

The AquaDEB project: Physiological flexibility of aquatic animals analysed with a generic dynamic energy budget model (phase II)

Marianne Alunno-Bruscia^{a, *}, Henk W. van der Veer^b, Sebastiaan A.L.M. Kooijman^c

^a French Research Institute for Exploitation of the Sea (Ifremer), Dept. of Biological Resources and Environment RBE-PFOM-PI, 11 Presqu'île du Vivier, 29840 Argenton-en-Landunvez, France

^b Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg Texel, The Netherlands

^c VU University, Faculty of Earth and Life Sciences, Dept. of Theoretical Biology, de Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

* Corresponding author : Marianne Alunno-Bruscia, email address : marianne.alunno.bruscia@ifremer.fr

Abstract:

This second special issue of the *Journal of Sea Research* on development and applications of Dynamic Energy Budget (DEB) theory concludes the European Research Project AquaDEB (2007–2011). In this introductory paper we summarise the progress made during the running time of this 5 years' project, present context for the papers in this volume and discuss future directions. The main scientific objectives in AquaDEB were (i) to study and compare the sensitivity of aquatic species (mainly molluscs and fish) to environmental variability within the context of DEB theory for metabolic organisation, and (ii) to evaluate the inter-relationships between different biological levels (individual, population, ecosystem) and temporal scales (life cycle, population dynamics, evolution). AquaDEB phase I focussed on quantifying bio-energetic processes of various aquatic species (e.g. molluscs, fish, crustaceans, algae) and phase II on: (i) comparing of energetic and physiological strategies among species through the DEB parameter values and identifying the factors responsible for any differences in bioenergetics and physiology; (ii) considering different scenarios of environmental disruption (excess of nutrients, diffuse or massive pollution, exploitation by man, climate change) to forecast effects on growth, reproduction and survival of key species; (iii) scaling up the models for a few species from the individual level up to the level of evolutionary processes. Apart from the three special issues in the *Journal of Sea Research* –including the DEBIB collaboration (see vol. 65 issue 2), a theme issue on DEB theory appeared in the *Philosophical Transactions of the Royal Society B* (vol 365, 2010); a large number of publications were produced; the third edition of the DEB book appeared (2010); open-source software was substantially expanded (over 1000 functions); a large open-source systematic collection ecophysiological data and DEB parameters has been set up; and a series of DEB tele-courses and symposia have been further developed and expanded, bringing together people from a wide variety of backgrounds (experimental and theoretical biologists, mathematicians, engineers, physicists, chemists, environmental sciences, computer scientists) and training levels in DEB theory. Some 15 PhD students graduated during the running time of AquaDEB with a strong DEB component in their projects and over 15 will complete their thesis within a few years. Five post-doctoral projects were also part of the training network. Several universities (Brest, Marseille, Lisbon, Bergen) included DEB courses in their standard curriculum for biology students.

1. Introduction

The aim of DEB research is to develop a quantitative framework for metabolic organisation physics style, formalised on the basis of explicit assumptions, axioms if you wish (Sousa et al., 2008; Lorena et al., 2010). This systematic approach is ideal for multidisciplinary collaboration, where people with non-biological backgrounds are easily confused by a massive heap of facts, semi-facts and lies that frequently characterises descriptive biology (Sousa et al., 2010). The standard model turns out to have unique properties (Lika and Kooijman, 2011); in combination with the impressive array of realistic predictions so far, this motivates substantial effort investment in this line of thought.

The AquaDEB project aims to apply this approach to aquatic species (molluscs, fish, micro-algae, plankton), although DEB theory is meant for all species in all environments. The idea is that this application not only leads to a better understanding of quantitative relationships in relatively simple environments, but different species are also better comparable because the same model is applied to them and the comparison can be on the basis of parameter values (Freitas et al., 2010). DEB theory also comes with implied rules for the covariation of parameter values among individuals, which helps in filling in gaps of knowledge. The intra-specific variation is typically small relative to the inter-specific variation. These gaps become apparent by using such a systematic approach. Predictions can subsequently be used to prioritise future experimental research and to test and further develop the theory. This is how the development of theory benefits from this type of applications. Theory is a tool in our understanding and the value of a tool is in its use. DEB theory strongly stimulates a careful analysis. Where a lot of literature on respiration is fussy about the difference between intra- and inter-specific comparisons, DEB theory distinguishes them carefully. A unit of tissue of a young (small) individual respire more than that of an old (large) one because it grows faster. This explanation cannot hold for fully-grown individuals of a small-bodied and a large-bodied species. DEB theory explains the latter by the differential contribution of reserve to weight; similar phenomena, very different explanations.

Inspired by applications, DEB theory evolved rapidly during the AquaDEB project, as summarized in the third edition of the DEB book (Kooijman, 2010). The previous edition used the simplifying assumption that the maturity and somatic maintenance rates coefficients are equal, with the consequence that stage transitions occur at fixed amounts of structural mass and maturity as state variable only plays an academic role. Further research revealed, however, that this assumption does not hold generally and in particular situations, such as the study of effects of toxicants, even problematic. So this assumption was removed; the role of maturation is more explicit, *e.g.* to understand the observed variation in size at birth and at puberty while the maturity levels remain constant. The dynamics of development of the zebrafish could be understood in very much detail, this way (Augustine et al., 2011a). Recently strong support was found for the way DEB theory deals with maturation: some species of tadpoles speed up maturation to shorten the time to metamorphosis to frogs (Mueller et al., 2011); this comes with a sudden increase of respiration at hatching, before birth, in combination a particular decrease of growth. Related species that do not live in temporal ponds do not sport this acceleration and follow the rules of the standard DEB model.

DEB theory extended into quite a few different directions, *e.g.* the impact of metabolism on stable isotope dynamics (Pecquerie et al., 2010; Emmery et al., 2011), generalisations of the κ -rule which deal with multiple structures (organs, body parts), metabolic acceleration (Augustine et al., 2011b; Kooijman et al., 2011), effects of mixtures of chemical compounds (Baas et al., 2009; Baas et al., 2010; Jager et al., 2010), evolution of DEB systems (Kooijman and Troost, 2007; Troost et al., 2008; Muller et al., 2009; Kooi and van der Meer, 2010). We finally understand, we think, why the life span of endotherms increases with maximum body size amount species, but is almost independent of body size in ectotherms: it is in the ageing acceleration, which is (almost) zero in ectotherms (van Leeuwen, 2007; van Leeuwen et al., 2010; Kooijman, 2010). The subsections below further detail some of the

developments. These developments came with the need to become even more rigorous in the notation, which was also vital to the further extension of the DEBtool software, written in Matlab and Octave, which now has over 1000 functions in 14 toolboxes. The reference section lists DEB-related publications that appeared in the period 2007-2011 of members of the AquaDEB group and persons who played an active role in the DEB tele-courses and symposia. The comments on the DEB book try to summarise the scientific progress in the DEB arena since its appearance.

This final special issue is composed by a number of papers that include:

- i) “theoretical” papers among which two by Lika et al. (2011a,b) who present a statistical procedure, the covariation method, involving the simultaneous estimation of all core parameters of the DEB model from various empirical observations in a single-step procedure; while the third contribution also by Lika and Kooijman (2011) compare from a theoretical perspective 20 classes of energy budget models that differ in internal energy allocation;
- ii) papers on bivalves (blue mussels, Pacific and pearl oysters, cockles) with a core group presenting different targeted applications of the DEB theory in shellfish culture (Handå et al., 2011; Rosland et al., 2011; Thomas et al., 2011a,b; Alunno-Bruscia et al., 2011; Bernard et al., 2011; Emmery et al., 2011) based on empirical estimation of DEB parameters and/or on a calibration procedure to get consistency among parameters; including also one contribution by Saraiva et al. who apply the covariation method to the blue mussel, and two papers presenting a model comparison of DEB vs scope for growth SFG (Barillé et al., 2011; Filgueira et al., 2011);
- iii) papers on fish dealing with the metabolic handling of starvation and rejuvenation in teleost fish larvae (Augustine et al., 2011b), with the acceleration of fish metabolism during the life cycle *i.e.* pointing out the role of metamorphosis (Kooijman et al., 2011), with the prediction of variations in life-history traits among five species of Pacific salmon (Pecquerie et al., 2011), with explaining the disappearance of the European eel from the western Wadden Sea based on a 50-yr dataset of eel catches (van der Meer et al., 2011), and with investigating food conditions encountered by sand gobies by analysing seasonal growth trajectories (Freitas et al., 2011);
- iv) papers exploring the entrainment behaviour of cell division in phytoplankton (Muller et al., 2011) and interpreting mechanistically the effects of polyphenol in a marine polychaete (Jager and Selck, 2011).

2. Results of the AquaDEB project

2.1. Parameter estimation

Knowledge of parameter values is typically the first step in the application of models. Those values are needed to judge the applicability of the model in a particular case, *e.g.* to arrive at the conclusion that the fit of best-fitting parameter values is not good at all. The systematic search for the ‘why’-question is among the most useful aspects of application of mechanistic models.

The first phase of the AquaDEB project (Alunno-Bruscia et al., 2009) focussed on the development of methods for parameter estimation from data and applying these methods to data from the literature, from archives of experimental results obtained in the past and from results of experiments that have been set up to acquire specific data. We went through a learning trajectory, discovering that a particular combination of data, such as age and size at birth, maximum size and reproduction, contains sufficient information for some parameters, no information for other parameter and little information for a third class of parameters. So the identification of parameters is not a matter of white and black, but also has shades of grey, which complicates the problem. It became apparent that all the different types of data

had to be considered simultaneously. We first made an inventory of the relationship between the type of data and the functions of parameters that can be estimated from them (Kooijman et al., 2008). The role of compound parameters became clear: functions of parameters that have simple dimensions. There were quite a few cases where compound parameters could be estimated from data, while each of the contributing parameters could not. Although the standard DEB model has been kept as parameter sparse as possible (each metabolic process typically has only one or two parameters), the number of parameter rapidly increases with the number of different type of data. This is not a problem of DEB theory, but of biology. Lengths, wet mass, dry mass, ash-free dry mass, C-moles, grams, energy content are all, but different quantifiers for size, each involving its own conversion parameters. It is extremely difficult to measure the dry mass of a whale, or the wet mass of a bacterium for practical reasons. We also had to consider the sensitivity of parameter estimates on variations in data; a complex problem indeed, especially because none of the basic modelling variables (reserve, structure, maturity, reproduction buffer) can be measured directly, only indirectly (Lika et al., 2011a,b).

The second phase of the project aimed at estimating all (primary) parameters simultaneously from sets of data, supplementing them with circumstantial evidence from other species. Related species typically have similar values for particular parameters, and can be used as supplemental evidence if necessary. Lack of data is and will remain a pertinent problem. We also learned that this approach works for some parameters, but less for others (specific evolutionary or ecological adaptations). We started to collect data from a wide variety of species and estimate all parameters of the standard DEB model, the `add_my_pet` collection. It is possible to trace exactly where a particular parameter values came from. Even the code that has been used to arrive at the estimate is available for each species; the code is species-specific because the type of data that available is frequently rather unique. The collection now already has some 60 species; as far as we know it is the largest collection on earth of all aspects energetics. This will facilitate the estimate of parameter of other species (Bruggeman et al., 2009).

One of the things we already learned from this exercise is the unexpected large role of water in the estimation of (some) parameters, and especially the volume-specific costs for structure. The value for a jellyfish is obviously less than for a mammal, in view of their very different ratios of dry and wet mass. The estimation of this parameter is coupled to that of others, so the problem affects most parameters. One can wonder about the water-content of reserve. Does it differ from that of structure? An answer can be found in the comparison of the relative decrease in wet and dry mass during the early stages of starvation, given that reserve is used. We do not know of such measurements.

2.2. Variability

One of the aims of the AquaDEB project was to understand variability of biological data and to learn how to handle it, or even exploit it for various purposes. DEB theory offers a number of handles. First of all the parameter values are individual-specific, partly controlled by genetics along the idea of quantitative genetics. We are just starting the study of the relationships of the parameter values of parent and their offspring.

Second, survival is inherently stochastic, because aging and effects of chemical compounds are modelled via the hazard rate. Recent modules for effects of extreme starvation (shrinking and rejuvenation) also act via the hazard rate: defence is thought to be a component of maturation maintenance to capture the idea that lack of adequate nutrition makes the individual more vulnerable, e.g. for pathogens (Augustine et al., 2011b). Not only the hazard rate but also the actions of Synthesizing Units (SUs), which play an important role at several places in DEB theory, are inherently stochastic. This stochasticity of is less importance for the role of SUs in metabolic transformations (large number of molecules), but very important in their role of modelling behaviour (low rates of binding events), with natural links to Markovian approaches, but now in combination with functional aspects of behaviour. The

analysis of the behaviour of non-linear deterministic systems with stochastic inputs is far from easy, and just started (Kooijman et al., 2007; Kooijman and Troost, 2007; Kooijman, 2009). Third, time and space are not homogeneous, so environmental conditions vary. The most important aspects are food (or nutrient and or light) availability and temperature. This calls for tight links with physical transport models, even at the individual level. Much to our satisfaction, we see an increasing number of successful DEB applications to field data, examples are Cardoso (2007), Ren (2009), Rosland et al. (2009), Grangeré et al. (2009), Maar et al. (2009), Troost et al. (2010), Pecquerie et al. (2011), Saraiva et al. (2011), Bernard et al. (2011), Barillé et al. (2011), Alunno-Bruscia et al. (2011), Thomas et al. (2011a,b) and van der Meer et al. (2011). Given the notorious scatter of such data, we can conclude that the model is not too complex for such applications and it has sufficient robustness properties. The explicit role of surface areas in DEB theory links is naturally to such transport models. Deviations from isomorphy, e.g. in connection to metabolic acceleration (Kooijman et al., 2011) surprisingly leads, in combination with temporal variability of food availability, to permanent changes in parameter values. Parameters that depend on surface areas, notably the surface area specific assimilation rate and the energy conductance, start changing interactively when deviations from isomorphy occur. Metabolic acceleration turns out to be more frequent than originally thought, which is why this extension of the standard models has been build into the `add_my_pet` collection. It typically occurs in some fish and most bivalves just after birth, where metamorphosis marks the transition back to isomorphy. The overall effect is that the energy conductance of embryos is substantially lower than that of late juveniles and adults; this conductance controls reserve mobilisation, so the fuelling of metabolism.

Fourth, the nutritional value of food varies in time, and sometimes in predictable ways. During the project we learned that light-limited carbon fixation in micro-algae is insensitive for temperature, while nutrient uptake is. The effect is that carbohydrates are damming up at lower temperatures, increasing the nutritional value for e.g. bivalves. These changes in food quality further amplify the stochastic nature of nutritional inputs. Nutrition in combination with metabolic performance are key to the understanding of geographic variations and limits the natural distribution of species (Campos and van der Veer, 2008; Campos, 2009; Campos et al., 2009; Freitas et al., 2010; Freitas, 2011).

2.3. Comparison with other approaches

We naturally paid due attention to the comparison of DEB theory with other approaches, such the SFG (van der Veer et al., 2009; Barillé et al., 2011; Filgueira et al., 2011), species-specific (descriptive) models, the Metabolic Theory of Ecology (MTE, van der Meer, 2007; White et al., 2011), biochemical systems theory (Vinga et al., 2010), biophysical modelling (Kearney et al., 2010). Our general conclusion is that DEB theory performs very well in terms of being mechanistic, simple (quantified as numbers of variables and parameters) and realistic (quantified in goodness of fit with data). The comparison with other approaches suffers, however, from the problem that DEB theory deals with a rather large number of interacting processes, while other models treat particular processes, such as growth separately, simply ignoring for growth is modified by other processes, such as feeding, reproduction or maintenance. Some of these alternative approaches, such as biophysical modelling, naturally link up with DEB theory and will doubtlessly further integrated. Other approaches have fundamental inconsistencies with DEB theory, such as SFG and MTE, and will probably fade away eventually in view of their internal inconsistencies or will be restricted to very few particular applications.

2.4. Reconstructions

The AquaDEB group has been creative in all sorts of applications, we cannot be complete here. An example is a class that can be called reconstruction methods, where a measured

biological signal, e.g. opacity profiles in fish otoliths (Pecquerie et al., 2009, 2011; Fablet et al., 2011), growth profiles (Freitas et al., 2009) is used to reconstruct trajectories of environmental variables (food availability and/or temperature). Such reconstructions can be used for climate research, but also for size-dependent food selection. The idea is here to correlate reconstructed food with measured potential food sources. The problems are deep in this sector. It is rather easy to access chlorophyll density of surface layer for remote image data (Omta et al., 2009b; Thomas et al., 2011a), but chlorophyll itself is not digestible for animals and the chlorophyll/carbon ratio varies a lot. One can try to measure total carbon, but a lot of it is cellulose and cellulose is also not digestible for animals (without symbionts). Some algal species are abundant but not digestible; if deleted from algal counts good quantifiers for the nutritional value of phytoplankton can result (Bourlès et al., 2009; Alunno-Bruscia et al., 2011). Then we have detritus (Saraiva et al., 2011), but its nutritional value is probably varying. The tiny neonates of fish feed on very different type and size of food than the adults; the nutritional aspects for fish fry is important to understand fish population dynamics (Pecquerie, 2008; Pecquerie et al., 2009; Augustine et al., 2011b).

2.5. Effects of toxicants

DEB theory is unique in its implied rules for the covariation of parameter values of the standard DEB model, known as body size scaling relationships in the literature. This label is, however, less appropriate for DEB theory, because the maximum body size of an individual is itself a result of underlying processes, rather than an independent variable; contrary to the standard approach in such relationships, the rules purely follow for the structure of the theory and has no descriptive elements. Yet the predictions are very accurate, which gives strong support for the basic structure of the theory. White et al. (2011) conclude that DEB theory is the only existing theory that can explain why respiration in encrusting bryozoans scales with weight to the power $\frac{1}{2}$ rather than the more typical $\frac{3}{4}$, whereby the explanation is in its growth and the contribution of growth overheads to respiration. Similar rules could also be developed for the standard toxicokinetic model: the one-compartment model (Kooijman et al., 2007; Jager and Kooijman, 2009; Kooijman et al., 2009), from which effect modules follow (Jager et al., 2010). The behaviour of extensions of this model, e.g. the popular film models for chemical transport in the environment, also follows from these rules. The interaction of these rules for the behaviour of metabolism and toxicokinetics has great potential for extrapolation purposes across species and chemical compounds. Such extrapolations can be used to prioritise and optimise experimental research.

Good progress has been made in the understanding of effects of complex mixtures of chemical compounds, both for a few, where the toxico-dynamics each of the compounds is followed in detail, as well as for many (Baas et al., 2007; Baas, 2010; Baas et al., 2010; Baas and Kooijman, 2010; Jager et al., 2010). The theory is rather straightforward for lethal effects (Jager and Selck, 2011), but can become complex for non-lethal effects, where interaction of the various compounds in the mixture can be direct on the same target parameter (such as the specific somatic maintenance costs), or indirect by acting on different parameters. The interaction is then via metabolism, as quantified by DEB theory. The simultaneous analysis of effects on different endpoints (growth, feeding, reproduction) is essential here (Jager et al., 2007; Swain et al., 2010; Jager and Selck 2011; Wren et al., 2011; Agatz et al., 2011). Knowledge of which parameters are affected is of importance for the extrapolation of effects on individuals to consequences for population dynamics (Billoir et al., 2007; Klok, 2007; Klok et al., 2007; Ducrot et al., 2010; Jager and Klok, 2010; Svendsen et al., 2011).

2.6. Population and ecosystem levels

Core DEB theory deals with the metabolism of the individual, be it a bacterial cell or a whale or tree, and how it interacts with the environment. In combination with rules for the interaction between individuals (including their movements) and for the fate of abiotic factors (nutrients,

light, temperature) these ideas can be used to capture population and ecosystem dynamics. The simplest set of rules is that individuals only interact via competition for food and live in a homogeneous environment that is closed for mass but has light input. An implication of the environment being homogeneous is that nutrient re-distribution is instantaneous and the position of all individuals is fussy. To avoid the need to deal with all species, extra assumptions are typically made, such as the mineralisation of dead organic matter is instantaneous. This list already reveals quite a few potential problems. A lot of progress has been made since the start of the development of this advanced type of mathematical bookkeeping in 1979 (Diekmann and Metz, 2010), but some fundamental problems still wait for solution, such as how to include that structured populations are feeding on other structured populations. Matters easily become very complex and can only partly be solved with individual-based population models (IBMs), which follow each individual (Martin et al., 2011). Most literature on population dynamics simply ignores mass conservation and implements simplistic rules for the dynamics of the lower trophic levels. Even then the situation can be quite complex and calls for advanced numerical methods (Bruggeman et al., 2007; Broekhuizen et al., 2008).

In view of the great need for predictions at the higher levels of organisation, a lot of effort has been invested to find the fine balance between simplicity and realism (Klok, 2007; Klok et al., 2007; Nisbet et al., 2010). The ecological effects of chemical compounds on organisms are only of societal significance that the population and ecosystems levels (Billoir et al., 2007; Ducrot et al., 2010; Jager and Klok, 2010), for instance. The use of bifurcation analysis to analyse the potential behaviour of population and ecosystem models has been further developed for DEB-structured ones (van Voorn et al., 2007, 2008, 2010; Doedel et al., 2009; Stiefs, 2009; Stiefs et al., 2010), revealing a very rich asymptotic behaviour. Where deterministic models typically show multiple attractors, stochastic variants of these models behave much smoother and the system can move from one attractor to the other (Kooijman et al., 2007). Where deterministic models can suddenly switch from a point attractor to a cyclic behaviour when the total nutrient load of a system is increased (the famous paradox of enrichment), stochastic variants show a smooth transition. Toxicants can modify the behaviour of integrated systems in complex ways and quite a bit of progress has been made to understand how (Kooi et al., 2008a,b; Liebig et al., 2008; Bontje et al., 2009, 2010, 2011). Ways have been explored to reduce the number of variables that has to be followed in ecosystem model by focussing on trait-based approaches and refrain from following species individually. Particular patterns in the distributions and abundance of micro-algae can be understood this way (Bruggeman and Kooijman, 2007; Bruggeman 2009; Merico et al., 2009). The same motivation inspired the development of models for infinitely connected food webs, where each animals preys on all other in a given size range relative to its own, irrespective of the species (Maury et al., 2007a,b).

Where predation-prey interactions dominate the literature on population dynamics, our results point to the importance of syntrophic interaction as one of the mechanisms for maintenance of biodiversity (Muller et al., 2009; Eynaud et al., 2011). Nutritional details and the dynamics of biodegradation can have large effects on system properties (Eichinger et al., 2009, 2010; Poggiale et al., 2010), a worrying observation.

We only started to explore the implementation of DEB systems in physical transport models (Omta et al., 2007, 2008, 2009; Pecquerie 2008; Pecquerie et al., 2009; Grangeré et al., 2010). Such implementation is essential to understand the effect of primary production on atmospheric carbon dioxide, for instance (Omta, 2009; Omta et al., 2009a).

2.7. Evolution

No biological theory makes sense without an appropriate evolutionary setting. While ideas on metabolism of extinct forms have intrinsically speculative elements, a logical and consistent scenario is better than no scenario. DEB theory has the unique property that it is possible to

split and merge systems that follow DEB rules and the result again follows DEB rules, if done in a particular way. Such splitting and merging occurred frequently in evolutionary history. The class of models for the mobilisation of reserve that has this property is really small; that of the standard DEB model might be the only member. It is rather sure that metabolic systems evolved from multiple systems of prokaryotes and early eukaryotes to single reserve systems of animals. Scenarios for the quantitative details and the links with the evolution of various forms of homeostasis are discussed in Kooijman and Troost (2007) and Kooijman (2010).

Reserve can be seen as a form of metabolic memory, the larger the individual, the longer its metabolic memory, both intra- and inter-specifically. The rules for the covariation of parameter values result in a maximum reserve capacity scaling with maximum body length of a species. An implication is that cyclic (seasonal) forcing can lead to an evolutionary increase of maximum body size, empirically known as Cooper's law (Troost et al., 2008, 2009). The study of evolutionary changes of traits is the territory of adaptive dynamics. We discovered that this field can be seen as a special case of bifurcation analysis (Troost et al., 2007; Kooijman and van der Meer, 2010), which opens the door for the large body of theory and software that has been developed for bifurcation theory.

3. Education and dissemination

A research group like AquaDEB cannot do without a well-developed education and dissemination module. Apart from a few news-paper articles, several papers for a broad public were written (van Leeuwen, 2007; Baas et al., 2009; Kooijman et al., 2009; Kooijman, 2011). The summary of DEB concepts is meant for a fast introduction to the DEB book that is used in the DEB courses. We had 15 PhD graduations during the AquaDEB project (2007: Sousa, Omholt, Cardoso; 2008: Eichinger, Flye Sainte-Marie, Pecquerie, Bodiguel; 2009: Omta, Campos, van Voorn, Bruggeman, Stiefs, Grangeré, Rico-Villa, Thomas; 2010: Baas, Bernard, Bontje; 2011: Freitas) in which DEB theory played an important role. Some other 15 will complete their thesis within the next 3 years. Five post-doctoral researchers also participated actively to AquaDEB (2008: Laugen; 2009: Campeas, Eichinger; 2010: Flye Sainte-Marie; 2011: Pethybridge). This illustrates the dynamics of the research group and the wide scope of applied and theoretical aspects. The bi-annual DEB tele-courses play an important role in networking, especially because the 2009 (Brest) and 2011 (Lisbon) editions were linked with a practical part of the course and a symposium; in view of the success these elements will be further developed (Texel 2013, Marseille 2015, Bergen 2017).

4. Further developments

In view of the rapid build up of the parameter collection for a wide variety of species, the analysis of patterns in parameter values will start soon. Theories for ecological and evolutionary adaptations are likely to result for those analyses and will be used to further facilitate and improve parameter estimation. We can now already make the important observation that will change evolutionary theories: the observed allocation to reproduction, as revealed by the estimated value of the partition coefficient κ , is typically much lower than value that maximizes reproductive output (Lika et al., 2011b); the difference is so big that details of how the latter should be quantified exactly hardly matter. The availability of reliable parameter values will boost practical applications, such as the optimisation of bio-production (e.g. aquaculture, Omholt, 2007) and of harvesting (fisheries, forestry). It is basic to the solution of reconstruction problems, such as growth trajectories, which can be used to access food selection under field conditions.

We already started the analysis of two-reserve systems to understand food selection, in an attempt to link up the geometric framework for nutrition (Kearney et al., 2010) and behavioural ecology. We played with social and syntrophic interactions on the basis of Synthesizing Units to study effects on the maintenance of biodiversity in ecosystem models.

This maintenance is a notorious problem in simple ecosystem models. The relationships between biodiversity and ecosystem functioning urgently need further elucidation; we hope to make some progress soon.

We expect to see a further merging of the toxicity modules of DEB theory with stress ecology more generally (e.g. Flye Sainte Marie, 2008). The simultaneous analysis of multiple endpoints will become a rule, rather than an exception, to identify the mode of action of chemical compounds. The combination of effects with (bio)degradation and environmental fate modelling will become key for risk assessment purposes. A strong effect of a chemical compound is less of a problem if combined with a very short residence time in the environment; the degradability of compounds (e.g. Lika and Papadakis, 2009; Eichinger et al., 2010) is of more environmental relevance than its effects, but the combination is what matters. Extrapolation from effects of one compound to that of the other, from effects on one species to other species of organism, from effects on individuals to that on populations and ecosystems will need to be integrated with effect-fate studies.

Although a large amount of work has been done since the start of DEB theory in August 1979, the development and application of DEB theory is still in an early stage. Applying the theory has a rather long learning curve, and extending it even longer. We believe that the accumulation of promising results will stimulate an increasing number of research workers to make this effort investment.

Acknowledgements

We like to thank all members of the European AquaDEB-group, as well as all active external European and international colleagues who contributed actively to the group, for the very productive interaction we have had in the past 5 years. We do hope that the network will remain functional, using the DEB tele-courses and symposia as backbone. We also like to thank Ifremer and the LEMAR/CNRS (Lab. des Sciences de l'Environnement Marin/Centre National de la Recherche Scientifique) for the financial support, which, in retrospect, has been a very fruitful investment with some 25 publications, 3 PhD's and 1 post-doc per year. Detailed information about DEB and the AquaDEB project can be found at various web sites, respectively: <http://www.bio.vu.nl/thb/deb/deblab/> for the AquaDEB project.

References

- Agatz, A.R.A., Albert, C., Ducrot, V., Galic, N., Hendriks, A.J., Jager, T., Kretschmann, A., O'Connor, I., Rubach, M.N., Ruotsalainen, M., Schmitt, W., Stadnicka, J., van den Brink, P., Preuss, T.G., 2011. Toxicokinetic-toxicodynamic modelling of quantal and graded sub-lethal endpoints - a brief discussion of concepts. *Environ. Toxicol. Chem.* (in press).
- Alunno-Bruscia, M., van der Veer, H.W., Kooijman, S.A.L.M., 2009. The AquaDEB project (phase I): Analysing the physiological flexibility of aquatic species and connecting physiological diversity to ecological and evolutionary processes by using Dynamic Energy Budgets. *J. Sea Res.* 62, 43–48.
- Alunno-Bruscia, M., Bourlès, Y., Maurer, D., Robert, S., Mazurié, J., Gangnery, A., Gouletquer, P., Pouvreau, S., 2011. A single bio-energetics growth and reproduction model for the oyster *Crassostrea gigas* in six Atlantic ecosystems. *J. Sea Res.* (this volume).
- Augustine, S., Gagnaire, B., Adam, C., Kooijman, S.A.L.M., 2011a. Developmental energetics of zebrafish, *Danio rerio*. *Comp. Physiol. Biochem. A* 159, 275–283.
- Augustine, S., Litvak, M.K., Kooijman, S.A.L.M., 2011b. Stochastic feeding in fish larvae and their metabolic handling of starvation. *J. Sea Res.* (this volume).
- Baas, J., van Houte, B.P.P., van Gestel, C.A.M., Kooijman, S.A.L.M., 2007. Modelling the effects of binary mixtures on survival in time. *Environ. Toxicol. Chem.* 26, 1320–1327.

- Baas, J., Willems, J., Jager, T., Kraak, M.H.S., Vandenbrouck T., Kooijman, S.A.L.M., 2009. Prediction of daphnid survival after in situ exposure to complex mixtures. *Environ. Sci. Technol.* 43, 6064–6069.
- Baas, J., 2010. Effects of mixtures explained: From laboratory tests to effects in the environment. Ph.D. thesis, Vrije Universiteit, Amsterdam.
- Baas, J., Kooijman, S.A.L.M., 2010. Chemical contamination and the ecological quality of surface water. *Environ. Pollut.* 158, 1603–1607.
- Baas, J., Stefanowicz, A.M., Klimek, B., Laskowski, R., Kooijman, S.A.L.M., 2010. Model-based experimental design for assessing effects of mixtures of chemicals. *Environ. Pollut.* 158, 115–120.
- Barillé, L., Lerouxel, A., Dutertre, M., Haure, J., Barillé, A.-L., Pouvreau, S., Alunno-Bruscia, M., 2011. Growth of the Pacific oyster (*Crassostrea gigas*) in a high turbidity environment: comparison of model simulations based on scope for growth and dynamic energy budget models. *J. Sea Res.* (this volume).
- Bernard, I., de Kermoisan, G., Pouvreau, S., 2011. Effect of phytoplankton and temperature on the reproduction of the Pacific oyster *Crassostrea gigas*: investigation through DEB theory. *J. Sea Res.* (this volume).
- Billoir, E., Péry, A.R.R., Charles, S., 2007. Integrating the lethal and sublethal effects of toxic compounds into the population dynamics of *Daphnia magna*: A combination of the debtox and matrix population models. *Ecol. Modell.* 203, 204–214.
- Bontje, D., Kooi, W.M., Liebig, M., Kooijman, S.A.L.M., 2009. Modelling long-term ecotoxicological effects on an algal population under dynamic nutrient stress. *Water Res.* 43, 3292–3300.
- Bontje, D., Kooi, B.W., van Voorn, G.A.K., Kooijman, S.A.L.M., 2010. Feeding threshold for predators stabilises predator-prey systems. *Math. Model. Nat. Phenom.* 4, 92–110.
- Bontje, D., Kooi, B.W., van Hattum, B., 2011. Sublethal toxic effects in a generic aquatic system. *Ecotox. Environ. Saf.* (in press)
- Bourlès, Y., Alunno-Bruscia, M., Pouvreau, S., Tollu, G., Leguay, D., Arnaud, C., Gouletquer, P., Kooijman, S.A.L.M., 2009. Modelling growth and reproduction of the Pacific oyster *Crassostrea gigas*: application of the oyster-DEB model in a coastal pond. *J. Sea Res.* 62, 62–71.
- Broekhuizen, N., Rickard, G.J., Bruggeman, J., Meister, A., 2008. An improved and generalized second order, unconditionally positive, mass conserving integration scheme for biochemical systems. *Appl. Num. Math.* 58, 319–340.
- Bruggeman, J., Kooijman, S.A.L.M., 2007. A biodiversity-inspired approach to aquatic ecosystem modeling. *Limnol. Oceanogr.* 52, 1533–1544.
- Bruggeman, J., Burchard, H., Kooi, B.W., Sommeijer, B., 2007. A second-order, unconditionally positive, mass conserving integration scheme for biochemical systems. *Appl. Num. Math.* 57, 36–58.
- Bruggeman, J., 2009. Succession in plankton communities: A trait-based perspective. Ph.D. thesis, Vrije Universiteit, Amsterdam.
- Bruggeman, J., Heringa, J., Brandt, B.W., 2009. Phylopars: estimation of missing parameters values using phylogeny. *Nucleic Acids Res.* 37, W179–W184.
- Campos, J., van der Veer, H.W., 2008. Autecology of *Crangon crangon* (L.) with an emphasis on latitudinal trends. *Oceanogr. Mar. Biol. Annu. Rev.* 46, 65–104.
- Campos, J., 2009. The eco-geography of the brown shrimp in Europe. Ph.D. thesis, Vrije Universiteit, Amsterdam.
- Campos, J., van der Veer, H.W., Freitas V., Kooijman, S.A.L.M., 2009. Contribution of different generations of the brown shrimp *Crangon crangon* (L.) in the Dutch Wadden Sea to commercial fisheries: a dynamic energy budgets approach. *J. Sea Res.* 62 106–113.
- Cardoso, J.F.M.F., 2007. Growth and reproduction in bivalves; an energy budget approach. PhD thesis, Groningen University.
- Diekmann, O., Metz, J.A.J., 2010. How to lift a model for individual behaviour to the population level? *Phil. Trans. R. Soc. B* 365, 3523–3530.

- Doedel, E.J., Kooijman, B.W., van Voorn, G.A.K., Kuznetsov, Y.A., 2009. Continuation of connecting orbits in 3D-odes" (ii): cycle-to-cycle connections. *Int. J. Bifurcation Chaos*, 19, 159–169.
- Ducrot, V., Péry, A.R.R., Lagadic, L., 2010. Modelling effects of diquat under realistic exposure patterns in genetically differentiated populations of the gastropod *Lymnaea stagnalis*. *Phil. Trans. R. Soc. B* 365, 3411–3590.
- Eichinger, M., Kooijman, S.A.L.M., Sempéré, R., Poggiale, J.-C., 2009. Consumption and release of dissolved organic carbon by marine bacteria in a pulsed-substrate environment: from experiments to modelling. *Aqua. Microb. Ecol.*, 56, 41–54.
- Eichinger, M., Sempéré, R., Grégori, G., Poggiale, J.-C., Lefèvre, D., 2010. Increased bacterial growth efficiency with environmental variability: results from DOC degradation by bacteria in pure culture experiments. *Biogeosciences* 7, 1861–1876.
- Emmery, A., Lefebvre, S., Alunno-Bruscia, M., Kooijman, S.A.L.M., 2011. Understanding the dynamics of ^{13}C and ^{15}N in soft tissues of the oyster *Crassostrea gigas* facing environmental fluctuations in the context of Dynamic Energy Budgets (DEB). *J Sea Res.* (this volume).
- Eynaud, Y., Nisbet R.M., Muller, E.B., 2011. Impact of harmful radiation on energy budgets in scleratinian corals. *Ecol. Modell.* (in press).
- Fablet, R., Pecquerie, L., Pontual, H.D., Hoie, H., Millner, R., Mosegaard, H., Kooijman, S.A.L.M., 2011. Shedding light on fish otolith biomineralisation using a bioenergetic approach. *Proc. Natl. Acad. Sci.* (under review).
- Filgueira, R., Rosland, R., Grant, J., 2011. A comparison of Scope For Growth (SFG) and Dynamic Energy Budget (DEB) models applied to the blue mussel (*Mytilus edulis*). *J Sea Res.* (this volume).
- Flye Sainte Marie, J., 2008. Ecophysiology of brown ring disease in the Manila clam *Ruditapes philippinarum*, experimental and modelling approaches. Ph.D. thesis, Brest University & Vrije Universiteit, Brest & Amsterdam.
- Freitas, V., Cardoso, J.F.M.F., S. Santos, S., Campos, J., Drent, J., Witte, J.I.J., Kooijman, S.A.L.M., van der Veer, H.W., 2009. Reconstruction of food conditions for Northeast Atlantic bivalve species based on Dynamic Energy Budget theory. *J. Sea Res.* 62, 75–82.
- Freitas, V., Cardoso, J.F.M.F., Lika, D., Peck, M., Campos, J., Kooijman, S.A.L.M., van der Veer, H.W., 2010. Temperature tolerance and energetics, a dynamic energy budget-based comparison of north Atlantic marine species. *Phil. Trans. R. Soc. B* 365, 3553–3565.
- Freitas, V., 2011. Climate induced changes in estuarine predator-prey systems: a DEB approach. Ph.D. thesis, Vrije Universiteit, Amsterdam.
- Freitas, V., Lika, K., Witte, J.I.J., van der Veer, H.W., 2011. Food conditions of the sand goby *Pomatoschistus minutus* in shallow waters: an analysis in the context of Dynamic Energy Budget theory. *J Sea Res* (this volume).
- Grangeré, K., Ménesguen, A., Lefebvre, S., Bacher, C., Pouvreau, S., 2009. Modelling the influence of environmental factors on the physiological status of the Pacific oyster *Crassostrea gigas* in an estuarine embayment; The Baie des Vey (France). *J. Sea Res.* 62, 147–158.
- Grangeré, K., Lefebvre, S., Bacher, C., Cugier, P., Ménesguen, A., 2010. Modelling the spatial heterogeneity of ecological processes in an intertidal estuarine bay: dynamic interactions between bivalves and phytoplankton. *Mar. Ecol. Prog. Ser.* 415, 141–158.
- Handå, A., Alver, M., Edvardsen, C.V., Halstensen, S., Olsen, A.J., Øie, G., Reitan, K.I., Olsen, Y., Reinertsen, H., 2011. Growth of farmed blue mussels (*Mytilus edulis* L.) in a Norwegian coastal area; comparison of food proxies by DEB modelling. *J Sea Res.* (this volume).
- Jager, T., Crommentuijn, T., van Gestel, C.A.M., Kooijman, S.A.L.M., 2007. Chronic exposure to chlorpyrifos reveals two modes of action in the springtail *Folsomia candida*. *Environ. Pollut.* 145, 452–458.
- Jager, T., Kooijman, S.A.L.M., 2009. A biology-based approach for quantitative structure-activity relationships (QSARs) in ecotoxicity. *Ecotoxicol.* 18, 187–196.
- Jager, T., Klok, C., 2010. Extrapolating toxic effects on individuals to the population level; the role of Dynamic Energy Budgets. *Phil. Trans. R. Soc. B* 365, 3531–3540.

- Jager, T., Vandenbrouck, T., Baas, J., Coen, W.M.D., Kooijman, S.A.L.M., 2010. A biology-based approach for mixture toxicity of multiple endpoints over the life cycle. *Ecotoxicology*. 19, 351–361.
- Jager, T., Selck, H., 2011. Interpreting toxicity data in a DEB framework; a case study for nonylphenol in the marine polychaete *Capitella teleta*. *J Sea Res.* (this volume).
- Jager, T., Albert, C., Preuss, T., Ashauer, R., 2011. General unified threshold model of survival - a toxicokinetic toxicodynamic framework for ecotoxicology. *Environ. Sci. Technol.* 45, 2529–2540.
- Kearney, M., Simpson, S.J., Raubenheimer, D., Helmuth, B., 2010. Modelling the ecological niche from fundamental traits. *Phil. Trans. R. Soc. B* 365, 3469–3483.
- Klok, C., 2007. Effects of earthworm density on growth, development, and reproduction in *Lumbricus rubellus* (Hoffm.) and possible consequences for the intrinsic rate of population increase. *Soil Biol. Biochem.* 39, 2401–2407.
- Klok, C., Holmstrup, M., Damgaard, C., 2007. Extending a combined dynamic energy budget matrix population model with a bayesian approach to assess variation in the intrinsic rate of population increase. an example in the earthworm *Dendrobaena octaedra*. *Environ. Toxicol. Chem.* 26, 2383–2388.
- Kooi, B.W., Bontje, D., van Voorn, G.A.K., Kooijman, S.A.L.M., 2008a. Sublethal contaminants effects in a simple aquatic food chain. *Ecol. Modelling* 112, 304–318.
- Kooi, B.W., Bontje, D., Liebig, M., 2008b. Model analysis of a simple aquatic ecosystems with sublethal toxic effects. *Math. Biosci. Eng.* 5, 771–787.
- Kooi, B.W., van der Meer, J., 2010. Bifurcation theory, adaptive dynamics and DEB-structured populations of iteroparous species. *Phil. Trans. R. Soc. B* 365, 3579–3590.
- Kooijman, S.A.L.M., Troost, T.A., 2007. Quantitative steps in the evolution of metabolic organisation as specified by the dynamic energy budget theory. *Biol. Rev.* 82, 1–30.
- Kooijman, S.A.L.M., Grasman, J., Kooi, B.W., 2007. A new class of non-linear stochastic population models with mass conservation. *Math. Biosci.* 210, 378–394.
- Kooijman, S.A.L.M., Sousa, T., Pecquerie, L., Van der Meer, J., Jager, T., 2008. From food-dependent statistics to metabolic parameters, a practical guide to the use of Dynamic Energy Budget theory. *Biol. Rev.* 83, 533–552.
- Kooijman, S.A.L.M., 2009. Social interactions can affect feeding behaviour of fish in tanks. *J. Sea Res.* 62, 175–178.
- Kooijman, S.A.L.M., Baas, J., Bontje, D., Broerse, M., van Gestel, C.A.M., Jager, T., 2009. Ecotoxicological applications of Dynamic Energy Budget theory. In J. Devillers, (ed.), *Ecotoxicology Modeling*, Springer Berlin, pp. 237–259.
- Kooijman, S.A.L.M., 2010. *Dynamic Energy Budget theory for metabolic organisation*. Cambridge University Press.
- Kooijman, S.A.L.M., 2011. Energy budgets. In A. Hastings and L. Gross, (eds.), *Sourcebook in Theoretical Ecology*. Univ. California Press (in press).
- Kooijman, S.A.L.M., Pecquerie, L., Augustine, S., Jusup, M., 2011. Scenarios for acceleration in fish development and the role of metamorphosis. *J Sea Res.* (this volume).
- Liebig, M., Schmidt, G., Bontje, D., Kooi, B.W., Streck, G., Traunspurger, W., Knacker, T., 2008. Direct and indirect effects of pollutants on algae and algivorous ciliates in an aquatic indoor microcosm. *Aquat. Toxicol.* 88, 102–110.
- Lika, K., Papadakis, I.A., 2009. Modelling biodegradation of phenols by algae. *J. Sea Res.* 62, 135–146.
- Lika, K., Freitas, V., van der Veer, H.W., van der Meer, J., Wijsman, J.W.M., Pecquerie, L., Kearney, M.R., Kooijman, S.A.L.M., 2011a. The “covariation method” for estimating the parameters of the Dynamic Energy Budget theory I: philosophy and approach. *J Sea Res.* (this volume)
- Lika, K., Kearney, M.R., Kooijman, S.A.L.M., 2011b. The “covariation method” for estimating the parameters of the Dynamic Energy Budget theory II: properties and preliminary patterns. *J Sea Res.* (this volume).
- Lika, K., Kooijman S.A.L.M., 2011. The comparative topology of energy allocation in budget models. *J Sea Res.* (this volume).

Lorena, A., Marques, G., Kooijman, S.A.L.M., Sousa, T., 2010. Stylized facts in microalgal growth – interpretation in a DEB context. *Phil. Trans. R. Soc. B* 365, 3509–3521.

Maar, M., Bolding, K., Petersen, J.K., Hansen, J.S.L., Timmermann, K., 2009. Local effects of blue mussels around turbine foundations in an ecosystem model of Nysted off-shore wind farm, Denmark. *J. Sea Res.* 62, 159-174.

Martin, B., Zimmer, E., Grimm, V., Jager, T., 2011. Dynamic energy budget theory meets individual-based modelling: a generic and accessible implementation. *Meth. Ecol. Evol.* (under review).

Maury, O., Faugeras, B., Shin, Y.-J., Poggiale, J.-C., Ben Ari, T., Marsac F., 2007a. Modeling environmental effects on the size-structured energy flow through marine ecosystems. part 1: The model. *Progr. Oceanogr.* 74, 479–499.

Maury, O., Shin, Y.-J., Faugeras, B., Ben Ari, T., Marsac, F., 2007b. Modeling environmental effects on the size-structured energy flow through marine ecosystems. part 2: Simulations. *Progr. Oceanogr.* 74, 500–514.

Merico, A., Bruggeman, J., Wirtz, K.W., 2009. A trait-based approach for downscaling complexity in plankton ecosystem models. *Ecol. Modell.* 220, 3001–3010.

Mueller, C., Augustine, A., Kooijman, S.A.L.M., Kearney, M.R., Seymore, R., 2011. Differential acceleration of development in Australian Myobatrachid frogs, captured by DEB theory. *Comp. Physiol. Biochem. A* (submitted)

Muller, E.B., Kooijman, S.A.L.M., Edmunds, P.J., Doyle, F.J., Nisbet, R.M., 2009. Dynamic Energy Budgets in syntrophic symbiotic relationships between heterotrophic hosts and photoautotrophic symbionts. *J. Theor. Biol.* 259, 44–57.

Muller, E.B., Ananthasubramaniam, B., Klanjšček, T., Nisbet, R.M., 2011. Entrainment of cell division in phytoplankton with Dynamic Energy Budgets. *J Sea Res.* (this volume).

Nisbet, R.M., McCauley, E., Johnson, L.R., 2010. Dynamic energy budget theory and population ecology: lessons from *Daphnia*. *Phil. Trans. R. Soc. B* 365, 3411-3590.

Omholt, A.M., 2007. Modelling, instrumentation and control in marine larviculture. Ph.D. thesis, Trondheim University.

Omta, A.-W., Kooijman, S.A.L.M., Dijkstra H.A., 2007. Influence of (sub)mesoscale eddies on the soft-tissue carbon pump. *J. Geophys. Res.* 112:doi:10.1029/2007JC004189.

Omta, A.-W., Kooijman, S.A.L.M., Dijkstra H.A., 2008. Critical turbulence revisited: the impact of submesoscale vertical mixing on plankton patchiness. *J. Mar. Res.* 66, 61–85.

Omta, A.-W., 2009. Eddies and algal stoichiometry: Physical and biological influences on the organic carbon pump. Ph.D. thesis, Vrije Universiteit, Amsterdam.

Omta, A.-W., Bruggeman, J., Kooijman, S.A.L.M., Dijkstra, H. A., 2009a. The physics of the biological carbon pump. *J. Sea Res.* 62, 179-187.

Omta, A.-W., Llido, J., Kooijman, S.A.L.M., Garçon, V., Dijkstra, H.A., 2009b. How to interpret satellite chlorophyll observations: a case study about the Mozambique channel. *Deep Sea Res.* 56, 974-988.

Pecquerie, L., 2008. Bioenergetic modelling of the growth, development and reproduction of a small pelagic fish: the Bay of Biscay anchovy. Ph.D. thesis, Agrocampus Rennes & Vrije Universiteit, Amsterdam

Pecquerie, L., Petitgas, P., Kooijman, S.A.L.M., 2009. Modelling fish growth and reproduction in the context of the Dynamic Energy Budget theory to predict environmental impact on anchovy spawning duration. *J. Sea Res.* 62, 93–105.

Pecquerie, L., Nisbet, R.M., Fablet, R., Lorrain, A., Kooijman, S.A.L.M., 2010. The impact of metabolism on stable isotope dynamics: a theoretical framework. *Phil. Trans. R. Soc. B* 365, 3455–3468.

Pecquerie, L., Johnson, L.R., Kooijman, S.A.L.M., Nisbet, R.M., 2011. Analyzing variations in life-history traits of Pacific salmon in the context of Dynamic Energy Budget (DEB) theory. *J Sea Res.* (this volume).

Poggiale, J.-C., Baklouti, M., Queguiner, B., Kooijman, S.A.L.M., 2010. How far details are important in ecosystem modelling: the case of multi-limiting nutrients in phytoplankton - zooplankton interactions. *Phil. Trans. R. Soc. B* 365, 3495–3507

Ren, J. S., 2009. Effects of food quality on energy uptake. *J. Sea Res.* 62, 72-74.

- Rosland, R., Strand, Ø., Alunno-Bruscia, M., Bacher, C., Strohmeier, T., 2009. Applying Dynamic Energy Budget (DEB) theory to simulate growth and bio-energetics of blue mussels under low seston conditions. *J. Sea Res.* 62, 49-61.
- Rosland, R., Bacher, C., Strand, Ø., Aure, J., Strohmeier, T., 2011. Modelling growth variability in longline mussel farms as a function of stocking density and farm design. *J. Sea Res.* (this volume).
- Saraiva, S., van der Meer, J., Kooijman, S.A.L.M., Sousa, T., 2011. DEB parameters estimation for *Mytilus edulis*. *J. Sea Res.* (this volume).
- Sousa, T., Domingos T., Kooijman, S.A.L.M., 2008. From empirical patterns to theory: A formal metabolic theory of life. *Phil. Trans. R. Soc. B* 363, 2453-2464.
- Sousa, T., Domingos, T., Poggiale J.-C., Kooijman, S.A.L.M., 2010. Formalised DEB theory restores coherence in core biology. *Phil. Trans. R. Soc. B* 365, 3413-3428.
- Stiefs, D., 2009. Relating generalized and specific modeling in population dynamical systems. Ph.D. thesis, Oldenburg University & Vrije Universiteit, Amsterdam
- Stiefs D., van Voorn G.A.K., Kooi, B.W., Gross, T., Feudel, U., 2010. Food quality in producer-grazer models – a generalized analysis. *Am. Nat.* 176, 367-380.
- Svendsen, C., Jager, T., Haddad, S., Yang, R.S.H., Dorne, J.L.C.M., Broerse, M., Kramarz, P., 2011. Toxicokinetics and toxicodynamics. In: C. van Gestel (ed)., *Mixture toxicity. Linking approaches from ecological and human toxicology.* CRC Press, Boca Raton, FL, US.
- Swain, S., Wren, J., Stürzenbaum, S.R., Kille, P., Morgan, A.J., Jager, T., Jonker, M.J., Hankard, P.K., Svendsen, C., Owen, J., Hedley, B.A., Blaxter, M., Spurgeon, D., 2010. Linking toxicant molecular and physiological mode of action in *Caenorhabditis elegans*. *BMC Biol.* 4, 32.
- Thomas, Y., Garen, P., Pouvreau, S., 2011. Application of a bioenergetic growth model to larvae of the pearl oyster *Pinctada margaritifera* L. *J. Sea Res.* (this volume).
- Thomas, Y., Mazurié, J., Alunno-Bruscia, M., Bacher, C., Bouget, J.-F., Gohin, F., Pouvreau, S., Struski, C., 2011. Modelling spatio-temporal variability of *Mytilus edulis* (L.) growth by coupling a dynamic energy budget model with satellite-derived environmental data. *J. Sea Res.* (this volume).
- Troost, T.A., Kooi, B. W, Kooijman, S. A. L. M. 2007. Bifurcation analysis can unify ecological and evolutionary aspects of ecosystems. *Ecol. Mod.* 204, 253-268.
- Troost, T.A., Kooi, B.W., Dieckmann, U., 2008. Joint evolution of predator body size and prey-size preference. *Evol. Ecol.* 22, 771-799.
- Troost, T.A., van Dam, J., Kooi, B.W., Tuenter, E., 2009. Seasonality, climate cycles and body size evolution. *Math. Model. Nat. Phenom.* 4, 137-157.
- Troost, T.A., Wijsman, J., Saraiva, S., Freitas, V., 2010. Modelling shellfish growth with Dynamic Energy Budget (DEB) models: an application for cockles and mussels in the Oosterschelde (SW Netherlands). *Phil. Trans. R. Soc. B* 365, 3567-3577.
- van der Meer, J., 2007. Laws on growth and heat. *Trends Ecol. Evol.* 22, 392-393.
- van der Meer, J., van der Veer, H.W., Witte, J.I.J., 2011. The disappearance of the European eel from the western Wadden Sea. *J. Sea Res.* (this volume).
- van der Veer, H.W., Cardoso, J.F.M.F., Peck, M.A., Kooijman, S.A.L.M., 2009. Physiological performance of plaice *Pleuronectes platessa* (L.): A comparison of static and dynamic energy budgets. *J. Sea Res.* 62, 83-92.
- van Leeuwen, I.M.M., 2007. Vive rápido, muere joven; matemáticas en biología del envejecimiento. *La Gaceta De La RSME*, 10, 71-96.
- van Leeuwen, I.M.M., Vera, J., Wolkenhauer, O., 2010. Dynamic energy Budget approaches for modelling organismal ageing. *Phil. Trans. R. Soc. B*, 365, 3443-3454.
- van Voorn G.A.K., Hemerik, L., Boer, M., Kooi, B.W., 2007. Heteroclinic orbits indicate overexploitation in predator prey systems with a strong allee effect. *Math. Biosci.* 209, 451-469
- van Voorn G.A.K., Stiefs, D., Gross, T., Kooi, B.W., Feudel, U., Kooijman, S.A.L.M., 2008. Stabilization due to predator interference: Comparison of different analysis approaches. *Math. Biosci. Eng.* 5, 567-583.

van Voorn, G.A.K., Kooijman, B.W., Boer, M.P., 2010. Ecological consequences of global bifurcations in some food chain models. *Math. Biosci.* 226, 120–133.

Vinga, S., Neves, A.R., Santos, H., Brandt, B.W., Kooijman, S.A.L.M., 2010. Subcellular metabolic organization in the context of Dynamic Energy Budget and biochemical systems theories. *Phil. Trans. R. Soc. B* 365, 3429–3442.

White, C.R., Kearney, M.R., Matthews, P.G.D., Kooijman, S.A.L.M., Marshall, D.J., 2011. A manipulative test of competing theories for metabolic scaling in animals. *Am. Nat.* (in press).

Wren J.F., Kille P., Spurgeon, D., Swain, S., Sturzenbaum, S.R., Jager, T., 2011. Application of physiologically based modelling and transcriptomics to probe the systems toxicology of aldicarb for *Caenorhabditis elegans* (Maupas 1900). *Ecotoxicology* 20, 397–408.