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# Body size scaling relationships in flatfish as predicted by Dynamic Energy Budgets (DEB theory): implications for recruitment

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## Abstract

In this paper, we apply the general Dynamic Energy Budget (DEB) framework to the growth and reproduction of flatfish at varying food densities with the aim to work out the various relationships between physiological and ecological variables and body size in a systematic manner. The DEB theory predicts that maximum body size is independent of temperature and only determined by 4 parameters: the environmental food conditions, the maximum surface area-specific assimilation rate, the fraction of energy spent on (somatic) maintenance and growth and the volume-specific cost of maintenance. Differences between species can be captured in differences in the environmental food conditions, the maximum surface area-specific assimilation rate and the fraction of energy spent on maintenance and growth. The DEB theory predicts that due to the latitudinal trend in environmental food conditions, maximum body size will increase with latitude, both within as well as among species. Since size at first maturation, size at hatch, larval size and size at metamorphosis directly scale with maximum body size, similar trends with latitude in these variables are expected. The DEB theory further predicts that egg and larval stage duration are related to egg volume<sup>0.25</sup>. Field data provide a strong support for the various model predictions. Implications for recruitment in flatfish are discussed.

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## 1. Introduction

Since the beginning of the last century, it is generally accepted that year-class strength in marine fishes appears to be primarily determined by mortality processes operating during the early life history stages (Hjort, 1914, 1926) by a combination of coarse control during the period of egg and/or larval drift

generating among-year variability, followed by a second interval of finer scale regulation later in the early life history where among-year variability is reduced (for review see Leggett and DeBlois, 1994). An ongoing debate is the extent to which the processes determining recruitment are species and/or area specific or, alternatively, are part of a more general pattern affecting more than one species or species group. Arguments in support of the presence of general patterns in fish are founded in links between the factors controlling recruitment and species- or genus-specific early life history patterns (Roff, 1982;

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Rothschild and DiNardo, 1987). Further support for this view is provided by the fact that adjacent populations of a species often show synchrony in year-class strength over spatial scales of hundreds of kilometres (Walsh, 1994; Myers et al., 1997; Fox et al., 2000).

The fact that year-class strength in marine fishes appears to be primarily determined by processes operating during the pre-juvenile stage of the life history implies that the population egg production and the survival of these eggs and of the resulting larvae are key elements (Cushing, 1995; Rickman et al., 2000). This justifies an analysis of the relevant body size scaling relationships related to egg production and survival. The overwhelming amount and variability of biological information has already led to the establishment of numerous empirical relationships of biological rates as simple functions of body size, volume or other variables. In this respect the work of Peters (1983) in the field of descriptive ecology on interspecific size relations can be considered a landmark. However, such empirical allometric regressions do not offer mechanistic explanations and even they might obstruct the evolution of new insight into the underlying principles.

Therefore, in our opinion any analysis of scaling relationships should be built upon a consistent framework of quantitative bioenergetics to evaluate the quantitative aspects of energy allocation, growth and reproduction and such a framework should be based on simple mechanisms that are not species-specific. In this paper, we focus on flatfish and have chosen to adopt a framework based on dynamic energy budgets (DEB theory, Kooijman, 1988, 2000). The DEB theory quantifies growth and reproduction in relation to food uptake. Using this framework, a comparison of the various aspects of the life histories and energetics of individual species (Van der Veer et al., 2001), and species complexes, can be investigated. Firstly, the predictions according to the DEB theory of various scaling relationships between physiological and ecological variables and body size are worked out in a systematic manner. Secondly, information on flatfish is analysed to allow a comparison of predictions with field data and finally the implications of variability in energy allocation on recruitment are discussed.

## 2. Material and methods

### 2.1. The dynamic energy budget model

The quantitative aspects of energy budgets are assumed to follow the rules as specified by the Dynamic Energy Budgets (DEB) theory (Kooijman, 1988, 2000). The DEB theory is based on a set of general assumptions regarding food uptake, storage and utilisation. It characterises an individual using two state variables: structure and reserve, and assumes that body size exerts its influence through surface area and volume. The DEB model describes the energy flows through an animal (Fig. 1) and the changes in these flows in environments in which food densities and temperatures vary. The model considers three life stages (embryos, which neither feed nor reproduce; juveniles, which feed but do not reproduce; and adults which both feed and reproduce) and three main body fractions (structural biovolume (somatic tissue); stored reserves and gonads (i.e. stored energy reserves allocated to reproduction)). The contribution of these body fractions to total biovolume changes with time. The chemical composition of each of these fractions is assumed to remain constant (homeostasis).

Food uptake is assumed to follow a type II functional response curve (Holling, 1959), in which the intake rate depends hyperbolically on the available

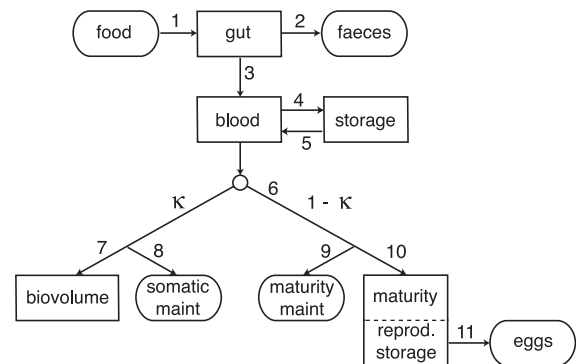


Fig. 1. Energy flow through an organism in the DEB model, after Van Haren (1995). Rates: 1 ingestion (uptake), 2 defecation, 3 assimilation, 4 demobilisation of energy into reserves, 5 mobilisation of energy from reserves, 6 utilisation, 7 growth, 8 somatic maintenance, 9 maturation maintenance, 10 maturation,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

food density, and to be proportional to the organisms' surface area. Food converts to reserve with a constant efficiency. Mobilised reserve is allocated to growth, somatic and maturation maintenance, and to maturation or reproduction. A fixed fraction  $\kappa$  of utilised reserve is allocated to growth plus somatic maintenance while the remainder  $(1-\kappa)$  is allocated to maturity maintenance plus maturation or reproduction (Kappa rule). Maintenance has priority over growth, and hence growth ceases when all the reserve allocated to somatic maintenance plus growth is required for somatic maintenance. The mobilisation rate of reserve is proportional to the ratio of reserve density (i.e. the ratio of reserve and structure) and volumetric length (the cubic root of structure's volume). The energy costs of maintenance are proportional to structure's volume. At constant food densities, the reserves are in equilibrium with the environment and consequently growth of structural biovolume represents a weighted difference between surface area and volume and corresponds with Von Bertalanffy growth (Kooijman, 2000). The reserves that are allocated to maturation in embryos and juveniles are allocated to reproduction in adults. This flux of reserve is temporarily stored in a buffer, which is emptied during oviposition. For a more detailed description of the DEB model and its assumptions, see Kooijman (1993, 2000).

Since an organism consists of structure, reserve and reproductive storage or eggs, it will depend on the biology of the organism how size measures relate to the amount of structure. For the interpretation of size measures, two conditions are essential. It is assumed that the contribution of reserves and reproductive tissue in body length or wet mass is small, so length quantifies structure. We also assume that the shape of the fish is relatively constant during growth, so that surface area is approximately proportional to the length squared. An appropriate length measure (standard SL or total length TL, etc.) can be converted into volume by multiplying it by the shape coefficient ( $\text{volume}^{1/3} \text{length}^{-1}$ ) and raising the result to the third power. This shape coefficient is species-specific and depends on the way length is measured. It is further assumed that the specific density of structure, reserve, and reproductive mass is close to 1, so the mass of  $1 \text{ m}^3$  is about 1000 kg.

The DEB model quantifies growth and reproduction at varying food densities. The DEB model

describes the energetics of a species via a number of parameters of which the most important ones are:

- (1) the maximum surface area-specific ingestion rate;
- (2) the volume-specific costs of maintenance per unit time;
- (3) the fraction of energy spent on maintenance plus growth.

In the DEB theory, intraspecific variability is caused by differences in the state variables not in parameter values and in contrast, interspecific variability is the result of differences in parameter values. The link between physiological and ecological variables is formed by the extensive parameters, such as for instance, egg and larval volume. These parameters relate to physical design and scale with maximum body size. For those physiological quantities that can be represented as functions of extensive parameters, body size scaling relationships can be derived (Kooijman, 1986, 2000).

## 2.2. Data acquisition

Most of the data presented in this study were assembled from the literature, but in addition some unpublished data were used. In all cases, basic references are listed. The analyses were restricted to females only. Most information available consisted of length estimates instead of volumes. In some cases, length measurements were converted into volumes by taking an average shape coefficient for flatfish of 0.219 after Van der Veer et al. (2001). For each species information on species type (boreal, temperate, subtropical, tropical) was based on FishBase (Froese and Pauly, 2003) and was combined with the following parameters: the maximum length  $L_{\max}$ , female length at 50% maturation  $L_{50}$ , range of egg diameters (minimum-maximum), range of larval size at hatching (minimum-maximum) and egg and larval development time. Information about North Atlantic flatfish species was collected from Miller et al. (1991), and for Indopacific species from Shuozeng (1995). In addition, estimates of  $L_{\max}$  were obtained from Whitehead et al. (1986) and complemented with recent literature references. Information on egg and larval size and egg development time were based on Hempel (1979) and Pauly and Pullin (1988) in combination

with more recent references. Information on female size at 50% maturation was based on various literature references. The focus was to collect a complete data set for a number of representative flatfish species. For almost all species the data assembled originated from various sources.

### 3. Model predictions

The model predictions as to how the various variables depend on body size are based on Kooijman (1986). The reasoning boils down to the observation that all DEB parameters are either intensive (do not depend on the size of the organism) or extensive, while ratios of extensive parameters are intensive. In other words: all parameters that depend on body size do so in the same way. This means that parameter values tend to co-vary among species.

In this paper, the various relationships between physiological and ecological variables and body size are estimated based on the general assumptions of the DEB theory concerning the quantitative nature of energy budgets. Because the DEB model is, apart from energy-structured also volume structured, the length of the various life stages is directly related to growth. Therefore, the various physiological and ecological variables are split into volume or size-related and growth-related ones. Since the size dependence may work out in a different way within a species compared to between species, both aspects are estimated separately.

#### 3.1. Volume/size

##### 3.1.1. Maximum size

The DEB theory predicts that the maximum structural volume or length of an organism is determined by the resources available and maintenance requirements. This relationship is described as follows:

$$V_{\max}^{1/3} = \kappa \{p_{Am}\} / [p_M] \quad [1]$$

where  $V_{\max}^{1/3}$  is the maximum volumetric length (m);  $\kappa$  is the fraction of utilised reserve spent on somatic maintenance plus growth (-);  $\{p_{Am}\}$  is the maximum surface area-specific assimilation rate ( $\text{W m}^{-2}$ ) and  $[p_M]$  is the volume-specific cost of maintenance

( $\text{W m}^{-3}$ ). The parameters  $[p_M]$  and  $\kappa$  are intensive, and  $\{p_{Am}\}$  is extensive, from which follows that  $\{p_{Am}\}$  must be proportional to  $V_{\max}^{1/3}$  among species. This means that all extensive parameters must be proportional to the maximum volumetric length of a species. The reasoning is simple and powerful, but easy to overlook. The ultimate volumetric length relates to the maximum one as  $V_{\infty}^{1/3} = f V_{\max}^{1/3}$ , where  $f$  is a measure of food supply defined in terms of Holling's functional response curve (-).

Both  $\{p_{Am}\}$  and  $[p_M]$  are similarly temperature-dependent, hence the ratio is inherently species-specific and is not likely to vary with latitude. At least in flatfish,  $\kappa$  appears to be species-specific (Van der Veer et al., 2001); however within a species it does not seem to vary over latitude (Fig. 2). With respect to  $f$ , the scaled functional response that quantifies food supply, it seems that the standing stock of food tends to be positively correlated with latitude (Petersen and Curtis, 1980; Gross et al., 1988), and hence the absolute quantity of food available is likely to diminish toward the tropics. At high latitudes, seasonal temperature oscillations divide the year into times of very high and very low production. During times of low food availability due to starvation, and elevated levels of predation resulting from the weakened energy state of individuals, populations are culled and thinned. The consequence is that during periods of high food production the energy available per surviving individual is high. In the tropics, temperature oscillations are much reduced, as are seasonal variations in production. Food availability per individual is therefore more constant year round and culling effects are likely to be gradual rather than episodic as in temperate or polar regions. The consequence could be lower population sizes, lower individual growth rates, lower reproductive output, or a combination of all of the above. The more constant food densities at lower latitude select for small body volumes, since a small volume aids survival due to its lower maintenance costs. Fluctuating food densities at high latitudes select for larger body volume, because a large volume gives better survival over prolonged periods of starvation. Therefore, the DEB theory predicts a geographic trend in body size caused by a decreasing trend in food availability from the poles towards the tropics both within a species and between species.

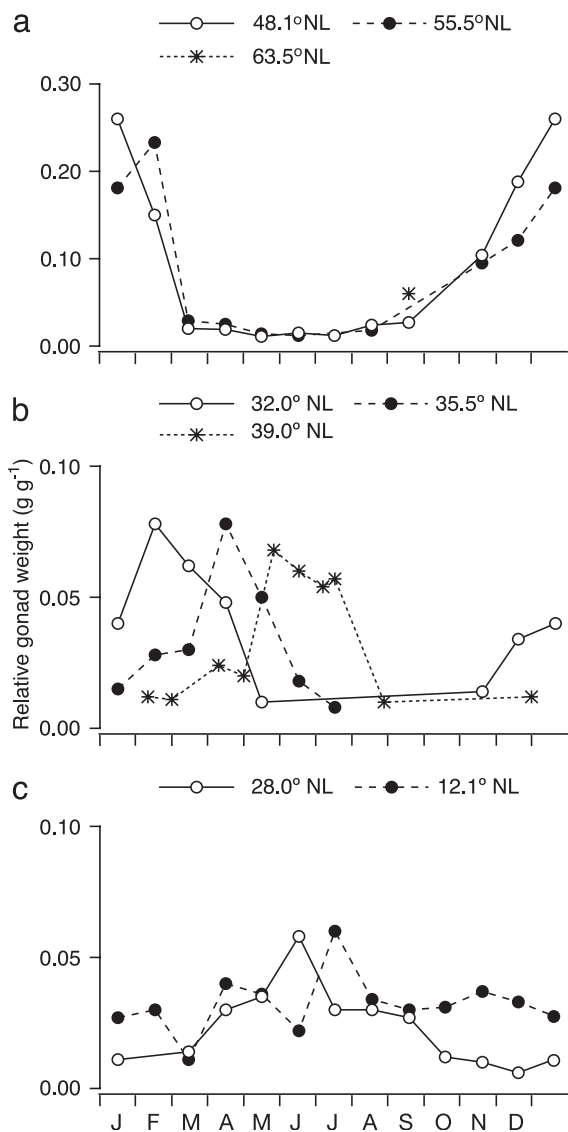


Fig. 2. Seasonal pattern in storage for reproduction in a temperate (a: plaice, *Pleuronectes platessa*), subtropical (b: Japanese flounder, *Paralichthys olivaceus*) and a tropical species (c: *Achirus lineatus*). The relative gonad mass (RG;  $\text{g g}^{-1}$ ) is expressed as fraction of the total wet mass ( $W_w$ ; g) minus gonad mass ( $G_w$ ; g):  $RG = (G_w / (W_w - G_w))$ . All data after Van der Veer and Witte (unpubl.), except for plaice data for France (Deniel, 1981), plaice data for Irish Sea (Dawson and Grimm, 1980) and Japanese flounder data (Tanaka et al., 1997).

### 3.1.2. Size at reproduction

Energy allocation to development is used for maturation in embryos and juveniles, whereby the

transition from a juvenile to an adult occurs if the cumulative investment to increase the state of maturity exceeds specified amounts. Since in the DEB theory the threshold for the investment in the increase of the state of maturity is thought to be proportional to volume, between species the volume or size at first reproduction will also be proportional to respectively maximum volume or maximum size. Since these life stage parameters may vary among different taxa, variation in the volume ratio or size at reproduction and maximum volume or size might be expected. Within a species, growth and the rate of maturation will vary depending on the food conditions; however, this will not affect the volume or size of first reproduction of a species. It will be related to ultimate maximum structural volume or size. Experimental data support this prediction (Kooijman, 2000). In case a geographic trend in maximum body size exists from the poles towards the tropics, as a consequence a similar trend will occur in size at first reproduction, both within and between species.

### 3.1.3. Egg size

In the DEB model the volume of the hatchling must be proportional to the maximum volume of the adult, because the threshold for the investment in the increase in the state of maturity is thought to be proportional to volume. However, just after fertilisation, the contribution of structural volume will be negligible and the egg volume will consist almost completely of reserve energy. This reserve density is not constant between species, but scales with body volume<sup>1/3</sup> (length). Total energy content of the eggs will therefore scale with body volume<sup>4/3</sup>. So egg volume will scale with body volume<sup>4/3</sup>, which also means that body volume scales with egg volume<sup>3/4</sup>. Especially these life stage parameters may vary among different species and taxa. Therefore, the tendency of egg volume to be proportional to ultimate body volume<sup>4/3</sup> only holds for related species at best. In case a geographic trend in body size exists from the poles towards the tropics, a trend in egg size will also be present both within and between species.

### 3.1.4. Size at hatch

In the DEB model the length of the various life stages is closely related to growth, due to the fact that the DEB model is energy as well as volume struc-

tured. According to the DEB theory, between species the volume of birth of a hatchling will be proportional to ultimate maximum female volume. Larger hatchlings consist of more structural mass and they will develop from larger eggs. In other words species with a larger maximum volume will produce larger eggs which develop into larger hatchlings (see 3.1.3). Within a species, these relationships are different. Size at hatch is strongly related to maximum body size, which will be apart from food conditions constant within a species. Hence, within a species it will be independent of variations in egg size.

### 3.2. Development

#### 3.2.1. Egg stage

During egg development the reserves decline and due to this decline, the growth rate in the egg slows down. Between species, incubation time, i.e. the time required to reach hatching size, simply scales with the energy content of the egg, since larger eggs produce larger hatchlings which takes more time. Since total energy content of the eggs scale with body volume<sup>4/3</sup> between species, egg volume scales with body volume<sup>4/3</sup>, or body volume scales with egg volume<sup>3/4</sup>. In combination with the fact that incubation time scales with body volume<sup>1/3</sup> (length), this implies that incubation time also scales with egg volume<sup>1/4</sup>. Within a species the pattern is different. Large eggs, i.e. large initial energy supplies, result in short incubation times and will hatch earlier if the structural biomass of the hatchling is the same, because more stored energy for a similar-sized hatchling allows a higher development rate.

#### 3.2.2. Larval stage

The relationship between larval and juvenile stage duration is consistent with and similar to that of egg development. The main difference between egg development on the one hand and larval and juvenile development on the other, is that from hatching onwards when feeding starts, energy uptake processes become important. Therefore, larval and juvenile stage duration are dependent on food densities, and the minimum developmental time only holds true at high food densities, whereby  $f$ , the measure of food supply defined in terms of Holling's functional response curve, will approach 1. At such high food

densities, the length of the larval and juvenile period for different species will in a similar way as for egg development scale linearly with body length (Kooijman, 1986). The ultimate maximum adult size is already reflected in the egg, larval and juvenile size. However, it also takes more time to develop and build up a larger adult even if the larvae are already larger. Within a species the pattern is different. Geographic patterns in maximum body volume or size are thought to be the consequence of differences in food conditions in the adult stage, but not in the larval and juvenile stages. Therefore, within a species, larval and juvenile stage duration will be independent of ultimate maximum body size.

## 4. Comparing model predictions with empirical data

### 4.1. Volume/size relationships

#### 4.1.1. Maximum body size

Maximum body size and geographical patterns were analysed for the north-eastern Atlantic and the Mediterranean based on the taxonomic guide of Whitehead et al. (1986). For each flatfish species listed, the maximum fish length was combined with an estimate of the midpoint of the distribution of the species. Next, all length data were converted into estimates of the maximum female body volume by assuming a shape coefficient for all families of 0.219 (see Van der Veer et al., 2001). In addition, for a few species information of maximum length in relation to latitude was compiled. There appeared to be a general trend between maximum length and latitude. Although small flatfish species occurred at all latitudes the maximum size of flatfish species increased from about 20 cm standard length at low latitudes to about 200 cm at high latitudes (Fig. 3a). This trend was associated with a shift in the predominant family from Cynoglossidae in tropical waters to Pleuronectidae in cold waters. Maximum volume of flatfish species had a clearer pattern (Fig. 3b), increasing from about 1000 cm<sup>3</sup> to 50 000 cm<sup>3</sup> with latitude. Within a species, the available information on maximum size over the range of distribution of the species was variable (Fig. 4). In plaice and Japanese flounder maximum length appeared to increase with latitude. In long

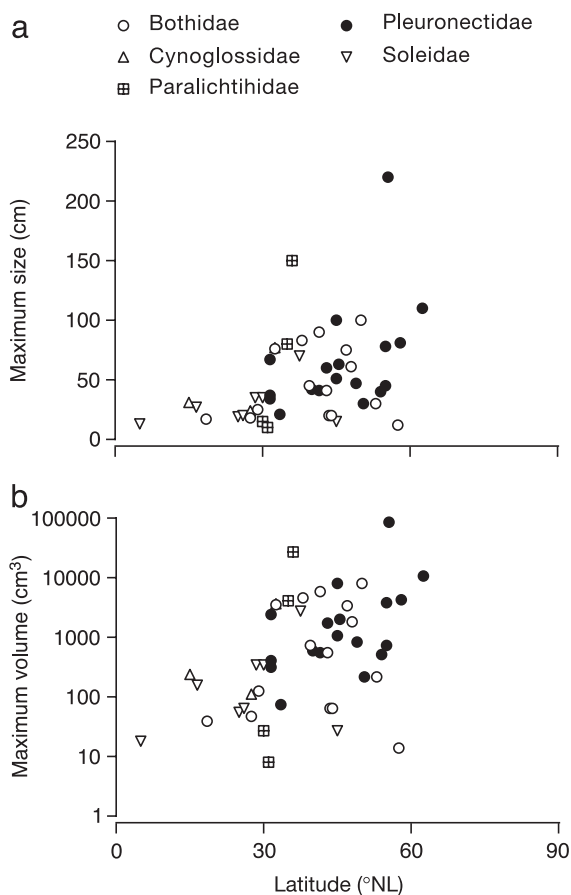


Fig. 3. Maximum length (a: cm) and maximum volume (b: cm<sup>3</sup>) of various North-eastern Atlantic and Mediterranean flatfish species in relation to the estimated midpoint of their distribution. Data after Whitehead et al. (1986). For more information see text.

rough dab such a trend was only present for populations along the east coast of the North Atlantic. On the west coast of the North Atlantic, however, a decreasing trend with latitude was observed. This might be related to the fact that in contrast to the east coast, temperature and probably also food conditions did not show a clear trend with latitude along the west coast (Walsh, 1994).

#### 4.1.2. Maturation

In total 53 combinations of estimates of female size at 50% maturation and of maximum female size were found for 5 flatfish taxa. Most estimates were for species belonging to the Bothidae and to the Pleuronectidae. For all data combined, a significant linear

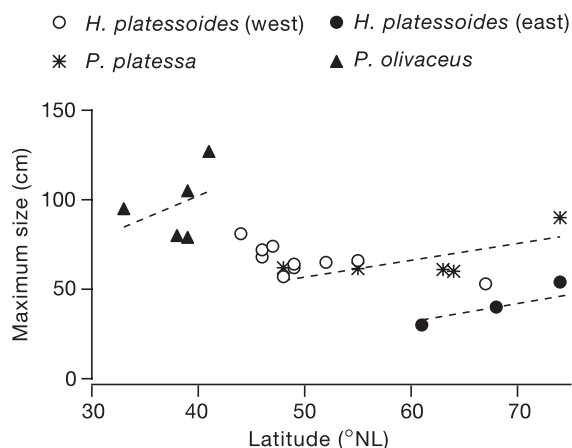


Fig. 4. Maximum size (cm) of various flatfish species in relation to latitude. Data for plaice (*Pleuronectes platessa*) after Deniel (1981), Kovtsova and Boitsov (1995) and Van der Veer and Witte (unpubl.); for Japanese flounder (*Platichthys olivaceus*) after Shuozen (1995) and Tanaka (pers. comm., 2003); for long rough dab (*Hippoglossoides platessoides*) after Walsh (1994).

relationship between size at reproduction and maximum female size was observed ( $R^2=0.95$ ) as predicted by the DEB theory. Also there were no significant differences between the various taxa and range of distribution of the various species (Fig. 5; Table 1). On average, females of the various flatfish species became mature at about 40% of their maxi-

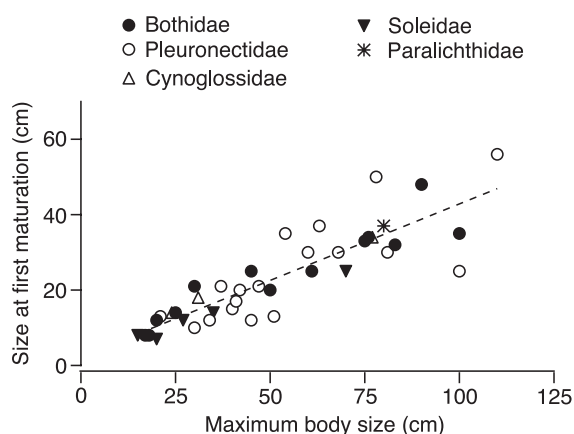


Fig. 5. Relationship between length at first maturation (cm) and estimated maximum female fish length (cm) for various flatfish species of different taxa. For more information and data source see text.

Table 1

ANOVA of length at 50% maturation ( $L_{50}$ ; cm) in flatfish in relation to maximum female body length  $L_{max}$ ; cm), species type (Type; polar, temperate, subtropical, tropical) and family (Taxa; Bothidae, Pleuronectidae, Cynoglossidae, Soleidae, Paralichthidae), according to the model:  $L_{50} = L_{max} + \text{Type} + \text{Taxa}$ . Dependent variable:  $L_{50}$ ,  $N = 40$ , multiple  $R = 0.976$ , multiple  $R^2 = 0.953$

Source	Sum of Squares	df	Mean-Square	F-ration	P(2 tail)
$L_{max}$	7004.264	1	7004.264	173.831	0.000
Type	170.418	3	56.806	1.410	0.258
Taxa	46.135	4	11.534	0.286	0.885
Error	1289.395	32	40.294		

imum body size, which corresponds with  $0.40^3$  or about 6.5 % of their maximum volume.

#### 4.1.3. Egg size

Information on the egg diameter of flatfishes was compiled for 52 species belonging to 5 taxa. For 52 species information on the minimal egg diameter was present and for 46 species there were also estimates of the maximum egg diameter. All information on egg diameters was converted into egg volumes using:

$$\text{Eggvolume} = \left(\frac{\pi}{6}\right) \times (\text{Eggdiameter})^3 \quad [2]$$

Although egg volume was significantly related to maximum female body volume (Fig. 6; Table 2), the relationship was not consistent with the predictions of the DEB theory, since the exponent was less than  $4/3$ , even less than 1. This occurred for both the estimates of the minimum egg volume (not shown) and for the maximum egg volume ( $R^2 = 0.31$  and  $R^2 = 0.51$  respectively). No significant differences between the various taxa and between the range of distribution of the various species were found. It suggested that the investment in egg volume was lower than predicted.

#### 4.1.4. Hatchling size

Combinations of minimum larval and minimum egg size were found for 36 species, belonging to 5 taxa. In 24 species information on maximum larval size was also available. Egg diameters were converted into egg volumes according to [2]. Estimates of larval volume at hatch were obtained by applying a similar shape coefficient for all species of 0.219 (see Van der

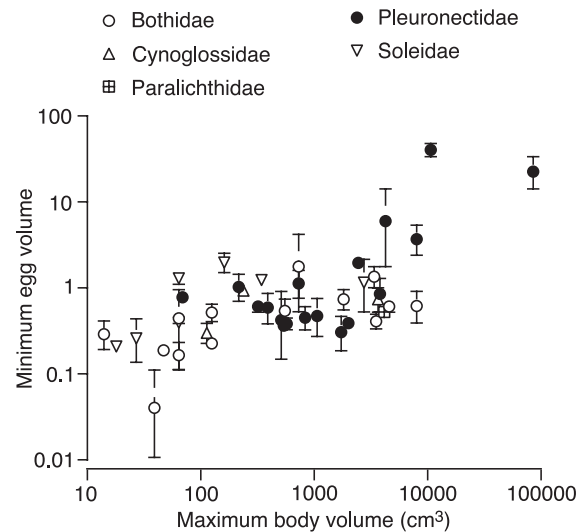


Fig. 6. Relationship between average minimum egg volume ( $\text{mm}^3$ ) with 95% confidence interval and estimated maximum female fish volume ( $\text{cm}^3$ ) for various flatfish species of different taxa. For more information and data source see text.

Veer et al., 2001) to convert the length measurements into volumes:

$$\text{Hatchlingvolume} = (0.219 \times \text{larvallength})^3 \quad [3]$$

Larval volume at hatch was significantly positively related to the volume of the egg (Fig. 7; Table 3), as predicted. This holds true for both the estimates of the minimum larval volume at hatch and for estimates of the maximum larval volume at hatch ( $R^2 = 0.83$  and  $R^2 = 0.70$  respectively). No significant differences between the various taxa and between the range of distribution of the various species were found.

Table 2

ANOVA of maximum egg volume ( $\text{Eggmax}$ ;  $\text{mm}^3$ ) in flatfish in relation to maximum female body size  $L_{max}$ ; cm), species type (Type; polar, temperate, subtropical, tropical) and family (Taxa; Bothidae, Pleuronectidae, Cynoglossidae, Soleidae, Paralichthidae), according to the model  $\text{Eggmax} = L_{max} + \text{Type} + \text{Taxa}$ . Dependent variable:  $\text{Eggmax}$ ,  $N = 43$ , multiple  $R = 0.711$ , multiple  $R^2 = 0.505$

Source	Sum of Squares	df	Mean-Square	F-ration	P(2 tail)
$L_{max}$	1032.943	1	1032.943	19.796	0.000
Type	39.835	3	13.278	0.254	0.858
Taxa	85.696	4	21.424	0.411	0.800
Error	1826.245	35	52.178		

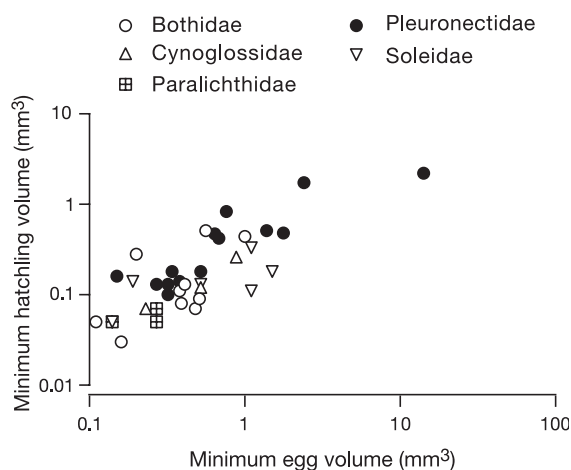


Fig. 7. Relationship between minimum larval volume at hatch ( $\text{mm}^3$ ) and minimum egg volume ( $\text{mm}^3$ ) for various flatfish species of different taxa. For more information and data source see text.

There was also a significant positive relationship between maximum female volume and the larval volume at hatch, both for the minimum larval volume and for the maximum larval volume,  $R^2=0.78$ ;  $n=35$  and  $R^2=0.64$ ;  $n=25$  respectively (Fig. 8; Table 4), but with an exponent less than 1. There were no significant differences between range of distribution of the various species or between the various taxa (Table 4).

#### 4.1.5. Size at metamorphosis

For 45 species, belonging to 5 taxa, combinations of minimum size at metamorphosis and maximum female size were found. For 27 species information on maximum size at metamorphosis was also available. Size at metamorphosis was converted into estimates

Table 3

ANOVA of minimum larval volume at hatch (Larfm<sub>in</sub>;  $\text{mm}^3$ ) in flatfish in relation to minimum egg volume; (Eggm<sub>in</sub>;  $\text{mm}^3$ ), species type (Type; polar, temperate, subtropical, tropical) and family (Taxa; Bothidae, Pleuronectidae, Cynoglossidae, Soleidae, Paralichthidae), according to the model  $\text{Larfm}_{in} = \text{Eggm}_{in} + \text{Type} + \text{Taxa}$ . Dependent variable: Larfm<sub>in</sub>,  $N=36$ , multiple  $R=0.910$ , multiple  $R^2: 0.829$

Source	Sum of Squares	Df	Mean-Square	F-ration	P(2 tail)
Eggm <sub>in</sub>	3.555	1	3.555	55.624	0.000
Type	0.407	3	0.136	2.121	0.120
Taxa	0.304	4	0.076	1.191	0.337
Error	1.790	28	0.064		

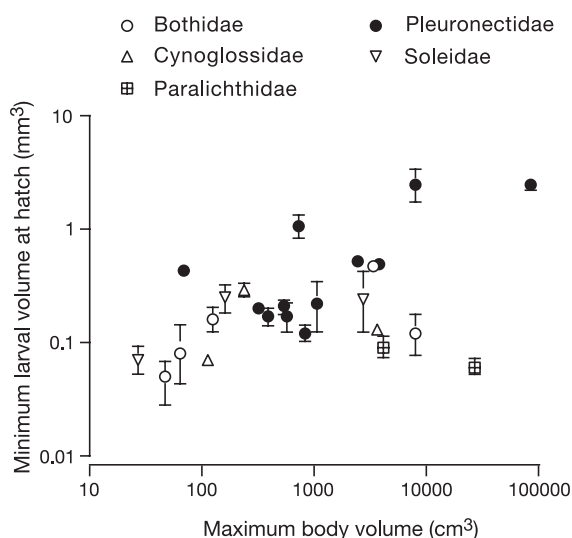


Fig. 8. Relationship between minimum larval volume at hatch ( $\text{mm}^3$ ) with 95% confidence interval and estimated maximum female fish volume ( $\text{cm}^3$ ) for various flatfish species of different taxa. For more information and data source see text.

of volume by applying a similar shape coefficient for all species of 0.219 (see Van der Veer et al., 2001) in a similar way as done for larval size according to [3]. The estimates of volume at metamorphosis were significantly positively related to the maximum female volume (Fig. 9), but with an exponent less than 1. This holds true for both the estimates of the minimum volume at metamorphosis and for estimates of the maximum volume at metamorphosis ( $R^2=0.26$  and  $R^2=0.25$  respectively). No significant differences between the various taxa and between the range of distribution of the various species were found.

Table 4

ANOVA of minimum larval volume at hatch (Larfm<sub>in</sub>;  $\text{mm}^3$ ) in flatfish in relation to maximum body volume; (Vmax;  $\text{cm}^3$ ), species type (Type; polar, temperate, subtropical, tropical) and family (Taxa; Bothidae, Pleuronectidae, Cynoglossidae, Soleidae, Paralichthidae), according to the model  $\text{Larfm}_{in} = \text{Vmax} + \text{Type} + \text{Taxa}$ . Dependent variable: Larfm<sub>in</sub>,  $N=35$ , multiple  $R=0.881$ , multiple  $R^2: 0.776$

Source	Sum of Squares	Df	Mean-Square	F-ration	P(2 tail)
Vmax	2.977	1	2.977	34.335	0.000
Type	0.609	3	0.203	2.340	0.096
Taxa	0.910	4	0.228	2.625	0.057
Error	2.341	27	0.087		

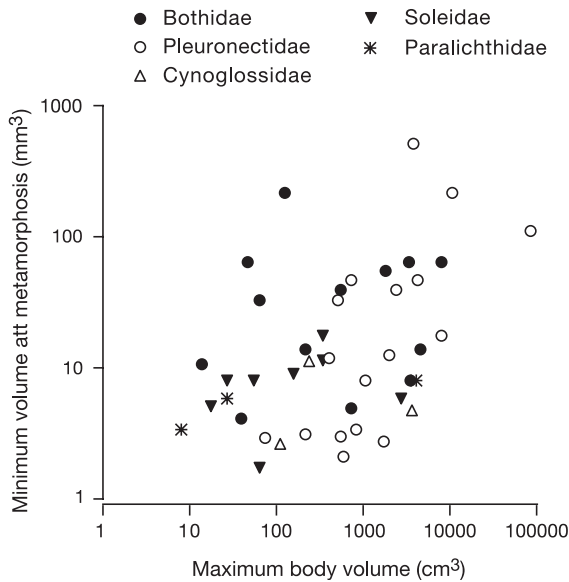


Fig. 9. Relationship between minimum larval volume at metamorphosis (mm<sup>3</sup>) and estimated maximum female fish volume (cm<sup>3</sup>) for various flatfish species of different taxa. For more information and data source see text.

4.2. Development

4.2.1. Egg development

For 10 species, data on egg development in relation to water temperature and egg size or volume were found. In 6 species, information was available on egg development at various water temperatures. The total data set consisted of 36 observations. The impact of differences in water temperature on egg development was described by means of the Arrhenius relationship, which is based on the Van 't Hoff equation:

$$\dot{k}(T) = \dot{k}(T_1) \exp[T_A/T_1 - T_A/T] \tag{4}$$

where  $\dot{k}$  is a physiological rate,  $T$  is absolute temperature (K),  $T_1$  is a chosen reference temperature (K), which has been set in this paper at 283 K (= 10 °C) and  $T_A$  is the -species-specific- Arrhenius temperature (K). The relationship between egg development and volume was analysed by the following model:

$$D = a * V^b \tag{5}$$

where  $D$  is the development time (d),  $V$  is egg volume (mm<sup>3</sup>) and  $a$  and  $b$  are constants. Four different

models were applied with increasing complexity. All models consisted of [5] and [4]. Models 1 and 2 were applied to the whole data set. In model 1,  $b$  was fixed at 0.25 according to the predictions of the DEB model:

$$D = a * V^b * \exp[T_A/T_1 - T_A/T] \tag{6}$$

For models 3 and 4 the data set was restricted to those species for which egg development times were available at different temperatures (6 species). For both Model 3 and 4 different Arrhenius temperatures for the different species were assumed, whereby in Model 3,  $b$  was again fixed at 0.25:

$$D = a * V^b * ((SPECIES = 1) * \exp[T_{A1}/T_1 - T_{A1}/T] + (SPECIES = 2) * \exp[T_{A2}/T_1 - T_{A2}/T] + \dots + (SPECIES = 6) * \exp[T_{A6}/T_1 - T_{A6}/T]) \tag{7}$$

whereby  $T_{Ai}$  is the Arrhenius temperature of species  $i$ . Models 1 and 3, in which  $b$  was fixed at 0.25, and models 2 and 4, in which  $b$  was set as parameter, all resulted in significant relationships (Table 5). Also in models 2 and 4, a value of  $b=0.25$  fell within the 95 confidence limits of the estimate of  $b$ . The correlation improved in models 3 and 4, where different Arrhenius temperatures for the various species were assumed. The observed range in Arrhenius temperatures varied between the species from 5698–12800 K. Nested analyses indicated that the relationship significantly improved by incorporating different Arrhenius temperatures for the various species (F-

Table 5

ANOVA of minimum egg development time (Eggdevmin; d) in flatfish in relation to minimum egg volume (Eggvolmin; mm<sup>3</sup>) and temperature (TEMP, °C) according to the model: Eggdevmin =  $a * \text{Eggvolmin}^b * (\exp(-T_A/283 + T_A/(273 + \text{TEMP})))$ . Model 1 and 3:  $b=0.25$ ; Model 3 and 4: different  $T_A$  for different species

Model	a	b	95% CI	T <sub>A</sub>	r <sup>2</sup>	n
1	6.931	0.25*		11569	0.82	35
2	7.226	0.172	0.078–0.266	12447	0.82	35
3	7.732	0.25*		6016–12500	0.97	27
4	7.664	0.276	0.166–0.386	5698–12800	0.98	27

test Model 4 versus 2  $F_{[1,21]} = 11.39$ ; model 3 versus 1  $F_{[1,22]} = 13.43$ ). For  $b$  set as parameter this was not the case.

#### 4.2.2. Larval development

For 5 species, 19 observations on larval development time from hatching until metamorphosis in relation to temperature and larval size were present. In 4 species, information was available at different temperatures. In a similar way as for the analysis of egg development, the same four different models were applied to analyse larval development. Larval development time was related to egg volume and to larval volume at hatch. Larval development showed a significant relationship with egg volume<sup>0.25</sup> (Table 6). Both models 1 and 3, in which  $b$  was fixed at 0.25, and models 2 and 4, in which  $b$  was variable, resulted in significant relationships. Also in models 2 and 4, a value of  $b = 0.25$  fell within the 95 confidence limits of the estimate of  $b$ . The correlation improved in models 3 and 4, where different Arrhenius temperatures for the various species were assumed. The observed range in Arrhenius temperatures varied between the species from 12800 and 20600 K. Nested analyses indicated that the relationship significantly improved by incorporating different Arrhenius temperatures for the various species (F-test model 4 versus 2  $F_{[1,11]} = 16.02$ ; model 3 versus 1  $F_{[1,12]} = 20.08$ ). For  $b$  set as parameter this was not the case. The same held true for the relationship between larval development time and larval volume at hatch (Table 7). All models resulted in significant relationships, and the highest correlation was observed in models 3 and 4, where species-specific Arrhenius temperatures were assumed. Nested

Table 6

ANOVA of minimum larval development time (Larvdevmin; d) in flatfish in relation to minimum egg volume (Eggvolmin; mm<sup>3</sup>) and temperature (TEMP, °C) according to the model: Larvdevmin =  $a * \text{Eggvolmin}^b * (\exp(-TA/283 + TA/(273 + \text{TEMP})))$ . Model 1 and 3:  $b = 0.25$ ; Model 3 and 4: different  $T_A$  for different species

Model	a	b	95% CI	$T_A$	$r^2$	n
1	41.265	0.25*		19849	0.78	19
2	49.320	0.071	-0.154–0.296	15161	0.76	19
3	40.908	0.25*		11800–20611	0.97	17
4	40.584	0.289	0.082–0.497	11326–21361	0.97	17

Table 7

ANOVA of minimum larval development time (Larvdevmin; d) in flatfish in relation to volume at hatch (Hatchvolmin; mm<sup>3</sup>) and temperature (TEMP, °C) according to the model: Larvdevmin =  $a * \text{Hatchvolmin}^b * (\exp(-TA/283 + TA/(273 + \text{TEMP})))$ . Model 1 and 3:  $b = 0.25$ ; Model 3 and 4: different  $T_A$  for different species

Model	a	b	95 % CI	$T_A$	$r^2$	n
1	54.029	0.25*		9828	0.72	14
2	54.675	0.039	-0.204–0.283	11982	0.75	14
3	47.636	0.25*		9031–14076	0.88	13
4	48.920	0.90	-0.137–0.317	8954–15235	0.90	13

analyses indicated that the relationship significantly improved by incorporating different Arrhenius temperatures for the various species (F-test model 3 versus 1  $F_{[1,9]} = 5.17$ ). For  $b$  set as parameter this was not the case.

## 5. Discussion

### 5.1. Scaling relationships: why apply dynamic energy budgets?

Although the literature on quantitative bioenergetics in fish is already extensive, we have selected a framework that until recently had not been applied in this field: the theory of dynamic energy budgets (DEB theory) developed by Kooijman (1988, 2000). The reason is that the DEB theory is based on simple mechanistic rules that are not species-specific. Therefore, this quantitative framework can be applied to all living organisms (numerous examples -varying from bacteria to whales- have shown that this is true). A second argument in support of the DEB theory is that a large number of classic models are special aspects and cases of the DEB theory, for example the Michaelis–Menten kinetics, the temperature dependence of physiological rates, Von Bertalanffy growth, Holling's hyperbolic functional response and microbial product formation (for overview see Kooijman, 2000, 2001). Thirdly, in a previous paper the dynamic energy budgets were successfully utilised for the intra- and interspecies comparison of energy flow in some North Atlantic flatfish species (Van der Veer et al., 2001). The quantitative aspects in terms of energy flow of growth and reproduction in plaice *Pleuronectes*

*platessa*, flounder *Platichthys flesus*, dab *Limanda limanda* and sole *Solea solea*) could be described in a single model, whereby the diversity between species could be captured in differences in parameter values. The validity of the DEB model was further highlighted by the successful application of the same model in the analysis of energy flow in various bivalve species (Van Haren and Kooijman, 1993; Cardoso et al., 2001). Finally, the correct predictions of various body size scaling relationships -except for the exponent of reproductive output- are the strongest empirical support for the conclusion that the DEB model realistically captures the main features of animal energetics. Therefore, body size scaling relationships and recruitment will be linked via various life history parameters that represent strategic choices concerning energy allocation and critical size for switching between life stages (e.g. maturation) since these are likely to be adaptive (Nisbet et al., 2000).

### 5.2. Away from empirical regressions towards underlying mechanisms

The link between bioenergetics and life history has been around for a long time (Kleiber, 1961; Ware, 1980; West et al., 1997, 2001). In applying the DEB theory we do not intend to replace the numerous concepts that have been proposed over the years, but to add a general framework consisting of a consistent set of general rules based on mechanisms for energy uptake, storage and utilisation. The correct predictions for the various body size scaling relationships are a strong support in favour of the general assumptions underlying the DEB theory. There are two essential differences between the DEB theory and other energy models. Firstly, in all life stages, energy is allocated to maturation or reproduction. In embryos and juveniles it is used for maturation, while in adults it is used for reproduction. The other essential difference concerns the fact that within the DEB theory there is no direct relationship between food intake on the one hand and processes such as growth, maintenance and reproduction on the other hand. Food is first converted into reserves and these reserves are utilised and allocated to growth, maintenance and maturation or reproduction. For arguments and experimental

support of these two essential assumptions see Kooijman (2000). This means that in the light of the DEB theory, conventional fish bioenergetic studies in which food intake is related to growth, respiration and maintenance are incorrect.

An important link between most conventional budget studies and the DEB theory is formed by the Von Bertalanffy growth equation, of which the basic ideas go back to Pütter (1920), and perhaps even further back in time. Despite the fact that the process of growth is complex, size-at-age data of numerous species from different phyla, including fishes, can be fitted to the Von Bertalanffy growth curve. Consequently, growth in most energy models is assumed to occur according to a Von Bertalanffy growth curve. In the DEB theory, growth of an organism follows the Von Bertalanffy growth curve only if the food density in the environment is constant during the growth period. This is because at constant food densities, the stored energy reserves are in equilibrium with the environment and consequently growth of structural biovolume represents a weighed difference between surface area and volume and corresponds with Von Bertalanffy growth (Kooijman, 1988). The growth curve is also of a Von Bertalanffy type if the food density fluctuates around a mean level with a period that is small compared to the growth period (Kooijman, 1988, 2000). From the point of view of the DEB theory, the fact that Von Bertalanffy growth curves frequently fit data from animals in the field over a range from the tropics to the poles suggests that they all live at relatively constant (mean) food densities during their growth season. Mathematically it turns out that under such conditions within a species, the inverse of three times the Von Bertalanffy growth rate is linear to ultimate length (Kooijman, 1988). Additionally, the intercept and slope correspond with two compound parameters in the DEB model, which contain two terms that determine the maximum body size (see above), the volume-specific cost of maintenance and the maximum surface area -specific assimilation rate. The consequence is that due to this link, parameters of the Von Bertalanffy growth curve can directly be interpreted and related to physiological traits (Kooijman, 1988, 2000) and this offers an opportunity to get away from empirical regressions towards underlying mechanisms.

### 5.3. Scaling relationships: implications for recruitment

Recruitment success simply depends on the egg production and the survival during in the early life history (Cushing, 1995). The fact that fecundity is positively related to body size within a species, despite a high variability among individuals (Millner et al., 1991; Rijnsdorp, 1994) justifies a focus on body size, especially since stocks with high fecundity also seem to have higher recruitment variability (Rickman et al., 2000). The importance of body size is further illustrated by the strong link between growth and mortality processes and the experimental evidence of a relationship to body size during teleost early life stages (Pearcy, 1962; Ursin, 1973; Cushing, 1974; Ware, 1975) and implied by size-spectrum theory (Peterson and Wroblewski, 1984). In this respect, flatfishes do not seem to differ from other teleosts in aspects of their life history that might influence recruitment (body size, fecundity, egg size and egg development and mortality).

Implications of the various body size scaling relationships, as predicted by the DEB theory and confirmed by data on various flatfish species, are that recruitment characteristics of a variety of marine teleosts can be linked to the way in which they invest surplus energy to satisfy the conflicting demands of persistence (growth) and replacements (reproduction) at different levels of stock. Given the differences in ultimate size that are related to latitude in flatfishes, it is to be expected that species occupying higher latitudes will have larger egg sizes, longer hatching times, and a larger size at hatching, as shown by Miller et al. (1991). The link between body size and survival is twofold, by means of the direct relationship of survival with egg size and of the consequence for the stage duration (development time). This relationship is different within and between species. Within a species, an inverse relationship between egg size and egg mortality rate has been observed in flatfishes and in other teleosts and appears to hold true for teleost species in general (Rijnsdorp and Jaworski, 1990; Rijnsdorp and Vingerhoed, 1994). Chambers and Leggett (1992), and Hjort (1926) have shown that mortality rate tends to vary inversely with stage duration (development rate/time) because short-

er stage durations mean shorter periods of exposure to predators during the given stage. The positive relationship between egg size and development rate is thus consistent with the broader relationship between egg size and mortality rate and could be the underlying basis for that relationship as and where it exists within a species. Across species the pattern is less clear. Development time increases with egg size, because bigger eggs produce larger larvae, and this takes longer. So, between species, this increase in stage duration counteracts a reduction in direct egg mortality with increasing egg size. For the larval stage, the importance of body size is illustrated by the size-dependent relationships between the susceptibility of fish larvae to predation and the predator: prey size ratio (Pepin et al., 1987; Miller et al., 1988) and that larval size explains a significant fraction of larval mortality (Pepin and Myers, 1991). The above findings support the suggestion by Houde (1997) of a highly probable functional relationship between body size and stage specific productivity, which ultimately is related to recruitment level and variability.

A consistent pattern that emerges and supports the assumptions of the DEB theory in an indirect way is the negative relationship between egg diameter and ambient water temperature in a variety of fish species (Ware, 1975; Blaxter and Hunter, 1982; Kashiwagi et al., 1987). In subtropical and temperate flatfish species, there is a clear trend of a decrease in egg size during the period of spawning (Minami and Tanaka, 1992; Rijnsdorp and Vingerhoed, 1994). This pattern has also been observed in other teleost species. Bagenal (1971) has hypothesised that this trend results from seasonal changes in food availability. However, an equally valid argument can be made for the change being a compensation for the faster development rate associated with increases in temperature as the season advances. Between species, larger egg volumes are related to a larger size at hatching and because it takes more time to 'build' a larger larva at hatching, a larger egg volume means a longer development time. This is confirmed by the analysis of hatching time in marine fish eggs in relation to temperature and egg size by Pauly and Pullin (1988). They concluded that larger eggs develop more slowly than small eggs, all other factors being equal. Also in this study, both egg and larval

development time were related to egg volume according to the predictions of the DEB theory. Furthermore, in the DEB theory larger eggs result in a larger size at hatching and metamorphosis, both occurring in flatfish. These findings are in agreement with the conclusion that egg size seems to correlate with the size and other attributes of larvae hatching from them and that size differences established in the earliest days of a fish's life tend to be retained for at least several weeks into the larval period and perhaps longer (Chambers, 1997). By determining the resources available to the offspring for early growth and development, progagule size can exert a strong influence on offspring fitness.

In conclusion, in studying life history responses of individuals and populations to environmental variability, one should realise that the observed phenotypic plasticity is built on a general bioenergetics framework. Variability and trends in environmental conditions are reflected in various body size relationships and latitudinal trends, both within and among species. The DEB theory offers a tool to study the life history responses of individuals and populations to environmental variability from an energetic point of view, such as the energetic consequences of reproduction in relation to energy reserves (Lambert and Dutil, 2000). However, special attention should be paid to the evolution of egg and offspring size (Schliekelman and Ellner, 2001). Life history theory suggests that a trade-off between egg size and egg numbers exists as a response to environmental variability (Roff, 1992; Stearns, 1992). The DEB theory suggests that this trade-off is limited by the fact in principle egg volume is simply related to maximum adult body volume. Although data indicate that there is indeed a significant relationship between egg volume and maximum body volume, energy investment in egg size/volume in the various flatfish species is much less than predicted by the DEB theory, suggesting a strong selection for increasing egg numbers at the expense of egg volume and hence of an increase in development time.

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