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Intra- and interspecies comparison of energy flow in North Atlantic flatfish species by means of dynamic energy budgets

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Abstract

The quantitative aspects of growth and reproduction in four flatfish species (plaice, flounder, dab, sole) in terms of energy flow are described on the basis of a dynamic energy budget (DEB theory). This theory consists of general assumptions about energy uptake, storage and utilisation and describes an individual by two state variables: structure and reserve, whereby body size exerts its influence through the ratio between surface area and volume. Comparison between model estimates and field data shows that the DEB model successfully describes the energetics of growth and reproduction in a number of flatfish species. Differences between species could be captured in the same model using different parameter values. Intraspecific differences in growth between males and females are mainly caused by differences in maximum surface area-specific ingestion rates. Differences between species are reflected in the surface area-specific maximum ingestion rate, the energy partitioning over growth and reproduction, and in egg volume. According to these parameters at 283 K (10°C), the species could be ranked as follows: surface area-specific maximum ingestion rate (W m^{-2}) plaice: 56.6; flounder: 54.5; sole: 45.1 and dab: 36.1 W m^{-2}. Fraction of energy allocated to reproduction (–): flounder: 0.35; plaice: 0.15; dab: 0.15 and sole 0.10. As a consequence of these differences in surface area-specific maximum ingestion rate and in the fraction of utilised energy allocated to reproduction, the gonad masses (g) of females of 0.5 kg wet mass differ considerably: flounder: 149 g; plaice: 86 g; sole: 70 g; and dab: 69 g. However, due to differences in egg size between species, the potential annual egg production shows a completely different pattern: dab: 2200 10^3; flounder: 1560 10^3; sole: 343 10^3 and plaice: 130 10^3 eggs.

Keywords: Dynamic energy budgets; Juvenile; Flatfish; Growth; Reproduction; Plaice; Flounder; Dab; Sole

1. Introduction

A juvenile fish should experience a benign abiotic environment, adequate food and refuge from predation in order to grow, obtain sexual maturity and reproduce. So far most studies on the growth of fish are restricted to the impact of temperature and food (Scofiani and Hawkins, 1985; Jobling, 1993; for flatfish see Fonds and Rijnsdorp, 1988; Fonds et al., 1992; Van der Veer and Witte, 1993; Van der Veer et al., 1994). This lack of information about other factors and their interactions was criticised by Neill et al. (1994). They proposed a conceptual model based on Fry's scheme of the effects of environmental factors on the physiology of fish (Fry, 1947,1971). The underlying philosophy of this framework is that all of the environment can be resolved into five classes of physiological effects: controlling, limiting, lethal, masking and directive factors. However, this

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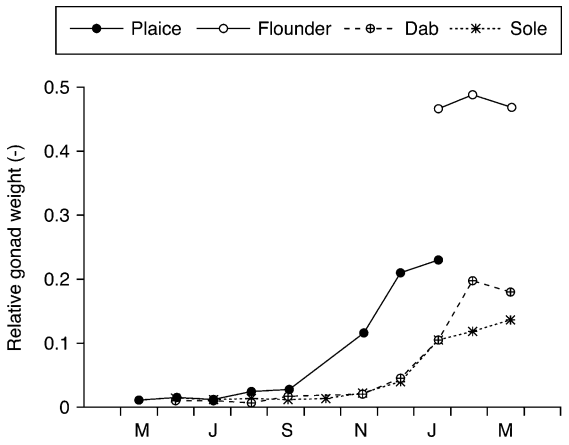


Fig. 1. Seasonal pattern in energy storage in reproduction in female plaice, flounder, dab and sole, based on information of Deniel (1981) for the Baie of Douarnezez (French coast). The relative gonad mass (RG; g g^{-1}) is expressed as fraction of the total wet mass (W_w; g) minus gonad mass (G_w; g): $RG = G_w/(W_w - G_w)$.

framework is restricted to an analysis of the environment in a qualitative way only, and lacks the power to expand it to a quantitative analysis. A general theory on energy budgets could fill this gap, and although literature about energy budgets in fish is considerable, it is merely species-specific. To our knowledge no general framework exists in which the quantitative aspects of the energy allocation over growth and reproduction are described in a coherent way.

In this paper we introduce such a quantitative framework, based on a theory of dynamic energy budgets (DEB) developed by Kooijman (1988, 2000). The DEB theory aims to quantify the energy flow through an individual organism during its lifetime. Key processes are feeding, digestion, storage, maintenance, growth, development, reproduction and ageing. Central in the DEB theory is the fundamental role of surface/volume ratios and reserves. From this starting point the relationship between various physiological and ecological processes is derived in a systematic way (Kooijman, 2000).

The aim of the present paper is to introduce the DEB model for growth and reproduction of some North Atlantic flatfish species, with special emphasis on plaice *Pleuronectes platessa* L. and to apply the model for the comparison of species. The comparison is restricted to the juvenile and adult demersal stages and does not include egg and larval stages. Furthermore, the analysis is mainly focused on females. Our goal is to improve the comparison of the various aspects of the life histories and energetics of species by capturing diversity into the parameter values of a single model.

2. Species characteristics

The flatfish species studied belong to the family Pleuronectidae [plaice *Pleuronectes platessa* L.; flounder *Platichthys flesus* (L.); dab *Limanda limanda* (L.)] and the family Soleidae [sole *Solea solea* (L.)]. The species are shallow-water, bottom-living flatfishes and they all show a depth-related distribution with a pattern of movements towards deeper water with increasing age. Dab and plaice can be regarded as typical cold-water species with a spatial distribution from the Barents Sea in the north to the Bay of Biscay in the south. Flounder and sole belong more to the warm-water species, with a distribution from the Mediterranean in the south to the northern North Sea (sole) and the Norwegian coast (flounder). Flounder is the only euryhaline species, since its life cycle includes freshwater, brackish and marine habitats. In the other species, the juveniles use the shallow coastal areas and estuaries as a nursery and the adults are found in the open sea. With respect to growth and reproduction the various species show considerable differences (Wheeler, 1978). Maximum age in female plaice is 30 years, in which they can obtain a length of about 0.9 m and a mass, including reproductive storage, of about 6 kg. Female flounder can reach a maximum mass of about 2 kg at a size of 0.5 m, and has a maximum life span of about 10–15 years. The maximum mass of female sole is about 3 kg at a size of about 0.6 m and its maximum life span is about 20 years. The maximum size and mass of dab is much lower, in the order of 0.4 m and 1.3 kg, respectively, at a maximum age of about 10–12 years.

The differences in growth and reproductive characteristics of the various species can also be illustrated by the general patterns in energy allocation over growth and reproduction (Fig. 1). The seasonal pattern in energy storage in reproduction in female flatfish, expressed as fraction of the body mass minus the gonad mass shows large differences between species. The fraction of energy stored in

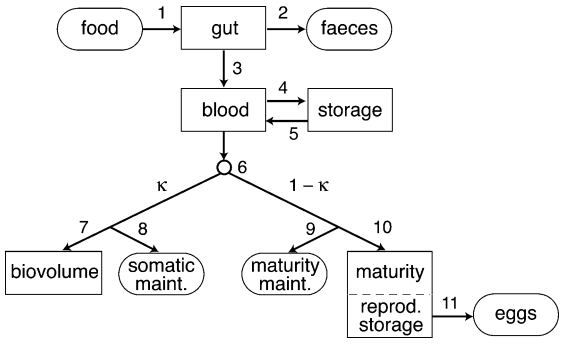


Fig. 2. Energy flow through an organism in the DEB model, after Van Haren (1995). Rates: 1 ingestion (uptake), 2 defecation, 3 assimilation, 4 demobilisation of energy into reserves, 5 mobilisation of energy from reserves, 6 utilisation, 7 growth, 8 maintenance, 9 maturation maintenance, 10 maturation,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

reproduction is highest in flounder (up to 0.45), intermediate in plaice and dab (about 0.20) and lowest in sole (about 0.15).

3. Dynamic energy budget (DEB) model

This section briefly describes the DEB model. A conceptual introduction can be found in Kooijman (2001); a full description is given in Kooijman (2000). The DEB model describes the energy flows through an animal (Fig. 2) and also changes therein in environments with varying food densities and temperatures. 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 components (structural biovolume or somatic tissue; stored energy reserves; and gonads and/or stored energy reserves allocated to reproduction) are distinguished. Homeostasis for each fraction is assumed, i.e. the ability to keep the chemical composition constant despite changes in the chemical composition of the environment. However, the contribution of these body fractions to total biovolume changes with time.

Food uptake is assumed to follow a type II functional response according to Holling (1959), which means that the rate depends hyperbolically on food density. Food uptake is proportional to an organism's surface area, and converted into reserves with a constant efficiency. Stored energy is utilised from these reserves and is allocated to growth, maintenance and reproduction. A fixed fraction of the utilised energy (κ) is allocated to somatic maintenance and growth while the remainder ($1 - \kappa$) is allocated to maturity maintenance and development or reproduction. Maintenance has priority over growth, and hence growth ceases when food densities are low. The energy costs of maintenance are proportional to the amount of structure. At constant food densities, the stored energy reserves are proportional to the structure and consequently growth of structural biovolume is a weighed difference between surface area and volume. Embryos and juveniles allocate energy to development, i.e. the increase of the state of maturity; adults use this flux for reproduction. This energy is stored temporarily in a buffer, which is emptied at spawning.

Since an organism consists of mass, reserves 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 hardly changes during growth, so that surface area is about proportional to squared length. An appropriate length measure (SL or TL, etc.) can be converted into volume by multiplying it by the shape coefficient (volume$^{1/3}$ length^{-1}) and to raise 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 m^3 is about 1000 kg.

The DEB model is based on growth and reproduction at varying food densities and its state variables are structure and reserve. Based on the underlying assumptions described above, five equations together fully determine feeding, growth, survival and reproductive behaviour (see Kooijman, 2000, p. 120–123). These equations are coded in STELLA® 5.0. The various primary variables and parameters of the DEB model are listed in Table 1. The notation and symbols in this paper follow those in Kooijman (2000) and the following main rules apply:

Table 1
Variables and parameters of the DEB model, together with dimension and interpretation after Kooijman (2000)

Symbol	Dimension	Interpretation
Variables		
T	time	time
E	energy	energy storage
Primary parameters		
V_p	length^3	volume at start reproductive stage
$\{\dot{p}_{Xm}\}$	energy length^{-2} time^{-1}	maximum surface area-specific ingestion rate
$\{\dot{p}_{Am}\}$	energy length^{-2} time^{-1}	maximum surface area-specific assimilation rate
$[E_m]$	energy length^{-3}	maximum storage density
$[\dot{p}_M]$	energy length^{-3} time^{-1}	volume-specific maintenance costs per unit of time
$[E_G]$	energy length^{-3}	volume-specific costs for growth
κ		fraction of utilised energy spent on maintenance plus growth
δ_m		shape coefficient

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

In principle, the parameter values are expressed in SI units. To prevent confusion, commonly used units are also given.

4. Parameter estimation

In addition to the parameters that are required to describe feeding, maintenance, growth and reproductive output, there are three other aspects:

1. the shape coefficient, determining how length translates to volume,
2. the effect of temperature,
3. the start of the reproductive stage.

4.1. Shape coefficient

The shape of an individual determines how a specific length measure relates to volume. Individual volumes (V; m^3) can be calculated from wet masses (W_w; kg), according to:

$$W_w = d_w V$$

where d_w is the specific density (kg m^{-3}). For marine species an average salinity of about $S = 34$ can be assumed, which corresponds with a specific density d_w of 1025 kg m^{-3} at 5°C (Lalli and Parsons, 1993). At higher temperatures and lower salinities, this value will approach 1000. Therefore, in all calculations a specific density of 1000 kg m^{-3} has been taken. Shape coefficients (δ_m) follow from:

$$V = (\delta_m L)^3 \quad (1)$$

whereby all volumes are based on wet mass minus gonad mass measurements, since gonad mass is considered not to represent structural body mass or reserve.

For the different species, the shape coefficients for total length are similar over the size range studied, suggesting isomorphic growth (Fig. 3). Also, no differences could be observed between juveniles, females or males. There is a suggestion that isomorphic growth is restricted to the juvenile and adult stages and that larval stages have a different shape coefficient: in dab and also in plaice, the shape coefficients drop at low total length values. The shape coefficients for the various flatfish species are rather similar. Plaice, flounder and dab have almost equal shape coefficients of 0.219, 0.224 and 0.213, respectively. Sole has a lowest coefficient of 0.192.

4.2. Temperature

Temperature has an effect on all physiological rates. In DEB, the Arrhenius description has been selected to describe the effect of temperature and it is based on the Van't Hoff equation. The Arrhenius

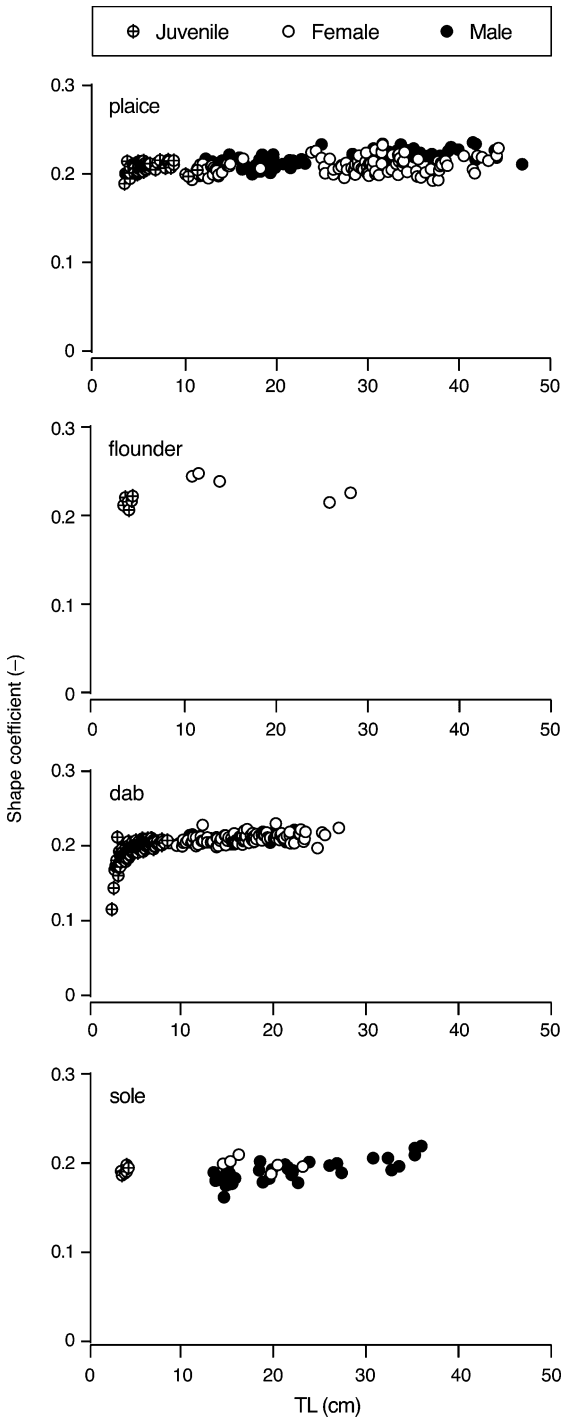


Fig. 3. Shape coefficient ($V^{1/3}\,L^{-1}$) in relation to total length (cm) for the different flatfish species, under the assumption of $d_w = 1.00$. All masses are in wet mass minus gonad or testis masses.

relationship—using absolute temperatures (K)—is as follows:

$$\dot{k}(T) = \dot{k}(T_1) * \left[\frac{T_A}{T_1} - \frac{T_A}{T} \right] \quad (2)$$

where $\dot{k}$ is a physiological rate, T is ambient temperature (K), T_1 is a chosen reference temperature (K), which was set in this paper at 283 K ($= 10°C$) and T_A is a species-specific coefficient, the so-called Arrhenius temperature (K). The Arrhenius relationship implies that a plot of $\ln(\dot{k})$ against $1/T$ gives a straight line with a slope of T_A. Examples of rates are for instance respiration rate. The Arrhenius temperature can be compared with the conventional Q_{10} values, according to:

$$\frac{1}{10}\ln Q_{10} = \frac{T_A}{T_1 \times (T_1 - 10)} \quad (3)$$

There was some variability between the various estimates, not only between species but also between estimates (Table 2). Dab has the lowest mean value of about 4500 K, followed by plaice: 7000 K, and flounder and sole: 8500 K. This range corresponds with Q_{10} values from 1.78 to 3.00.

4.3. Start of reproduction

The DEB theory assumes that the transition from juvenile to adult occurs when the cumulated energy invested in maturation exceeds a certain threshold value. Field studies show that flatfish mature according to a trajectory in the length and hence age space (see for plaice: Rijnsdorp, 1993). However, this window can be regarded as the result of becoming sexually mature when the fish has passed some fixed size-threshold (Roff, 1991) in combination with a distinct spawning period of only once a year. Therefore, fish volume at the transition from juvenile to adult can be estimated from the minimum length observed of a flatfish becoming mature.

Minimum length at maturity is different for males and females. In general, males become mature at a smaller size (Table 3). Dab becomes mature at the smallest size of 10 cm for males and 11 cm for females. Plaice has the largest size: 15 cm for males and 22 cm for females. The corresponding volumes range from 9.7 cm^3 in

Table 2
Mean Arrhenius temperature (K) for various flatfish species, calculated from literature information on juvenile flatfish. Non-linear weighted least-squares (WLS) regressions were applied. For more information see text

Species		Arrhenius temperature	SE	N	R^2	Reference
Plaice	oxygen consumption	5878	221	110	0.95	Fonds et al. (1992)
	maximum food intake	7963	347	50	0.96	Fonds et al. (1992)
Flounder	oxygen consumption	6957	323	40	0.96	Fonds et al. (1992)
	maximum food intake	11134	495	50	0.96	Fonds et al. (1992)
Dab	oxygen consumption	3958	864	13	0.93	Fonds (unpublished)
	maximum food intake	4931	2337	13	0.85	Fonds (unpublished)
Sole	maximum food consumption	7305	506	50	0.83	Fonds and Saksena (1977)
	maximum food intake	9708	544	50	0.96	Fonds and Saksena (1977)

dab (males) to 106.5 cm^3 in plaice (female), and converted into volumetric length ($V^{1/3}$) the range between the species is from 2.13 to 3.23 cm in males and from 2.43 to 4.74 cm in females (Table 3).

4.4. Feeding

The DEB theory assumes that food uptake is proportional to an organism's surface area, and converted into reserves with a constant efficiency. The maximum surface area-specific ingestion rate $\{\dot{p}_{Xm}\}$ at the reference temperature of 283 K (10°C) can be computed from data at different temperatures (Temp; °C) according to:

$$\dot{p}_X = \{\dot{p}_{Xm}\} * f * V^{2/3} * \exp\left(\frac{T_A}{283} - \frac{T_A}{(273+\text{Temp})}\right) \quad (4)$$

whereby $\dot{p}_X$ is the ingestion rate (W d^{-1}), f is a function of the food density, which approaches 1 under excess food conditions, and V is volume (m^3). Therefore, $\{\dot{p}_{Xm}\}$ (W m^{-2}) can be estimated from data on maximum food intake of flatfish in relation to size and temperature. Experiments on maximum daily food intake have been published for juvenile plaice and flounder by Fonds et al. (1992) and for sole by Fonds and Saksena (1977). For juvenile dab, only a limited amount of information is available (Fonds, unpublished). In all four species, the relationship between maximum daily food intake and fish mass is described for a range of temperatures. In combination with the length-mass relationship presented in the same papers, the maximum daily food intake can be related to $V^{2/3}$, which corresponds with $(\delta_m L)^2$. The maximum surface area-specific ingestion rate was estimated by non-linear weighted least-squares regression of model (4). The estimates of $\{\dot{p}_{Xm}\}$ at 283 K for plaice, flounder and dab were similar 63 W m^{-2}; however, the 95% confidence intervals differed considerably: plaice: 60–67 W m^{-2}; flounder: 58–68 W m^{-2}; dab: 43–84 W m^{-2}. In sole the maximum surface area-specific ingestion rate was lower, about 35 W m^{-2}, with a 95% confidence interval of 29–42 W m^{-2}.

Only part of the energy ingested will be assimilated. The maximum surface area-specific assimilation rate refers to the 'assimilated' energy, which is defined as the free energy intake minus all losses in relation to digestion and in faeces. In the DEB theory, the energy loss in urine is tied to three

Table 3
Minimum length (cm), wet mass (g) and volumetric length (cm) at maturity of various flatfish species. Data after Fonds (unpublished). Values of minimum length at maturity between brackets are estimates

	Plaice		Flounder		Dab		Sole	
	male	female	male	female	male	female	male	female
Minimum length at maturity (cm)	15	22	11	(13)	10	(11)	(12)	15
Minimum mass/volume at maturity (g; cm^3)	33.8	106.5	13.3	22.0	9.7	12.9	17.3	30.8
Minimum volumetric length at maturity ($V^{1/3}$; cm)	3.23	4.74	2.37	2.80	2.13	2.43	2.58	3.23

processes: assimilation maintenance and growth. The contribution via maintenance probably dominates. The maximum surface area-specific assimilation rate will depend on type of food and therefore it is in principle a diet-specific parameter. Brett and Groves (1979) estimated the overall loss in faeces to be on average 20%. Therefore, for all four flatfish species the maximum surface area-specific assimilation rate is estimated as:

$$\{\dot{p}_{\mathrm{Am}}\} = 0.80 * \{\dot{p}_{\mathrm{Xm}}\} \quad (5)$$

4.5. Maintenance

According to the DEB theory, the energy costs of maintenance are proportional to the amount of structure. The volume-specific maintenance costs per unit of time $[\dot{p}_{\mathrm{M}}]$ can be deduced from mass and energy loss during starvation, when growth ceases and hence the energy spent will be proportional to maintenance plus storage in reproduction. In some species, among which plaice, feeding and growth stop during the spawning period, even in immature individuals (Dawson and Grimm, 1980; Rijnsdorp and Ibelings, 1989), and this provides an opportunity to estimate the costs of maintenance under field conditions. Dawson and Grimm (1980) describe the seasonal changes in energy reserves in adult female plaice in body mass (carcass and liver) and the gonads. The carcass is the main source of lipid and protein reserves during the period of starvation from December to March when reproduction takes place. Over the period February–March, the energy content of the carcass decreases from 1936 to 1810 kJ = 126 kJ and that of the liver from 65.1 to 28.6 = 36.5 J, in total 162.5 kJ. Over this period the energy content of the gonad decreases from 1112 to 29.4 kJ due to spawning. Under the assumption that the energy flow from the carcass into the gonads over this period is negligible, this means that the decrease in energy content of the carcass and liver represents the metabolic costs over this 28 day period. With a body mass of 406 g wet mass in February, this means a volume-specific maintenance cost $[\dot{p}_{\mathrm{M}}]$ of 14.3 J cm^{-3} d^{-1} at about 6–7°C, or 17.2 J cm^{-3} d^{-1} at 10°C which is equivalent to 199 W m^{-3}. Rijnsdorp and Ibelings (1989) obtained an estimate of between 17 and 24 J cm^{-3} d^{-1} for adult females and of 19 J cm^{-3} d^{-1} for adult males, which corresponds with a range of 196–278 W m^{-3} for females and with 221 W m^{-3} for males. Their estimate did not take into account the slight increase in body size during spawning and must be considered to be maximum estimates. No field or laboratory observations are available for the other species.

4.6. Growth and reproduction

With respect to the processes of growth and reproduction, three parameters are of importance:

1. the maximum storage density,
2. the volume-specific costs for growth,
3. the fraction of utilised energy spent on somatic maintenance plus growth, the remaining proportion being used for maturity maintenance plus development or reproduction.

An estimate of the maximum storage density $[E_{\mathrm{m}}]$ can be obtained in species with a contracted spawning period in which no feeding occurs and reproduction is supported from energy reserves. The assumption is that in such capital spawners, the energy density of the fish is maximal at the beginning of the spawning period and almost zero at the end. The decrease in energy reflects the maximum storage density. Plaice and flounder are such capital spawners and for plaice the data of Dawson and Grimm (1980), who describe the seasonal changes in energy reserves in adult female plaice in the carcass, allow an estimate of the maximum storage density. In November, at the end of the growing season, the energy content of the carcass and the liver is maximal; a 495 g female then contains in total 3200 kJ. At the end of the spawning period in February, the energy content has decreased to 2003 kJ, corresponding with an energy loss of 2.54 kJ cm^{-3}. There are no data to estimate the maximum storage density for the other species.

The estimate of the volume-specific costs for growth $[E_{\mathrm{G}}]$ is based on data on the energy density of the fish at the beginning of the spawning period when storage density is maximal. In November, at the end of the growing season when the energy content of the carcass and the liver is maximal, a 495 g female plaice contains in total 3200 kJ, which is equal to 6.46 kJ cm^{-3}. 2.54 kJ cm^{-3} of this energy content represents storage (see above), which means that the structural mass amounts to about 4 kJ cm^{-3}. Assuming a conversion efficiency of about 60%, this

Table 4
Maximum surface area-specific ingestion rate $\{\dot{p}_{Xm}\}$ (W m^{-2}) at 283 K with 95% confidence interval (95% C.I.) for the various flatfish species, estimated by means of non-linear weighted least-squares (WLS) regressions together with number of observations (N) and correlation coefficient (R^2). Between brackets corresponding values in J cm^{-2} d^{-1}

Species	$\{\dot{p}_{Xm}\}$		95% C.I.	N	R^2	Reference
	W m^{-2}	(J cm^{-2} d^{-1})				
Plaice	63.43	(548)	60.0–66.9	50	0.95	Fonds et al. (1992)
Flounder	63.07	(545)	57.7–68.3	50	0.96	Fonds et al. (1992)
Dab	63.43	(548)	43.3–83.7	50	0.85	Fonds (unpublished)
Sole	35.30	(305)	28.8–41.7	13	0.96	Fonds and Saksena (1977)

would mean a costs for growth of about 7 kJ cm^{-3}. No field or laboratory observations are available for the other species. Literature data indicate that the energy content of individuals of the various species is rather constant for animals in good condition, i.e. between 21 and 23 kJ g^{-1} dry mass (Fonds et al., 1989; Rijnsdorp and Ibelings, 1989; Fonds, unpublished). Therefore, it is assumed that the values of $[E_m]$ for the other species will be in the same order of magnitude.

The fraction of utilised energy spent on maintenance plus growth (κ) can be estimated from the energy flow in an organism. According to Dawson and Grimm (1980) an adult female plaice of 6 years old, and a total length of 32.6 cm in May, in 1 year increases to 35.9 cm length and from 323.9 to 455.6 g wet mass, or 131.7 cm^3 volume. In combination with the volume-specific costs for growth of 7 kJ cm^{-3}, this means that the costs of 131.7 cm^3 amounts to 922 kJ. Over this same time period, the energy content of the carcass also increases from 1638 to 2306 kJ ($=668$ kJ) minus the energy content of the newly formed mass of 131.7*4 kJ ($=524$ kJ), which amounts to 144 kJ. The costs of maintenance during the year can be roughly estimated as four times that during the period of spawning from December to March of 1018 kJ = 4072 kJ. The energy loss due to spawning during its seventh year amounts to 983 kJ. This means that the total energy flow amounts to about 6120 kJ, of which 983 is used for spawning. This results in an estimate of κ of (6120–983)/(6120) = 0.85. In this way, κ will be slightly overestimated since it does not take into account the maturity maintenance costs. No field or laboratory observations are available for the other species.

4.7. Consistency between the various parameters

A useful parameter for all species is the estimate of their maximum length and hence maximum volume. According to the DEB model (Kooijman, 2000) under optimal food conditions ($f=1$), the maximum structural volume ($V_{m;}$ cm^3) is defined by only three parameters, κ, the maximum surface area-specific assimilation rate $\{\dot{p}_{Am}\}$ and the volume-specific maintenance costs $[\dot{p}_M]$ according to:

$$V_m^{\frac{1}{3}} = \kappa * \frac{\{\dot{p}_{Am}\}}{[\dot{p}_M]} \quad (6)$$

Only for plaice, are estimates of all three parameters available. In plaice, a κ of 0.85 in combination with a maximum structural mass of a female of about 5 kg results in a ratio between $\{\dot{p}_{Am}\}$ and $[\dot{p}_M]$ of 0.20 m^{-1}, which corresponds with a ratio between $\{\dot{p}_{Xm}\}$ and $[\dot{p}_M]$ of 0.25^{-1}. The volume-specific cost of maintenance was estimated to be about 225 W $m^{-3.}$ This would require $\{\dot{p}_{Xm}\}$ to be in the order of 56.6 W m^{-2}. This estimate is close to the lower limit of the 95% confidence interval.

For the other species, only estimates of the maximum surface area-specific assimilation rate $\{\dot{p}_{Am}\}$ are available based on feeding experiments (Table 4). For flounder, dab and sole, the assumption is that the volume-specific cost of maintenance is similar to that in plaice. The general patterns in energy allocation over growth and reproduction indicate that the annual production allocated to reproduction in flounder is higher than that in plaice (Fig. 1), which

Table 5
Observed and estimated maximum mass or volume (g or cm^3) and maximum length of plaice, flounder, dab and sole based on the DEB model parameters at 283 K (10°C) under the assumption of maximum food conditions. Adjustments in parameter values have been restricted to $\{\dot{p}_{Xm}\}$ and κ. For discussion see text

	Unit	Plaice	Flounder	Dab	Sole
Field data					
W_{max}	g	5000	2000	1300	3000
L_{max}	cm	78	56	51	75
DEB model					
κ		0.85	0.65	0.85	0.9
ratio $\{\dot{p}_{Xm}\}/[\dot{p}_M]$	m^{-1}	0.20	0.19	0.13	0.16
$[\dot{p}_M]$	W m^{-3}	225	225	225	225
estimated $\{\dot{p}_{Am}\}$	W m^{-2}	45.3	43.6	28.9	36.1
losses due to digestion	–	0.2	0.2	0.2	0.2
estimated $\{\dot{p}_{Xm}\}$	W m^{-2}	56.6	54.5	36.1	45.1

means that κ will be much lower in flounder: in the order of 0.65. In combination with a maximum mass of about 2 kg, this results in a maximum surface area-specific ingestion rate $\{\dot{p}_{Am}\}$ of 54.5 W m^{-2} (Table 5). This value is near the lower 95% confidence limits of the estimate (Table 4). In dab, κ seems to be similar to that in plaice (Fig. 1). In combination with a maximum mass of about 1.3 kg, this requires a $\{\dot{p}_{Xm}\}$ of about 36 W m^{-2}. This value is outside the 95% confidence limits of the estimate; however, this does not seem unrealistic since the calculation of the maximum ingestion rate was based on very few data. In sole, the general patterns in energy allocation over growth and reproduction suggest that the annual production allocated to reproduction is lower than that in plaice (Fig. 1), which implies a κ of about 0.90. The maximum mass in sole is about 3 kg; this results in a $\{\dot{p}_{Xm}\}$ of about 45 W m^{-2}, which is in the range of the upper level of the 95% confidence limit.

5. Simulations with the DEB model

The standard analysis of the DEB model (see Appendix A) has been carried out under optimal food conditions, which means $f = 1$ at a temperature of 10°C. In addition, analyses were run at temperatures of 6, 10, 14 18 and 22°C. For some species the lower and upper temperatures may be outside their temperature range, but this aspect was not taken into account in the present analyses. For all species the following simulations were performed and compared with field data:

1. the total length–age relationship at various temperatures,
2. the growth of an individual fish of 5 cm at various temperatures,
3. the annual energy location over body growth and reproduction,
4. the development of gonad mass in relationship to body mass,
5. egg production in relationship to body mass.

The input parameters used for the various species in the different simulations are those listed in Table 5. Gonad mass is calculated from the annual energy stored in reproduction. For all species, 10% costs have been assumed for the conversion of energy into structural gonad mass. Next, the structural gonad mass is converted into number of eggs by means of the species-specific energy content per egg. Finally, these egg numbers are converted into gonad wet mass applying a species-specific factor (Table 6). According to Nash et al. (2000) for plaice this factor is 1500 eggs per g wet mass. For the other species, this factor has been corrected for the differences in egg volume relative to plaice.

The factors used and the model structure in STELLA are listed in Appendix A.

5.1. Plaice (Fig. 4)

During the spawning period from December to the

Table 6
The egg costs, energy content of the eggs and number of eggs per g gonad weight for female plaice, flounder, dab and sole. Gonad costs, the costs to convert energy into gonad structure, are assumed to be 10% in all species. Energy content of the eggs after Fonds (unpublished). Number of eggs per gram wet weight after Nash et al. (2000) for plaice. Data for flounder, dab and sole are based on the information for plaice after a correction for differences in energy content of the eggs

	Units	Plaice	Flounder	Dab	Sole
DEB model					
Egg costs	–	0.10	0.10	0.10	0.10
Energy content egg	J egg^{-1}	5	0.7	0.4	1.5
Eggs per g wet weight	n	1500	10500	18750	4950

end of February, the assimilation of food—and also growth—has been set to zero in the model, similar to the field situation. Therefore, although the growth curves at the various temperatures all correspond with the Von Bertalanffy growth, the maximum asymptotic length is only about 80 cm. The model results are in good correspondence with the field observations. In some areas (Iceland) growth seems to be lower than predicted under maximum food conditions, which might indicate suboptimal growth conditions at higher age. A comparison of predicted growth with observed growth in the laboratory under excess feeding conditions (Fonds et al., 1992) of a 5 cm individual shows a good fit in the range of about 6 and 18°C. Predicted and observed growth showed a similar slope, suggesting that the Arrhenius temperature is in the right order of magnitude. The model simulations suggest that above 18°C, temperature conditions are no longer optimal for plaice. Also the simulated annual energy allocation in reproduction shows a good correspondence with field observations (Deniel, 1981). A good correspondence between model simulations and field data is also found in the relationship between wet mass and gonad mass and annual egg production, respectively. Some field data are lower than predicted; however, since plaice is a batch spawner (Rijnsdorp and Vingerhoed, 1994) this might simply indicate that these individuals were already spawning. Data on egg production show the large variability in plaice. The estimates of model fit with the data of Deniel (1981) off the French coast; however, Rijnsdorp (1991) provides higher egg production figures for the North Sea. Overall, the input parameters seem to describe the growth and reproduction of plaice.

5.2. Flounder (Fig. 5)

During the spawning period from December to the end of February, the assimilation of food—and also growth—has been set to zero in the model, similar to the field situation. The growth of female flounder off the French coast fits within the various growth curves estimated at different temperatures according to the model; however, in the field females are not over 8 years old. The size of the largest individuals (40 cm) is even smaller than the maximum length according to the literature (50 cm). The maximum length according to the model is in the range of 55 cm. The estimates of the maximum growth rate of a 5 cm individual between 10 and 18°C showed a perfect correspondence with the observed growth in the laboratory under excess feeding conditions (Fonds et al., 1992). This suggests that the estimates of both the various parameters and of the Arrhenius temperature are correct. The temperature optimum for flounder seems to be at about 18°C. The model estimates of the energy investment in reproduction show a good correspondence with the field data (Deniel, 1981). The higher investment of flounder in reproduction than in plaice is reflected in the higher gonad masses as a fraction of body mass. Both the estimates of the gonad masses and the egg production in relation to body mass correspond with the field data. The fact that the model estimates seem to be higher than the field data is—as in plaice—a reflection of the fact that the flounder is a batch spawner. The field samples represent individuals that could have spawned already one or more times. The annual egg production is even much higher in flounder than in plaice, since egg volume and energy content in flounder are much

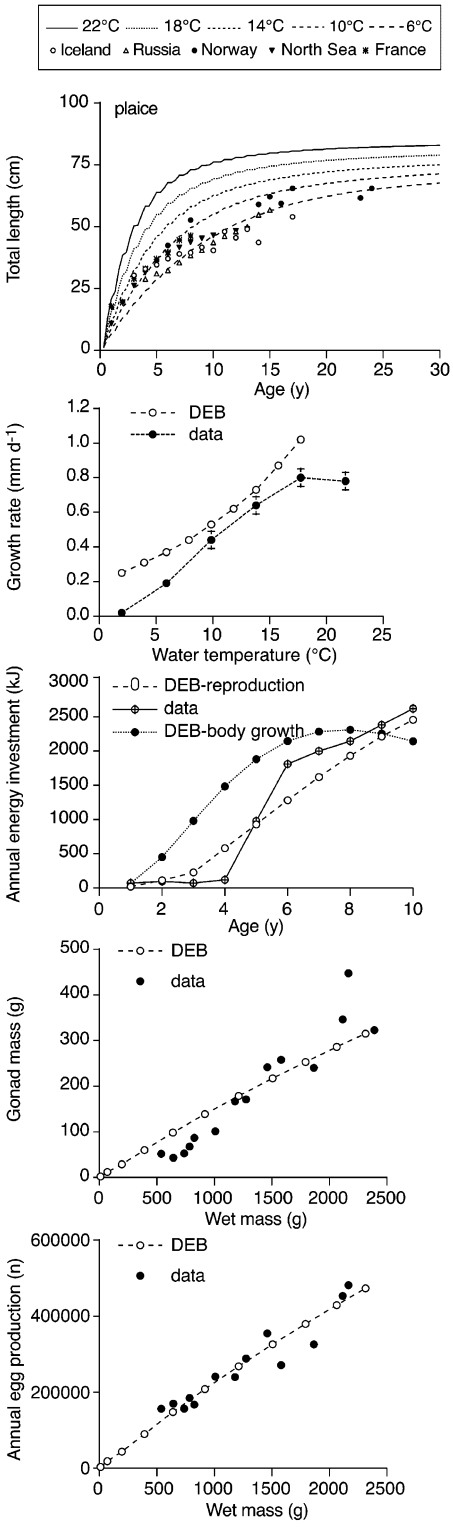


Fig. 4. Comparison of field data on plaice (after Deniel, 1981; Fonds et al., 1992) with estimates of the DEB model (see Appendix A) under optimal food conditions ($f = 1$) for: total length (cm) − age (year) relationship at various temperatures; growth (mm d^{-1}) of an individual fish of 5 cm at various temperatures; annual energy location (kJ) over body growth and reproduction; gonad mass (g wet mass) and egg production (n) in relationship to body mass (g wet mass).

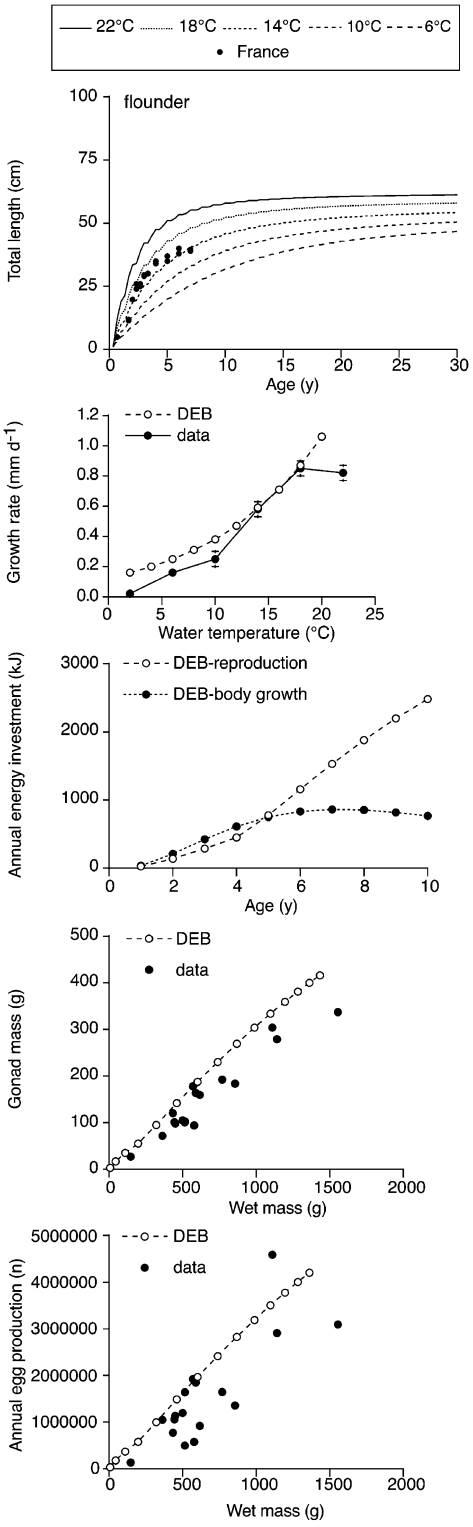
smaller than in plaice. The input parameters seem to capture the growth and reproduction of flounder in the field.

5.3. Dab (Fig. 6)

Field data on the growth of female dab fit within the range of the model growth curves at the various temperatures; however, in some areas (Scotland, Iceland) there is a suggestion that in the older age classes, growth might not be maximal. The maximum growth of a 5 cm individual at different temperatures in the laboratory (Fonds, unpublished) is lower than the estimates of the model over almost the whole temperature range and also the slope of the predicted growth seems lower than that of observed growth. This suggests that both the growth rate and the Arrhenius temperature are too low. The lower level of the predicted growth rate compared to the observed growth suggests that some of the parameter estimates need some fine-tuning. The annual energy investment in body growth and reproduction in dab is much lower than that in plaice and flounder. No accurate field data are available. Both the estimates of the gonad masses and the egg production in relation to body mass show a reasonable fit with the field data off the French coast (Deniel, 1981).

5.4. Sole (Fig. 7)

The maximum length according to the model of about 75 cm shows a good fit with two records of very large female sole caught in the North Sea (Van der Veer and Witte, unpublished data). Field data on growth fit within the range of growth curves estimated by the model at various temperatures; however, again there is a suggestion that growth might not be maximal for the older age groups. A comparison of predicted maximum growth according to the model with observed maximum growth in the laboratory



shows a good fit between 15 and 20°C, suggesting that the estimates of both the various parameters and of the Arrhenius temperature are correct. The annual energy investment in body growth and reproduction in sole is lower than that in plaice and flounder, but higher than in dab. Both the estimates of the gonad masses and the egg production in relation to body mass show a reasonable fit with the field data off the French coast (Deniel, 1981).

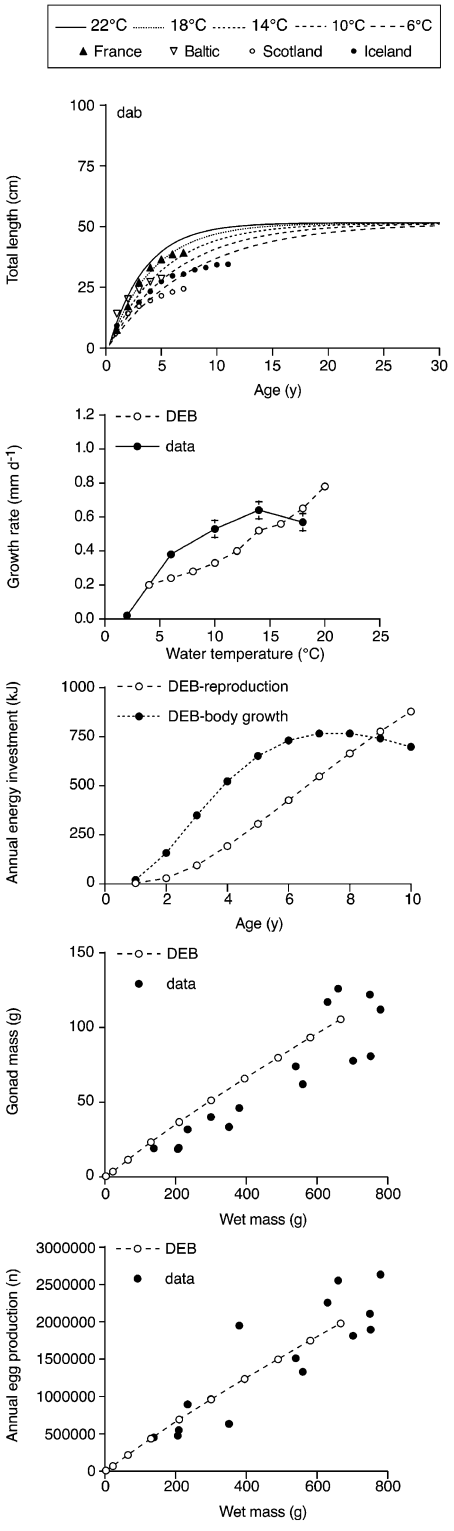
6. Discussion

6.1. Accuracy of estimates

In principle, the various parameters of the DEB model can be estimated from literature data. However, for most species not enough information is available to allow such an exercise. In this study, the most complete set of parameters was derived for plaice. In flounder, sole and dab, essential information is lacking and hence some parameters could only be roughly estimated. Even in plaice, the various estimates are either based on a number of completely independent data sources or based on indirect estimates. Therefore, the quality of the data and the accuracy of the estimates can be questioned in some cases.

One of the problems is the temperature dependence of various parameters. To relate the various temperature-dependent parameters to each other the primary parameters ($\{\dot{p}_{Xm}\}$, $\{\dot{p}_{Am}\}$, $[\dot{p}_M]$) need to be converted to a standard temperature with the Arrhenius temperature. The various estimates of the Arrhenius temperature showed a rather large variability, both within a species and between species. Especially for dab, more data seem to be required for a more precise estimate. Nevertheless, the temperature dependence of the various processes seems to differ between the species. Plaice and dab with the most northerly distribution seem to have the lowest Arrhenius temperature,

Fig. 5. Comparison of field data on flounder (after Deniel, 1981; Fonds et al., 1992) with estimates of the DEB model (see Appendix A) under optimal food conditions ($f = 1$) for: total length (cm) − age (year) relationship at various temperatures; growth (mm d^{-1}) of an individual fish of 5 cm at various temperatures; annual energy location (kJ) over body growth and reproduction; gonad mass (g wet mass) and egg production (n) in relationship to body mass (g wet mass).



while in sole and flounder with a more southern geographical distribution the Arrhenius temperature seems to be higher. Furthermore, it might well be that the Arrhenius temperature varies between geographical areas. However, at present such data are lacking.

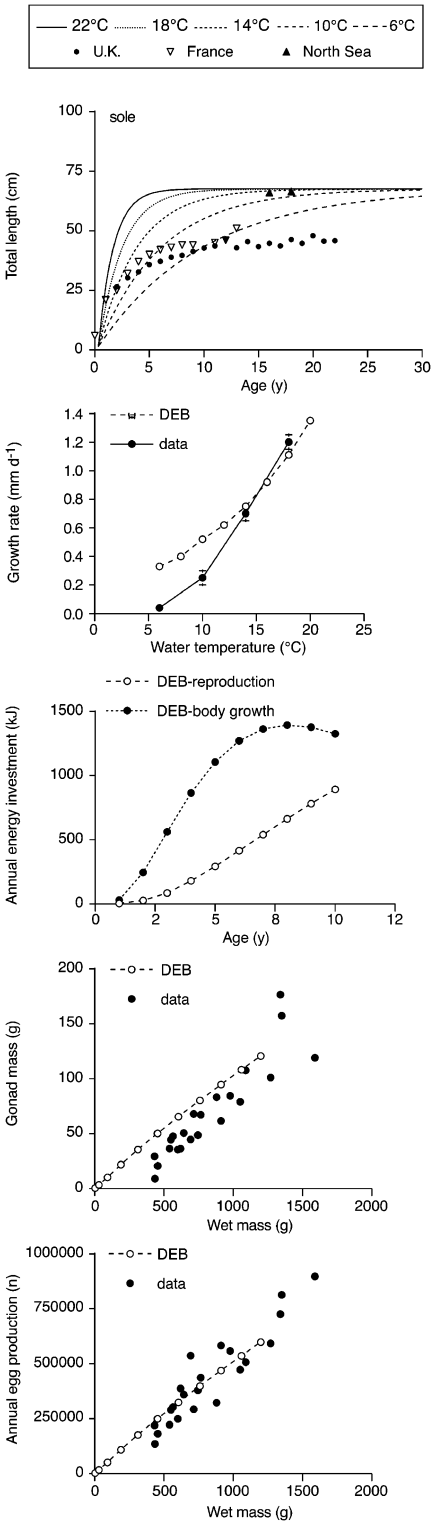
With respect to the analysis of the various parameters, two aspects need to be distinguished:

1. the partition of energy over growth and reproduction,
2. the rate of flow.

The partition of energy over growth and reproduction is reflected in the relationship between total length and age and wet mass with gonad mass and with annual egg production. In all species, the energy partition seems to be in the correct order of magnitude. The predicted relationships between wet mass and gonad mass and annual reproduction fit with field data. The same holds true for the age–total length relationships.

With respect to the rate of energy flow, there seems to be some discrepancy with field data. In all species, the maximum length observed in the field seems to be lower than that predicted by the model simulations under optimal food conditions. This might imply that food intake in the field is lower than maximally possible. However, whether this is a consequence of searching and handling of prey or whether food is limited in the field remains an open question at the moment. With respect to the growth rate of a juvenile in relation to temperature, the model simulations for plaice, flounder and sole show a very good fit with the field data. However, in dab there is some discrepancy between model simulations and observed growth in the laboratory. In dab the slope of increase with temperature seems too low and also at too low a level. This might suggest that in dab not only the Arrhenius temperature is underestimated, but also some parameters need fine-tuning.

Fig. 6. Comparison of field data on dab (after Deniel, 1981 and Fonds and Rijndorp, 1988) with estimates of the DEB model (see Appendix A) under optimal food conditions ($f = 1$) for: total length (cm) − age (year) relationship at various temperatures; growth (mm d^{-1}) of an individual fish of 5 cm at various temperatures; annual energy location (kJ) over body growth and reproduction; gonad mass (g wet mass) and egg production (n) in relationship to body mass (g wet mass).



6.2. Intraspecific comparison of species

Within a species, two aspects are especially of importance in generating individual differences: firstly differences in sex and secondly the differences in abiotic and biotic conditions over the range of distribution of a species.

With respect to differences between males and females, the literature shows that in all flatfish species—plaice, flounder, dab and sole—the females grow to a much larger size, and hence body volume, than the males do (see for instance for plaice and dab: Garstang, 1909; Bohl, 1957). Furthermore, this also holds true for reproductive investment (see for plaice: Rijnsdorp and Ibelings, 1989). On the other hand, length-mass data show that when gonad and testis masses are excluded, there are no differences with respect to structural body mass. Seasonal differences in total mass between males and females are exclusively caused by differences in energy investment in reproduction.

In DEB this diversity of the energetics of the two sexes must be reflected in different parameter values. No differences in parameter values are expected in the volume-specific maintenance costs, in the volume-specific costs for growth $[E_G]$ and in the maximum storage density. Since in the DEB model, the maximum structural volumetric length ($V_m^{1/3}$; cm) is defined by κ, the maximum surface area-specific assimilation rate $\{\dot{p}_{Am}\}$ and the volume-specific maintenance costs $[\dot{p}_M]$, this means that κ and $\{\dot{p}_{Am}\}$—and therefore $\{\dot{p}_{Xm}\}$—should be different. Differences in κ are supported by the observed smaller reproductive investment in males than in females in plaice (Rijnsdorp and Ibelings, 1989). However, differences in κ cannot account for the observed differences in maximum length. κ is even higher in males, which would result in an even higher maximum structural volume and length. Therefore, differences between

Fig. 7. Comparison of field data on sole (after Deniel, 1981, and Fonds and Rijndorp, 1988) with estimates of the DEB model (see Appendix A) under optimal food conditions ($f = 1$) for: total length (cm) − age (year) relationship at various temperatures; growth (mm d^{-1}) of an individual fish of 5 cm at various temperatures; annual energy location (kJ) over body growth and reproduction; gonad mass (g wet mass) and egg production (n) in relationship to body mass (g wet mass).

males and females must be reflected in differences in food intake. For dab, lower food intake rates have indeed been found in the field (Lozán, 1992). In the juvenile phase the reduced food or energy intake will not be fully reflected in a lower growth rate, but is partly compensated for by a higher investment in growth by the higher κ. This figure is a simplification, since in reality κ does not seem to be constant in a species, but might even show marked regional differences between populations, as has been found in the blue mussel (Van Haren and Kooijman, 1993). The impact of $\{\dot{p}_{Xm}\}$ on the ultimate maximum length is much larger than variations in κ are. A similar mechanism is assumed to operate between males and females in the other species.

Over the range of distribution of a species, temperature is a main abiotic factor that varies and affects the energy budget of fish. κ, the volume-specific costs for growth $[E_G]$ and the maximum storage density $[E_m]$ will remain unaffected because they are temperature-independent. Only food intake and maintenance are temperature-dependent; however, from an energetic point of view the functioning of the organism will remain the same as long as these processes vary in a similar way. In reality food intake levels off at high temperatures as has been described for plaice and flounder by Fonds et al. (1992), while the volume-specific maintenance costs $[\dot{p}_M]$ will continue to rise with increasing temperatures. The consequence is that theoretically under optimal food conditions the ultimate maximum length will remain the same with increasing temperature until the optimum temperature of a species is reached, followed by decrease in ultimate length with further increase of temperature. However, a detailed analysis of this mechanism is beyond the scope of the present paper.

6.3. Interspecific comparison of species

A comparison of the various flatfish species is complicated by the uncertainty in some essential parameter values. Despite these uncertainties, the present analysis provides some insight into differences between species. Both the field data and the model simulations illustrate that the various species differ especially with respect to their surface area-specific maximum ingestion rate. Plaice has the highest surface area-specific maximum ingestion rate, followed by flounder, sole and dab. With a κ of 0.85 in plaice 15% of the energy is stored in reproduction. As a result a female of 500 g wet mass has an average gonad mass of 86 g wet mass. Such a female produces on average about 129 10^3 rather big eggs with an average volume of 3.56 mm^3. In flounder the surface area-specific maximum ingestion rate is about 10% lower than in plaice. However, despite this lower surface area-specific maximum ingestion rate a female flounder of 500 g wet mass still has a much larger gonad mass of about 149 g wet mass, because the lower food intake is more than compensated for by the fact that twice the amount of their energy is stored in reproduction (30% compared with 15% in plaice). Since egg volume in flounder is only about 15% of that in plaice, the egg production of a female flounder of 500 g is about 10 times higher (ca. 1563 10^3) than that of plaice. In sole, the surface area-specific maximum ingestion rate is much lower than in flounder. Also only 10% of their energy is stored in reproduction. As a consequence, a female sole of 500 g wet mass has a gonad mass of only about 70 g, which is even lower than that in plaice. However, since egg volume in sole is much lower than in plaice, total egg production of a 500 g female sole is, with 343 10^3 eggs, still nearly three times higher than that in plaice, but also still only 20% of the egg production of flounder. In dab the surface area-specific maximum ingestion rate seems to be even slightly lower than that in sole; however, the gonad mass of a 500 g female dab is about the same as in sole because dab spend more energy in reproduction (15%) than sole (10%). Egg volume of dab is smallest and this means that despite their relatively small gonad masses, the egg production is highest of all species: about 2000 10^3 eggs.

The above comparative analysis of growth and reproduction in the four flatfish species is preliminary and only on outlines. Not only some fine-tuning of the various parameters is required, but also more details should be incorporated with respect to differences between species, such as for instance variability in κ over the range of a species (Van Haren and Kooijman, 1993).

6.4. The next step

The aim of the present paper is to introduce a framework in which the quantitative aspects of the energy allocation to growth and reproduction in

flatfish are described in a coherent way. The Dynamic Energy Budgets introduced in this paper appear to be applicable to flatfish energetics. The DEB model successfully describes the energy allocation to growth and reproduction in a number of species and the intra- and interspecific differences between species can be captured in the same model using only different parameter values. This offers a new approach of the physiology and energetics of flatfish species.

Some fine-tuning of the parameters seems desirable. A link between the quantitative DEB model with Fry's qualitative scheme of the effects of environmental factors on the physiology of fish (Fry, 1947,1971) seems promising. Another spin-off is an analysis of the various size-dependent physiological variables such as metabolism, respiration, egg size etc. (Kooijman, 1986a,b,c). The DEB model also provides an opportunity to link physiology with various trade-offs in the life history of the flatfish (see for instance Roff, 1991). However, these aspects fall outside the scope of the present paper.

Acknowledgements

Thanks are due to our colleague Mark Fonds for putting his published and unpublished original experimental data at our disposal, and to Henk Hobbelink for graphical assistance. This is NIOZ publication No. 3590.

Appendix A. Structure and parameters of the DEB model

A.1. Model structure

```
Body_growth(t) = Body_growth(t − dt) +
        (flow_to_growth − Starvation_return)*dt
INIT Body_growth = 0
flow_to_growth = kappa*utilization_rate −
        flow_to_main
Starvation_return = IF(assimilation_rate = 0)
        THEN flow_to_growth ELSE 0
Body_main(t) = Body_main(t − dt) +
        (flow_to_main)*dt
INIT Body_main = 0
flow_to_main =
        vol_costs_maintenance*body_volume
Energy_storage(t) = Energy_storage(t − dt) +
        (assimilation_rate + Starvation_return −
        utilization_rate)*dt
INIT Energy_storage = 5
assimilation_rate = IF(Season > 0.70) THEN 0
        else (max_surf_ass_rate*
        functional_response*body_volume^(2/3))
Starvation_return = IF(assimilation_rate = 0)
        THEN flow_to_growth ELSE 0
utilization_rate = (Eg*(max_surf_ass_rate/
        Em)*body_volume^(−1/3) +
        vol_costs_maintenance)/(kappa/
        body_volume + Eg/Energy_storage)
Mat_and__Repr(t) = Mat_and__Repr(t − dt) +
        (flow_to_mat_and_rep)*dt
INIT Mat_and__Repr = 0
flow_to_mat_and_rep = (1 −
        kappa)*utilization_rate − flow_to_mat_main
Mat_main(t) = Mat_main(t − dt) +
        (flow_to_mat_main)*dt
INIT Mat_main = 0
flow_to_mat_main = MIN(Vp*(1 − kappa)/
        kappa*vol_costs_maintenance,body_
        volume*(1 − kappa)/kappa*vol_costs_
        maintenance)
pool(t) = pool(t − dt) + (utilization_rate −
        flow_to_main − flow_to_growth −
        flow_to_mat_main −
        flow_to_mat_and_rep)*dt
INIT pool = 0
utilization_rate = (Eg*(max_surf_ass_rate/
        Em)*body_volume^(−1/3) +
        vol_costs_maintenance)/(kappa/
        body_volume + Eg/Energy_storage)
flow_to_main =
        vol_costs_maintenance*body_volume
flow_to_growth = kappa*utilization_rate −
        flow_to_main
flow_to_mat_main = MIN(Vp*(1 − kappa)/
        kappa*vol_costs_maintenance,body_
        volume*(1 − kappa)/kappa*vol_costs_
        maintenance)
flow_to_mat_and_rep = (1 −
        kappa)*utilization_rate − flow_to_mat_main
```

A.2. Input parameters

```
actual_temp = 10
```

```
Arrhenius_temp = 7000
Eg = 7000
Em = 2500
food_density = 690000
functional_response = 1/(1 +
      saturation_coefficient/food_density)
kappa = 0.85
loss_due_to_digestion = 0.20
max_surf_ass_rate = (1 −
      loss_due_to_digestion)*max_surf_ing_rate
max_surf_ing_rate = 630*temp_correction
saturation_coefficient = 184000
Season = SIN(2*PI*(TIME + 75)/360)
shape = 0.219
temp_correction = 1*EXP(Arrhenius_temp*(1/
      (273 + 10) −1/(273 + actual_temp)))
vol_costs_maintenance = 20.8*temp_correction
Vp = 106.5
```

A.3. Output parameters

```
Annual_repr(t) = Annual_repr(t − dt) +
      (reprod_rate − spawning)*dt
INIT Annual_repr = 0
reprod_rate = flow_to_mat_and_rep
OUTFLOWS:
spawning = PULSE(Annual_repr,360,360)
body_volume = Body_growth/Eg + 0.03375
eggs = Gonads/J_per_egg
Eggs_per_g_wet_weight = 1500
Egg_costs = 0.10
Energy_content = E_divided_by_V*tot_wet_weight
E_divided_by_V = Energy_storage/body_volume
Gonads = Annual_repr*(1 − Egg_costs)
Gonad_wet_weight = eggs/Eggs_per_g_wet_weight
J_per_egg = 5
k_wet = tot_wet_weight/TL^3
test_use_utilisation = flow_to_growth +
      flow_to_main + flow_to_mat_and_rep +
      flow_to_mat_main
TL = (body_volume^(1/3))/shape
tot_wet_weight = body_volume +
      Gonad_wet_weight
```

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