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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

Marianne Alunno-Bruscia[a, *], Henk W. van der Veer[b] and Sebastiaan A.L.M. Kooijman[c]

[a] French Research Institute for Exploitation of the Sea (Ifremer), Dept. of Functional Physiology of Marine Organisms 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] Free 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

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Abstract:

The European Research Project AquaDEB (2007–2011, http://www.ifremer.fr/aquadeb/) is joining skills and expertise of some French and Dutch research institutes and universities to analyse the physiological flexibility of aquatic organisms and to link it to ecological and evolutionary processes within a common theoretical framework for quantitative bioenergetics [Kooijman, S.A.L.M., 2000. Dynamic energy and mass budgets in biological systems. Cambridge University Press, Cambridge]. The main scientific objectives in AquaDEB are i) to study and compare the sensitivity of aquatic species (mainly molluscs and fish) to environmental variability of natural or human origin, and ii) to evaluate the related consequences at different biological levels (individual, population, ecosystem) and temporal scales (life cycle, population dynamics, evolution). At mid-term life, the AquaDEB collaboration has already yielded interesting results by quantifying bio-energetic processes of various aquatic species (e.g. molluscs, fish, crustaceans, algae) with a single mathematical framework. It has also allowed to federate scientists with different backgrounds, e.g. mathematics, microbiology, ecology, chemistry, and working in different fields, e.g. aquaculture, fisheries, ecology, agronomy, ecotoxicology, climate change. For the two coming years, the focus of the AquaDEB collaboration will be in priority: (i) to compare energetic and physiological strategies among species through the DEB parameter values and to identify the factors responsible for any differences in bioenergetics and physiology; and to compare dynamic (DEB) versus static (SEB) energy models to study the physiological performance of aquatic species; (ii) to consider 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) to scale up the models for a few species from the individual level up to the level of evolutionary processes.

1. Introduction

Variability is a universal feature of the functioning of biological systems, seen at every level of organisation from molecules to ecosystems. Aquatic systems are no exception as they are exposed to high spatial and temporal variability. Many factors can be responsible for environmental variability and because it acts on different scales, modelling is essential for the study of its consequences for ecosystems. Models of population or community dynamics (Tuljapurkar & Caswell, 1996) and food-web dynamics (Pauly et al., 2000) provide valuable tools for analysis and prediction. Models based on the conservation law for mass and energy in biology can be used to evaluate and predict how the environment operates on individual aquatic organisms through their metabolism, and how it affects population dynamics. However, in order to be reliable and to make not just qualitative but also realistic quantitative predictions, models should be built on a precise description of the physiological processes within individuals.

The study and modelling of mechanisms involved in acquisition and use of energy by individuals is vital for estimating their life history traits (*e.g.* growth, reproductive effort, survival, age and size at maturation), and thus for describing population and community dynamics. Growth, reproduction and survival are activities requiring energy, for which living organisms need substrates (nutrients, light, food). Fry (1947, 1971) defined activity as including all the physiological work an animal does, not just for movement but also for growth and physiological regulation of its internal environment. Energy generated in this way is essential not only for individual organisms, and for the populations and communities they form in nature (Stearns, 1992 ; Nisbet et al., 2000), but also for whole ecosystems because trophic fluxes rely on energy (*e.g.* Begon et al., 1996).

Energy allocation within organisms is closely linked to metabolism and depends both on their genotypes (Leroi et al., 1994a,b ; Ernande et al., 2004) and the environment, where variation operates on animals' activity through their metabolism (Fry, 1947). Organisms exposed to environmental change can respond by different adaptive mechanisms depending on the time scale. In the short-term, i.e. over shorter timescales than a lifetime, organisms can show rapid and reversible transformations in their physiology, behaviour and morphology, which refer to the principle of phenotypic flexibility (Piersma & Drent, 2003). Variation and selection are key to evolutionary change. The evolution of organisms represents their long term adaptation to environmental change. Energy allocation strategies with a genetic basis can be modified by the evolutionary process in response to changing environments and probably much more so than the short term adaptive capacities of the same organisms (Leroi et al., 1994a,b ; Jørgensen et al., 2006). Such evolutionary changes in energy allocation strategy can have serious long term implications for population dynamics and ecosystems because they have indirect effects on life history traits and trophic fluxes (Jørgensen et al., 2006).

Many empirically based population and evolutionary studies of energy budgets use "net production" models (e.g. Ross & Nisbet, 1990; Gurney & Nisbet, 1998) or "static energy budgets" (SEB) models (e.g. Paloheimo et al., 1982) derived from the "scope for growth" (SFG) concept. In "net production" or "scope for growth" models (e.g. Fry, 1947; Bayne & Newell, 1983), the assimilated energy is immediately available for maintenance, the remainder is used for growth and or is deposited as reserves (e.g. Ren & Ross, 2005). Another category of models that have been developed are the (dynamic) energy budget (DEB) or "assimilation models" (see Nisbet et al., 2000; Ren & Ross, 2005; Van der Meer, 2006). A very comprehensive body of theory now exists on DEB (Kooijman, 2000, 2010). DEB models use ordinary differential equations to describe the rates at which individual organisms assimilate and use energy from food for maintenance, growth, reproduction, development and ageing. According the DEB theory, a fixed proportion *kappa* of the available energy is allocated to somatic maintenance and growth combined, and the remaining *1-kappa* to either maturation (for embryos and juveniles) or to reproduction and maturity maintenance (for adults). The DEB model has several advantages over other bio-energetic models: *i/* DEB is a mechanistic and dynamic model that relies on simple physiological principals common to all species; *ii/* it has a limited number of parameters, which simultaneously integrate genetic and environmental effects on the animal; *iii/* its structure allows the comparison of energetic (and physiological) management between species, as inter-specific differences appear in the model parameter values. An important difference between DEB and SFG models is in the interpretation of respiration. SFG subtracts respiration from assimilation as losses that are not available for growth (or reproduction), while DEB includes the overhead costs of growth and reproduction in respiration. This is a fundamental difference in bookkeeping.

Using the DEB theory also allows to describe and to quantify the path between different levels of organisation, from the individual (or even the molecule) to the population and ecosystem (Nisbet et al., 2000; Kooijman et al., 2001). Because the theory is based on precise knowledge of energy partitioning within organisms, it can be used to analyse the effects of environmental factors, on demographic characters (growth, reproduction, survival) and deduce effects on population dynamics. Principal environmental factors taken into account by the DEB model include temperature and trophic resources (food density), which are forcing variables for energy partitioning (e.g. Van der Veer et al., 2006; Pouvreau et al., 2006; Ren & Ross, 2005). Other environmental factors included are the effects of pollutants (*e.g.* Péry et al., 2002; Casas & Bacher, 2006), pathogens, competitors, predators or man, notably through fishing pressure on certain species, communities or ecosystems. The theory also allows the integration of different time scales: life cycle, ecological time and evolutionary time. Because the dynamics of energy partitioning are considered throughout the life cycle of an individual, the repercussions for life history traits can be known and from this the population dynamics derived in turn and even the invasion fitness consequences (Metz et al., 1992) which determine the evolutionary dynamics of organisms and their characters.

2. Scientific objective of the AquaDEB project

Working within a common theoretical framework for quantitative bioenergetics based on the dynamic energy budget (DEB) theory (Kooijman, 2000, 2010), the main objectives of the AquaDEB project are *i/* to study and compare the sensitivity of aquatic species (molluscs and fish) to environmental variability of natural or human origin, *ii/* to evaluate the related consequences at different biological levels (individual, population, ecosystem) and temporal scales (life cycle, population dynamics, evolution).

The approach consists of a three step process:

(1) applying the standard DEB model to a selection of species, and build, if necessary, species-specific extensions that allow the comparison of species on the basis of parameter values. The main deliverable is to provide generic DEB models for each species and in analyse the intra-species variability in parameters;

(2) comparing the response of the various species to environmental fluctuations in terms of energy allocation strategy using the DEB model parameters. What is at stake is to identify and explain the inter-species variability in the DEB parameters. A comparison between outputs of static energy budget (SEB) and dynamic energy budget (DEB) models is also planned for some species;

(3) scaling up analysis to the population level, and then to the ecological and evolutionary levels. More specifically, what is at stake is to examine how some disturbances related to pollutants, new diseases, parasites and climate, or fisheries modify the strategies of energy allocation in aquatic organisms, as well as their life history traits (growth, size and age for sexual maturity, fertility and survival) with inferences on population dynamics. The disturbances include the

effects and the fate of chemical toxicants in aquatic organisms (e.g. kinetics of bioaccumulation of contaminants in the individual, sensitivity of the population dynamics to contamination and environmental factors, bio-transformation processes, transfer of contaminants over generations). The AquaDEB project is focused on two groups of aquatic organisms: molluscs (e.g. *Crassostrea gigas*, *Tapes philippinarum*, *Mytilus edulis*, *Cerastoderma edule, Lymnaea stagnalis*) and fish (e.g. *Solea solea*, *Pleuronectes platessa, Merluccius merluccius*, *Engraulis encrasicolus, Dicentrachus labrax, Danio rerio)*. These species were selected according to two sets of criteria: *i*) they are important from an ecological point of view, i.e. bio-geographic distribution, different scales for time and space, some are important for human activities (aquaculture, fisheries, impact of invasive species) and all are useful bio-indicators for the risk assessment of contaminants affecting aquatic animals; *ii*) they belong to widely separated phyla and exhibit contrasting reactions to environmental constraints on behaviour and physiology. For the purpose of this special issue, this list of species has been extended to crustaceans (e.g. *Crangon crangon*) and microalgae.

Over the last two years (2007-2008; Phase I), the AquaDEB collaboration has focused on steps 1 and 3 by means of two regular annual meetings in combination with (electronic) communication among partners. It has been also acting as a training network for young PhD and post-doc researchers: doctoral degrees and/or joint post-doctoral supervision among some AquaDEB partners have strengthened the collaborative work. The biannual DEB tele-courses support the training network. The AquaDEB partnership involves research teams at: Ifremer (French Research Institute for Exploitation of the Sea), IRD (French Research Institute for Development), and the Universities of Brest, Caen, Nantes in France; the NIOZ (Royal Netherlands Institute for Sea Research) Texel, the IMARES (Institute for Marine Resources and Ecosystem Studies) Wageningen and the Department of Theoretical Biology of the Free University of Amsterdam in Holland. This consortium has enlarged with the active participation of external European partners from INRA (French National Institute for Agricultural Research) and IMR (Norwegian Institute of Marine Research), from the Universities of Bergen (UiB, Norway) and of Mediterranea (Marseille, France), and from the Instituto Superior Técnico of the University of Lisbon (Portugal), and finally Telecom Bretagne (France) and BIO-LITTORAL (France).

The overall mid-term results are in accordance with expectations (see steps (1) and (3)) and are crystallised in the various contributions of this special volume. Most of these results, as well as other recent DEB applications on other species and new developments in different fields, have been presented and gathered during the 1st International Symposium on DEB theory, the DEB2009 Symposium which was held at Brest (France) from the 19th to the 22nd of April 2009 (http://wwz.ifremer.fr/index.php/deb2009); this symposium was linked to the DEB tele-course 2009. The AquaDEB project naturally occurs in the continuity of a previous bilateral Dutch-French collaboration entitled DEBIB “Dynamic Energy Budget in Bivalves” (Van der Veer & Alunno-Bruscia, 2006; see *Journal of Sea Research*, vol. 56 issue 2). This special issue is opening the way for other AquaDEB results which will appear soon (e.g. Rico-Villa et al. submitted for publication; Eichinger et al., submitted for publication; Pecquerie et al. submitted for publication; Campeas et al. in preparation; Bourlès et al. in preparation), while a theme issue on DEB theory and its applications of the *Philosophical Transactions of the Royal Society* entitled “Developments in DEB theory and its applications” will appear in 2010.

3. Structure of this special issue

This special issue includes the main results of the AquaDEB group at mid-term activity of the project regarding step 1 (i.e. building up generic DEB models and collecting a set of DEB parameters for different aquatic species) and step 3 (i.e. scaling up to the ecological level by coupling the individual DEB models to ecosystem and bio-accumulation/perturbation models). This issue also benefits from external contributions, which are thematically ”DEB-related” to the AquaDEB project.

In the first paper of this special issue, Rosland et al. (2009 -this issue) provide realistic estimates of key DEB parameters for an important shellfish commercial species, the blue mussel (*Mytilus edulis*) under low seston environments in Norway. Rosland et al. (2009 -this issue) validate the model by comparing simulations with growth data on mussels from different sites in southern Norway, and also assess the quality of the estimated DEB parameters and the model robustness to changes in parameter values, initial conditions and environmental forcing, i.e. temperature and chlorophyll *a* concentration as the only available food quantifier for mussels.

In the second contribution by Bourlès et al. (2009 -this issue) extends the standard DEB model to include more detail in food selection and nutrition for another important commercial bivalve species, *Crassostrea gigas*. The DEB model was first validated for the Pacific oyster by Pouvreau et al. (2006); now it is applied at a rearing site of *C. gigas* where temperature variations are broader and different food quantifiers are available for food density. This extended version of the oyster-DEB model is run with the different food quantifiers: phytoplankton enumeration demonstrates its reliability to represent the best the available food explaining the oyster growth, compared to chlorophyll *a*. The updated oyster-DEB model presented Bourlès et al. (2009 -this issue) supports the “aim for generality” proposed in the earlier paper (Pouvreau et al. 2006) and has been further tested in different environments on the French Atlantic coast where *C. gigas* is cultured (Bourlès et al. in prep).

Next, Ren (2009 -this issue) is testing the DEB model on the greenshell mussel *Perna canaliculus*, another important commercial shellfish. By using experimental data on mussel feeding experiments, Ren (2009 -this issue) demonstrates that inorganic particles, which concentration may fluctuate in the natural seston, plays an important role in the functional response of energy uptake by *P. canaliculis* and that the inclusion of the inorganic term may reduce some uncertainty in the half-saturation coefficient and improve the estimation of ingestion rate. These first three papers by Rosland et al. (2009 -this issue), Bourlès et al. (2009 -this issue) and Ren (2009 -this issue) all underline that the choice of appropriate quantifiers for food quantity and quality is important and even critical in the parametrisation of DEB models and may help to explain and control for some uncertainty or variability of the half-saturation coefficient in a DEB model. As a complementary approach, the feeding processes could be defined more precisely in bivalves (Bourlès et al. 2009, Rosland et al. 2009 -this issue).

In a reverse approach, Freitas et al. (2009 -this issue) apply the DEB model to dynamically reconstruct the food conditions of Northeast Atlantic coastal bivalve species, i.e. the Baltic clam *Macoma balthica*, the soft-shell clam *Mya arenaria*, the cockle *Cerastoderma edule* and the blue mussel *M. edulis*. By focusing on the food (energy) assimilated rather than on the potential food available, Freitas et al. (2009 -this issue) propose an approach to assess food limitation in the field which has several implications for growth and production of bivalve stocks. For all bivalve species, their results suggest food limitation over the range of locations. In general, reconstructed food intake indicates better conditions for *C. edule* compared to the other species, while *M. edulis* presented the lowest food conditions in all the areas. Despite the indications for a latitudinal trend in primary production, no clear pattern or relationship between reconstructed food conditions and latitude was observed suggesting that any trend may be overruled by local conditions.

In the next two contributions, the standard DEB model is applied on two fish species: the plaice *Pleuronectes platessa* (Van der Veer et al. 2009-this issue) and the anchovy *Engraulis encrasicolus* (Pecquerie et al. 2009 -this issue). For the plaice, Van der Veer at al. (2009 -this issue) use the DEB model to derive body size scaling relationships describing the physiological performance of *P. platessa* and make a comparison with allometric relationships derived from a static energy budget (SEB) model. Their results indicate that *i*) DEB models can correctly predict the physiological performance of plaice within variable environments, and *ii*) DEB are preferred over SEB approaches because they are neither descriptive nor species-specific, and they can be used for extrapolations beyond the range of experimental data iii) SEB approaches have a serious problem because the allometric coefficients vary. Van der Veer et al. (2009 -this issue) discuss how SEB-derived information can be used in a DEB-context. The authors point out that some aspects of the DEB model can still be improved, e.g. processes underlying the temperature tolerance range, temperature acclimation and the relationship between optimal temperature and body size; the contribution of various processes to metabolism; and the incorporation and quantification of Fry's scheme of the environment, especially of masking (e.g. sub-optimal salinity conditions) and limiting (e.g. low oxygen conditions) factors.

In the case of the anchovy, Pecquerie et al. (2009 -this issue) extend the DEB theory to investigate how environment variability impacts the spawning timing and duration of a multiple-batch spawning fish species. The model is successfully applied to reproduce the growth and reproduction of anchovy in the Bay of Biscay. The model captures realistically the start and ending of the spawning season, including the timing of the spawning events, and the change in egg number per batch. Based on the results from different simulation scenarios to validate the model predictions under starvation conditions and to quantify the impact of fluctuating forcing conditions of the spawning pattern of *E. encrasicolus*, Pecquerie et al. (2009 -this issue) conclude that the model can be used to realistically predict spawning in spatially and temporally varying environments and provide initial conditions for bio-physical models used to predict larval survival for fisheries applications.

Spawning timing and duration is also a key issue for the commercial fisheries of the brown shrimp *Crangon crangon* from the Dutch Wadden Sea. In that context, Campos et al. (2009 -this issue) apply the DEB model on *C. crangon* to contribute to the debate on which generation, i.e. winter generation from the previous year or summer generation from the current year, sustains the autumn fishery catches in the Wadden Sea. Firstly, the authors estimate the DEB parameters based on published information on this species. Then, they evaluate the reliability of the DEB parameters by comparing the model output with published experimental data on shrimp growth in relation to water temperatures. Finally, the DEB model is applied to calculate maximum growth under optimal food conditions at the prevailing water temperature in the Wadden Sea for both the summer and winter generations. On the basis of these simulations, Campos et al. (2009 -this issue) conclude that this is likely the summer generation from the previous year that contributes to the bulk of the fisheries recruits in autumn.

In the subsequent papers, the effects of some disturbances (disease, pollutants) on the physiological traits of aquatic species are analysed by using Dynamic Energy Budgets and individual DEB models are coupled to bio-accumulation or hydro-biogeochemical models to scale up the analysis to the ecosystem level (see step 3).

Flye Sainte Marie et al. (2009 -this issue) propose an approach allowing a quantitative estimation of the energetic cost of a bacterial disease, the Brown Ring Disease (BRD), on the Manila clam *Ruditapes philippinarum* by using DEB. On the basis of starvation data of infected and uninfected clams, these authors show that an energetic cost can be associated to high intensity of BRD development, independently of the decrease in filtration activity and that during an infection the maintenance cost can almost double compared to the uninfected situation.

Bodiguel et al. (2009 -this issue) study factors impacting accumulation of organic pollutants in the European hake (*Merluccius merluccius*) through the fish ontogeny in the framework of Dynamic Energy Budgets. The bioaccumulation model that they proposed is a comprehensive approach that relates evolution of hake PCB contamination to physiological information about the fish, such as diet, metabolism, reserve and reproduction status. The model describes the total and the lipid-normalised concentration of 4 PCB congeners in male and female hakes from the Gulf of Lions (NW Mediterranean sea) and the Bay of Biscay (NE Atlantic ocean). Results of the model simulations clearly demonstrate the relative effects of food contamination, growth and reproduction on the PCB bioaccumulation in hake. The same species living in different habitats and exposed to different PCB prey concentrations exhibit marked difference in the body accumulation of PCBs. At the adult stage, female hakes have a lower PCB concentration compared to males for a given length. Bodiguel et al. (2009 -this issue) successfully simulate these sex-specific PCB concentrations by considering two mechanisms: a higher energy allocation to growth for females and a transfer of PCBs from the female to its eggs when allocating lipids from reserve to eggs.

Among organic pollutants, phenols constitute a group found in many near-shore marine systems, which degradation by bacteria and fungi has been extensively studied both experimentally and theoretically, but only relatively recently the capabilities of some algae for phenols biodegradation has gained interest. Lika & Papadakis (2009 -this issue) describe the aerobic biodegradation of phenolic compounds by microalgae using the DEB model and qualitatively validate against experimental data. A microalgal cell has the ability to produce biomass via the autotrophic assimilation (uptake of light and dissolved inorganic carbon), the heterotrophic assimilation (uptake of dissolved organic carbon) and, to a lesser extend, via the biodegradation of phenols. The rules of synthesizing units are used for the uptake and interactions of substrates and for the merging of assimilates. The model is capable of making predictions under oxygen and carbon (inorganic and organic) limiting conditions. Model predictions cover a wide range of experimental evidence, but also give a possible explanation for the inhibition of bioremoval of phenols (due to the lack of oxygen) in the presence of glucose. Model analysis suggests that this inhibition may be due to the competition for oxygen between glucose and phenol assimilation. In general, the balance between the benefits and costs of the different types of assimilation determines the microalgal growth rates as well as the phenol biodegradation rates. Being based on general assumptions, the model can be applied to the biodegradation of a wide variety of aromatic compounds.

Next, Grangeré et al. (2009 -this issue) couple the individual DEB model for *C. gigas* (see Bourlès et al. 2009 -this issue) which simulates growth and reproduction (i.e. gametogenesis and spawning), and a biogeochemical sub-model, which simulates trophic resources of oysters (i.e. phytoplankton biomass via chlorophyll a). Adequate simulation of oyster growth dynamics requires a relevant food quantifier compatible with outputs of the biogeochemical sub-model (i.e. chlorophyll a concentration). The authors use the phytoplankton carbon concentration as quantifier for food, as it is a better estimator of the energy really available to oysters. The transformation of chlorophyll a concentration into carbon concentration using a variable chlorophyll a to carbon ratio enable to improve the simulation of oyster growth especially during the starvation period (i.e. autumn and winter). Once validated, the coupled model is a suitable tool to study the influence of the year-to-year variability of phytoplankton dynamics and water temperature on the gonado-somatic growth of the Pacific oyster. Four years with highly contrasted meteorological conditions (river inputs, water temperature and light) 2000, 2001 (both wet years), 2002 and 2003 (both dry years), are simulated. Significant variability of the response of oysters to environmental conditions are highlighted between wet and dry years. In the wet years, an increase in loadings of river nutrients and suspended particulate matter led to a shift in the initiation and the magnitude of the phytoplanktonic spring bloom, and consequently to a shift in oyster growth patterns. In the dry years, an increase in water temperature -especially during summer- resulted in early spawning. Thus, the gonado-somatic growth pattern of oysters was shown to be sensitive to variations in river loadings and water temperature.

In a similar approach of coupling DEB with biogeochemical model, Maar et al. (2009 -this issue) model the growth and feed-backs of blue mussels in natural beds and on turbine foundations in an off-shore wind farm (OWF) located in a shallow coastal ecosystem by coupling a DEB model to a small scale 3D hydrodynamic–biogeochemical model. The model results show that blue mussels located higher up in the water column on turbine pillars achieved a 7-18 times higher biomass than those located on the scour protection because the former experience an enhanced advective food supply. Secondly, the high biomasses of blue mussels on foundations created local ‘hot spots’ of biological activity and changed ecosystem dynamics due to their feed-backs e.g. ingestion of microplankton and copepods, excretion of ammonium and egestion of faecal pellets. These results are supported by field measurements around foundations of Chl a concentrations and biomasses of the fauna community. This study emphasised that OWFs seem to be particularly favourable for blue mussels in the western Baltic Sea and that the functioning of the OWFs as artificial reef ecosystems depends upon how the blue mussels interact with their local pelagic and benthic environment.

In the next paper, Kooijman (2009 -this issue) extends the standard DEB model with a simple stochastic module for interaction between individuals (with identical parameters) to mimic social interactions in fish from the same tank (and from the same clutch of eggs) and to explain differences in fish size. The remarkable result obtained by Kooijman (2009 -this issue) is that length-at-age of two individuals in a tank where the number of food particles is kept constant closely follow von Bertalanffy growth curves with very different parameters, while in reality the individuals have identical parameters. The empirical observation demonstrates that fish are close to the supply end of the supply-demand spectrum and that age-based models for growth do not apply to supply systems.

Finally, in the context of the soft-tissue carbon pump (i.e. growth, sinking and remineralisation of phytoplankton), Omta et al. (2009 -this issue) develop a plankton physiological model with a novel representation of the effect of temperature and light on plankton stoichiometry in the context of Dynamic Energy Budgets. This model predicts that the effect of temperature on the carbon:nutrient ratio depends on the light conditions. Using this model combined with a mechanistic model for the mixed layer, Omta et al. (2009 -this issue) study the biological carbon pump at the Bermuda Atlantic Time-Series site and at various locations along a meridional transect through the Atlantic Ocean. Their results suggest that the soft-tissue carbon pump is stronger at mid-latitudes than in the (sub-)tropics and near the poles as consequence of latitudinal variations in algal stoichiometry.

4. Challenges for the next two years of AquaDEB

Until the end of the project (2009-2010; Phase II), a special emphasis in the AquaDEB collaboration will be put in priority on : *i*) the analysis of intra-specific variability in the DEB parameters, e.g. reducing some variability or uncertainty of the half-saturation coefficient and improving the estimation of ingestion rate in bivalves, linking some intraspecific genetic variability with parameter variability (see step 1); *ii*) the interspecific comparison of energy flows by means of variability in the various DEB model parameters towards a more quantitative understanding of the broad patterns in physiological diversity; as well as the model comparisons (see step 2); *iii*) considering different scenarios of environmental disruption (e.g. diffuse or massive pollution, fisheries pressure on marine species stocks, climate change) to forecast effects on growth, reproduction and survival of key species and to better understand the survival and expansion strategies of these species, in relation to their different capacities for adaptation and reproduction.; (*iii*) scaling up the models for a few species from the individual level up to the level of evolutionary processes.

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