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Intra- and interspecies comparison of energy flow in bivalve species in Dutch coastal waters by means of the Dynamic Energy Budget (DEB) theory

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Abstract

The energy flow in various bivalve species (*Macoma balthica*, *Mya arenaria*, *Cerastoderma edule*, *Mytilus edulis* and *Crassostrea gigas*) in different habitats (intertidal, subtidal and offshore areas) of Dutch coastal waters was analysed by comparing growth observations in the field with model simulations by means of the Dynamic Energy Budget (DEB) theory. The reconstruction of the seasonal food conditions suggested that with respect to food consumption, *M. balthica* and *C. edule* are the most successful species, followed by *M. arenaria*, and *M. edulis* and *C. gigas*. Positive growth was correlated with the beginning of the spring bloom in primary production and food limitation between species was lowest during this period. After the spring bloom, severe food limitation during the summer period was found. As a result, negative body growth occurred during most of year. DEB model simulations both on an annual and a seasonal basis also showed that, at the prevailing water temperatures, growth of the different species was not maximal. It remains uncertain whether the suboptimal food conditions were the consequence of food limitation or also of reduced filtration efficiency due to the high sediment load in the water.

Keywords: Interactions; Growth; Food limitation; Dynamic Energy Budget; *Macoma balthica*; *Mya arenaria*; *Cerastoderma edule*; *Mytilus edulis*; *Crassostrea gigas*; Wadden Sea

1. Introduction

The fact that the macrobenthic biomass in temperate estuaries can be predicted from primary production data (Herman et al., 1999) suggests that food limitation might be a common phenomenon. Long-term studies in the western Dutch Wadden Sea, where changes in phytoplankton were associated with parallel changes in zoobenthic biomass (Beukema et al., 2002) support this view. Also on a local scale, competition for food has been reported from stomach content analysis of filter-feeding bivalves (Hummel, 1985; Kamermans et al., 1992; Kamermans, 1993; Cognie et al., 2001) and from observations that bivalve filtration indeed results in particle depletion of the overlying water mass (Asmus et al., 1992; Jonsson et al., 2005). This evidence suggests that food may be the prime limiting factor for benthic biomass in estuarine systems and it points to strong intra- and interspecies interactions.

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Environmental changes in temperature and food conditions will affect the energy available for the different physiological processes and determine rates of growth and reproduction. Therefore, any analysis on the role of intra- and interspecific interactions on the population dynamics of macrozoobenthos requires as a starting point a comparative study into the physiology of the various species. Ideally, such a comparative bioenergetic study should be based on a general framework built on first principles. The Dynamic Energy Budget (DEB) theory (Kooijman, 1988, 2000) offers this framework for a quantitative description of the energy flow through an individual and the allocation of energy over growth and reproduction in relation to environmental conditions and food intake. The same model can be applied to different species, whereby intraspecific variability in growth and reproduction is caused by differences in environmental conditions (temperature, food), and interspecific variability is caused by differences in parameter values, in combination with differences in environmental conditions (Kooijman, 2000).

The elegance of the DEB model is two-fold; (1) it is based on first principles and (2) only a few equations and parameters fully determine and describe feeding, growth and reproduction. Once these species-specific parameters are known, growth and reproduction can be determined if the fluctuations in temperature and food are known. The DEB model can also be applied the other way around for the reconstruction of environmental conditions from observed growth and reproduction patterns in the field. This innovative approach to reconstruct food conditions for various species under field conditions provides insight into the presence of food limitation and competition among species.

In this paper, we apply the DEB model for the reconstruction of food conditions for macrobenthic species in Dutch coastal waters. The focus is restricted to the most common bivalve species, not only because they are abundant and have similar food sources, but also because their age and hence growth can be determined from the analysis of annual shell growth marks. Only a few bivalve species account for most of the biomass; in the present study, five species were selected: the Baltic tellin *Macoma balthica* (L.), the edible cockle *Cerastoderma edule* (L.), the blue mussel *Mytilus edulis* L., the soft-shell clam *Mya arenaria* L. and the recently introduced Pacific oyster *Crassostrea gigas* (Thunberg) (Beukema, 1976, 1979; Dankers and Beukema, 1983; Dekker, 1989; Holtmann et al., 1999; Cardoso et al., in press). In the Dutch Wadden Sea and adjacent coastal waters, these species occupy different habitats (Wolff, 1983). *M. balthica* can be found from the upper regions of the intertidal and the subtidal to the outer parts of the tidal inlets in the coastal zone. *M. arenaria* occurs mainly from the upper regions of the intertidal to the subtidal but in other areas it extends to considerable depths offshore. *C. edule* is present from mid tide to just below the low water mark and *M. edulis* occurs from high in the intertidal zone to below low water in the subtidal. *C. gigas* can be found on hard substrate (stones, mussel and cockle banks) in the intertidal. *M. arenaria*, *C. edule*, *M. edulis* and *C. gigas* are suspension-feeding species, while *M. balthica* is a deposit-feeder also capable of suspension-feeding (Hummel, 1985).

This paper is built on a number of contributions. Extensive field data on seasonal patterns in growth and reproduction of the various species in relation to habitat (intertidal, subtidal, offshore) have been collected by regularly sampling over the years 2001–2003 (Cardoso et al., in press, in preparation-a,b,c). At the same time, the complete set of DEB parameters for the various bivalve species was determined in a systematic way based on various field and laboratory datasets (Van der Veer et al., 2006-this issue). The final objective of this paper is to reconstruct food conditions for the various species and habitats by applying the DEB model (c.f. Kooijman, 2000; Van der Meer, 2006-this issue).

2. Materials and methods

2.1. Field data

Field data on growth and reproduction of the various bivalves in Dutch coastal waters were collected during a monthly sampling programme of about 1.5 years between mid 2001 and 2003 (details can be found in Cardoso et al., in press, in preparation-a,b,c). In short, about 100 individuals of each species were sampled, if possible, every month, and water temperature was also measured at each sampling date. For each collected bivalve, age, shell length, ash-free dry mass of body and reproductive organs were determined. In this way, it was possible during each sampling to split up the sample into age groups and to estimate the mean somatic mass (total body mass excluding gonads) for each species and habitat. Next, these monthly samples allowed determining the seasonal variation in somatic mass up per age group for each species and location.