

CHAPTER 9

Synthesis

Introduction

In this thesis, intra- and interspecific interactions between bivalve species of the Wadden Sea were analysed. The Dynamic Energy Budget (DEB) theory (Kooijman 1988, 2000) was selected as framework to quantify interactions among bivalve species. Since the DEB theory is based on energy flows in organisms, inter- and intraspecies interactions, such as food competition, can be analysed. After a general introduction (Chapter 1), the basic information on various bivalves was collected by studying growth and reproductive output of the different species in relation to environmental conditions (Chapters 2-5). An introduction to the DEB model was presented and its assumptions regarding body-size scaling relationships were tested (Chapter 6), followed by the estimation of the required parameters for the various bivalve species (Chapter 7). The DEB model was then applied to simulate bivalve growth under water temperature conditions observed in the field and various food levels. By comparing the simulation results with field data, intra- and interspecies competition in terms of food was determined and the seasonal pattern in food conditions for the various species and habitats was reconstructed (Chapter 8). This approach provided insight into the presence of food limitation and competition among species. In the present chapter, the main conclusions from the previous chapters are summarized. Limitations to using the DEB approach and suggestions for further research are discussed.

Field studies

Field data on growth and reproductive output of *Macoma balthica*, *Mya arenaria*, *Cerastoderma edule*, *Mytilus edulis* and *Crassostrea gigas* were collected with the final aim to test the predictions of DEB model simulations with field data. However, such descriptive studies also gave insight into the physiology of these species in the western Wadden Sea.

In chapter 2, the reproductive investment of the blue mussel *M. edulis* was studied with the aim to test whether reproductive failure could be the cause for the low recruitment of *M. edulis* observed in the western Dutch Wadden Sea. Results showed that, despite the increase in mean winter temperature during the last decades, no significant relationship was found between body condition in late winter and mean winter temperature. Hence, reproductive failure due to a negative effect of increasing temperature on body condition and reproductive output will not have been a cause for the low recruitment in recent years. Nevertheless, reproductive investment by the mussel population studied was not optimal since complete spawning hardly occurred. Resorption of gonadal tissue due to unfavourable environmental conditions (too high temperature and/or food limitation during summer) was also suggested by the high gonadosomatic ratio at the end of the summer. Reduced recruitment could be due to poor spawning (as a result of resorption) but other factors that exert their influence after spawning (predation on larvae or postlarvae, lack of settlement substrate) or on the adult

population (decrease in number of spawners) are also likely to be involved in the observed low recruitment during the last years.

In chapter 3, the timing of spawning and reproductive investment of the soft-shell clam *M. arenaria* and the cockle *C. edule* were followed. The aim was to analyse whether differences in timing of spawning and reproductive investment between species could be responsible for the observed differences in recruitment success in the field, which is in general higher in *C. edule* than in *M. arenaria*. Timing of spawning was similar in both species but individual reproductive investment was higher in *M. arenaria* than in *C. edule*. Moreover, due to the differences in body mass composition between species, absolute reproductive output of the *M. arenaria* population seems to be much higher than that of the *C. edule* population. Hence, differences in recruitment success between species are probably not due to differences in reproductive output. Differences in post-larval processes (such as differential predation pressure in early life stages) are more likely to be responsible for the observed recruitment patterns.

In chapter 4, growth and reproductive output of the Baltic clam *M. balthica* were determined in different habitats (intertidal and subtidal areas in the Wadden Sea, and a coastal North Sea area) to analyse which (sub)population contributes more to the persistence of the *M. balthica* population in the western Dutch Wadden Sea. Significant differences in growth and reproductive investment were found between locations. Young individuals were mostly found in the intertidal area, where growth in terms of somatic mass was good. In the subtidal, where the highest densities were found, somatic mass and gonadal mass indexes were low. Coastal areas had the lowest densities and showed high growth in terms of shell length and body mass. The subtidal habitat contributed the most to the reproductive output of the western Dutch Wadden Sea population (due to the high densities found) although the highest reproductive output per individual was in the coastal area.

The aim of chapter 5 was to test whether the latitudinal decrease of temperature towards the poles could potentially determine the ultimate northern limit of the geographical distribution of the Pacific oyster *C. gigas*. To analyse the physiological performance of this species, spatial and temporal variation in growth and reproductive output of *C. gigas* were studied in three populations, from France to the Netherlands. An increase in maximum shell length, somatic and gonadal mass was observed from France to the Netherlands. In addition, mean oocyte diameter decreased significantly from south to north. The combination of increasing gonadal mass and decreasing oocyte volume suggests an increasing reproductive output in terms of egg numbers from France to the Netherlands. Smaller eggs (oocytes) are thought to have a longer development time than larger eggs because small eggs need more time to reach a similar larval size (Kooijman 2000). This suggests that the environmental conditions along the Dutch coast may result in increased larval dispersal and possibly further population expansion. The fact that population expansion in the Wadden Sea appeared to be rather irregular might indicate that successful larval dispersal occurs only in years with a high

reproduction, since with increasing development time also losses due to predation and other mortality factors increase.

The DEB model

Estimation of parameters

To be able to apply the DEB model to simulate growth in bivalves and to reconstruct food conditions in the field, several steps were taken. First, the assumptions of the DEB model regarding body-size scaling relationships for the comparison of species were tested. To this end, DEB model predictions for bivalves were validated with field and laboratory observations from literature (Chapter 6). Significant relationships were found between body size and, respectively, size at first reproduction and the Von Bertalanffy growth rate (coefficient); and between egg and larval size (volume) and egg and larval development time. The main discrepancy between field observations and DEB predictions was in the relationship between egg and larval volume and adult body volume. It was suggested that for successful settlement, the size or volume of the larvae must be in balance with the sediment composition, that is, the size or volume of the larvae must be similar to or larger than sediment grain size.

Next, DEB model parameter values were determined for each species, based on published experimental data (Chapter 7). Problems with parameter estimation were mainly due to the lack of reliable datasets. For none of the bivalve species, a complete set of DEB parameters could be estimated based on existing field data. Similarities among species were found in their volume-specific maintenance costs, the costs for growth and the maximum storage energy density. Differences between species were expressed in differences in some DEB parameters, especially the maximum surface area-specific assimilation rate and in the fraction of energy allocated to reproduction. These differences are reflected on the theoretical maximum total shell length of the species.

Model application

The estimated parameters from chapter 7 were used to run the model, with temperature and food conditions as input variables (Chapter 8). Field data (from Chapters 2-5) were combined with DEB model simulations and a reconstruction of the seasonal pattern in food conditions for the different species in the different habitats was made. Two types of simulations were done: [1] annual growth in shell length of the various species was predicted under prevailing temperature conditions and a range of food levels, expressed in the form of a functional response curve with values between 0 (starvation) and 1 (food *ad libitum*); and [2] seasonal variation in food level was reconstructed for each species in each habitat by simulating mass variation along the year under prevailing temperature conditions, and comparing the simulated mass with the observed mass in the field. This allowed a study of the interactions

between bivalve species, and between different habitats of a species, in terms of food competition.

The reconstruction of the annual food conditions suggested that with respect to food consumption, *M. balthica* and *C. edule* are the most successful species, with an annual simulated food level between 0.7 and 1.0. The seasonal variation in food conditions showed high values of food level in spring and summer, corresponding to the main growing season. After the summer, the amount of food (phytoplankton and phyto-benthos) in the water and sediment surface declines. As a result, the simulated food level for the various species decreased during summer and/or autumn, suggesting that strong food competition between species must have occurred during these periods. Overall, DEB model simulations, both on an annual and seasonal basis showed that, at the prevailing water temperatures, growth of all species studied was not maximal. This leads to the conclusion that for the various species in the different habitats, food conditions were different and insufficient for maximum growth.

Food limitation in suspension-feeding bivalves has been suggested by several authors (Beukema et al. 2002, Hummel 1985, Kamermans et al. 1992, Kamermans 1993, Cognie et al. 2001, Asmus et al. 1992, Jonsson et al. 2005). The results presented in this thesis suggest that food limitation also occurs in bivalve species in the Wadden Sea, pointing out to the importance of food as a limiting factor for benthic biomass and productivity. However, it is still questionable whether the apparent suboptimal food conditions (i.e. food conditions insufficient for maximum growth) for most species and habitats during most of the year are due to lack of food or/and to environmental conditions which limit feeding efficiency (such as silt content in the water).

Limitations and suggestions

Overall, the DEB model was successfully applied for the simulation of growth and reconstruction of food conditions in bivalves. To achieve this, several aspects are important. These are: field data on growth of bivalves, water temperature data and estimation of DEB parameters. With respect to field data, a correct age estimation of the different species is essential. For some species, such as *M. balthica* and *C. edule*, the analysis of external growth rings on the shell surface seems to give an accurate estimation of age. However, in other species, it is still unsure how to estimate age correctly. Therefore, validation of age determination in Wadden Sea bivalve species is essential in the near future. This could be done, for example, by marking experiments or by analysing carbon and oxygen isotopes. Since in many species age cannot be determined in an easy and straightforward way, a first impression of the pattern in seasonal food conditions can be given by reconstructing the seasonal functional response from variation in somatic mass index.

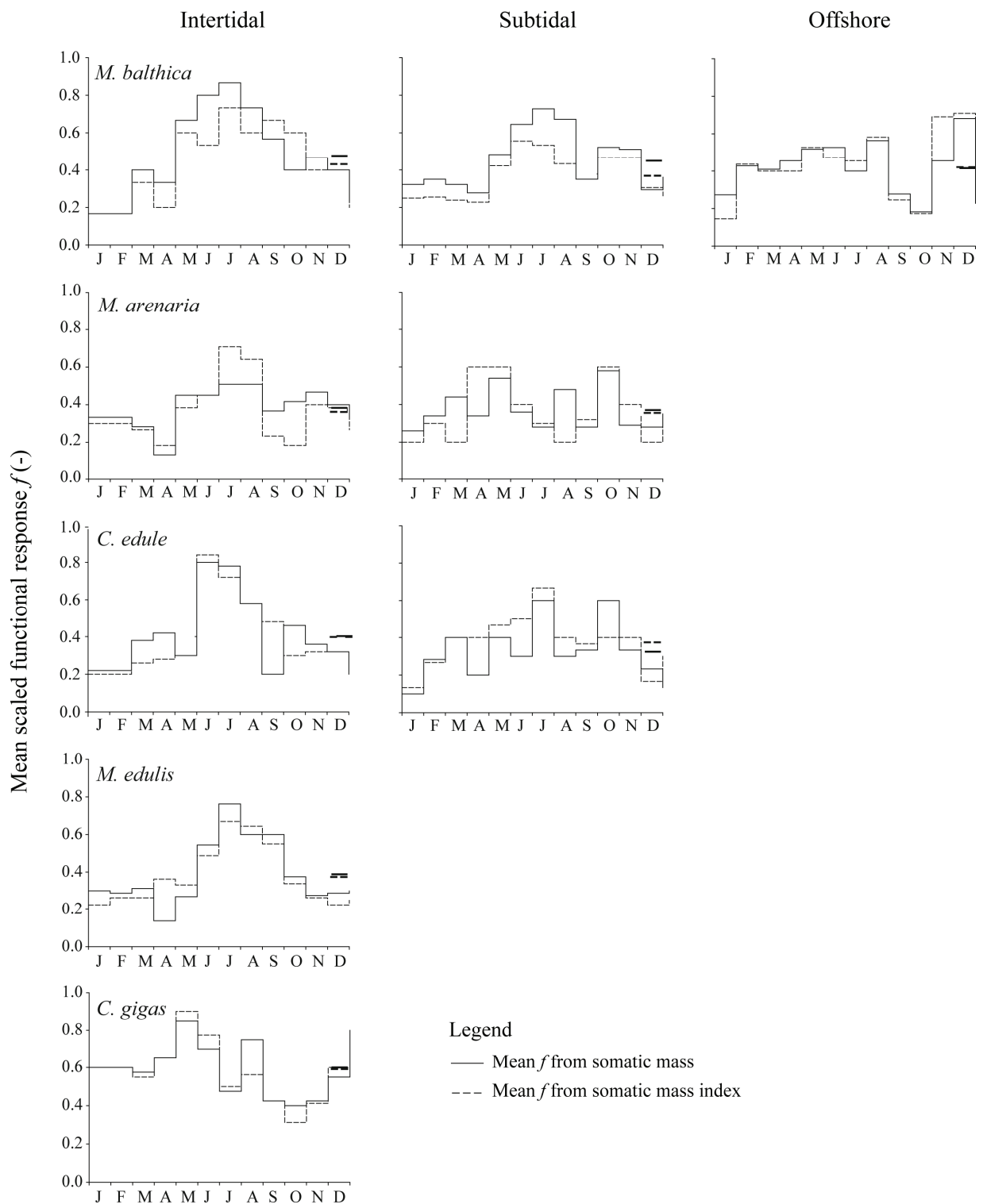


Fig. 9.1. Mean seasonal functional response (f , -) based on the reconstruction of food conditions for each age class (—; data from Chapter 8) and based on the reconstruction of food conditions using variation in somatic mass index (- -). Thicker marks indicate yearly mean. Simulations were done as described in Chapter 8.

However, it should be kept in mind that growth in terms of somatic mass index does not take into account the contribution of length growth over time and, therefore, during the growing season it will result in an underestimation of the reconstructed food patterns. Such underestimation will especially occur in fast growing, short living species and in younger age classes, since in older individuals there is hardly any change in somatic mass with age (Chapter 8). For the studied species, the seasonal reconstruction of food conditions by the two methods (somatic mass and somatic mass index) did not show large differences (Fig. 9.1).

Both the seasonal patterns as well as the yearly means are similar. However, the reconstructed functional response from somatic mass index was not always lower than the one from the instantaneous growth rate in somatic mass, as theoretically expected. This is a reflection of the large variability in individual growth. Also the lack of long-term data series on growth of bivalves may lead to some discrepancies between field data and model simulations since the variability in growth due to differences in environmental conditions from year to year was not considered.

With respect to temperature data, it is important to have accurate temperature measurements in the studied areas. Information on water temperature is necessary for model simulations. Continuous temperature measurements in the water column and the upper sediment layer by using temperature loggers would have been better. Also the availability of long-term data sets for the study areas is of interest since individuals are exposed to year-to-year variability in environmental conditions, which was not considered in this study. Furthermore, temperature was considered here the only environmental factor that controlled growth but differences in other factors such as salinity and water current speed, which have not been considered, could also influence growth.

The estimation of the DEB parameters for the different species was based on published literature data, mostly from laboratory experiments. However, the lack of good datasets led to difficulties in estimating some parameters and a protocol had to be adopted to fill in missing gaps and achieve parameter consistency (Chapter 7). For a reliable estimation of parameters, it is important to have well-designed experiments which allow a simultaneous determination of growth, reproduction, respiration, assimilation and body condition under varying feeding conditions and food intake. Furthermore, parameter values were considered species-specific, although some variability may be expected (Kooijman 2000). The fact that, in blue mussel *M. edulis*, resorption of gonads seems to occur due to unfavourable environmental conditions (too high temperature and food limitation during summer; Chapter 2), suggests that the parameter k may vary along the year. Also the shape coefficient of *M. balthica* was seen to differ between Wadden Sea areas (Luttikhuisen et al. 2003), and sediment load in the water seems to influence a bivalve's gill-palp ratio (Honkoop et al. 2003) and filtration efficiency (Kooijman 2006). Intra-specific variability in DEB parameters could be responsible for some patterns attributed to food conditions. A possibility for testing the intra-specific variability in DEB parameter is by applying the model to another area, using the same species-specific

parameter values and changing only temperature conditions. A trial was done by applying the model to simulate growth in a northern European location (Valosen estuary, Bodø, Norway). Growth in the field was simulated for 4 different species and annual food conditions were reconstructed (Fig. 9.2), according to the methods described in chapter 8. For all species except *C. edule*, growth could be simulated without problems since the observed shell growth fell within the simulated curves. In *C. edule*, shell growth was faster than the maximum growth predicted by the DEB model, under maximal food conditions ($f=1$). The lack of accurate growth and temperature data could be responsible for this discrepancy (see above). However, variability in DEB parameter values can also not be ruled out. Applying the DEB model to simulate growth and to reconstruct food conditions in bivalves from other latitudes and habitats could be a first approach to evaluate with more detail the specificity of the parameters.

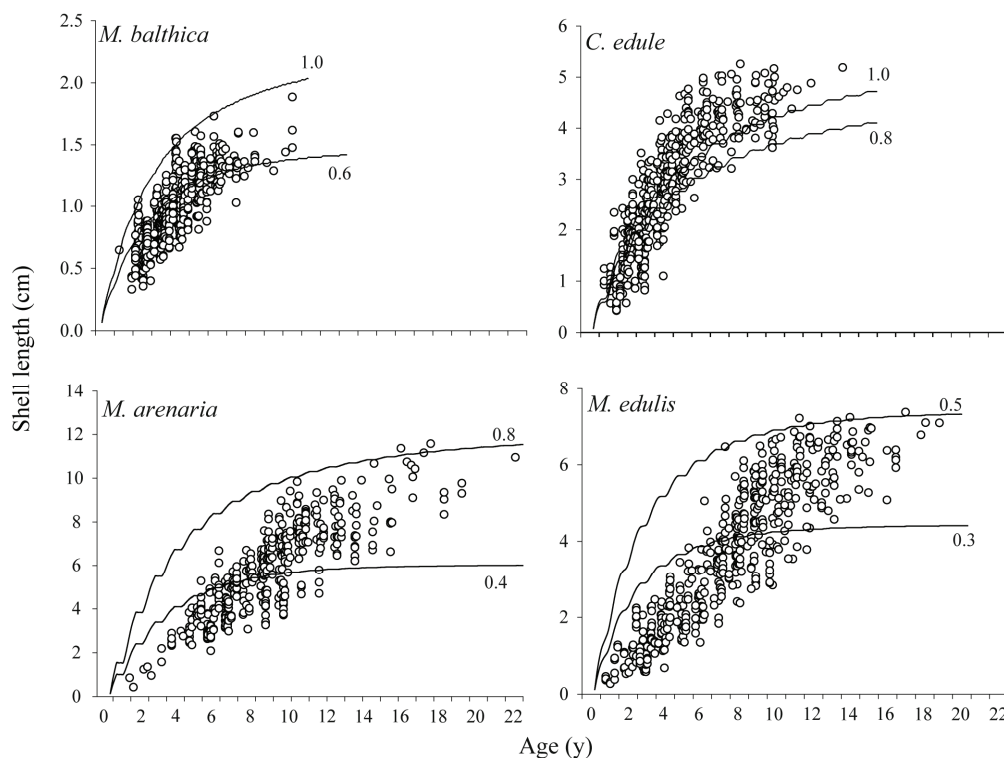


Fig. 9.2. Observed shell length (cm) with age (y) of *M. balthica*, *M. arenaria*, *C. edule* and *M. edulis* in Norway (Campos and Freitas, unpubl. data). Simulated growth curves were added for fast and slow growing individuals. Values indicate the average functional response used to simulate the curves under current water temperature conditions. Simulations were done as described in Chapter 8.

Concerning the recent attention and effort put into studying global climate change and its consequences in marine ecosystems, the DEB approach could to be an important tool to analyse the impact of climate change on bivalve productivity.

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