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Body-size scaling relationships in bivalve species: A comparison of field data with predictions by the Dynamic Energy Budget (DEB) theory

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Abstract

In this paper, we apply the Dynamic Energy Budget (DEB) theory to bivalve species (1) to provide basic body-size scaling relationships that can be used to predict species characteristics when basic information is lacking, and (2) to analyse the discrepancy between DEB predictions based on energetic constraints and field observations, in order to identify potentially important factors in life history strategy of bivalves. Body-size scaling relationships were identified for size at first reproduction, Von Bertalanffy growth parameter, and egg and larval development time in relation to egg and larval volume and temperature conditions. Due to their small egg volume, bivalve species are characterised by a relatively short pelagic larval stage. The main discrepancy between field observations and DEB predictions was in the relationship between egg and larval volume and adult body volume. In bivalves, the characteristics of the early life stages are not related to body size of the species. Since the minimum size of settling larvae is always larger than 125 μm, it is suggested that successful settlement might be the key factor. Settlement size or volume of the fragile larvae must be in balance with the sediment composition, i.e. similar to or larger than that of the sediment grain size.

Keywords: Body size; Dynamic Energy Budget; Bivalve; Von Bertalanffy; Egg; Larva; Development; Growth; Recruitment

1. Introduction

The benthic community of estuarine coastal systems is characterised by a mosaic of species, including a variety of bivalves (for a general overview see: Ketchum, 1983; Mathieson and Nienhuis, 1991). In the western Dutch Wadden Sea, various bivalve species account for most of the biomass (Beukema, 1976). Although the maximum age of the various species is about the same (Tebble, 1966), they differ with respect to growth and reproduction. For instance, their maximum length differs by more than a factor of 10 (Tebble, 1966; Carriker and Gaffney, 1996; Poppe and Goto, 1993). Despite these large differences, annual spatfall and subsequent recruitment of all species is successful (Beukema et al., 2001; Van der Meer et al., 2001) indicating that different life history strategies can be adopted successfully in these fluctuating estuarine environments.

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Any analysis of life history strategies in terms of the trade-off between growth and reproduction requires a general framework to compare the energetics of the different species in a systematic way. The Dynamic Energy Budget (DEB) theory (Kooijman, 1993, 2000) offers this general framework. DEB models can be used in various ways. First of all, various aspects in the life history and energetics of different species can be captured in a single model whereby differences between species are reflected in differences in parameter values only. Van der Veer et al. (2006) provide estimates of the various DEB parameters and a comparison of sets for a number of abundant bivalve species in Dutch coastal waters. Based on these, Cardoso et al. (2006) applies the DEB model to analyse the intra- and interspecies comparison of the energy flow in bivalve species in Dutch coastal waters.

A second application of the DEB theory is the prediction of various body-size scaling relationships. Such relationships have already been under study and under debate for decades since the pioneering work of Kleiber (1932) on the scaling of metabolic rate with body size. Thus numerous empirical relationships of biological rates as simple functions of body size and other variables have been established (for an overview see Peters, 1983). Although this descriptive ecology has proved to be valuable, it has been criticised for seeking post-hoc explanations of observed patterns without experimental tests of hypotheses (Blackburn and Gaston, 1999). The DEB theory of Kooijman (1993, 2000), based on surface- and volume-related processes can be considered as a clear response to this criticism. However, the DEB theory has so far not been recognised as such. Despite the fact that it was introduced in the late 1980s, recent literature is still suggesting that we lack a general theory on body-size scaling relationships based on first principles (e.g. Blackburn and Gaston, 1999; Brown et al., 2004; Harte, 2004). To our knowledge, the DEB theory is the only theory that is based on a set of general assumptions regarding food uptake, storage and utilisation that predicts many types of intra- and interspecific scaling relationships (Kooijman, 2000). In this paper, we develop the predictions of the DEB theory for bivalves with the aims of:

(1) providing basic body-size scaling relationships that can be applied to predict species characteristics in case basic information is lacking;
(2) analysing the discrepancy between DEB predictions based on energetic constraints and field observations to identify potentially important factors in life history strategy of bivalves.

2. DEB model predictions

A conceptual introduction of the DEB theory can be found in Kooijman (2001), and a full description is given in Kooijman (2000). The DEB theory describes the energy flow through an animal (Fig. 1) and also changes therein in environments with varying food densities and temperatures. In the model, three life stages (embryos, which neither feed nor reproduce; juveniles, which feed but do not reproduce; adults which both feed and reproduce) and three main body components (structural biovolume or somatic tissue; stored energy reserves; and gonads and/or stored energy reserves allocated to reproduction) are distinguished. Five equations with a small number of parameters (Table 1) can fully determine feeding, growth, survival and reproductive behaviour (see Kooijman, 2000).

The DEB theory implies interspecific body-size scaling relationships via a classification of its parameters into intensive parameters (which do not depend on the body size of the organism) and extensive parameters (which do depend on body size). In the DEB theory, size is measured in terms of volume. However, since literature data on volume is scarce, the volumetric length (i.e. the cubic root of the volume) is used to quantify body size.

Some of the volume- and growth-related relationships are temperature dependent and need to be corrected for temperature differences before a comparison between species can be made. Therefore, we corrected for differences in temperature using the Arrhenius relationship, which is an alternative to the Q_{10} (for details see Kooijman, 1993, 2000). The predictions of various

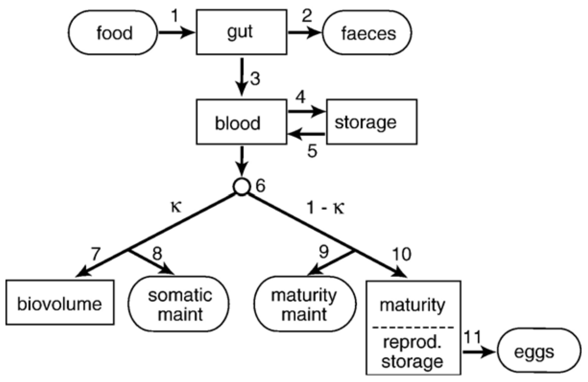

Fig. 1. Energy flow through an organism in the DEB model, after Van Haren (1995). Rates: 1 ingestion (uptake), 2 defecation, 3 assimilation, 4 demobilisation of energy into reserves, 5 mobilisation of energy from reserves, 6 utilisation, 7 growth, 8 somatic maintenance, 9 maturation maintenance, 10 maturation,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

Table 1
Primary and compound parameters of the DEB model. Notation after Kooijman (2000)

Symbol	Dimension	Interpretation
T_A	K	Arrhenius temperature
$\{\dot{j}_{Xm}\}$	J cm^{-2}d^{-1}	Maximum surface area-specific ingestion rate
	–	Losses due to digestion
$\{\dot{p}_{Am}\}$	J cm^{-2}d^{-1}	Maximum surface area-specific assimilation rate
$[\dot{p}_M]$	J cm^{-3}d^{-1}	Volume-specific maintenance costs
$[E_m]$	J cm^{-3}	Maximum storage density
$[E_G]$	J cm^{-3}	Volume-specific costs of growth
$[E_V]$	J cm^{-3}	Volume-specific structural energy content
κ	–	Fraction of utilized energy spent on maintenance plus growth
δ_m	–	Shape coefficient
$\dot{v}=\{\dot{p}_{Am}\}/[E_m]$	cm d^{-1}	Energy conductance
$\dot{k}_M=[\dot{p}_M]/[E_G]$	d^{-1}	Maintenance rate constant
$g=[E_G]/\kappa[E_m]$	–	Investment ratio
$\dot{r}_B$	a^{-1}	Von Bertalanffy growth constant

body-size scaling relationships are based on Kooijman (1986). There are three types of relationships: (1) primary scaling relationships, which can be derived from the structure of the DEB model and do not involve empirical arguments; (2) secondary scaling relationships, which can be derived from primary relationships and require empirical arguments; and (3) tertiary scaling relationships, which derive from the assumptions of the DEB model but require extra assumptions about individual interactions. While primary (predictions 1, 2 and 3) and secondary (predictions 4, 5 and 6) scaling relationships consider that two species show the same behaviour with respect to energetics as long as food density is constant (the so-called "invariance property"), tertiary scaling relationships (prediction 7) invoke indirect effects via the population level, such as competition for food.

2.1. Prediction 1: Maximum theoretical body volume is independent of temperature

According to the DEB theory, under optimal food conditions, the maximum theoretical body volume or length of a species is determined by the resources available and by maintenance requirements, according to Kooijman (2000; page 94):

$$V_{\max}^{1/3} = \kappa\{\dot{p}_{AM}\}/[\dot{p}_M] \tag{1}$$

wherein: $V_{\max}^{1/3}$ is the maximum volumetric length (δ*L; m); κ is the fraction of utilised reserve spent on somatic maintenance plus growth (−); $\{\dot{p}_{Am}\}$ is the maximum surface-area-specific assimilation rate (J cm^{-2} d^{-1}) and $[\dot{p}_M]$ is the volume-specific cost of maintenance (J cm^{-3} d^{-1}).

Both $\{\dot{p}_{Am}\}$ and $[\dot{p}_M]$ are similarly temperature dependent; hence the ratio is inherently species specific and not dependent on temperature.

2.2. Prediction 2: Egg volume is proportional to maximum theoretical body volume$^{4/3}$

Just after fertilisation, eggs consist almost completely of reserve energy; from then on and until birth, structure develops at the expense of the reserves. Birth is the moment of transition from a non-feeding stage to a feeding stage. Between species, the reserve density at birth, which is the ratio of the amount of reserve and structure, scales with volumetric length because the amount of energy an organism is able to store is dependent on its size (volume). Therefore, the amount of reserve in an egg, and thus the egg volume, will scale with maximum body volume$^{4/3}$. However, there is a large variation in egg size between taxa, thus the tendency of egg size to be proportional to maximum volumetric length only holds for related species (Kooijman, 2000), such as bivalves.

2.3. Prediction 3: Volume at first reproduction is proportional to maximum theoretical body volume

The κ-rule of the DEB theory states that a fixed fraction κ of the utilised reserve is allocated to somatic maintenance plus growth, the rest to maturity maintenance plus maturation (or reproduction in adults). Juveniles have to mature and become more complex while the increase in size (structure) in adults does not include an increase in complexity. The energy spent on development in juveniles is spent on reproduction in adults. In this way, stage transitions (from embryo to juvenile or from juvenile to adult) occur if the cumulative investment in maturation exceeds a specified threshold. In the DEB theory, this threshold is thought to be proportional to maximum structural volume because more complex organisms (with higher structural volume) will take more time to reach maturity. Therefore, volume at first reproduction also scales with maximum body volume. However, this relationship may vary between taxa (Kooijman, 2000).

2.4. Prediction 4: Volume at hatching and settlement is proportional to the maximum observed body volume

The maximum observed body volume an individual can achieve will depend on the actual prevailing food conditions, according to Kooijman (2000; Eq. (3.23), page 95):

$$V_\infty^{1/3} = fV_{\max}^{1/3} \tag{2}$$

where $V_\infty^{1/3}$ is the ultimate volumetric length (δ*L; m); f is the scaled functional response (−), which is a measure of food supply (Holling, 1959) and $V_{\max}^{1/3}$ is the maximum volumetric length (δ*L; m).

Since settlement represents a stage in the development of an individual bivalve, it is natural to scale the size at settlement with that at birth (hatching) and puberty (start of allocation to reproduction). The DEB model is volume structured rather than age structured, and therefore the length of the various life stages is closely related to growth. Species with larger maximum volume will produce larger eggs (see prediction 2), which develop in larger hatchlings because more energy reserves in the egg lead to the production of more structural mass. In this way, larger hatchlings consisting of more structural mass will develop from larger-sized species. The same arguments hold true for the volume at settlement, because large hatchlings with large structural mass will have a large size (volume) at settlement.

2.5. Prediction 5: Egg and larval development time are related to respectively egg and larval volume$^{1/4}$

Egg volume only represents reserve energy for development and hardly contains any structural mass. Therefore the relationship between egg volume and maximum body volume between species is based on the relationship between reserve energy and body volume. Between species, the energy content of an egg is not constant because it scales with body volume$^{1/3}$ (volumetric length). Since hatching volume of a species is proportional to the maximum body volume (Kooijman, 2000), total energy content of the egg must scale with body volume$^{4/3}$. Since reserve density of the egg is roughly similar between species, egg volume will scale with adult body volume$^{4/3}$, which also means that body volume scales with egg volume$^{3/4}$ and that volumetric length scales with egg volume$^{1/4}$. Egg development time scales with the energy content of an egg, and this implies that egg development time is related to egg volume$^{1/4}$.

After hatching, feeding starts and uptake processes start to become important. Therefore, the minimum developmental time holds true only at optimal food densities. At optimal food conditions, the length of the larval and juvenile period will, as for egg development, scale linearly with body size (volumetric length) and hence with larval volume $^{1/4}$ (Kooijman, 1986). The observed maximum adult size is already reflected in the egg, larval and juvenile size. However, it takes more time to develop and build up a larger adult if the larva is already larger.

2.6. Prediction 6: Von Bertalanffy growth rate scales approximately with the maximum observed body volume$^{-1/3}$

Under constant food conditions, or under abundant food conditions in view of the hyperbolic functional response f (Kooijman, 1988), the parameter values of the Von Bertalanffy growth curve can be interpreted from an energetic point of view (Kooijman, 2000; Eq. (3.22), page 95) according to:

$$\frac{1}{3\dot{r}_B} = -\frac{1}{\dot{v}}V_{\max}^{1/3} + \frac{1}{\dot{k}_M} \tag{3}$$

in which $V_{\max}^{1/3}$ is the maximum length (m); $\dot{r}_B$ is the Von Bertalanffy growth constant (a^{-1}); $\dot{v}$ is the energy conductance (m d^{-1}); $\dot{k}_M$ is the maintenance rate constant (d^{-1})

Under such conditions, and between species, the Von Bertalanffy growth rate decreases almost linearly with the observed maximum body volume to the power 1/3.

2.7. Prediction 7: Maximum observed body volume is positively related to latitude

Energy constraints on distribution patterns of organisms are mainly related to the quantity and quality of the available food. There is some evidence that latitudinal trends in food conditions do exist. Oceanic (=pelagic) primary productivity seems to be higher, on a global scale, in temperate habitats than in arctic and tropical ones (Gross et al., 1988; Behrenfeld and Falkowski, 1997; Falkowski et al., 1998). Trends of productivity in coastal areas are more complicated since, in addition to pelagic production, also benthic primary production becomes an important component. Furthermore, coastal areas are under the direct influence of local hydrodynamic and morphological conditions. A comparison of a subarctic, temperate and tropical marine coastal shelf ecosystem suggests on the one hand a trend of increasing planktonic primary production towards the tropics, but on the other hand a more efficient transfer of energy to higher trophic levels at high latitudes (Petersen and Curtis, 1980). As an explanation, reduced metabolism and higher conservation of organic matter at low temperatures are suggested (Petersen and Curtis, 1980).

In the DEB theory the maximum body volume of a species is determined by three DEB parameters (see Prediction 1) according to:

$$V_{\max}^{1/3} = \kappa\{\dot{p}_{Am}\}/[\dot{p}_M] \quad (1)$$

Whether a species is able to achieve its maximum volume will depend on prevailing food conditions f (see Prediction 4) according to:

$$V_{\infty}^{1/3} = fV_{\max}^{1/3} \quad (2)$$

Within species, the larger amount of food at higher latitudes, as suggested by the observed trend of more efficient transfer of energy to higher trophic levels at high latitudes, will lead to a larger ultimate size. Hence, a trend of increasing body size/volume with latitude is expected for species covering a wide distributional range. Among species, a size increase towards the poles would be an advantage in surviving long periods of starvation and fluctuating food densities, despite the low temperatures. This is because maximum body volume tends to be proportional to the maximum storage density, which is to the amount of storage material per unit of structural volume (somatic tissue). Small species can only cope with low food levels if these are constant, as it happens in the tropics. Moreover, small body volumes at lower latitudes would help survival because a smaller body volume has lower maintenance costs. Therefore, among species, the DEB theory predicts an increase of body size with latitude.

3. Methods

3.1. Data acquisition

Most of the data presented in this study were assembled from the literature but some unpublished data were added. In all cases, basic data sources of individual references are listed (Appendix A). Most information available consisted of length estimates rather than volumes. Publications by Loosanoff and Davis (1963) on the rearing of bivalve larvae, Tebble (1966) on the British bivalve seashells and Strathmann (1987) on the reproduction and development of marine invertebrates of the Northern Pacific coast were starting points. Information on individual species was compiled by means of literature searches on the Web of Science®. The objective was to gather enough information to be able to test the predictions, and not to collect published information about all species.

3.2. Statistical analysis

In order to test whether the different relationships based on field data are in agreement with model predictions, we tested the proportionality of the relationships. Thus, it was assumed that $y=a\cdot x^b$ and that $b=1$ or -1 (depending on whether the expected relationship is positive or negative), and linear regression models were run after double-log transformation. If the estimated b was not significantly different from the predicted b, then field data fit with model predictions and the predictions were not falsified.

4. Results

Since data on the shape coefficient of most of the bivalve species used in this paper were not available, body volume could not be corrected for differences in shape between species and therefore size measures are presented in terms of length.

4.1. Prediction 1: Maximum theoretical body volume is independent of temperature

To our knowledge no field or laboratory information is available for bivalves to allow a test and falsification of the prediction that maximum volumetric length is independent of temperature.

4.2. Prediction 2: Egg volume is proportional to maximum theoretical body volume$^{4/3}$

Since there is no information on the maximum theoretical body volume, maximum body length found in the literature was used. Egg dimensions were mostly presented as egg diameter measurements. For most species, egg diameter (μm) varied between individuals and populations; however between species the range between minimum and maximum egg diameter was similar (Fig. 2a). With respect to minimum egg diameter, the range observed varied between about 40 and 120 μm. Minimum egg diameter was not significantly positively related with maximum body size$^{4/3}$(b was significantly different from 1; Fig. 2b). In contrast to predictions, this relationship was even slightly negative, although not significantly. This information falsified the prediction.

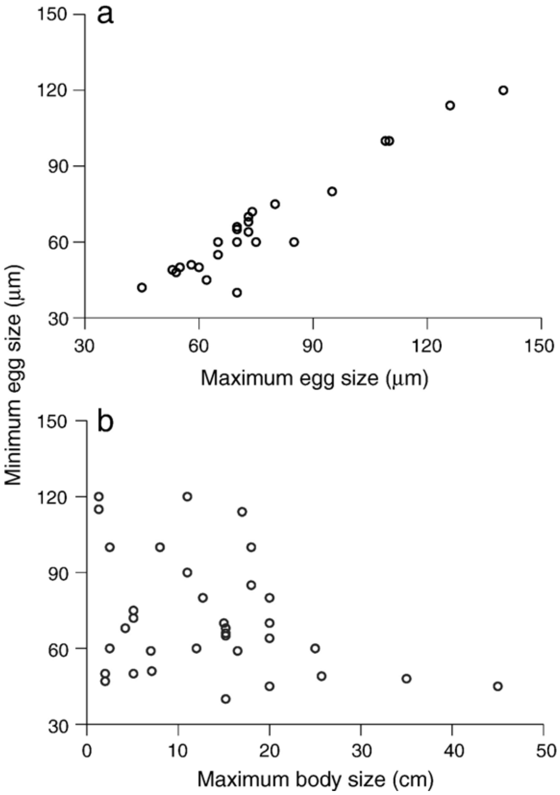

Fig. 2. Minimum egg size (um) in various bivalve species in relation to (a) maximum egg size (μm) and (b) maximum body size (cm).

4.3. Prediction 3: Volume at first reproduction is proportional to the maximum theoretical body volume

Information on body size at first reproduction was scarce and limited to female bivalves (Fig. 3). Size at first reproduction was significantly related to the observed maximum body size. Linear regression revealed that *b* was not significantly different from 1. Differences in shape between the bivalve families will have been responsible for part of the observed variability. On average, female bivalves became mature at about 15% of their maximum body size. This information did not falsify the prediction.

4.4. Prediction 4: Volume at hatching and settlement is proportional to maximum observed body volume

For larvae, also only lengths rather than volume measurements were available. For both hatchlings and settling larvae, the minimum and the maximum length were significantly positively related (not shown). Linear regression between minimum egg diameter and minimum length at hatching revealed that *b* was not significantly different from 1 (Fig. 4a) but no significant relation was found between minimum egg diameter and minimum length at settlement (Fig. 4c). Nevertheless, a positive relationship was observed. Part of the scatter in data might be due to differences in shape. Also minimum length at hatching was not positively related to maximum body length, as revealed by the fact that *b* was significantly different from 1 (Fig. 4b). Minimum length at hatching seemed to vary between about 60 and 200 μm irrespectively of maximum body length. The same was observed for the relationship between minimum length at settlement and maximum body length (Fig. 4d). The lowest observed length at settlement was about 150 μm while the largest settling larvae were in the range of about 375 μm. This information falsified the prediction.

4.5. Prediction 5: Egg and larval development time are related to respectively egg and larval volume$^{1/4}$

Information on egg development in relation to water temperature was scarce and observations differed with respect to prevailing water temperature (range 10–24 °C). In total, information for 14 species could be found. Only for three species, information was available at different temperatures. Observations on larval development were available for 27 species and 35 combinations of water temperature (range 9–33 °C) and development time. However, information at different temperatures was only available for four species. The relationship between egg/larval development time and egg/larval volume was analysed by the following model:

$$D = a^{*}V^{b*}\exp[-T_A/T_1 + T_A/T] \qquad (5)$$

where *D* is the egg development time (h) or the larval development time (d), *V* is the egg or larval volume at

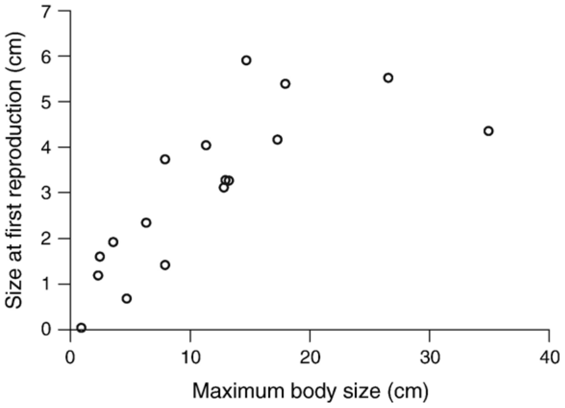

Fig. 3. Body size at first reproduction (cm) in various bivalve species in relation to maximum body size (cm).

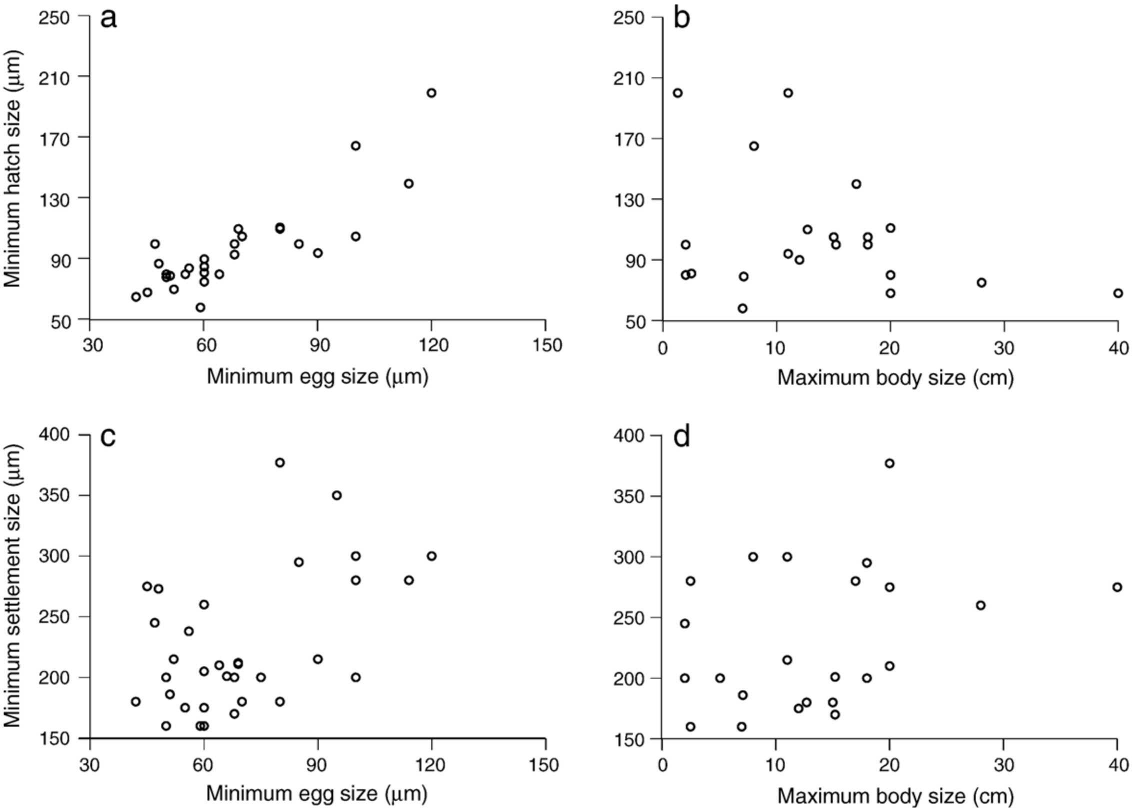

Fig. 4. Minimum hatching size (µm) and minimum settlement size (µm) of various bivalve species in relation to (a and c) minimum egg size (µm) and (b and d) maximum body size (cm).

hatching (mm^3), *a* and *b* are constants, T is experimental temperature (K), T_1 is a chosen reference temperature (K), which has been set in this paper at 293 K (=20 °C) and T_A is the (species specific) Arrhenius temperature (K). Egg and larval volumes were estimated from minimum egg and larval size and assuming a spherical shape. Two different models were applied (Table 2). In model 1, *b* was fixed at 0.25 according to the predictions of the DEB model, and in model 2 *b* was set as a parameter. For both egg and larvae, no significant differences were found between the two models (F-test, $F_{(1,13)}=0.68$, $p=0.42$ for eggs, $F_{(1,32)}=0.13$, $p=0.72$ for larvae), which was confirmed by the fact that the value of $b=0.25$ fell within the confidence limits of the estimated *b* (Table 2). When only one observation per species was used instead of the whole data set, the same result was found. However, especially in case of eggs, large variability was found in the Arrhenius temperature, suggesting that more data points should be used for a more correct estimate of the relation between egg size

Table 2
ANOVA of egg and larval development time (D: h or d) in various bivalve species in relation to minimum egg and larval volume at hatching (V; mm^3) and temperature (TEMP, °C) according to the model: $D=a * V^b * \exp[-T_A/293+T_A/(273+TEMP)]$

Model	*a*	*b*	95% CI	T_A	95% CI	r^2	n
Eggs							
1	559.8	0.250		7487.8	2979.7–11995.9	0.634	16
2	1792.4	0.390	0.019–0.760	6999.7	2178.4–11820.9	0.652	16
Larvae							
1	124.5	0.250		7779.7	5927.6–9631.9	0.705	35
2	96.7	0.214	0.024–0.405	7656.3	5793.1–9519.4	0.707	35

Model 1: $b=0.25$; model 2: *b* estimated.

and egg development time. Nevertheless, the information above did not falsify the prediction.

4.6. Prediction 6: Von Bertalanffy growth rate scales approximately with the observed maximum body volume $^{-1/3}$

Data on growth rates and maximum body length were found for 67 species in the Web of Science®. The relationship between the Von Bertalanffy growth rate and maximum length was negative but not significant (b was significantly different from −1) (Fig. 5a). Part of the scatter might be due to differences in shape between species and the fact that no correction was made for temperature differences. For nine species, however, these corrections could be made, using rough estimates of the mean annual temperature and data on shape coefficients (Bayne and Worrall, 1980; Rodhouse et al., 1984; Page and Hubbard, 1987; Van Haren and Kooijman, 1993; Kooijman, 1993, 2000). By correcting growth rates to a temperature of 20 °C, considering an Arrhenius temperature of 5800 (according to Van der Veer et al., 2006), the Von Bertalanffy growth rate scaled inversely with maximum length, and b was not significantly different from −1 (Fig. 5b). In addition, the slope of the regression was close to −1, in accordance with the DEB theory. However, it should be noted that for one of the species, the mussel *Mytilus edulis*, six data points were presented in contrast to one data point for the other species. Intraspecies trends might be interfering with the interspecies comparison. Nevertheless, if the data on mussel were not considered, the significant relationship would still be observed. Therefore, this prediction was not falsified.

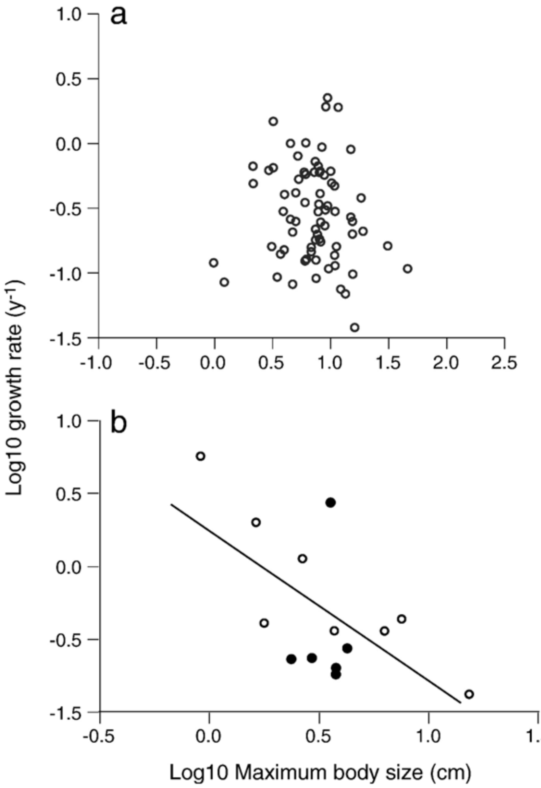

Fig. 5. Von Bertalanffy growth rate (y^{-1}) as a function of maximum body size (cm). (a) Complete dataset collected with no correction for temperature and shape differences; (b) dataset corrected for differences in temperature and shape (see text; full circles correspond to data for *Mytilus edulis* only; open circles are data from different species). The line has a slope -1, as expected on the basis of the DEB theory.

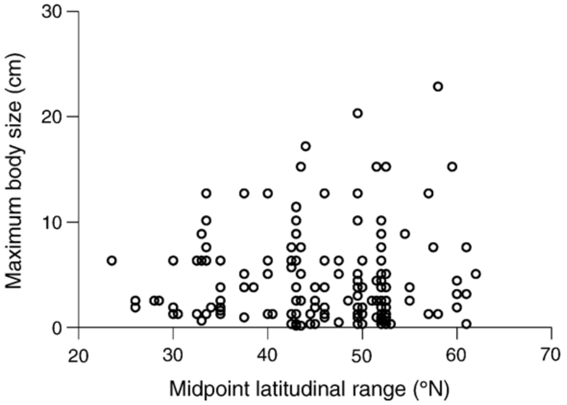

Fig. 6. Maximum body size (cm) of various bivalve species in relation to their latitudinal distribution. Data after Tebble (1966), one point per species is represented.

4.7. Prediction 7: Maximum observed body volume is positively related to latitude

In relation to the interspecific trends, there was hardly any information available on the ultimate volumetric length that different bivalve species achieve. Indirect information was obtained from Tebble (1966), who described the distributional range and maximum observed size for bivalves occurring around Britain. For various species, the maximum size (cm) was combined with an estimate of the midpoint of the distribution of the species. The observed trend between maximum size and latitude suggested that small species occur over the whole range while larger sized species are only observed with increasing latitude towards the pole (Fig. 6). Similar information for north-eastern Pacific bivalves suggested no relationship between body size and latitude (Roy and Martien, 2001).

Latitudinal trends within species may be affecting the observed trend. Within the temperature limits of a species, food conditions seem to determine the rate of growth, not only over the distributional range of the species (Ansell, 1968), but also within local areas (De Montaudouin, 1996). Nevertheless, information on trends in maximum body size/volume with latitude within species is contradictory. In the hard clam *Mercenaria mercenaria*, a positive trend with latitude is suggested (Ansell, 1968; Heck et al., 2002). However, in the Baltic clam *Macoma balthica* a negative relationship with latitude was found along the North American Atlantic coast, while no trend was observed along the European Atlantic coast (Beukema and Meehan, 1985). The yellow clam *Mesodesma macroides* also showed a negative relationship with latitude (Fiori and Morsán, 2004). So it seems that within bivalve species, other factors besides food availability are important as well, influencing the expected latitudinal trend of body size.

Due to the variability in the dataset and information available, we concluded that the data are too variable to allow an interspecies comparison and to support the prediction.

5. Discussion

5.1. Body-size scaling relationships

By focusing on the predictions according to the DEB theory of various scaling relationships between physiological and ecological variables on the one hand and body size on the other hand, we were able to analyse a number of predictions, by comparing them with field data on different bivalve species. For the volume at first reproduction, egg and larval development time and the Von Bertalanffy growth rate, field data did not falsify the predictions by the DEB model. A similar pattern as for flatfish species (Van der Veer et al., 2003) was found in this study (Table 3). In flatfish, egg development time also scaled with egg volume and temperature (Van der Veer et al., 2003). However, both in flatfish and bivalves, a discrepancy is observed in the relationship of egg and larval volume with maximum body volume. The fact that body length of bivalves was used, instead of body volume, may have added variability to the different relationships, as differences in shape between species were not considered.

The predictions of the DEB model also seem to apply, at least partly, for other groups of invertebrates. A clear relationship between egg and larval size and development time has been reported for various species (Steele, 1977; Strathmann, 1977; Todd and Doyle, 1981; Chester, 1996; Marshall and Keough, 2003; Miner et al., 2005). The data by Todd and Doyle (1981) on nudibranch molluscs are extensive enough to convincingly illustrate that irrespectively of development type (planktotrophic, lecithotrophic, direct), egg development is related to egg volume$^{1/4}$, as predicted by the DEB theory. Miner et al. (2005) also showed that egg size in echinoderms was positively correlated to the length of the facultative feeding period, suggesting that larger eggs with higher energy content would allow a longer developmental period. The negative relationship between the Von Bertalanffy growth rate and maximum size has also been demonstrated for several other invertebrate groups (Kooijman, 1993, 2000).

Table 3
Body-size scaling relationships, comparison between predictions by the DEB theory (Kooijman, 1993, 2000) and field data for respectively bivalve (this study) and flatfish species (after Van der Veer et al., 2003)

	DEB prediction	Bivalves	Flatfish
I	Maximum body volume-temperature	?	?
II	Egg volume-maximum body volume$^{4/3}$	–	–
III	Vol. at first reproduction-maximum body volume	+	+
IV	Hatchling/settling volume-ultimate body volume	–	–
V	Egg/larval development-egg/larval volume$^{1/4}$	+	+
VI	Von Bertalanffy parameters	+	+
VII	Ultimate body volume-latitude	–	+

?: no data; +: prediction not falsified; –: prediction falsified.

In contrast to allometric scaling relationships, which are only descriptive and often species-specific, the various body-size relationships predicted by the DEB theory can be used for extrapolations beyond the range of data on which they are based. This holds true especially for the relationship between volume at first reproduction, egg and larval development time in relation to egg and larval volume and temperature, and the Von Bertalanffy growth parameter. For example, model 1 of Table 2 can be used to determine development time of eggs and larvae if egg and larvae volume are known. The aspect of the larval stage duration is especially of interest. Due to their small egg size, bivalve species are characterised by a relatively short pelagic larval stage in the order of a few weeks at 10 °C. For instance, an egg size of 60 µm has a larval stage of 24 d. For a relatively large egg of 120 µm, the difference in pelagic larval stage duration is only about 2 weeks (40 versus 24 d; see Prediction 5). The consequence is that due to their small egg volumes, the period of dispersion of bivalve eggs and larvae will be relatively short in comparison with other marine species.

Besides body-size scaling relationships between species, the DEB model can also be applied to establish body-size relationships within a species, such as for growth, reproduction and respiration in relation to size, but this aspect is the focus of another paper (Cardoso et al., 2006).

5.2. Identification of potentially important factors in life history strategy of bivalves

The main discrepancy between model predictions and field data is related to the relationship between maximum body volume and egg and larval volume. For bivalves, no positive trend between maximum body size and egg size, or larval size at hatching and settlement was observed. In gastropods, such as *Crepidula* spp., egg size and hatch size were also not related to adult body size (Collin, 2003). Nevertheless, in flatfish, a positive trend was present; however in absolute values, flatfish invested less energy in individual eggs and larvae than predicted (Van der Veer et al., 2003). Although in fish a significant trend was seen between size at maturity and body size within the same family (Kooijman, 2000), no trend was seen in egg size or size at hatching and settlement within bivalves, even within the same family (not shown in the figures).

The consequence is that, in bivalves, the characteristics of the early life stages are not related to body size of the species. Although, in the DEB theory, egg volume is predicted to scale with maximum body size, large variations between taxa are expected to occur in this life stage parameter. If environmental conditions are unstable, small organisms may produce large eggs, which lead to large juveniles that are more adapted to such conditions. Therefore, the relationship between egg size and maximum body size is only expected in related species, with similar tolerance ranges for different environmental variables. Since small species occurred over the whole latitudinal range, any scaling relationship with body size might be biased because a similar body size does not correspond with similar environmental conditions.

The absence of a positive relationship between maximum body size of a bivalve species and larval size at settlement might be related to the sediment characteristics of the settling areas. Successful settlement and survival of bivalve larvae in highly dynamic intertidal environments will include a sequence of events, whereby the dominant factors are the hydrodynamics during settlement and the sediment dynamics in post larval re-suspension (e.g. Bouma et al., 2001). In addition, grain size might be a critical factor for survival of spat after settlement and during re-suspension. Successful settlement might only be possible when settlement size or volume of the fragile larvae is in balance with the sediment composition, which means similar to or larger than that of the sediment grain size. In estuarine and coastal areas such as the western Wadden Sea (Dapper and Van der Veer, 1981; Dekker and Waasdorp, 2004; Zwarts et al., 2004) and the Swedish west coast (Pihl and Rosenberg, 1984) median grain size of intertidal areas varies between 100 and 260 μm and this might explain why the minimum settlement size found in bivalves is above 125 μm. Even small bivalve species must produce settling larvae that are large enough to cope with the sediment characteristics with normal grain sizes of at least about 100 μm. In this respect, an interesting next step would be a comparison of the size of settling bivalve larvae with other benthic invertebrate species, to see whether other groups are also characterised by a minimum settling volume or size.

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Appendix A

Literature references used for the estimation of the different relationships (numbers refer to references in footnote)

Species	Size first repr	Min egg diam	Max egg diam	Min hatch size	Max hatch size
Abra tenuis	20	20; 1	1	1	1
Abra alba	20	20		20	20
Acar transversa				14	14
Anomia simplex		14	14	14	14
Arctica islandica	31	15	15	12	12
Bankia setacea		26		26	26
Cerastoderma edule	33	7; 14	7		
Chlamys varia				16	16
Crassostrea ariakensis	32	32	32		

Appendix A (*continued*)

Species	Size first repr	Min egg diam	Max egg diam	Min hatch size	Max hatch size
Crassostrea gigas	9	13; 14	13; 14	14	14
Crassostrea virginica		14	14	14	14
Donax trunculus	28	28			
Ensis directus	8	8; 14	14	14	14
Katelysia scalarina				10	10
Laevicardium montoni		14	14		14
Macoma balthica	33	7	7	14	
Marcia opima				19	19
Mercenaria mercenaria	11; 14	11; 14	11; 14	11; 14	11; 14
Modiolus modiolus		26		26	26
Modiolus demissus		14		14	14
Mya arenaria	3; 2	4; 3; 14; 26	4; 3; 14; 26	26; 14	26; 14
Mytilus edulis	33	7	7	26	26
Ostrea edulis	9	9	14	14; 9	14; 9
Ostrea lurida		26	26	26	26
Panopea abrupta	5	26		26	26
Pecten maximus		21	21		
Pecten irradians		14	14	14	14
Petricola pholadiformis		14	14	14	14
Pinctada mazatlanica	24				
Pitar morrhuana		14	14	14	14
Placuna placenta				18	18
Pteria sterna	24				
Rangia cuneata		27		27	27
Spisula solidissima		30		14	14
Spisula solidissima similis		29			
Tapes philippinarum	23			26	26
Tapes semidecussata		14	14	14	14
Teredo navalis		14	14	14	14
Tresus capax		26	26	26	26

Species	Min sett size	Max sett size	Larv dev time	Growth rate
Abra alba	20	20	20	34
Acar transversa	14	14	14	
Aequipecten operculus				35
Alasmidonta heterodon				36
Anomia simplex	14	14		
Arctica islandica	12	12	12; 17	
Bankia setacea	26		26	
Barnea candida				37
Cerastoderma edule	14	14		
Chlamys hastata			14	
Chlamys varia	16			
Corbicula japonica				38
Corbula trigona				39
Crassostrea iridescens				40
Crassostrea madrasensis				41
Crassostrea virginica	14	14	14	
Donax denticulatus				42
Donax dentifer				44
Donax incarnatus				45
Donax serra				43
Dosinia anus				46
Ensis directus	14		14	
Ensis macha				47; 48
Gari solida				49; 50
Haliotis fulgens				51
Haliotis mariae				52; 53
Hiatella artica				54
Katelysia scalarina	10			
Laevicardium montoni	14	14	14	
Lanternula elliptica				55
Macoma balthica	7			
Mactra chinensis				57
Mactra discors				46
Mactra murchisoni				46; 59
Marcia opima	19			
Mercenaria mercenaria	11	11	11; 14	
Mesodesma mactroides				60
Modiolus demissus	26	14	14	
Modiolus modiolus	14			
Mya arenaria	14; 26	14; 26	14	2
Mysella tumida	26	26		

(continued on next page)

Appendix A (*continued*)

Species	Min sett size	Max sett size	Larv dev time	Growth rate
Mytilus califonianus				
Mytilus edulis	26	26	25; 26	61; 62; 63; 64
Ostrea angasi				65
Ostrea edulis	14; 9	14	14	
Ostrea lurida	26	26	26	
Panopea abrupta	26		26	
Paphies donacina				59
Pecten irradians	14		14	
Pecten jacobaeus				66
Pecten maximus	21	21		
Petricola pholadiformis	14		14	
Pholas dactylus				37
Pitar morrhuana	14	14	14	
Placuna placenta	18		18	
Polymedosa radiata				67
Protothaca thaca				50
Rangia cuneata	27	27	27	
Ruditapes largillierti			10	
Ruditapes philippinarum				68
Semele solida				50
Solemya reidi	26			
Spisula aequilatera				46; 59
Spisula solida				69
Spisula solidissima	14		14	
Spisula solidissima similis		26		
Tagelus dombeii				48
Tapes philippinarum	26	14		
Tapes semidecussata	14		14	
Teredo navalis	14		14	
Tresus capax	26		26	
Tridacna derasa				70
Venus antiqua				48
Venus verrucosa				58

1 Bachelet, 1989; 2 Brousseau and Baglivo, 1988; 3 Brousseau, 1978; 4 Brousseau, 1987; 5 Campbell and Ming, 2003; 6 Casse et al., 1998; 7 Honkoop and Van der Meer, 1998; 8 Kenchington et al., 1998; 9 Kennedy et al., 1996; 10 Kent et al., 1998; 11 Kraeuter and Castagna, 2001; 12 Landers, 1976 ; 13 Cardoso, unpubl.; 14 Loosanoff and Davis, 1963; 15 Loosanoff, 1953; 16 Louro et al., 2003; 17 Lutz et al., 1982; 18 Madrones-Ladja, 1997; 19 Muthiah et al., 2002; 20 Nott, 1980; 21 Paulet et al., 1988; 22 Le Pennec et al., 2003; 23 Ponurovsky and Yakovlev, 1992; 24 Saucedo and Monteforte, 1997; 25 Sprung, 1984; 26 Strathmann, 1987; 27 Sundberg and Kennedy, 1992; 28 Tirado and Salas, 1998; 29 Walker and Obeirn, 1996; 30 Walker et al., 1996; 31 Witbaard, 1997; 32 Zhou and Allen, 2003; 33 Beukema and Dekker, pers comm.; 34 Bachelet and Cornet, 1981; 35 Heilmayer et al., 2004; 36 Michaelson and Neves, 1995; 37 Pinn et al., 2005; 38 Oshima et al., 2004; 39 Etim et al., 1998; 40 Melchor-Aragon et al., 2002; 41 Alam and Das, 1999; 42 Garcia et al., 2003; 43 Laudien et al., 2003; 44 Riascos and Urban, 2002; 45 Thippeswamy and Joseph, 1991; 46 Cranfield and Michael, 2001; 47 Baron et al., 2004; 48 Urban, 1996; 49 Urban and Tarazona, 1996; 50 Urban and Campos, 1994; 51 Shepherd et al., 1991; 52 Siddeek and Johnson, 1997; 53 Shepherd et al., 1995; 54 Sejr et al., 2002; 55 Urban and Mercuri, 1998; 56 Brey and Hain, 1992; 57 Sakurai, 1993; 58 Arneri et al., 1998; 59 Cranfield et al., 1996; 60 Fiori and Morsán, 2004; 61 Rodhouse et al., 1984; 62 Page and Hubbard, 1987; 63 Bayne and Worrall, 1980; 64 Seed, 1969; 65 Mitchell et al., 2000; 66 Peharda et al., 2003; 67 Campos et al., 1998; 68 Goshima et al., 1996; 69 Gaspar et al., 1995; 70 Pearson and Munro, 1991.

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