Chapter 1

General introduction
Objective

Bivalves are a main component of the benthic fauna of many marine and estuarine areas. Due to their high abundance (Dame 1996, Gosling 2003, and references therein), they are important as food source for other species, such as shorebirds, fishes, crustaceans (Braber and De Groot 1973, Hulscher 1982, Phil and Rosenberg 1984, Fréchette and Bourget 1985, Offringa 1993, Zwarts and Blomert 1992, Dekinga and Piersma 1993, Leopold 1996, Zwarts et al. 1996, Van der Veer et al. 1998, Mascaro and Seed 2000, Hiddink et al. 2002, Fox 2003, Beukema and Dekker 2005) as well as humans. Bivalve species can be found all around the globe in a variety of environments, from the poles to the tropics (Tebble 1966, Hayward and Ryland 1995, Dance and Ward 2002). Over such a range, differences in environmental conditions such as in water temperature, salinity, food availability and water current occur. These differences influence growth, survival and reproduction and, ultimately, they limit and determine the distribution of species.

At a latitudinal scale, physiological processes in bivalves are mainly affected by temperature. Latitudinal differences in growth rate of bivalves have been frequently related to latitudinal gradients in temperature (Gilbert 1973, Bachelet 1980, Appeldoorn 1983, 1995; Beukema and Meehan 1985, Hech et al. 2002, Fiori and Morsán 2004). Also gametogenesis and spawning are affected by temperature. In many bivalve species, spawning occurs once a specific threshold temperature is reached (Loosanoff and Davis 1963, Lammens 1967, De Wilde and Berghuis 1978, Giese and Kanatani 1987, Drent 2004). Overall, temperature is seen as a key factor directly or indirectly affecting physiological processes. After severe winters, the amount of settled bivalve larvae (spat) on the seafloor appears to be higher than after mild winters (Reise 1987, Beukema et al. 2001). In this case, temperature acts indirectly by reducing the amount of predators that feed on early life stages (Beukema 1992, Strasser and Günther 2001, Strasser 2002, Philippart et al. 2003).

At a local scale, physiological processes in bivalves are affected by other environmental factors as well. Food quality and quantity, tidal level and sediment type are known to influence growth and reproduction, and these seem to have locally a more important role (Newell and Hidu 1982, De Montaudouin 1996, Beukema and Cadée 1997, Honkoop and Beukema 1997, Beukema et al. 2002, Carmichael et al. 2004). Food availability is considered the most important factor influencing growth in bivalves at a local scale. For example, higher growth, body condition and reproductive output are usually observed at lower intertidal (exposed during low tide) areas than at higher ones (Jones et al. 1978, Guevara and Niell 1989, Roseberry et al. 1991, Jensen 1992, Wanink and Zwarts 1993, De Montaudouin 1996, Honkoop and Beukema 1997), due to the longer submersion time and thus longer possibility of food intake at lower intertidal areas. Furthermore, numerous intra- and interspecific interactions between bivalve species and other benthic fauna also occur within an area and these include competition for food (Hummel 1985, Kamermans et al. 1992, Kamermans 1993,
Herman et al. 1999, Cognie et al. 2001), predation (Van der Veer et al. 1998) or disturbance by other benthic organisms such as worms (Flach 1992). As a consequence, bivalve species experience differences in local conditions and, to be able to survive in a variable environment, they have strategies to maximize growth, reproduction and survival. These life history strategies include the timing of reproduction, their feeding and also their use of the different tidal levels.

In the shallow Wadden Sea, the largest estuarine area in northern Europe, in size around 10,000 km² (Wolff 1983), a few bivalve species constitute more than 65% of the total biomass of macrobenthos, both at intertidal and subtidal (always submersed) areas (Dekker 1989, Beukema 1991, Dekker et al. 2002, 2003; Dekker and Waasdorp 2004, 2005, 2006). These species (Fig. 1.1) include the Baltic tellin *Macoma balthica*, the edible cockle *Cerastoderma edule*, the blue mussel *Mytilus edulis*, the soft-shell clam *Mya arenaria*, the razor shell *Ensis americanus* and a recent invading species the Pacific oyster *Crassostrea gigas* (Beukema 1976, Wolff 1983, Dankers et al. 2006, Dekker and Waasdorp 2006).

Despite the similarities in their life cycles, there are differences in habitat use among the various species. In some of these species, such as *M. balthica* and *C. gigas*, spat is almost exclusively found in high densities in the intertidal zone, whereas in *C. edule*, *M. arenaria*, *E. americanus* and *M. edulis* settlement of spat is observed over a wider range in the intertidal and subtidal. Adults of all species are generally found over a wider tidal range (intertidal and subtidal) than the juveniles (Beukema et al. 1978, Beukema 1993). Differences in habitat use between the various species imply that differences in their life history characteristics must be involved. Therefore, spatial differences in food and growing conditions between tidal areas

**Fig. 1.1.** Most common bivalve species of the western Wadden Sea.
are expected to result in differences in, for example, age at maturity, maximum age and maximum size.

On the one hand, the fact that these species are widespread and common illustrates the strong persistence of the populations (c.f. Sinclair 1988) and hence their survival from year to year. On the other hand, environmental conditions in the Dutch Wadden Sea hardly seem favourable for growth and survival of bivalves, since food conditions appear to be suboptimal during most of the year. For example, low temperatures and low food availability during winter lead to weight loss in bivalve species such as *M. balthica*, *M. arenaria* and *C. edule* (Zwarts 1991). Additionally to these environmental stresses, there is also a high predation pressure and competition for food between bivalve species (De Vlas 1979, Kamermans et al. 1992). Therefore, despite their survival in the Dutch Wadden Sea, their yearly energy balance can be negative in some years, as seen in *M. balthica* (Hummel 1985).

The main aim of this thesis is to get insight on how different bivalve species are able to persist in an apparently unfavourable environment. First, variation in life history strategies among bivalve species in relation to environmental conditions is studied. The objective is to identify whether interspecific differences occur with respect to feeding, growth, reproductive investment and timing of spawning. Second, intraspecific differences in the various bivalves are analysed, whereby the outcome of the life history strategy of a species in different habitats is studied. Since food quantity, food quality and temperature are the main factors influencing physiological rates, such as feeding rates and respiration rates (Widdows 1973a, b; Newell and Bayne 1980, Møhlenberg and Kiørboe 1981, Smaal et al. 1997), this has been translated into a study of the physiology of bivalve species. Environmental conditions affect the energy available for growth and reproduction and therefore, differences in life history strategies among species are expected to result in differences in success of species.

**Approach**

This thesis focuses on growth and reproduction of bivalve species in different habitats of the western Dutch Wadden Sea and North Sea coastal zone in relation to environmental conditions. This approach allows a further analysis of intra- and interspecific interactions (such as competition for food) between those bivalve species. Such a comparative bi-energetic study should, ideally, be based on a general framework that can be applied to all species. The Dynamic Energy Budget (DEB) theory developed by Kooijman (1988, 2000) offers this framework. By applying the DEB model, it is possible to quantitatively describe the energy flow through an individual and to analyse the allocation of energy over growth and reproduction in relation to environmental conditions and food intake. The same model can be applied for different species whereby differences among species are expressed as differences in parameter values. The DEB model has already been successfully applied to analyse the effects of toxic components in mussels (Van Haren and Kooijman 1993), to compare life
history strategies of marine flatfish species (Van der Veer et al. 2001) and to simulate growth and reproduction in oysters (Bacher and Gangnery 2006, Pouvreau et al. 2006). The DEB model is applied in this thesis in two ways: [1] for the prediction of growth under various food and temperature conditions and [2] for the reconstruction of food intake under current temperature conditions and with observed bivalve growth in the field.

The work presented in this thesis is based on extensive field studies on growth and reproduction of various bivalve species in combination with DEB model simulations with the final aim to analyse differences in life history strategies among and within species in relation to habitat characteristics. This thesis consists of three parts:

[1] Field studies,
[2] Estimation of DEB model parameters for the various bivalve species,
[3] Application of the DEB model for the reconstruction of food conditions in the field to analyse intra- and interspecies competition.

Field studies

Studied species and their characteristics

Five bivalve species were studied in this thesis: the Baltic tellin *Macoma balthica*, the edible cockle *Cerastoderma edule*, the blue mussel *Mytilus edulis*, the soft-shell clam *Mya arenaria* and the Pacific oyster *Crassostrea gigas* (see Fig. 1.1). All species have a wide range of distribution, from cold to temperate or even subtropical waters (Tebble 1966, Hayward and Ryland 1995). Although in the Dutch Wadden Sea and adjacent coastal waters these species occupy different habitats (Wolff 1983), they share fundamental similarities in their life cycles. After fertilization in the water column and a short egg stage of maximum a few days, a free swimming planktonic larval period occurs. Usually, after three to four weeks in the water column, larvae are ready to settle on the seafloor. Once these bivalve spat have settled for a few weeks, it is common for them to redistribute over the intertidal or subtidal range.

*M. balthica* occurs from the upper regions of the intertidal and subtidal areas in the Dutch Wadden Sea to the outer parts of the tidal inlets in the coastal zone. *C. edule* and *M. edulis* occur from the intertidal to the shallow subtidal areas in the estuary. *M. arenaria* is present mainly from the upper intertidal to the shallow subtidal but it may be found, in offshore areas, at considerable depths. *C. gigas*, a native species from Japan, is now quite abundant and expanding in intertidal areas of the estuary, although it can also be found in the subtidal. Considerable differences in ultimate size are found between these species: *M. balthica* reaches a maximum shell length of 2.5 cm, *M. arenaria* of 10-15 cm, *C. edule* of 5 cm, *M. edulis* up to 15 cm and *C. gigas* up to 20 cm (Tebble 1966, Hayward and Ryland 1995, Reise 1998). All species live half or totally buried in muddy to sandy sediments although mussels and oysters always have to attach to hard substrate such as rocks or dead shells, being often found on stones of harbour piers. *M. balthica* and *M. arenaria* are able to bury deep in the sediment.
and protrude their long siphons over the surface for feeding and respiration. All species except for *M. balthica* are suspension-feeders, filtering food particles from the water column. Although *M. balthica* is capable of suspension-feeding, it is mainly a deposit-feeder, feeding on benthic algae from the sediment surface.

**Studied locations and methods**

Bivalve species were sampled at selected intertidal (above Low Low Water Spring (LLWS)) and subtidal (between LLWS and LLWS – 5 m) areas of the western Dutch Wadden Sea and in the North Sea coastal zone (called in this thesis “offshore”, between LLWS - 5 m and LLWS - 10 m), in such a way that representative samples could be collected (Fig. 1.2). Sediment composition varied from sand, in the vicinity of gullies and deeper channels, to muddy areas near the shore.

![Fig. 1.2. Two of the sampled stations in this study: a) intertidal, b) subtidal.](image)

Intertidal sampling areas were emerged for about 4 to 5 hours per tidal cycle. In these areas, sampling was done during low tide, by walking directly from the shore to the sampling area or by travelling first by boat to the tidal flat. On the tidal flat, *M. edulis*, *C. edule*, *M. arenaria* and *C. gigas* were collected by hand, by digging out with a fork, while *M. balthica* was sampled with a hand core (Fig. 1.3a). At subtidal areas, sampling was done by boat. *M. balthica* and *M. arenaria* were sampled with a ‘Reineck’ box corer (Fig. 1.3b) and *C. edule* was sampled with a 1.9 m beam trawl (Fig. 1.3c). At offshore areas, *M. balthica* was sampled by boat with a ‘Van Veen’ grab (Fig. 1.3d). Samples were then sieved over 1 mm mesh size. In addition to the sampling on the Wadden Sea, *C. gigas* was also sampled in an estuary in the south of the Netherlands (Oosterschelde estuary) and on the coast near La Rochelle in France. At each sampling station and sampling date, water temperature and salinity were measured.

After samples were collected, they were transported to the laboratory and stored in a refrigerator at 5 °C. During the following 48 hours, all individuals were processed. From each individual, shell length, shell height and shell width were measured with an electronic
calliper. Live bivalves were opened and flesh was removed. Flesh mass was immediately weighed in a balance while the shell was left to air dry and weighed the day after.

Reproductive tissue (gonad) was separated from the rest of the body tissue (soma) under a microscope and each part was put individually in ceramic pots. Tissues were then dried for 4 days in an oven at 60 °C and incinerated for 4 h in a furnace at 560 °C. After drying and incinerating, each pot was weighed to the nearest 0.01 mg. The ash-free dry mass (AFDM) of somatic and gonadal tissues was then determined by subtracting the ash weight from the dry weight. This AFDM was used to analyse differences in body condition and reproductive investment along the year among species and, within one species in different sampling locations.

The field data collected was used not only to test the predictions of the DEB model simulations with field data, but also to gather information on the life history strategies of the different species in relation to their current status in the Wadden Sea.

**Fig. 1.3.** Gear used to sample the different species: a) Hand core, b) Box corer, c) Beam-trawl and d) ‘Van Veen’ grab.
The DEB model

DEB model structure
The DEB theory is built on dynamic systems and quantifies the energy flow through an individual during its life-time. Key processes are feeding, digestion, storage, maintenance, growth, development, reproduction and ageing. The quantitative aspects of energy budgets were taken to follow the rules as specified by the Dynamic Energy Budget (DEB) theory (Kooijman 2000). The DEB model describes the energy flow through an animal (Fig. 1.4) and the changes in this flow in environments in which food densities and temperatures vary. The DEB model distinguishes three life stages: embryos, which neither feed nor reproduce; juveniles, which feed but do not reproduce; and adults which both feed and reproduce. In addition, also three main body fractions are considered: structural biovolume, or somatic tissue; stored reserves; and gonads, or stored energy reserves allocated to reproduction. The contribution of these body fractions to total biovolume changes with time. Storage materials (such as glycogen in bivalves) are continuously used and replenished while structural materials (such as proteins) are continuously degraded and reconstructed. The chemical composition of each of these fractions is taken to remain constant (homeostasis).

![Fig. 1.4. Energy flow through an organism in the DEB model, after Van Haren (1995). Rates: 1 ingestion (uptake), 2 defecation, 3 assimilation, 4 demobilisation of energy into reserves, 5 mobilisation of energy from reserves, 6 utilisation, 7 growth, 8 somatic maintenance, 9 maturation maintenance, 10 maturation, 11 reproduction. The rounded boxes indicate sources or sinks; the rectangles indicate state variables.](image)

The state of a system at a given moment is described by state variables. The DEB theory characterises an individual using two state variables: structure, quantified as body volume, and energy reserves, quantified as reserve density. State variables change with time and can
be described by a set of differential equations which have parameters (Table 1.1). The notation and symbols used here are the same as in Kooijman (2000):

1. variables are indicated by symbols and lower case symbols frequently relate to upper case ones via scaling;
2. quantities are expressed per unit of volume with square brackets [ ]; per unit of biosurface area with braces { }; and per unit of mass with angles < >;
3. rates have dots, indicating the dimension per time.

**Table 1.1.** Parameter set of primary and compound parameters of the DEB model. Notation after Kooijman (2000).

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Dimension</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary parameters</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( T_A )</td>
<td>K</td>
<td>Arrhenius temperature</td>
</tr>
<tr>
<td>( J )</td>
<td>( \text{J cm}^{-2} \text{d}^{-1} )</td>
<td>Maximum surface area-specific ingestion rate</td>
</tr>
<tr>
<td>( \rho )</td>
<td>-</td>
<td>Losses due to digestion</td>
</tr>
<tr>
<td>( \bar{p}_M )</td>
<td>( \text{J cm}^{-3} \text{d}^{-1} )</td>
<td>Volume-specific maintenance costs</td>
</tr>
<tr>
<td>( E_m )</td>
<td>( \text{J cm}^{-3} )</td>
<td>Maximum storage density</td>
</tr>
<tr>
<td>( E_G )</td>
<td>( \text{J cm}^{-3} )</td>
<td>Volume-specific costs of growth</td>
</tr>
<tr>
<td>( E_V )</td>
<td>( \text{J cm}^{-3} )</td>
<td>Volume-specific structural energy content</td>
</tr>
<tr>
<td>( \kappa )</td>
<td>-</td>
<td>Fraction of utilized energy spent on maintenance plus growth</td>
</tr>
<tr>
<td>( \delta_m )</td>
<td>-</td>
<td>Shape coefficient</td>
</tr>
<tr>
<td>Compound parameters</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \dot{v} = \frac{\bar{p}_{am}}{E_m} )</td>
<td>( \text{cm d}^{-1} )</td>
<td>Energy conductance</td>
</tr>
<tr>
<td>( \dot{k}_M = \frac{\bar{p}_M}{\sqrt{E_G}} )</td>
<td>( \text{d}^{-1} )</td>
<td>Maintenance rate constant</td>
</tr>
<tr>
<td>( g = \frac{E_G}{\kappa E_m} )</td>
<td>-</td>
<td>Investment ratio</td>
</tr>
<tr>
<td>( \dot{r}_B = \left( \frac{3}{\bar{k}_M + 3fV_m^{1/2}/\dot{v}} \right)^{-1} )</td>
<td>( \text{y}^{-1} )</td>
<td>Von Bertalanffy growth rate</td>
</tr>
</tbody>
</table>

Parameters are constants that are assumed to have a fixed value but may change with time. For example, parameters related to physiological rates (growth, filtration, respiration) depend on temperature and therefore, remain constant as long as temperature does not change. If temperature changes, then parameters change as well. With this respect, it is assumed that temperature affects all physiological rates in the same way, and a species-specific parameter
(the Arrhenius temperature) is used to correct physiological rates measured at different temperatures (Box 1). Intraspecific variability is caused by differences in state variables not in parameter values and in contrast, interspecific variability is the result of differences in parameter values. The elegance of the DEB model is the limited number of parameters which can fully describe the state of an organism.

**Box 1 - The Arrhenius temperature**

Temperature has an effect on all physiological rates. Each species can only tolerate temperature within a specific temperature range. Within part of the temperature tolerance range (i.e. the optimal temperature range), rates increase exponentially with increasing temperature. Outside the optimal temperature range, both at low and high temperatures, rates are reduced. In the DEB theory, the description proposed by Arrhenius describes the effect of temperature on physiological rates with acceptable accuracy within the temperature tolerance range of a species. The Arrhenius relationship is described by the equation

\[
\hat{k}(T) = \hat{k}(T_1) e^{\frac{T}{T_a} - \frac{T_1}{T_a}}
\]

in which \(\hat{k}\) is a physiological rate, \(T\) is the ambient temperature (in Kelvin), \(T_1\) is a chosen reference temperature (in this thesis all model simulations were done at 20 °C, that is 293 K) and \(T_a\) is the Arrhenius temperature. This relationship is used to correct different physiological processes for differences in temperature. By plotting \(\ln \hat{k}\) against \(\frac{T}{T_a}\), the result is a straight line with slope \(T_a\). The Arrhenius temperature is species-specific, which means that within one species, the relationship between different physiological rates and temperature is the same.

The DEB model is based on a set of general assumptions regarding food uptake, storage and utilisation (Table 1.2). Food uptake is assumed to be proportional to the organisms' surface area and to follow a type II functional response curve (Holling 1959), in which the intake rate depends hyperbolically on the food density in the environment (Box 2). Food is assumed to enter first a reserve pool and later mobilized reserve is allocated to growth, to somatic and maturation maintenance and to maturation or reproduction. That is, a fixed fraction \(\kappa\) of utilised reserve is allocated to growth plus somatic maintenance while the remainder fraction \((1-\kappa)\) is allocated to maturity maintenance plus maturation or reproduction. This rule is called ‘\(\kappa\)-rule’. The different life stages utilize energy in a different way. Juveniles have to mature and become more complex (i.e. develop new organs and regulation systems) while adults do not increase in complexity but reproduce. Therefore, the energy spent on development in juveniles is spent on reproduction in adults. If conditions are poor, reproduction is blocked and all energy is allocated to growth and somatic maintenance. However, maintenance has priority over growth, and hence growth ceases when all reserve that is allocated to somatic maintenance plus growth is required for somatic maintenance.
Box 2 - The functional response

Functional responses describe the relationship between consumption rate of an individual and food density. In the DEB model, the link between food conditions in the field and ingestion rate \( \left( \dot{J}_X \right) \) as a function of food density is described by a hyperbolic functional response (Kooijman 2000):

\[
\dot{J}_X = \frac{\dot{J}_{Xm}}{f} V^{2/3}
\]

where \( \dot{J}_{Xm} \) is the maximum ingestion rate per unit of surface area; \( V^{2/3} \) is the body surface area and \( f \) is the scaled functional response. This response curve corresponds with the type II response curve as proposed by Holling (1959). The type II functional response assumes that a predator spends its time either searching for a prey or handling a prey. Handling includes chasing, killing, eating and digesting. In this type of functional response, ingestion (consumption) rate increases with food density at a decelerating rate, until a maximum is reached above which ingestion rate remains constant (Fig. 1.5). The initial slope of the function is given by the searching rate while the asymptote is given by the reciprocal of the handling time. In bivalves, filtration rate decreases with increasing food concentration, leading to a constant ingestion rate because, at a certain moment in time, ingestion rate cannot increase further due to the time necessary for food digestion (Fig. 1.5). Values of the scaled functional response vary between 0 (starvation) and 1 (optimal, food ad libitum).

Fig. 1.5. Schematic representation of the type II functional response proposed by Holling (1959) about the relationship between food density and food ingestion (solid line) or filtration in bivalves (striped line).
Maintenance is defined as the energy requirement of an organism, excluding the energy necessary for growth of structural mass, reproduction and development. Maintenance costs are species-specific and depend on the size of the organism and on body temperature (Box 3).

A more detailed description of the DEB model can be found in Kooijman (2000).

**Table 1.2.** The basic assumptions of the DEB model (from Van der Meer 2006, following Kooijman 2000).

<table>
<thead>
<tr>
<th>Assumption</th>
<th>Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>a.</td>
<td>An organism is characterised by a structural body and a reserve density (i.e. amount of reserves per amount of structural body). The chemical composition of both structural body and reserves is constant, which is called the assumption of strong homeostasis.</td>
</tr>
<tr>
<td>b.</td>
<td>Each organism starts its life as an embryo (which does not feed and does not reproduce). When the embryo has reached a certain degree of maturation, it changes into a juvenile (which feeds, but does not reproduce). Similarly, a juvenile changes into an adult (which feeds and reproduces) when it exceeds a given threshold value.</td>
</tr>
<tr>
<td>c.</td>
<td>Ingestion is proportional to the surface area of the organism and depends upon food density by a Holling type II functional response. Recall that embryos do not feed.</td>
</tr>
<tr>
<td>d.</td>
<td>A fixed fraction of the ingested food is assimilated and enters a storage pool, which is characterised by the reserve density.</td>
</tr>
<tr>
<td>e.</td>
<td>The regulation of the reserve density follows a first-order process.</td>
</tr>
<tr>
<td>f.</td>
<td>A fixed fraction $\kappa$ of the utilisation rate goes to somatic maintenance, heating (for endotherms) and growth of the structural body (with a priority for maintenance), and the rest goes to maturity maintenance and (for embryos and juveniles) maturity or (for adults) reproduction.</td>
</tr>
<tr>
<td>g.</td>
<td>Maintenance rate is proportional to structural volume and heating rate is proportional to the surface area of the organism.</td>
</tr>
</tbody>
</table>

Estimation of parameters and DEB model simulations

Applying the DEB model requires the estimation of a set of parameters for the various species according to a standard procedure. For the estimation of parameters, published data on the various species was collected and, when data sets were lacking, a newly established standard procedure was used to determine missing parameters.

For each species, the DEB model can be used for: 1) the simulation of growth in the field if food and temperature conditions are known, 2) the reconstruction of the food level in the field if temperature conditions and growth are known, or 3) the reconstruction of temperature conditions in the field if food conditions and growth are known. In this thesis, DEB model simulations were done first to simulate annual growth by using the prevailing (current) temperature conditions at different scenarios of food level and compared to field results. Second, the DEB model was used to reconstruct the seasonal pattern in food level for the various species in the different habitats. Food conditions in the field were reconstructed by back-calculating food from observed growth in the field at the current temperature conditions.
Finally, the existence of food competition between species was analysed by comparing the estimates of the back-calculated food conditions for the various species.

**Box 3 - Maintenance**
In the DEB theory, maintenance of both somatic and gonadal tissues is proportional to body volume. Maintenance costs are species-specific and depend on the size of the organism. This is because a cell is a volume that uses a fixed amount of energy per unit of time for maintenance, i.e. to maintain its structure (or volume). In this way, a larger bivalve (with more cells) needs more energy to maintain its cells than a smaller one and the required energy is proportional to the amount of cells (volume) it needs to maintain. Maintenance costs \( \dot{p}_M \) are described by:

\[
\dot{p}_M = \left[ \dot{p}_M \right] \cdot V
\]

where \( \left[ \dot{p}_M \right] \) is the volume-specific maintenance costs and \( V \) is the body volume.

This implies that the volume-specific maintenance costs are independent of volume. This is because the size or volume of a cell is related to its complexity, therefore, the amount of energy necessary to maintain a cell is the same regardless of the size of the individual. Since the complexity of cells is similar between related species such as bivalves, the volume-specific maintenance costs are also considered to be similar.

**Outline of the thesis**
This thesis is divided in a number of components: field data collection (Chapters 2 to 5), DEB model predictions for bivalves (Chapter 6), estimation of DEB parameters (Chapter 7), simulation exercises and combination of DEB model simulations and field data (Chapter 8) and a synthesis with a final discussion (Chapter 9).

**Chapter 2**
The blue mussel *Mytilus edulis* is one of the most common bivalves in the Wadden Sea. From mid 1980’s to late 1990’s, strong declines in mussel populations have been observed. Part of the decrease in mussel densities has been due to fishing activities for seed mussels. Although measures were taken to protect mussel beds, densities are still much lower than in the 1970’s. The slow recovery of mussel beds in the intertidal of the western Dutch Wadden Sea suggests that factors involved in the survival of adults or recruitment success could be acting too. Water temperature is an important factor influencing various physiological processes in bivalves. In the Wadden Sea, lower body condition has been observed in several species after mild winters in comparison to severe winters. Therefore, the observed increase in water temperatures in the Dutch Wadden Sea suggests that an effect of temperature on the population dynamics of mussels might be expected. It is known that high winter temperatures enhance predation pressure on larvae and post-larvae. However, it is also possible that the increasing trend in water temperature during the last decades could have a negative effect on
the reproductive output of mussels. In order to test whether reproductive failure could be the cause for the low recruitment of *M. edulis* in the western Dutch Wadden Sea, the reproductive investment of the mussel was studied during one year and a long-term data series on body condition was analysed to assess whether the decrease in recruitment success could be due to a negative impact of increasing temperatures on body condition and, hence on reproductive output.

**Chapter 3**

In the Dutch Wadden Sea estuary, the common cockle *Cerastoderma edule* and the soft-shell clam *Mya arenaria* are found in intertidal and subtidal areas. These species present large differences in maximum size and age: 15 cm and 28 years in *M. arenaria* vs. 5 cm and 10 years in *C. edule*. In the western Dutch Wadden Sea, recruitment success of *C. edule* is usually higher than in *M. arenaria*. These differences in recruitment success can result from a number of factors, starting with differences in reproductive output or differences in larval and post-larval processes (such as growth, pelagic stage duration and mortality). The fact that egg size is similar in these species (57 µm in *M. arenaria* vs. 65 µm in *C. edule*) suggests that larval size and pelagic stage duration will also be similar. Therefore, differences in larval processes between species are not likely to be responsible for the observed differences in recruitment. As a starting point, this chapter focuses on the reproductive investment of *C. edule* and *M. arenaria* in two habitats of the western Wadden Sea by analysing the timing of spawning and the reproductive output of each species. The aim was to find out if differences in reproductive investment between these two species could be the cause for the observed differences in recruitment success in the western Wadden Sea.

**Chapter 4**

The bivalve *Macoma balthica* is an abundant species in intertidal and subtidal areas of the Dutch Wadden Sea and adjacent coastal waters. However, from an energetic point of view, at least the environmental conditions for the intertidal population hardly seem favourable due to exposure to high temperatures during the summer and the fact that significant food intake can only occur during submersion. Therefore, it is possible that recruitment in the Wadden Sea originates mainly from the subtidal and/or offshore stocks. In order to evaluate the importance of the different habitats to the persistence of the *M. balthica* population in the western Dutch Wadden Sea, growth and reproductive output in various habitats (intertidal, subtidal, offshore) was analysed.

**Chapter 5**

The Pacific oyster *Crassostrea gigas* is an invading species of the Dutch Wadden Sea which has become abundant during the last years. Since its recent expansion seems to be related to an increase in mean water temperature, it is possible that the latitudinal decrease of
temperature towards the poles might potentially determine the ultimate northern limit of the geographical distribution of \textit{C. gigas}. As a first approach to analyse the physiological performance of this species along a latitudinal gradient, spatial and temporal variation in growth and reproductive output were studied in three \textit{C. gigas} populations from France to the Netherlands. Focus was on the energy allocation to growth and reproduction of the various populations in relation to environmental conditions, with the aim of finding out how this species has been able to successfully invade and expand in the Dutch Wadden Sea.

Chapter 6
The DEB model predicts a set of body-size scaling relationships for the comparison of species. Body-size scaling relationships describe relationships between physiological variables (egg size, growth rate, size at settlement and maturation) and body size. The DEB model was used to analyse body-size scaling relationships that can be applied to predict species characteristics in case basic information is lacking. In addition, the discrepancies between DEB predictions based on energetic constraints and field observations were analysed to identify potentially important factors in the life history strategy of bivalves.

Chapter 7
The various DEB parameters were estimated for a number of bivalve species that are abundant in northern European waters, including the Dutch Wadden Sea. First, a brief overview was presented on how the various parameters can be estimated and what types of data sets are required. Next, a protocol was introduced on how to deal with missing estimates in case data sets are lacking and how to achieve consistency between various estimates. Finally, a complete and consistent set of DEB parameters was presented for various bivalve species.

Chapter 8
In chapter 8, the energy flow in the various bivalve species in different habitats of Dutch coastal waters was analysed by comparing growth observations in the field with model simulations by means of the DEB theory. The final objective was to reconstruct food conditions for the various species and habitats by applying the DEB model. For that, field data collected in the previous chapters were used, for the analysis of seasonal variation in somatic mass per age group for each species and location. In addition, the parameters estimated in chapter 7 were used to run the model, in combination with temperature and food conditions as input variables. At the end, DEB simulations were run to reconstruct food conditions for the various species at the various locations under the current water temperature conditions, in order to have an idea of the interactions between bivalve species in terms of food competition.
Chapter 9

In this chapter, the main conclusions from the previous chapters were summarized. Limitations for using the DEB model in relation to the quality of datasets available were discussed. Focus was put into the problem of age determination in bivalves and on the variability of species-specific parameters. In addition, suggestions for further research were presented.

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