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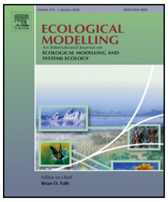

Production efficiency differences among populations can be explained by physiology

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ABSTRACT

Production efficiency may differ considerably among individuals and populations. Here we theoretically analyze to what extent differences in efficiency among populations relate to basic physiological processes. We derive characteristics for a stationary population of constant size using (1) an extended Bertalanffy growth equation and (2) Dynamic Energy Budget (DEB) theory to describe individual energetics and mortality combined with an additional thinning rule to provide a more realistic description of survival than the one usually made by only assuming constant background mortality. The production-assimilation ratio as predicted by DEB theory appeared to be strongly correlated with the Bertalanffy growth coefficient and the ultimate reproduction rate. Birds and to a lesser extent mammals have a much lower ratio than other taxa. Benthic marine invertebrate grazers, which are mainly molluscs, showed a higher ratio than pelagic grazers, mostly arthropods, which may have consequences for overall ecological efficiency when marine coastal systems get more dominated by the benthic compartment as a result of human impacts such as the construction of windfarms.

1. Introduction

Solar energy is captured by primary producers and transferred into chemical energy. The rate at which chemical energy arrives at the higher levels of the plant–herbivore–carnivore food chain not only depends on the net primary productivity, but also upon the ecological or trophic efficiency of succeeding links in the food chain. Ecological efficiency, also called Lindeman efficiency, is the ratio of the productivity of a trophic level and that of the level below (Lindeman, 1942). For animals the ecological efficiency can be decomposed as the product of (1) the consumption efficiency, which equals the ingested energy by a trophic level divided by the produced energy at the level below; (2) the assimilation efficiency, which is the ratio of the assimilated energy and the ingested energy; and (3) the production efficiency, which equals the ratio of the productivity of the trophic level and the assimilated energy (Chapin et al., 2002; Reiss, 1989).

Production efficiency differs considerably among individuals, populations and food chains (Van der Meer, 2020). Here we examine whether systematic differences exist in production efficiency among animal populations and what the most important underlying physiological processes, in terms of among other things food intake rate, maintenance rate, growth rate and reproductive rate, are in determining the efficiency.

In this paper we will use Dynamic Energy Budget (DEB) theory, as developed by Kooijman (2010), to predict production efficiency. DEB theory provides an integrated look at whole-organism energetics and, in contrast to simpler models, such as the Bertalanffy growth model (von Bertalanffy, 1934) or the extended ontogenetic growth model of the Metabolic Theory of Ecology (Hou et al., 2008), includes reserve dynamics and reproduction. In order to make the step from efficiency at the individual level to that at the population level, knowledge of organism energetics does not suffice, and the survival function has to be known as well. DEB theory only provides a survival function as a result of aging, but natural populations are prone to many other causes of death, such as predation, parasitism, diseases, starvation or accidents. Various types of survival functions will be examined, and for each type focus will be on the particular case that results in constant population size, that is when the population rate of increase equals zero.

At constant food availability, DEB theory predicts that isomorphic animals grow according to the Bertalanffy model, which can thus be considered as a simplified version of the standard DEB model for isomorphic animals. We first look at the efficiency predictions of the well-known Bertalanffy model (von Bertalanffy, 1934), but extended with a description of reproduction. The advantage of such simplified

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model is that an analytical approach is much easier, whereas for the more complicated DEB model we necessarily have to rely on simulations. We embroider on earlier work on a comparison between the efficiencies of poikilothermic and homeothermic species (Van der Meer, 2020) and on recent work by Kooijman et al. (2020), who linked DEB energetics and the thinning rule to population growth of animals.

Predicted production efficiencies will be compared among species from various taxa, which are extensively covered in the Add-my-Pet collection (Van der Meer et al., 2014; Marques et al., 2018). The DEB model has already been parametrized for more than four thousand different species. As an example of possible applications of the theory, we will explore efficiency differences between pelagic and benthic marine grazers. It has been noted that the benthic biomass of coastal marine systems, such as the North Sea, has increased over the last decades, while the pelagic part decreased. The idea exists that large-scale construction of windfarms and the associated increase in artificial hard structures will further increase the benthic compartment. We ask the question: How would this transition affect production efficiencies within the ecosystem?

2. Stationary Bertalanffy populations

Consider a stable population with zero population growth rate and constant age-specific birth and mortality rates. Assume further that the food assimilation rate of each individual is proportional to the surface area of the individual. For such stationary population the production-assimilation ratio r_P equals

$$r_P = \frac{\int_0^\infty f(x) q_t V(x) dx}{\int_0^\infty f(x)(\int_0^x aV(y)^{2/3} dy) dx} = \frac{q_t \int_0^\infty f(x) V(x) dx}{a \int_0^\infty S(x) V(x)^{2/3} dx} \tag{1}$$

where $f(x)$ is the density function (time^{-1}) of age at death x (time), q_t is the volume-specific energy content (energy length^{-3}), $V(x)$ is the volume (length^3) at age x, a is the area-specific assimilation rate (energy length^{-2} time^{-1}), $S(x)$ is the survival function (or stable age distribution) (-), and y is age (time) (Van der Meer, 2020). Note that $q_t V(x)$ (energy) equals the life-time production of an individual that dies at age x, and that $\int_0^x aV(y)^{2/3} dy$ (energy) equals the life-time assimilation of such individual.

If we further assume that the maintenance rate of an individual is proportional to its volume and that the individual growth rate is the difference between the food assimilation rate and the maintenance rate, we arrive at the Bertalanffy growth equation (Paloheimo and Dickie, 1965)

$$\frac{\mathrm{d}V}{\mathrm{d}y} = \frac{aV^{2/3} - bV}{q_r} \tag{2}$$

where b is the volume-specific maintenance rate (energy length^{-3} time^{-1}), and q_r is the energy required to create one unit of volume (energy length^{-3}). As there are always overhead costs of growth, implying that the energy that is required for tissue growth is more than the chemical energy that the created tissue actually contains, it follows that $q = q_t/q_r < 1$. At the individual level, the ratio between the production rate and the assimilation rate, which is given by $q(1 - V^{1/3}/V_\infty^{1/3})$, decreases linearly with length, starting at q when the organism is infinitely small and going to 0 when it reaches its ultimate size (Van der Meer, 2020). Note that when the organism is extremely small, maintenance rate is negligible compared to assimilation rate and all assimilated energy is put into growth, with a conversion efficiency of q. The organism approaches its ultimate size when the assimilated energy is just sufficient to pay for the maintenance, and no energy is left anymore for growth.

2.1. *Production-assimilation ratio when mortality rate is constant*

Returning to the population level and assuming a constant instantaneous mortality rate equal to λ, it follows that the density function equals $f(x) = \lambda \exp(-\lambda x)$, and the survival function $S(x) = \exp(-\lambda x)$. Solving Eq. (1) reveals

$$r_P = q \frac{\lambda}{\lambda + b/q_r} = q \frac{\lambda}{\lambda + 3\gamma} \tag{3}$$

where $\gamma = b/(3q_r)$ is the Bertalanffy growth coefficient (Van der Meer, 2020). Hence the population production efficiency depends upon the volume-specific maintenance rate b (scaled by the energy q_r required to create one unit of volume) relative to the instantaneous mortality rate λ. If the mortality rate is much higher than the scaled maintenance rate, the efficiency will approach the ratio q. This is logical, as a high mortality rate means that most animals die at a small size and these small animals have an efficiency, as was shown earlier, close to q (Van der Meer, 2020).

2.2. *Thinning implies that hazard rate is proportional to growth rate*

Yet, the notion of constant mortality is highly unrealistic for most marine organisms, where the numerous and usually unprotected tiny larvae are much more vulnerable than the larger adults. Following Kooijman et al. (2020) we add a ‘thinning rule mortality’ to the constant mortality rate. Thinning implies that the mortality rate is such that the total expected intake rate of an animal does not change over time. Expected assimilation rate equals

$$A(y) = S(y) \cdot aV(y)^{2/3} \tag{4}$$

Hence

$$\frac{dA(y)}{dy} = 0 \tag{5}$$

By definition, the rate of change of body volume V and survival fraction S are given by

$$\frac{dV(y)}{dy} = r(y)V(y) \tag{6}$$

$$\frac{dS(y)}{dy} = -h(y)S(y) \tag{7}$$

where $r(y)$ is the instantaneous growth rate and $h(y)$ the hazard rate at age y. From Eqs. (4) and (5) it follows that

$$\frac{dS(y)V(y)^{2/3}}{dy} = S(y)\frac{dV(y)^{2/3}}{dy} + V(y)^{2/3}\frac{dS(y)}{dy} = 0 \tag{8}$$

Combining with Eqs. (6) and (7) and noting that $dV(y)/dy = \frac{3}{2}V(y)^{1/3} \cdot dV(y)^{2/3}/dy$ and thus $dV(y)^{2/3}/dy = \frac{2}{3}r(y)V(y)^{2/3}$ it follows that

$$S(y)\frac{2}{3}r(y)V(y)^{2/3} - h(y)S(y)V(y)^{2/3} = 0 \tag{9}$$

which gives

$$h(y) = \frac{2}{3}r(y) \tag{10}$$

Hence, the thinning rule implies that the hazard rate equals 2/3 of the instantaneous body volume growth rate (Kooijman et al., 2020).

2.3. *Bertalanffy growth and thinning reveal the survival function*

In case of Bertalanffy growth this results in a hazard rate equal to

$$h(x) = \frac{2}{3}\frac{1}{q_r}\left(\frac{a}{V(x)^{1/3}} - b\right) = \frac{2b}{3q_r}\left(\frac{V_\infty^{1/3}}{V(x)^{1/3}} - 1\right) = 2\gamma\left(\frac{1}{1 - e^{-\gamma x}} - 1\right) \tag{11}$$

where $\gamma = b/(3q_r)$ is the Bertalanffy growth coefficient from the equation $V(x)^{1/3} = V_\infty^{1/3}(1-e^{-\gamma x})$. Adding a constant background hazard rate λ to the 'thinning rule' hazard rate gives

$$h(x) = \lambda + 2\gamma\left(\frac{1}{1-e^{-\gamma x}} - 1\right) \tag{12}$$

Recall that the survival function can be written as

$$S(x) = \exp\left(-\int_{x_0}^{x} h(y)dy\right) \tag{13}$$

where x_0 is the age at birth. It follows that

$$S(x) = \exp\left(-\int_{x_0}^{x}\left(\lambda + 2\gamma\left(\frac{1}{1-e^{-\gamma y}} - 1\right)\right)dy\right) \tag{14}$$

Solving the integral gives

$$S(x) = \exp\left((2\gamma - \lambda)\int_{x_0}^{x} 1dy - 2\gamma\int_{x_0}^{x}\frac{1}{1-e^{-\gamma y}}dy\right) \tag{15}$$

$$S(x) = \exp\left((2\gamma - \lambda)(x - x_0) - 2\gamma\frac{\log(e^{-\gamma y} - 1)}{\gamma} + c]_{x_0}^{x}\right) \tag{16}$$

$$S(x) = e^{(2\gamma-\lambda)(x-x_0)}\left(\frac{e^{\gamma x_0} - 1}{e^{\gamma x} - 1}\right)^2 \tag{17}$$

2.4. *Lifetime assimilation, maintenance, and production*

The expected lifetime production follows from

$$P_P = q_t\left(V(y_0) + \int_{y_0}^{\infty} S(y)g(y)dy\right) \tag{18}$$

where $V(0)$ is the volume at birth and $g(y)$ the growth rate

$$g(y) = \frac{aV(y)^{2/3} - bV(y)}{q_r} \tag{19}$$

Hence the lifetime production is the energy content of the newborn $q_t V(y_0)$ plus the lifetime assimilation minus the lifetime maintenance, both multiplied by q.

The expected lifetime assimilation of an individual, which for a stationary population equals the population assimilation when multiplied by the constant birth rate, follows from

$$A_P = \int_{y_0}^{\infty} S(y)A(y)dy \tag{20}$$

where

$$A(y) = aV(y)^{2/3} \tag{21}$$

Note that the survival function can be re-written as

$$S(y) = \left(\frac{e^{\gamma y}}{e^{\gamma y_0}}\right)^2\left(\frac{e^{\gamma y_0} - 1}{e^{\gamma y} - 1}\right)^2 e^{-\lambda(y-y_0)} \tag{22}$$

and the assimilation rate as

$$A(y) = aL_\infty^2\left(\frac{e^{\gamma y} - 1}{e^{\gamma y}}\right)^2 \tag{23}$$

Hence, Eq. (20) can be simplified to

$$A_P = aL_\infty^2(1 - e^{-\gamma y_0})^2\int_{y_0}^{\infty} e^{-\lambda(y-y_0)}dy \tag{24}$$

which gives

$$A_P = aL_\infty^2(1 - e^{-\gamma y_0})^2\frac{1}{\lambda} \tag{25}$$

saying that the lifetime assimilation equals the assimilation from a newborn divided by the background hazard rate λ.

Lifetime maintenance is given by

$$M_P = b\int_{y_0}^{\infty} S(y)V(y)dy \tag{26}$$

and by writing

$$V(y) = L_\infty^3\left(\frac{e^{\gamma y} - 1}{e^{\gamma y}}\right)^2(1 - e^{-\gamma y}) \tag{27}$$

it can easily be seen that Eq. (26) can be simplified to

$$M_P = bL_\infty^3(1 - e^{-\gamma y_0})^2\int_{y_0}^{\infty}(1 - e^{-\gamma y})e^{-\lambda(y-y_0)}dy \tag{28}$$

which gives

$$M_P = bL_\infty^3(1 - e^{-\gamma y_0})^2\left(\frac{1}{\lambda} - e^{-\gamma y_0}\frac{1}{\gamma + \lambda}\right) \tag{29}$$

or

$$M_P = bL_\infty^3(1 - e^{-\gamma y_0})^2\left(\frac{1}{\lambda} - \left(1 - \frac{L(y_0)}{L_\infty}\right)\frac{1}{\gamma + \lambda}\right) \tag{30}$$

An example of how survival, expected assimilation rate, expected maintenance rate and expected production rate depend upon age is shown in Fig. 1.

2.5. *Thinning increases the production-assimilation ratio*

Recall that $aL_\infty^2 = bL_\infty^3$ and $L(y_0) = L_\infty(1 - e^{-\gamma y_0})$. Hence, the ratio between production and assimilation, which is

$$r_P = \frac{q_t L(y_0)^3 + q(A_P - M_P)}{A_P} \tag{31}$$

can be written as

$$r_P = \frac{q_t\lambda}{b}\frac{L(y_0)}{L_\infty} + q\left(1 - \frac{L(y_0)}{L_\infty}\right)\frac{\lambda}{\lambda + \gamma} \tag{32}$$

which, in case that $L(y_0) \ll L_\infty$, simplifies to

$$r_P = q\frac{\lambda}{\lambda + \gamma} \tag{33}$$

So, apart from the minor adjustments due to taking into account the contribution of a newborn of size greater than zero, the ratio is larger than the case without thinning, where we had $\lambda+3\gamma$ in the denominator instead of $\lambda + \gamma$ (Fig. 2). Note that the assumption of an additional constant background mortality λ prevents that animals live forever, which would have been the case if one only considers thinning-based mortality. Alternatively, one can refrain from making the constant background mortality assumption and add instead a mortality-due-to-aging term, the most simple one being that of a maximum age y_m. In that case, expected lifetime assimilation becomes

$$A_P = aL_\infty^2(1 - e^{-\gamma y_0})^2(y_m - y_0) \tag{34}$$

expected lifetime maintenance gets

$$M_P = bL_\infty^3(1 - e^{-\gamma y_0})^2\left((y_m - y_0) + \frac{1}{\gamma}(e^{-\gamma y_m} - e^{-\gamma y_0})\right) \tag{35}$$

and their ratio is given by

$$r_P = \frac{q_t}{b(y_m - y_0)}\frac{L(y_0)}{L_\infty} + q\frac{1}{\gamma}\frac{e^{-\gamma y_m} - e^{-\gamma y_0}}{y_m - y_0} \tag{36}$$

3. Constant population size

Knowledge of the growth function and survival function is not sufficient to derive the population instantaneous rate of increase r. The reproduction rate, and how it varies with age, should also be known. The Bertalanffy model ignores reproduction, but here we will describe reproduction rate simply by a function of surface area. We assume that at maturity the animal increases the assimilation rate and that this additional assimilated material is directly transformed in reproductive material. So reproduction rate $R(y)$ in terms of number of progeny produced per unit of time is given by

$$R(y) = wL(y)^2/E_0 \tag{37}$$

where w is the additional area-specific assimilation rate, and this type of assimilation starts when the length of the animal is larger than the length at the puberty threshold, *i.e.* $L(y) > L_P$. The parameter E_0 gives the energy content of the newly produced animal.

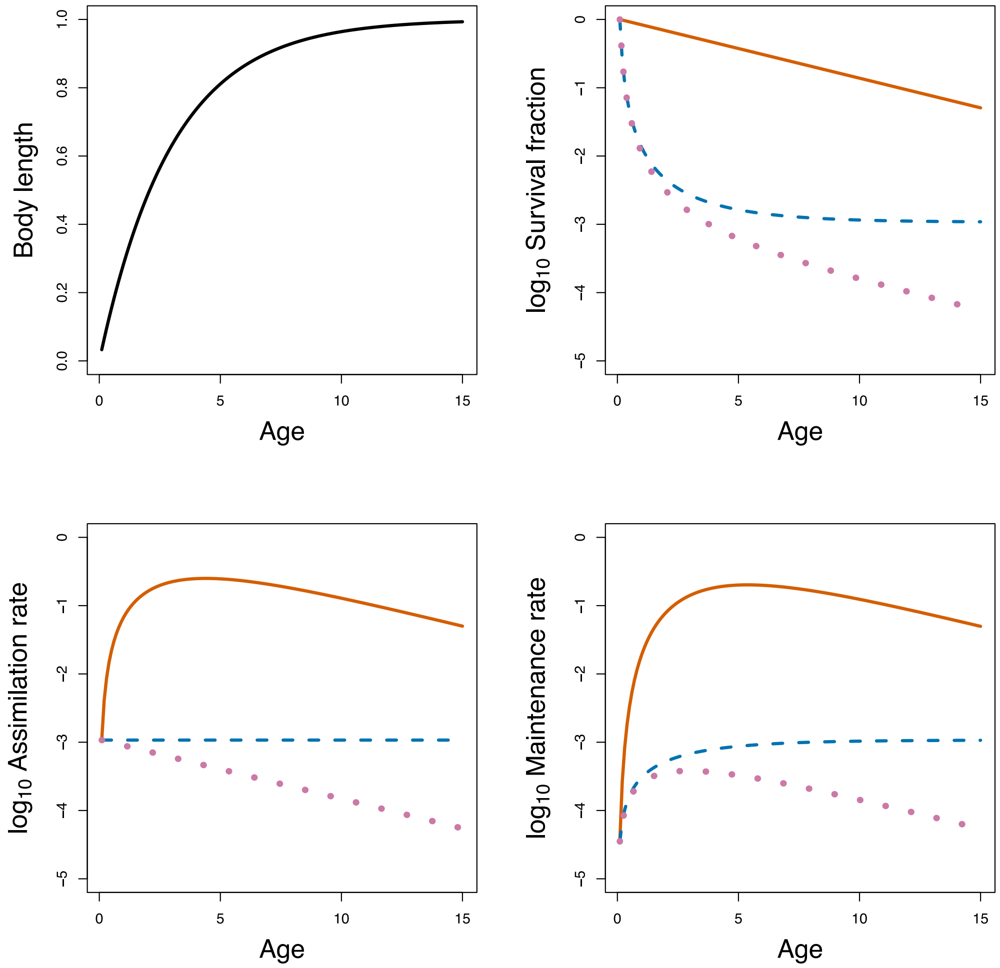

Fig. 1. Body length, survival fraction, expected assimilation rate, and expected maintenance rate versus age. Note the log-scales. Bertalanffy growth, with $a = 1$, $b = 1$, $q_t = 1$, $q_r = 1$, and $\lambda = 0.2$. Three different models: constant background mortality (red solid lines), thinning-rule mortality (blue dashed lines), and both (purple dotted lines).

The McKendrick characteristic equation (also attributed to others, *e.g.* Euler, Sharpe, Lotka, Von Foerster) can then be used to find the appropriate conditions under which the population size remains constant. For the second approach as sketched in the previous section, that is the thinning rule plus a background mortality λ, the question is: For what value of λ the population increase is zero? For the third approach, with thinning-rule mortality and with death by aging included, one may choose to vary the specific assimilation parameter a of the Bertalanffy growth equation, given the idea that this value will be lower at lower food availability, and find that value of a for which the population size is constant. The McKendrick equation follows from the idea that the renewal rate $B(t)$ of the population at time t is given by

$$B(t) = \int_{y_p}^{y_m} B(t-y)S(y)R(y)dy \tag{38}$$

which says that the renewal rate at time t is the integral of all animals that were previously born and are still alive times their reproduction rate at time t (Keyfitz and Keyfitz, 1997). Note that animals born less than the age of maturity y_p ago, do not contribute to the reproduction at time t. The same holds for animals born more than the maximum age y_m ago. An informed guess says that the population size and the birth rate changes exponentially over time, and Eq. (38) can be re-written as

$$Qe^{rt} = \int_{y_p}^{y_m} Qe^{r(t-y)}S(y)R(y)dy \tag{39}$$

or

$$1 = \int_{y_p}^{y_m} e^{-ry}S(y)R(y)dy \tag{40}$$

which, in case of a survival function that reveals $r = 0$, becomes

$$1 = \int_{y_p}^{y_m} S_0(y)R(y)dy \tag{41}$$

For the thinning-rule mortality with an additional constant background survival rate, we are looking for $\lambda = \lambda_0$ that gives

$$1 = \frac{w}{E_0} L_\infty^2 (1 - e^{-\gamma y_0})^2 \int_{y_P}^{\infty} e^{-\lambda_0 (y - y_0)} dy \tag{42}$$

which gives

$$1 = \frac{w}{E_0} L_\infty^2 (1 - e^{-\gamma y_0})^2 \frac{1}{\lambda_0} e^{-\lambda_0 (y_p - y_0)} \tag{43}$$

See also Eqs. (20) to (25) for understanding the mathematical steps that were taken to arrive at this result. Unfortunately, this is a complicated expression, and λ_0 has to be obtained by a root-finding procedure.

3.1. A simplifying assumption

If for the sake of convenience we assume that animals start to reproduce right at birth, λ_0 can be expressed explicitly as

$$\lambda_0 = \frac{wL_\infty^2 (1 - e^{-\gamma y_0})^2}{E_0} = wL(y_0)^2/E_0 \tag{44}$$

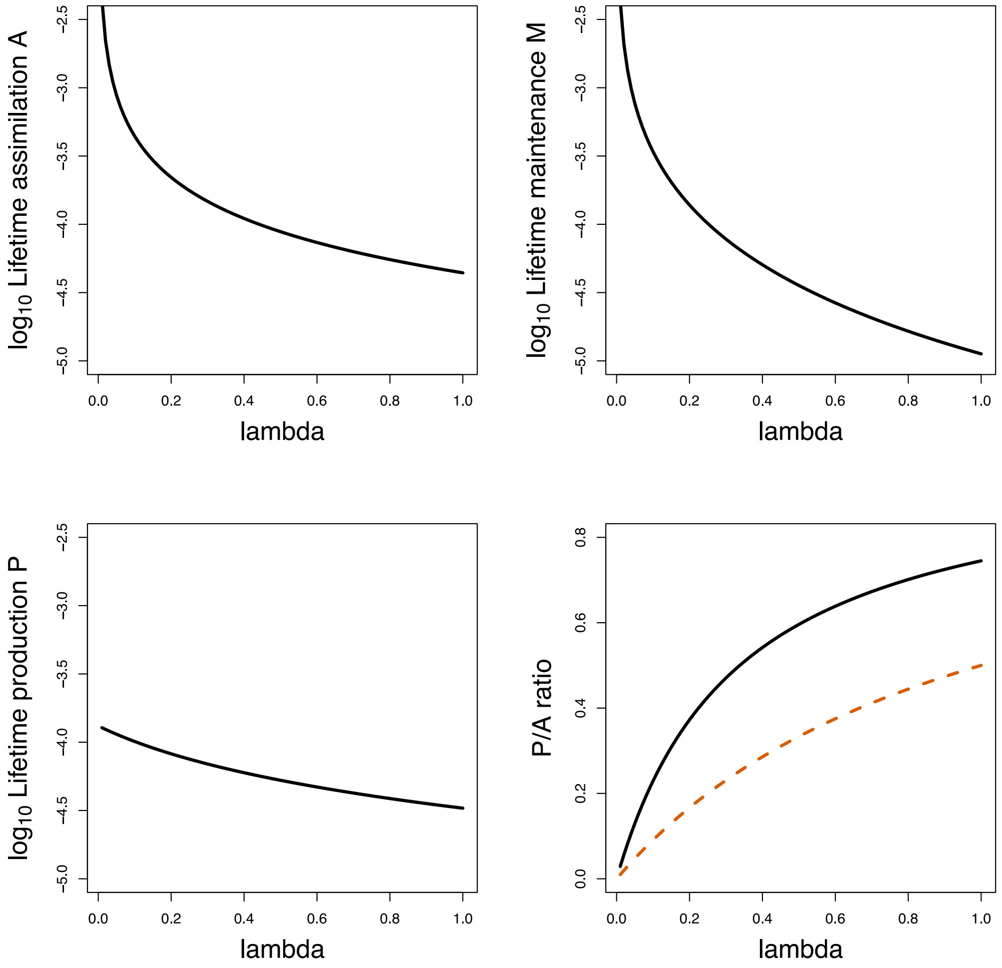

Fig. 2. Lifetime assimilation, maintenance, and production and the ratio between production and assimilation versus background mortality rate λ. Bertalanffy growth, with $a = 1$, $b = 1$, $q_t = 1$, $q_r = 1$. Two different models: constant background mortality (red line), and thinning-rule plus constant background mortality (black lines).

which says that the additional constant background hazard rate is equivalent to the ratio between the initial assimilation rate required for reproduction divided by the energy required to produce one offspring.

When the additional assimilation rate for reproduction is taken into account, the ratio between production and assimilation, is given by

$$r_P = \frac{q_t L(y_0)^3 + q(A_P - M_P)}{\frac{a+w}{a} A_P} \tag{45}$$

where A_P represents the assimilation channeled towards maintenance and growth. Assuming that $L(y_0) \ll L_\infty$ and combining with Eq. (44), the ratio between production and assimilation can be written as

$$r_P = q\frac{a}{a+w}\frac{\lambda_0}{\lambda_0+\gamma} = q\frac{a}{a+w}\frac{1/\gamma}{1/\gamma + E_0/(wL(y_0)^2)} \tag{46}$$

where $q = q_t/q_r < 1$ is the ratio between the energy content of somatic tissue and the energy required to produce it, and $\frac{a}{a+w}$ the relative contribution of the assimilation channeled towards growth and maintenance to the total assimilation, which is (as we will see below) similar to the DEB parameter κ. The reciprocal of the Bertalanffy growth coefficient $1/\gamma$ can be interpreted as the time it takes to grow to a specific relative size (that is relative to the ultimate size) and the ratio $E_0/(wL(y_0)^2)$ can be interpreted as the time it would take to produce one offspring when intake rate remains at the initial rate. Hence, the production-assimilation ratio is higher when (1) overhead costs of growth are low, (2) a larger proportion of the overall intake is channeled towards somatic growth and maintenance, and (3) the time it takes to grow is large compared to the time it takes to produce one offspring.

4. DEB modeling

The Bertalanffy individual, which immediately starts reproducing, has only one life-stage and can be described by only one state variable, *i.e.* volume. The standard DEB model organism is much more complicated (Kooijman, 2010). It has three succeeding life stages, the embryo, which neither feeds nor reproduces, the juvenile, which feeds but does not reproduce, and the adult, which feeds and reproduces. The organism is described by three state variables: (1) structural body volume V (length^3), (2) reserve density $[E]$ (energy length^{-3}), which is the amount of reserves per unit of structural body volume, and (3) maturity E_H (energy), which is the cumulative energy allocated to development.

Here we will not discuss the ideas and assumptions underlying the standard DEB model, but refer to Kooijman (2010) for a detailed treatment. More gentle introductions of DEB theory are provided by Van der Meer (2006, 2016, 2019, 2020). In the remaining section we will summarize the comparison between the Bertalanffy model and the standard DEB model as provided by Van der Meer (2020).

Table 1
Primary parameters of the standard DEB model.

Symbol	Dimension	Interpretation	Process
$\{\dot{p}_{Am}\}$	$eL^{-2}t^{-1}$	Surface-area-specific maximum assimilation rate	Assimilation
κ_X	–	Digestion efficiency	Digestion
$\dot{v}$	Lt^{-1}	Energy conductance	Mobilization
κ	–	Fraction of mobilization rate spent on maintenance plus growth	Allocation
$[\dot{p}_M]$	$eL^{-3}t^{-1}$	Volume-specific maintenance rate	Turnover/activity
$[E_G]$	eL^{-3}	Volume-specific costs of growth	Growth
$\dot{k}_J$	–	Specific maturity maintenance	Regulation/defence
κ_R	–	Reproduction efficiency	Egg formation
E_H^b	e	Maturity at birth	Life history
E_H^p	e	Maturity at puberty	Life history

Table 2
The DEB interpretation of the Bertalanffy model.

DEB process or parameter name	Bertalanffy	DEB
Total assimilation rate	$aV^{2/3}/\kappa$	$f\{\dot{p}_{Am}\}V^{2/3}$
Area-specific assimilation rate channeled to soma	a	$\kappa f\{\dot{p}_{Am}\}$
Volume-specific maintenance rate	b	$[\dot{p}_M]$
Volume-specific costs of growth including reserves for growth	q_r	$\kappa f\{\dot{p}_{Am}\}/\dot{v}+[E_G]$
Volume-specific energy content of structure including reserves	q_t	$\{f\dot{p}_{Am}\}/\dot{v}+[E_V]$

At constant food availability, the standard DEB model, in terms of somatic volume growth and reserve dynamics, resembles the Bertalanffy model. Volume growth is given by

$$\frac{\mathrm{d}V}{\mathrm{d}y} = \frac{\kappa f\{\dot{p}_{Am}\}V^{2/3} - [\dot{p}_M]V}{\kappa f\{\dot{p}_{Am}\}/\dot{v} + [E_G]} \tag{47}$$

The structure of the equation is similar to that of Eq. (2) and only parameters differ. See Table 1 for an explanation of all parameters of the standard DEB organism. When the mother has provided the embryo with the adequate amount of reserves, reserve density does not change at constant food availability. This implies that the structural volume V including the reserves $[E]V$, easily translates into the energy content of the total body by the proportionally coefficient

$$q_t = \frac{f\{\dot{p}_{Am}\}}{\dot{v}} + [E_V]$$

where $[E_V]$ is the energy density of the structural body (Van der Meer, 2020). That is the energy content of the structural body and the reserves summed equals $E_{E+V} = q_t V$. At constant food conditions, individual production rate (including reserves) $q_t dV/dt$ divided by the assimilation rate $\{\dot{p}_{Am}\}V^{2/3}$ thus equals

$$\kappa q(1 - \frac{V^{1/3}}{V_\infty^{1/3}}) \tag{48}$$

where $V_\infty^{1/3} = \kappa\{\dot{p}_{Am}\}/[\dot{p}_M]$. The conclusions on production efficiency for the Bertalanffy model thus more or less hold for the standard DEB model, apart of course from the reproduction part, which will be discussed next. Table 2 (taken from Van der Meer, 2020) provides the DEB interpretation of the Bertalanffy parameters. Van der Meer (2020) showed that under some simplifying assumptions the reproduction rate of the standard DEB model is given by

$$\dot{R} = \frac{\kappa_R}{R_0}(1-\kappa)\left(\dot{p}_C - \frac{[\dot{p}_M]}{\kappa}V_p\right) \tag{49}$$

where R_0 takes account of the energy investment in a single egg and egg mortality. The term $\dot{p}_C$ represents the rate at which the reserves are mobilized, which equals

$$\dot{p}_C = \frac{f\{\dot{p}_{Am}\}/\dot{v}}{\kappa f\{\dot{p}_{Am}\}/\dot{v} + [E_G]}\left(\dot{v}[E_G]V^{2/3} + [\dot{p}_M]V\right) \tag{50}$$

and thus depends on a weighted sum of surface area and volume. In conclusion, for the extended Bertalanffy model reproduction rate was proportional to surface area, but in the simplified standard DEB model described in this section, volume and volume at puberty are also involved.

5. Fitting the DEB model

Parameter estimates for all species for which a DEB model has been fitted are presented at the add-my-pet website at https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/index.html. The website also gives 'population traits', which include yield coefficients. For a stationary population the amount of living biomass does not change, and basically such population converts all food ingested into yield, which consists of either (1) faeces, (2) dead structure, (3) dead reserves, (4) carbon dioxide, (5) nitrogenous waste, (6) water, or (7) di-oxygen. The reported yield coefficients for faeces Y_P, dead structure Y_{Vd}, and dead reserves Y_{Ed} are expressed in C-moles produced per C-mole ingested. The same holds for the yield coefficient for carbon dioxide Y_C. The yield coefficient for nitrogenous waste Y_N is the yield in terms of N-moles per C-mole ingested and has to be multiplied by n_{CN}, which gives the number of C-moles per N-mole of the nitrogenous waste, to arrive at the nitrogenous waste yield in terms of C-moles produced per C-mole ingested. Here we are interested in the production (of dead structure and reserves) and assimilation (of food) in terms of C-moles and the yield of water and di-oxygen can therefore be ignored. The sum of Y_P, Y_{Vd}, Y_{Ed}, Y_C and Y_N n_{CN} equals 1 by definition and, because faeces are not assimilated, we calculated the production-assimilation ratio as $y_{PA} = (Y_{Vd} + Y_{Ed})/(1 - Y_P)$.

Yield coefficients were obtained by numerically solving the McKendrick equation as given here in Eq. (41), but with the appropriate DEB model (not necessarily the standard DEB model for isomorphs as discussed in this paper) and with mortality either due to aging (according the DEB aging rules, not discussed in this paper) or to thinning. Constant population size was achieved by adjusting the scaled functional response f. For further details we refer to Kooijman et al. (2020).

All DEB data (among other things the primary DEB parameters such as κ, compound parameters such as the Bertalanffy growth coefficient r_B, implied traits such as the ultimate reproduction rate R_i, and population traits such as the yield coefficient Y_{Vd}), were downloaded from the add-my-pet website (Marques et al., 2018) on January 2, 2024. Out of 4293 species from the collection, yield coefficients and relevant (compound) parameters were available for 3779 species.

Additionally, we classified all aquatic grazers species as either benthic or pelagic grazer based on the metadata available. An initial selection was made with only species that have an adult phase that consumes phytoplankton. From the resulting list, we classified the adult stages of the species using the available AmP ecocodes for 'Marine Benthic' and 'Marine Pelagic' environments. The original AmP classification uses tags for 'Coastal', 'Reef' and 'Intertidal' for many bivalve

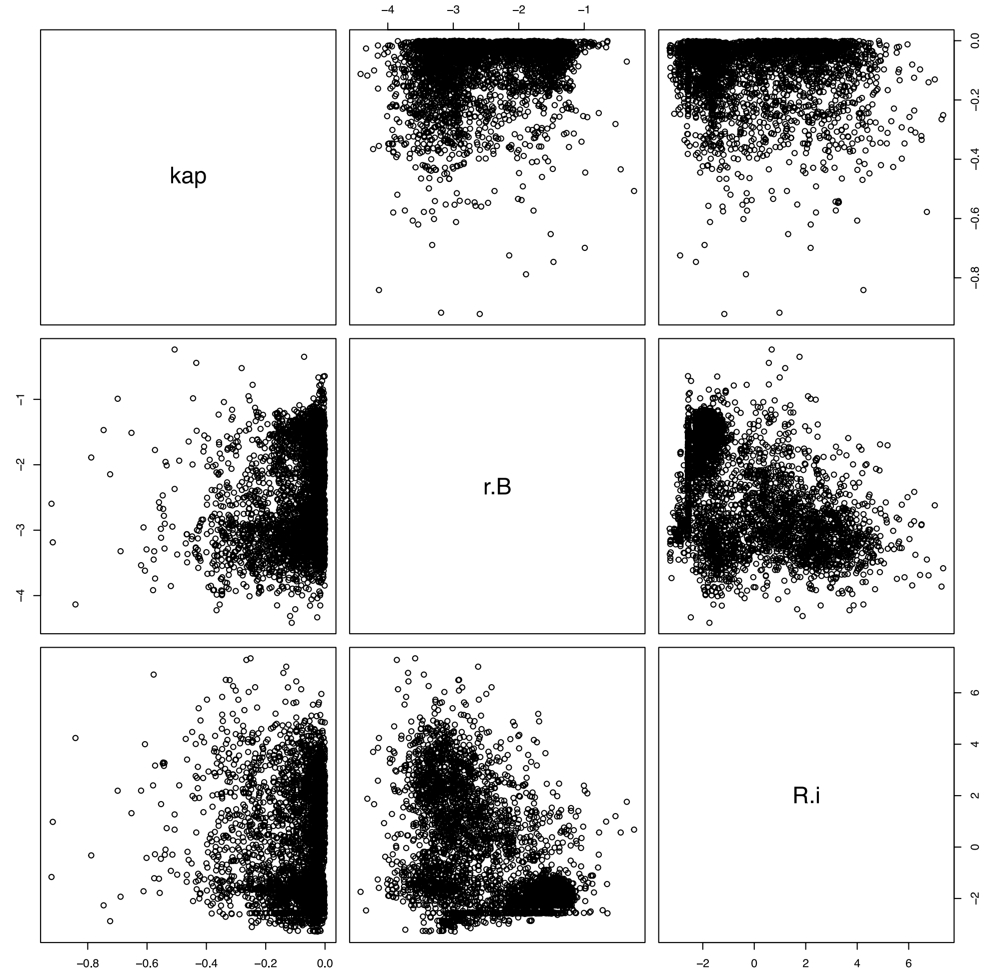

Fig. 3. The co-variation among the three selected DEB (compound) parameters/traits; the fraction of the mobilized reserves that is channeled towards somatic maintenance and growth κ, the Bertalanffy growth coefficient r_B, and the ultimate reproduction rate R_i. All panels show log10-transformed values; 3779 species.

and barnacle species. Since we are only interested whether the species is benthic or pelagic, we re-classified these two taxonomic classes as benthic species. Sponges and bryozoans were left out of the analysis due to the difficulty in determining biomass differences between individuals and colonies. The ecocodes used for freshwater grazer species are not valid for classifying between benthic and pelagic, thus this classification was done by taxonomic class or order. All freshwater gastropods, bivalves and gastrotrichs were considered benthic species, while all rotifers, tadpole shrimps and cladocerans where considered pelagic. Due to many species being labeled as general plankton eaters, and not specifically labeled as phytoplankton consumers, we had to manually attribute the taxonomic classes Appendicularia, Thaliacea, and the taxonomic orders Cyclopoida, Mysida, Euphausiacea to the pelagic compartment. We also manually attributed the class Ascidiacea, and the orders Scalpelliformes and Sessilia, as well as the copepod *Nitokra spinipes* to the benthic compartment. The resulting list was composed of 103 benthic grazers (from which 96 are molluscs) and 21 pelagic grazer species (20 arthropods).

The analysis of the extended Bertalanffy model indicated that the production-assimilation ratio is affected by among other things the fraction of the assimilated energy that is channeled towards reproduction, the Bertalanffy growth coefficient and the energy content of a newborn relative to the rate at which energy is initially channeled towards reproduction. So apart from estimating the production-assimilation ratio using the DEB approach, we also explored to what extent this ratio is related to the primary DEB parameter κ, which gives the fraction of the mobilization rate that is channeled towards somatic maintenance and growth (and thus not to reproduction and maturity), the compound DEB parameter Bertalanffy growth coefficient r_B, and the implied trait ultimate reproduction rate R_i (as a proxy for the time it takes to reproduce one offspring). Apart from a graphical analysis, a linear regression model was fitted to provide a simplified approximation of the underlying relationship as defined by DEB theory.

6. Results

The three selected (compound) DEB parameters/traits, for which the relation with the production-assimilation ratio was further explored, showed only minor covariation, which implies that the parameters of a multiple regression model between the production-assimilation ratio and these parameters/traits can be reliably estimated (Fig. 3). The production-assimilation ratio y_{PA} was most strongly related to the Bertalanffy growth coefficient r_B (Fig. 4). The relationship between the underlying DEB parameters and the production-assimilation ratio could best be summarized by a linear model with only the Bertalanffy growth coefficient r_B and the ultimate reproduction rate R_i as the steering variables. This simple relationship ‘explained’ about 69.85% of the total variation, and the difference with the model containing all three selected variables was negligible (69.86%). The relationship ($F_{2,3776} = 4375$, $p < 0.001$) is given by $\log(y_{PA}) = -3.234(SE = 0.026) - 0.669\ (SE = 0.010)\ \log(r_B) - 0.087\ (SE = 0.004)\ \log(R_i)$ (Fig. 5).

Most of the species in the add-my-pet collection are chordates (Table 3), which are by and large found higher up in the food chain as carnivores or even top-carnivores. The homeothermic mammals and

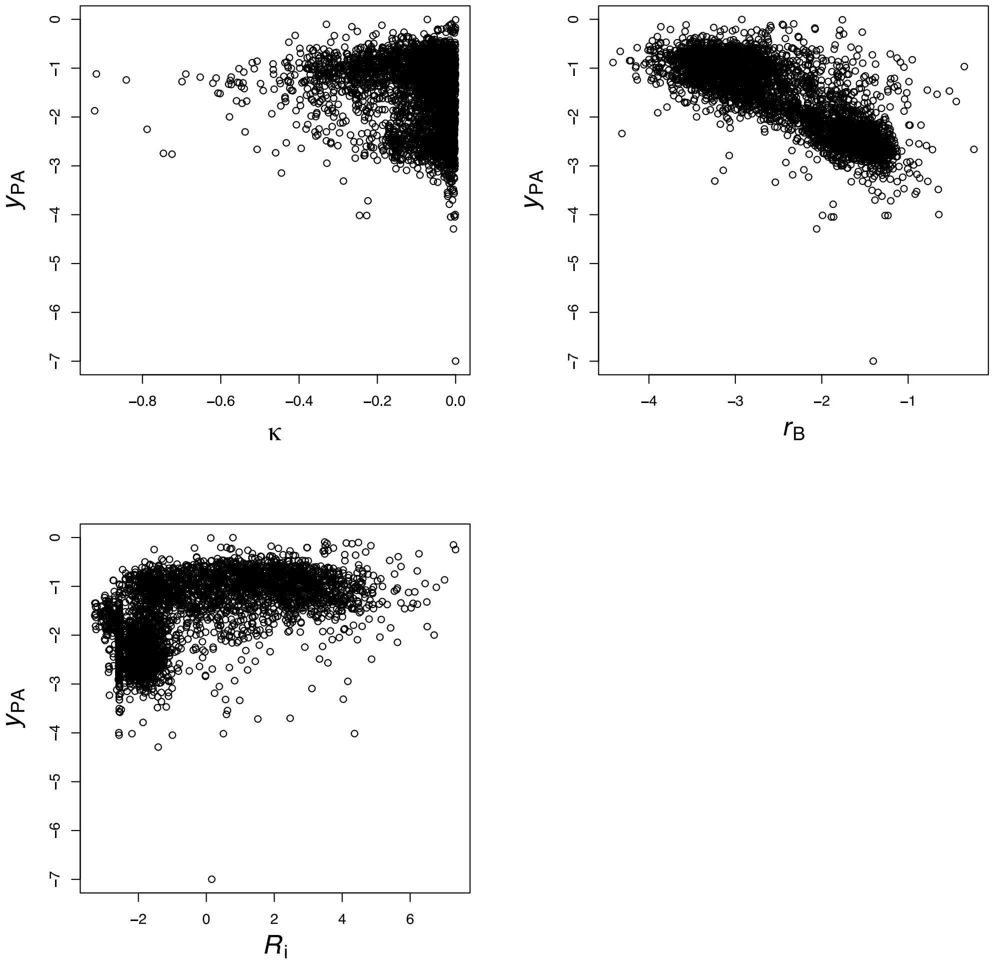

Fig. 4. The production-assimilation ratio y_{PA} versus the three selected DEB (compound) parameters; the fraction of the mobilized reserves that is channeled towards somatic maintenance and growth κ, the Bertalanffy growth coefficient r_B, and the ultimate reproduction rate R_i; 3779 species.

birds have a very low production-assimilation ratio, for birds as low as 0.3% (Table 4, Figs. 6 and 7). These low ratios are associated with a high Bertalanffy growth coefficient implying that maximum size is obtained relatively fast. The poikilothermic non-tetrapod chordates, mainly ray-finned fish (Actinopterygii), have a much higher production-assimilation ratio of about 10%. Molluscs showed a relatively high production-assimilation ratio too, which resulted in the selected benthic animals, which predominantly consist of molluscs (Table 3), having a mean production-assimilation ratio about 1.5 times higher than the selected pelagic species, which for the most part are arthropods.

Table 3
Number of species per phylum and per habitat code.

Phylum	All	Benthic	Pelagic
Acanthocephala	1	0	0
Annelida	17	0	0
Arthropoda	95	7	20
Brachiopoda	1	0	0
Bryozoa	2	0	0
Chaetognatha	1	0	0
Chordata	3402	0	0
Cnidaria	7	0	0
Ctenophora	4	0	0
Echinodermata	16	0	0
Gastrotricha	1	0	0
Mollusca	222	96	0
Nematoda	1	0	0
Nemertea	1	0	0
Porifera	1	0	0
Rotifera	2	0	1
Tardigrada	4	0	0
Xenacoelomorpha	1	0	0
All	3781	103	21

7. Discussion

This study embroiders on earlier work by Van der Meer (2020), who compared differences in the production-assimilation ratio of poikilotherms and homeotherms. He concluded that the higher efficiency in homeothermic mammals and birds has little to do with metabolic rate, but is merely the result of different energy allocation and life-history strategies. Birds, for example, have evolved to invest a large proportion of the assimilated energy in somatic growth and maintenance and to mature at a relatively large size. Therefore, their production efficiency as an adult individual is low. The focus of that study was mainly on individual organisms, but he also concluded that homeothermic populations with their high maintenance rate can only be as efficient as poikilothermic populations when the mortality rate keeps pace with the maintenance rate (see Eq. (3), also presented in Van der Meer (2020)). He suggested that in reality most likely the contrary occurs, and mortality rate is even lower in homeotherms than in poikilotherms.

In this study we go one step further and explicitly link mortality rate to individual energetics by using the ‘thinning rule’ (which says that the mortality rate is such that the total expected intake rate of an animal does not change over time) and the McKendrick characteristic

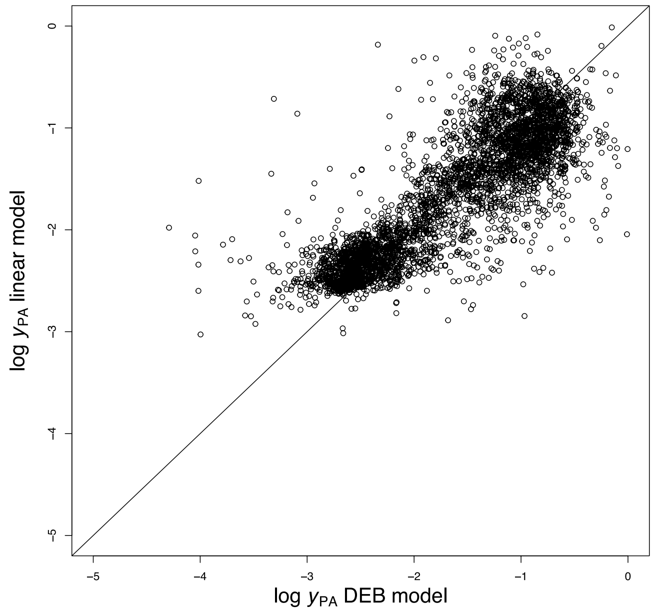

Fig. 5. The production-assimilation ratio as calculated on basis of DEB theory versus the subsequent prediction on basis of a linear model, where the DEB prediction is fitted versus the Bertalanffy growth coefficient and the ultimate reproduction rate R_i; 3779 species.

Table 4
Geometric mean production-assimilation ratio y_{PA} plus back-transformed SE for various taxa and ecological groups. n gives the number of species.

Group	n	Geometric mean	Antilog(SE)
Mammals	686	0.0082	3.03
Birds	986	0.0030	1.77
Other tetrapods	524	0.0578	2.37
Other chordates	1206	0.0980	2.40
Mollusca	222	0.1015	3.54
Others	157	0.0478	6.33
Pelagic grazers	21	0.0490	2.73
Benthic grazers	103	0.0753	4.84

equation (which says that when the product of the survival function and the reproduction function is integrated over all ages, the result should equal 1 at constant population size) to find the survival function, as was earlier done by Kooijman et al. (2020). Our analysis started with using the Bertalanffy growth equation, which we had to extend with a reproduction term in order to arrive at the survival function. This approach had the advantage that an explicit expression for the production-assimilation ratio in terms of the model parameters could be derived (see Eq. (46)). The equation tells that the production-assimilation ratio is higher when (1) overhead costs of growth are low, (2) a larger proportion of the overall intake is channeled towards somatic growth and maintenance, and (3) the time it takes to grow is large compared to the time it takes to produce one offspring.

To arrive at this interesting finding that these specific physiological characteristics can explain production efficiency differences among populations, we had to make some extremely simplifying assumptions, such as that animals start reproducing directly after birth. We therefore continued with using DEB theory, which provides a much more integrated and better tested look at whole-organism energetics; the disadvantage is that one has to rely on simulations and root-finding procedures, which might result in numerical problems. Furthermore, the link between the result in terms of the various yield coefficients and the many underlying DEB parameters remains somewhat hidden. In order to shed some light on this link, we used a linear model to relate the production-assimilation ratio, as derived by the DEB approach, to the most promising DEB (compound) parameters, as suggested by the previous Bertalanffy analysis.

It appeared that indeed the Bertalanffy growth coefficient (which says how long it takes an organism to reach a specific relative size) and the ultimate reproduction rate (which indicates how long it takes to produce an offspring) were a reliable short-cut to predict the production-assimilation ratio. Surprisingly, the parameter κ, which gives the fraction of the mobilized energy that goes to somatic maintenance and growth, did not improve the fit. But it could also be seen from Figs. 5 and 6 that a lot of the variation remained unexplained by this shortcut. Molluscs, for example, often showed a high production-assimilation ratios, even at relatively high growth coefficients and low reproductive rate.

Mollusc were also strongly represented in the benthic grazer group, which therefore showed a 1.5 times higher efficiency than the pelagic grazer group, which mainly consisted of arthropods. This result points to a possible higher trophic efficiency in marine coastal systems when the benthic compartment increases in importance, for example as a result of the construction of wind farms.

To exploit our theoretical findings even more in an applied context, a follow-up study could compare in detail the ecological efficiency of other groups from a specific marine ecosystem, at different trophic levels, or from different habitats. Comparing planktivorous (plankton-eating) and piscivorous (fish-eating) predators or comparing demersal fish and pelagic fish populations might be options. One could even try to conduct a complete 'food chain' analysis, looking at efficiencies across an entire chain. Finally, it should be noted that applied studies on ecological efficiency should not just look at the production efficiency, but also at the consumption efficiency and the assimilation efficiency. The add-my-pet collection provides information on the latter type, but it should be acknowledged that most of the figures in the database were 'guessed', as empirical information is almost completely lacking. Probably the same holds for data on the consumption efficiency.

CRediT authorship contribution statement

Jaap van der Meer: Writing – original draft, Software, Methodology, Formal analysis, Conceptualization. **Tan Tjui Yeuw:** Writing – review & editing, Data curation. **Karen van de Wolfshaar:** Writing – review & editing, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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We thank Dr Bas Kooijman for discussions on thinning, aging and many other interesting things. The research was funded by the Dutch Governmental program Ecological Impact of Wind at Sea (WOZEP).

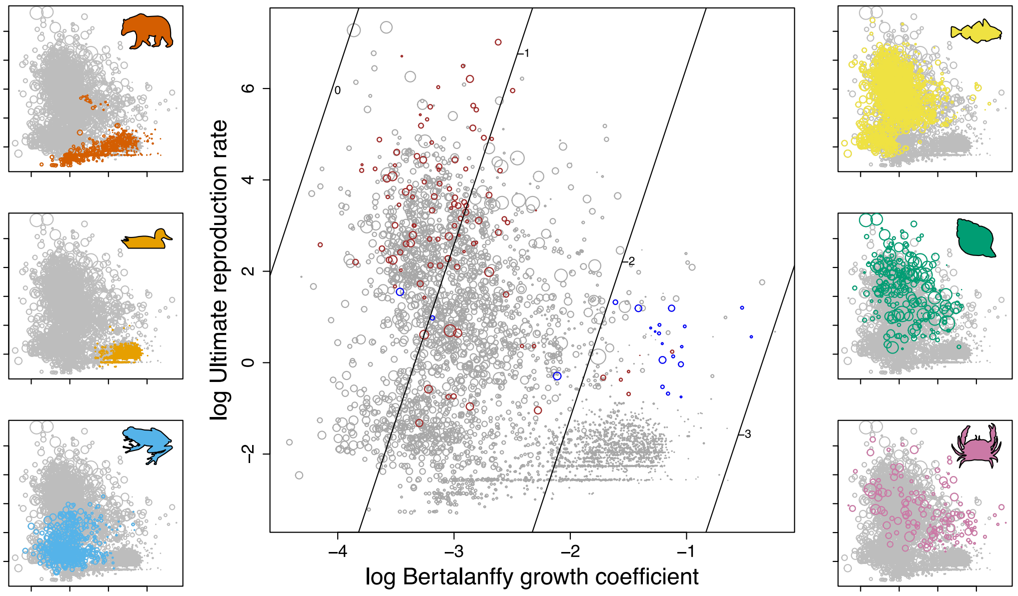

Fig. 6. The Bertalanffy growth coefficient r_B versus the ultimate reproduction rate R_i. The size of the symbols is proportional to the production-assimilation ratio y_{PA}. In the main panel lines show the predictions of the linear model, marine benthic grazers are shown in brown, and marine pelagic grazers in blue. Side panels show the data for (from upper left to lower right) mammals, birds, reptilians and amphibians, other chordates, molluscs, and all other species (not belonging to the chordates or the molluscs).

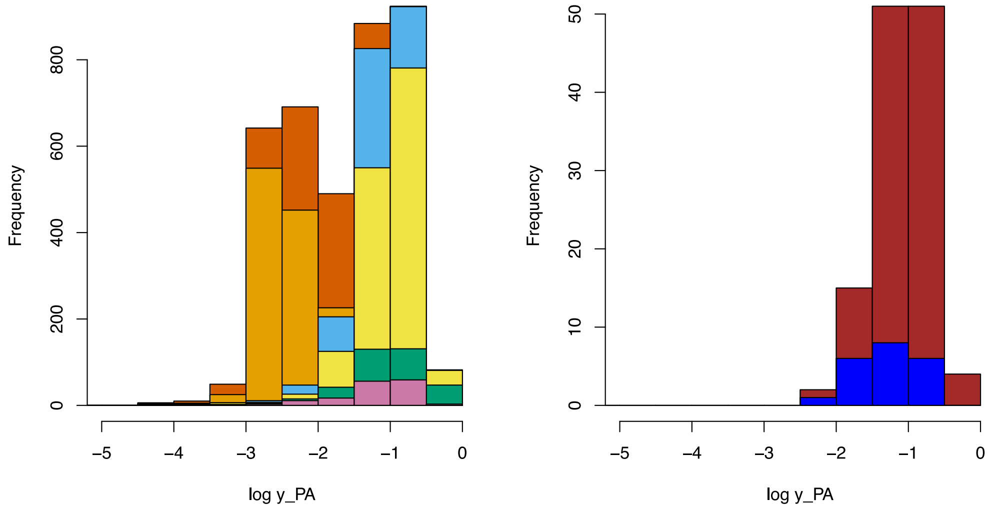

Fig. 7. Stacked frequency distribution of the $\log_{10}$ production-assimilation ratio. Left panel (3779 species) shows the taxa mammals (dark brown), birds (light brown), reptilians and amphibians (blue), other chordates (yellow), molluscs (green), and all other species (purple). Right panel (124 species) shows the marine benthic (brown) and pelagic (blue) grazers. Colors are similar to those in Fig. 6.

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