990). Meat content of mussels was fluctuating but there is no trend over time, hence the product quality has maintained. It is noticed that the total mussel production has shown a dramatic decline; although this is due to shortage of mussel seed, it can be argued that the farmers apparently succeeded in maintaining the quality of the product, by reduction of local stocks on mussel culture plots. Management of stocks by the farmers through translocation is a measure to maintain meat content (Smaal et al., 2001). In contrast to mussel culture, this culture practice is not applied for the wild cockles stock, and indeed an opposite response is apparent: cockle stock size has maintained but individual cockle growth has declined, apparently due to increased intraspecific competition.

We found a negative correlation between average annual mussel condition and total bivalve stock size. It implies that in years with a larger stock, individual growth is slower. This was demonstrated earlier by van Stralen and Dijkema (1994) for the Oosterschelde in the period 1981–1985: they found a negative relation between filtration capacity of mussels and cockles, and the average annual mussel condition, and concluded that expansion of mussel culture might induce lower meat yields. As shown in Fig. 4 mussel condition has maintained so far, and this can be attributed to the compensating measure of reducing the mussel stock. However, new techniques are now applied to increase the availability of mussel spat, by using suspended mussel spat collectors (Kamermans et al., 2002). Ropes and nets are brought into the system during the season from March till November and newly recruited mussel spat is harvested, eventually leading to an increase of the mussel culture stock. On-going expansion of the oysters, the appearance of new invasive species and an increase of the mussel stock will induce a further limit to the production carrying capacity.

4.4. Food

van Stralen and Dijkema (1994) found a highly significant positive relation between primary production and mussel condition for the period 1981–1990. This was also demonstrated by Smaal et al. (2001), for the period 1981–1997. The latter concluded that mussel growth in the Oosterschelde was food limited, but that production had been maintained through the positive feedback of the mussels to the primary production by effective nutrient regeneration and an increase in phytoplankton turnover. We did not find such a correlation for the period 1995–2009. Since the 1990s we observe a decrease in primary production, mussel production and cockle growth, and a rather stable level of mussel condition and cockle stock. The negative correlation between mussel condition and bivalve stock, and the reduced mussel production level indicate a surpassing, hence a decrease, of the production carrying capacity of the ecosystem. The expansion of the oyster population and the decline of primary production indicate overgrazing, hence a decrease of the ecological carrying capacity.

The overgrazing hypothesis is supported by the observation that, although there is a decrease of P, NH4 and Si concentrations over time, there is no nutrient limitation of primary production except for a period of 2–4 weeks in spring (Ihnken and Kromkamp, 2011) and a possible mild Si-limitation in early mid-summer for diatoms (see also Prins et al., 2012). In addition, Troost et al. (2009), describe a decrease of oyster larval abundance that may be due to increasing filtration pressure.

A switch of bottom-up to top-down control has also been demonstrated in mesocosm studies with variation in nutrient loads and mussel filtration (Prins et al., 1995). Indeed at some point grazing pressure becomes the limiting factor for primary production, and the dissolved nutrient pool increases, as was demonstrated by Prins et al., 1995. In the mesocosm study, there was also a further reduction of the primary production time. However, this is not observed in the Oosterschelde. In fact a limited but significant increase in primary production time was observed. This may be due to a relatively high proportion of picoplankton that is now apparent in the Oosterschelde and that escapes grazing. Preliminary data of 2010 and 2011 indeed show a fraction of 30% of the chlorophyll concentration to consist of picoplankton (Ihnken and Kromkamp, 2011; Malkin et al., 2010). In comparison to heavily overgrazed systems like Tracadie Bay in Canada (Cranford et al., 2009) with picoplankton values up to 80% of total phytoplankton, the picoplankton abundance in the Oosterschelde is still rather limited. However, for the Wadden Sea, with less grazing pressure, the picoplankton fraction is lower (ca 20%, Imares data). The occurrence of picoplankton may also explain the lack of correlation between primary production and mussel condition in our study, in contrast to previous Oosterschelde studies (van Stralen and Dijkema, 1994). Cranford et al. (2009) consider the fraction picoplankton as an indicator of overgrazing, and this might also be apparent for the Oosterschelde. In combination with only short-term spring limitation in nutrient concentrations in the Oosterschelde, a bivalve clearance time of less than 10 days, and a negative relation between standing stock and mussel growth, it can be concluded that overgrazing in the Oosterschelde is the most likely cause of the decrease in primary production.

By comparing a number of estuarine ecosystems, Herman et al. (1999) demonstrated a strong correlation between system averaged macrobenthos biomass and annual primary production. They also showed that the Oosterschelde standing stock was higher than could be expected from the correlation between stock size and primary production in the other ecosystems. In comparison with other estuarine ecosystems, the benthic biomass in the Oosterschelde has been relatively high, particularly given the annual primary production. The observed decline in primary production and the actual size of the filter feeder stock implies that both production and ecological carrying capacity seem to be surpassed.

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