Food supply and demand of bivalve suspension feeders in a tidal system
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Document Version
Publisher's PDF, also known as Version of record

Publication date:
1997

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
CONCLUDING REMARKS

This thesis has addressed the interaction between food supply and demand in bivalve suspension feeders. It will be remembered that the aims of the study were (i) to analyze the factors that regulate food requirements and acquisition of the bivalves, (ii) to test the hypothesis that food supply mismatches bivalve food demand when eutrophication-induced blooms of Phaeocystis become dominant, and (iii) to evaluate the role of bivalve suspension feeders in estuarine and coastal ecosystems, with special reference to the Oosterschelde situation. Below, the results of the research described in the preceding chapters are summarized in relation to these aims.

Food acquisition and requirements
Mussels acquire their food from a highly variable source. This thesis has shown that food supply in tidal systems fluctuates greatly with tide and season. Short-term seston dynamics are driven by tidal motion and wind-induced erosion. As shown in chapter 2 the resulting food supply was generally 1 - 20 % by weight of all material filtered by the bivalves. Food supply on bivalve beds was also influenced by filtration and pre-ingestive selection by the bivalves themselves. The investigations revealed that seston concentrations were higher on the bivalve beds than at the surface, but the food quality was poorer. A clear seasonality in food supply was also found: annual primary production in the central and western parts of the Oosterschelde was very significantly correlated with the growth of mussels on culture flats in corresponding years (Chapter 3). From this it can be inferred that phytoplankton is indeed the main food source for the mussels, and that phytoplankton dynamics determine seasonal fluctuations in food supply.

This thesis has confirmed that food requirements (i.e. metabolic demands for maintenance, growth and reproduction) depend on factors intrinsic to bivalve physiology, particularly body weight and the gametogenic cycle, and on external factors (primarily food composition and temperature), and that these interact greatly as food composition, temperature and gametogenesis follow annual cycles. The results of the seasonal experiment (Chapter 4) demonstrate that temperature did not fully account for seasonal variation in physiological processes in the mussel: clearance rates remained high during winter, and a good correlation was found between predicted peak spawning not only involved in N and P. The budgets showed no significantly different in N being retained in the mussel. The simulation model EMMY response to natural food found between predicted and P. The budgets showed no significantly different in N being retained in the mussel. 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supply and demand in the aims of the study.

Best and acquisition mismatches bivalve Phaeocystis become suspension feeders in the Oosterschelde in the preceding tide and season. This thesis has shown that tide and wind-induced influences on bivalve beds 

concentrations were food quality was found: annual primary production by the bivalves in culture plots in the Oosterschelde was very good, and in particular for the smaller individuals. The high physiological rates of cockles in summer correlated with spawning and temperature peaks, which covary, as cockles in the Oosterschelde estuary spawn in early summer.

The simulation model EMMY integrates the eco-physiology of the mussel in response to natural food. As explained in chapter 7, the model assumes that the mussel shows (i) adaptive responses to variation in food supply, (ii) physiological plasticity in food acquisition, and (iii) regulation of element partitioning between different tissue compartments for somatic growth, energy storage and gametogenesis. Its state variables are C and N content of somatic tissue, glycogen storage, organic shell matrix, gonads, gametes and blood. Tissue composition, timing and amount of spawning, growth in length and weight, and % flesh are presented as output. The validation runs conducted with food and temperature data from the Oosterschelde estuary as forcing functions were very similar to observed growth and condition. The model outcomes corroborate the hypothesis that the mussel's food requirements and food acquisition are physiologically regulated.

The EMMY model also makes clear that knowledge gaps exist with respect to the factors that determine clearance depression, selection efficiency, timing and amount of spawning; also for mucus and organic shell production, and partitioning between tissue compartments, assumptions had to be made.

good correlation was found between increased respiration and excretion rates, and the period of spawning, rather than with temperature. In contrast, clearance rates of cockles showed a seasonal cycle, with low values in winter, particularly for the smaller individuals. The high physiological rates of cockles in summer correlated with spawning and temperature peaks, which covary, as cockles in the Oosterschelde estuary spawn in early summer.

The results presented in chapter 5 show that the actual growth of mussels and their elemental composition could be predicted by estimating the scope for growth provided by the carbon, nitrogen and phosphorus available in the phytoplankton. During the spawning period, however, a large disparity was found between predicted and measured elemental growth. It seems that spawning not only involves loss of gametes, but also additional losses of C, N and P. The budgets show that the absorption efficiencies for C, N and P were not significantly different; relatively low rates of N excretion, however, result in N being retained in the animals much longer than C and P. This explains why the N content of the mussel is high in spite of the phytoplankton stoichiometry.
Further ecophysiological research of the responses of bivalves to different qualities of food is required to improve the model.

Yet, from the above it is concluded that food requirement shows a seasonal cycle which corresponds with the seasonality of gametogenesis and reproduction. More nitrogen is retained than carbon and phosphorus because relatively little is lost through excretion. Food acquisition is determined by filtration, selection, absorption and food supply. Selection and absorption stabilize the acquisition of food from a variable supply.

**Match/mismatch**

The experimental data presented in chapter 6 show that when food supply contains *Phaeocystis*, clearance rates are inversely related to the size and number of colonies, but also that solitary cells reduce the clearance rate. It seems likely that filtration at reduced clearance rate is not compensated by increased concentrations of particles. No adaptive responses to the diet were observed, yet the absorption of ingested *Phaeocystis* did not differ from the reference diet. It is nevertheless concluded that colonial *Phaeocystis* blooms have little nutritional value for the mussels, because mussels are unable to maintain filtration at higher colony concentrations.

The model simulation of the effects of *Phaeocystis* blooms in a scenario with prolongation of the bloom for about one month at relatively low concentrations did indeed show a 20 - 30% reduction of growth and reproduction (Chapter 7). The effects can be attributed to a depressed clearance rate which is a linear function of colony concentration up to a certain maximum. A scenario without *Phaeocystis* showed considerably higher growth rates in combination with an increased reproduction. Also the flesh content was higher.

These results indicate a mismatch between the relatively high food demand of the mussels and the food supply in the period of *Phaeocystis* blooms (May - July). As presented in chapter 6, these results corroborate field observations of Wadden Sea mussels, which have shown a retardation of glycogen formation, and a delay in tissue growth during a *Phaeocystis* bloom.

From the above it is concluded that *Phaeocystis* blooms have adverse effects on food acquisition of the mussels and that these effects coincide with periods of greater need for food. The ability of mussel populations to survive this mismatch depends on eutrophication is a reduction of N and P in the coastal ecosystem.

In the Oosterschelde, the coastal engineers observed a decrease of *Phaeocystis* during the period 1986 - 1987 (comm.). The yield of mussels in the same period was lower than expected. Although mussel spat, and *Phaeocystis* blooms in the Oosterschelde, the mussel spat showed no decreased *Phaeocystis* blooms in the reference results.

**Role in the ecosystem**

The interaction of mussels with their resources was examined in chapter 8. It was found that mussels filter the whole water column, including phyto- and zooplankton. Although mussel populations did not show a decrease in colony concentration, *Phaeocystis* blooms formed biode—decomposing biogenic material in the water column, (v) increasing the density of biogenic material.

Bivalve suspension feeders are adapted to these ecosystems by filtering large amounts of phytoplankton, (ii) forms biogenous material in the water column, (v) increasing the density of biogenic material. As presented in chapter 9, an increased level of biogenous material in the water column and a decrease of phytoplankton is observed.
responses of bivalves to different models.

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mismatch depends on the abundance and duration of the blooms. Given that eutrophication is a major stimulus of Phaeocystis blooms in coastal waters, the reduction of N and P loads will benefit mussel cultivation.

In the Oosterschelde estuary nutrient loads have reduced since 1987, owing to the coastal engineering project. Recent observations have shown a significant decrease of Phaeocystis concentrations, from a mean of 32.10⁶ cells.l⁻¹ in the period 1986 - 1988, to a mean of 3.10⁶ cells.l⁻¹ in 1993 - 1995 (Wetsteijn, pers. comm.). The yield of the mussel cultivation in the Oosterschelde has increased in the same period from 28.10⁶ to 49.10⁶ kg.yr⁻¹ (Van Dijk, pers. comm.). Although mussel yield depends on a variety of factors, such as availability of mussel spat, and exchange of mussel stocks between Wadden Sea and Oosterschelde, it seems likely that reduced nutrient inputs and subsequent decreased Phaeocystis blooms have contributed to the improved cultivation results.

Role in the ecosystem

The interaction between populations of bivalve suspension feeders and their resources was evaluated for a wide range of estuarine and coastal systems (Chapter 8). It was found that for most systems the time needed to potentially filter the whole system (clearance time) varies between 1 and 13 days. The water residence time in many of these systems (i.e. Bay of Brest, Marennes-Oléron, Oosterschelde, Ria de Arosa, Thau lagoon and Western Wadden Sea) is longer than the clearance time, which suggests bivalve control of phytoplankton. In these systems, bivalve biomass to volume ratio has been found to be typically in the range of 2 - 8 g.m⁻³. In more open systems, phytoplankton is still under bivalve control when biomass exceeds 8 g.m⁻³.

Bivalve suspension feeders exert a large impact on water column processes in these ecosystems by (i) filtering large quantities of material from the water column, (ii) controlling phytoplankton concentration and composition, (iii) forming biodeposits, (iv) increasing the inorganic nutrient release to the water column, (v) influencing the nutrient ratios in the water column, and (vi) increasing the phytoplankton turnover.

As presented in chapter 8, observations in the Oosterschelde estuary showed an increased benthic-pelagic coupling owing to the storm-surge barrier and
compartmentalization dams, because water residence times had doubled, and external nutrient loads decreased by 60%. Based on empirical and model results we estimated that the contribution of the mussel beds to the total nitrogen mineralization increased to about 30%, which should have a positive effect on the availability of nitrogen as a limiting nutrient for phytoplankton in the Oosterschelde after the spring bloom. Observations showed that the phytoplankton concentration had decreased after the completion of the barrier, but the primary production had maintained. Bivalve filtration and nutrient regeneration stimulated phytoplankton turnover, and consequently, the bivalves maintained their own food source.

Conclusions
The strong interactions between the bivalves and their resources make bivalves a key factor in estuarine and coastal systems, as they control phytoplankton biomass, affect the regeneration of inorganic nutrients and stimulate phytoplankton turnover. These mechanisms do not operate when eutrophication induced Phaeocystis blooms become dominant. These blooms not only cause a mismatch between food supply and demand of the bivalves, but also enhance the risk of destabilization of the ecosystem. The Oosterschelde case has shown that reduction of eutrophication went along with a decrease of Phaeocystis blooms and an increase of mussel productivity. It was also shown that stimulation of phytoplankton turnover by the bivalves attributed to maintenance of primary production, i.e. maintenance of food supply to the bivalves.