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

A.C. Smaal [a,*], T. Schellekens [a], M.R. van Stralen [b], J.C. Kromkamp [c]

[a] Imares, P O Box 77, 4400 AB, Yerseke, The Netherlands
[b] MarinX, Elkerzeeseweg 77, 4322 NA Scharendijke, The Netherlands
[c] NIOZ, P O Box 140 4400 AC, Yerseke, The Netherlands

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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.

* Corresponding author. Tel.: +31 317847039.
E-mail addresses: aad.smaal@wur.nl (A.C. Smaal), tim.schellekens@wur.nl (T. Schellekens), marinx@zeelandnet.nl (M.R. van Stralen), jacco.kromkamp@nioz.nl (J.C. Kromkamp).

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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).

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.

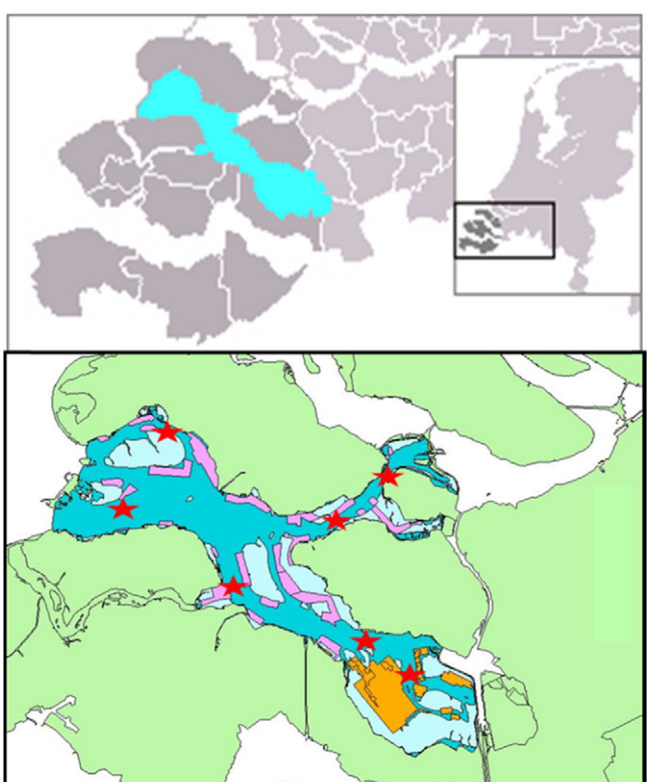

Fig. 1. The Oosterschelde estuary (SW Netherlands) with sampling stations for chlorophyll, suspended matter and primary production measurements (★) and mussel culture plots in the western and central parts (purple), and oyster culture plots in East (orange).

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