

# DEB2009 Symposium

**Dynamic Energy Budget :  
30 years of research for  
metabolic organization**



**1<sup>st</sup> international DEB symposium**



## **Welcome to the 1<sup>st</sup> international DEB symposium!**

We are pleased to welcome you to at the first Symposium on Metabolic organization in Brest, 19-22 April, 2009. This conference is being organized jointly by Ifremer (French Institute for the Research and Exploitation of the Sea), the Department of Theoretical Biology at Vrije Universiteit Amsterdam, the Universities of Brest (UBO), Marseille (LMGEM-UMR CNRS 6117), Caen (UMRPE2M, LBBM) and Lisbon (Instituto Superior Técnico), the IRD (French Research Institute for Development), the INRA (French National Institute for Agricultural Research), the NIOZ (Royal Netherlands Institute for Sea Research), the IMARES Wageningen (Institute for Marine Resources and Ecosystem Studies), as all these research teams are involved in research on DEB theory. You are 81 persons (at least!) from 12 different countries (Croatia, Denmark, France, Finland, Holland, Italy, Portugal, Mexico, New Zealand, Norway, United Kingdom, United States of America), who participate to this symposium.

Dynamic Energy Budget theory for metabolic organization is based in first principles and is central in biology. The aim of the symposium is to bring together people with an interest in DEB theory and its applications in the various fields, ranging from molecules to system earth, from fundamental to applied, from experimental to theoretical, covering biology, chemistry, physics, geology and mathematics. Few symposia can bring such a diversity of disciplines together, because specialists cannot recognize the coherence. Why should they waste time to lectures on topics they never meet again? DEB theory is unique, however, in revealing the required coherence for fruitful exchange, with the explicit aim to restore coherence in biology, and to develop a fundamental physical-style research program in biology. We seek to develop the theory on the basis of practical applications in fisheries, aquaculture, eco-toxicity, pharmacology, medicine, biotechnology, sewage water purification, sustainable development, economics.

Special issue 2 of the *Journal of Sea Research* 56 (2006) was exclusively devoted to applications of DEB theory in bivalves. A second special issue of *JSR* is planned for the summer 2009, which will be presented during the symposium. A theme issue on DEB theory and its applications of the *Philosophical Transactions of the Royal Society* is in preparation for 2010.

The meeting will include oral presentations and posters in four sessions, which will be opened by keynote speakers.

The organizing and scientific committees of the DEB2009 symposium

**Organizing committee:**

Marianne Alunno-Bruscia  
Arnaud Campeas  
Virginie Ducrot  
Marie Eichinger  
Jonathan Flye Sainte Marie  
Fred Jean  
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Jaap van der Meer  
Jean-Christophe Poggiale  
Philippe Pondaven  
Eric Rannou  
Henk van der Veer

## Conference overview

### Monday 20 April

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09:00-09:25	Introduction	Ifremer Plouzané
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12:50-14:20	Lunch	Ifremer Plouzané
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(conference room Lucien Laubier, Ifremer centre, Technopôle Brest Iroise, Plouzané)

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**Session 1: Introduction: general theory,  
formal aspects of DEB theory**

***Chairmen: J.-C. Poggiale & E. Rannou***

**Dynamic Energy Budget Theory:  
Reaching Consilience Between the Physical and the Biological Sciences  
through an Axiomatic Theory for Metabolism**

*Keynote speaker:*  
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*Key words: Dynamic Energy Budget theory, Occam's razor, consilience, metabolism*

**Abstract:** In contrast to what have been frequent statements in the ecological literature, DEB theory has shown that it is possible to obtain a unified mathematical theory for biology, similar to physical theories. At the same time, DEB has attained this aim by establishing a theory which is compatible with physical constraints, again something which is frequently disregarded in biology, thus ensuring Edwards Wilson's aim of consilience between the sciences.

Building on a recent axiomatic formalisation of DEB theory (Sousa, T., T. Domingos, S. A. L. M. Kooijman, 2008, From empirical patterns to theory: A formal metabolic theory of life, *Philosophical Transactions of the Royal Society of London B* 363: 2453–2464), here we show that DEB theory can be built from 1) the fundamental thermodynamic constraints that all processes obey mass and energy conservation but lead to entropy production, 2) a physical assumption of quite general applicability, that local flows are proportional to differences in intensive variables (and, hence, total flows are proportional to surface areas), 3) a biological assumption, that cells are metabolically very similar, independently of the organism or its size, and, 4) in a “systems theory” type of approach, an application of Occam's razor, in always choosing the simplest possible formulation of a mathematical theory (minimize the number of state variables; choose linear over non-linear functions; minimize the number of parameters).

Having condensed DEB theory in this compact definition, we then show how these fundamental assumptions lead to the strong and weak homeostasis principles, and then to partitionability of reserve dynamics and the reserve dynamics itself. With this, we obtain the von Bertalanffy growth curve and Kleiber's rule, for intra- and inter-specific comparisons.

## Scaling laws for entropy production within and across species: a mechanistic approach

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*Keywords: Metabolism, entropy, scaling laws*

**Abstract:** Metabolism describes the internal management of energy and mass of an organism and reflects its thermodynamic limitations; its quantification is usually done with statistical scaling rules. Although theoretically shallow, these rules can lead to interesting results, like approximately constant lifetime metabolized energy per mass for all mammals. However, such results can be abusive if the assumptions made are incorrect.

Beyond the fact that they do not explain the phenomena they describe and all the associated dimensional incoherencies, allometric rules can be overly simplifcative, for example by considering only one metabolic rate, as proportional to dioxygen use, to describe a system that is complex and multi-layered in terms of energy conversion and use.

This work uses a general theory for biological systems, Dynamic Energy Budget theory, to provide mechanistic quantifications and explanations for metabolic rates, absolute and mass-specific entropy production and a physiological time rate, both at the individual level and across related species, which allometric applications do not consider. Results indicate that power laws provide good approximations for most variables such as dioxygen consumption flux and metabolic rates in general but not so much for the entropy production and dissipated heat flux. Concurrently, recent results that point to equivalent mass specific entropy production for all organisms in the physiological time scale are flawed because they are dependent on the abusive use of allometrical scaling laws.

Such flaws are caused by the aggregation behind the concept of metabolic rate in allometry. While the allometric coefficient characterizing the dioxygen consumption rate depends on a certain mix of volume-proportional and surface area-proportional processes, there is no reason to believe that exactly the same mix is representative of the organism's entropy production. This is shown by the fact that each variables' power law exponent is different from the other's.

These exponents are, of course, resultant from different compromises when considering either intra or interspecies comparisons. In intraspecies, the growth of a single organism is followed, and the allometric exponent is directly related with the dependence of assimilation, dissipation and growth on shape. In interspecies, the allometric exponents depend on the evolution of design primary parameters across species, affecting indirectly the variables through the organisms' parameter sets.

The different behaviours of the various metabolic processes introduce differences in their scaling behaviour. For example, with entropy being related to dissipated heat flux and reserve residence time being related with the catabolic power rate, mass specific production of entropy in the reserve residence time lapse is not constant solely by the fact that these variables are not fundamentally affected in the same way by shape.

## Life Engine - Construction of a DEB module for videogames

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*Key words: Dynamic Energy Budget theory, Individual-Based model,*

**Abstract:** The Dynamic Energy Budget (DEB) theory has become a fundamental tool in modeling the metabolic behaviour of organisms. On the other hand, the videogame industry is striving for more realism in its products. The DEB group in IST has joined Biodroid, a game developing company, in the Life Engine project to build a game engine for metabolic modeling using DEB. Our goal is not only to have a module to be used in games but also a module for scientific use.

The project will start by implementing the standard DEB model for an organism with one reserve, one structure and one product feeding on one substrate. Along the three years of the project we will extend this module to include several reserves, several structures, several substrates and several products. These inclusions will have to be done automatically, based on standard rules, and not on a case by case implementation.

Another of the main implementation challenges will be the modeling of populations. We will start by focusing on an IBM (Individual-Based Model) approach, modeling each individual separately. Nevertheless, we will study the transition between IBMs and structured populations and aspire to construct a rule of thumb to choose between the two types of models.

In summary, we will present the Life Engine project, its main goals, foreseen challenges and expected results.

## DEB models with physiologically transparent state variables

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*Keywords: allocation strategy, blood, mammal reproduction, toxicology*

**Abstract:** Transparent connections between state variables in a DEB model and physiological observables greatly facilitate interpretation of experimental results. For example, many studies involve tracking assimilation and biotransformation of pulse-administered, labeled compounds. In such experiments, an adequate separation of short and long timescales, as well as representation of assimilation pathways and description of distribution of assimilate in the tissue is important. Such separation requires explicit representation of physiologically and/or anatomically relevant compartments, rather than the conceptual division of all tissue into reserves and structure practiced in most DEB models where even parts of the same cell get partitioned into different compartments.

We shall start by presenting a parameter-sparse DEB model enabling a more direct connection with measurable quantities (Klanjscek et al. 2007). The model was originally developed to study bioaccumulation of toxicants in large marine mammals and applied to the North Atlantic right whale. It captures the observed right whale life history, and correctly predicts contrasting male and female bioaccumulation patterns. The model distinguishes between structure and reserves in a physiologically differentiable way and has an explicit representation of the blood, which serves as an intermediary for all energy and toxicant fluxes between compartments.

Assimilated energy first enters the blood compartment where it can be utilized for maintenance, growth, reproduction, or transferred to energy storage. Maintenance is taken directly from the blood, while other processes - including energy storage - compete for energy. The resulting energy fluxes, together with the flux of energy from storage to the blood form a self-regulating system which produces a von Bertalanffy-like growth pattern. Gestation is triggered if reserves are above a critical level during the reproductive season. Flow of energy to reproduction is a balance between the demand of the offspring, and the ability of the mother to meet that demand. Toxicants entering the organism can be biotransformed by an organ (e.g. liver) in the blood, stored in the energy storage or structure where it may undergo a different mode of biotransformation, or transferred to the offspring at rates dictated by the concentration in the blood.

We shall propose that this approach to DEB modeling has broad applicability, as it incorporates dynamic energy allocation strategies related to life histories including, but not limited to, demand-driven allocation to reproduction, seamless transition to extreme starvation and swift resumption of growth following starvation, as observed in some species. The explicit representation of the blood compartment enables modeling and analyzes of organ-mediated toxicant metabolization, as well as effects of acute and starvation-induced exposure to toxicants and their metabolization.

### References :

Klanjscek, T., R.M. Nisbet, H. Caswell, and M.G. Neubert. 2007. A model for energetics and bioaccumulation in marine mammals with applications to the right whale. *Ecological Applications* 17:2233-2250.



## **Session 2: Perturbations studies, (eco)toxicity**

***Chairwomen (1<sup>st</sup> part): . V. Loizeau & V. Ducrot***  
***Chairwomen (2<sup>nd</sup> part): . V. Loizeau & M. Eichinger***

## What toxicants can teach us about metabolic organisation

*Keynote speaker:*

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*Keywords: toxicants effects*

**Abstract:** Organisms that are exposed to chemicals respond with changes in their life-history behaviour. These unlucky organisms may, for example, show a deviating growth curve compared to their unexposed relatives, and differ in the timing and rate of their reproduction. Clearly, such changes must reflect underlying changes in their energy budget. It is therefore essential to view toxicant effects as the response of a stressed system, where metabolic processes change under the influence of toxicants. The study of toxicant effects on (non-mammalian) organisms is the realm of eco-toxicology. Unfortunately, a process-based view is rare among ecotoxicologists, who generally appear to prefer a more descriptive view of toxic effects. In contrast, scientists working on metabolic organisation usually have little interest in toxicants. However, I will argue that the combination of energy budget theory and toxicants is a fruitful one for both fields. Firstly, existing theory on dynamic energy budgets can be applied to the practical problems of dealing with the enormous number of man-made chemicals, and aid in assessing their impacts on human and environmental health. Regulatory decisions require extrapolation from the results of laboratory tests to populations under field conditions, and any sensible extrapolation requires a thorough understanding of the system. Secondly, and more interesting scientifically, chemical stress offers a unique opportunity to test the allocation rules of energy-budget theory. Because of the huge diversity of chemicals, and their wide range of toxicity mechanisms, the organism can be stressed in far more (and far more specific) ways than with natural stressors such as food limitation.

The application of DEB theory to toxicants has become known as DEBtox. DEBtox started as a pragmatic simplification of DEB theory to be able to work with the data from standardised toxicity tests. However, in the last five years, we have taken the development of DEBtox further to analyse full life-cycle tests and mixtures of toxicants. The comparison of theoretical predictions to (dedicated) experimental data sets confirmed the usefulness of DEB theory, but also revealed limitations and raised new research questions. In this lecture, I will reflect on the history of DEBtox, provide an overview of the recent developments on life-cycle analysis and mixtures, and focus on the avenues that need to be explored in the near future.

## DEBtox models as a basis for population toxicological risk assessment

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*Keywords: population dynamics, biomarkers, ecotoxicology*

**Abstract:** In parallel to the DEB theory development, some applications have arisen in many domains. In particular, DEBtox mathematical models have been developed to study the effects of chemicals on organisms.

Energy-based models like DEBtox ones are particularly relevant to derive consequences on population from effects measured on individuals in toxicity tests. First, they offer the possibility to quantify mathematically effects on biological parameters to be used in population models, as a function of chemicals concentration. Second, time is incorporated explicitly through kinetics modelling, so that toxicity parameters estimated on relatively short exposure period can be used to assess effects on the entire life cycle. Third, as they describe perturbations of energy, they permit the study of biomass and density, for which modelling studies are scarce, in complement to the study of the population asymptotic growth rate.

We proposed a methodology to design toxicity tests, analyse their results and derive effects on population growth rate and density for the midge *C. riparius*. Prior to toxicity tests, experiments were performed to calibrate DEB description of the life cycle of the studied species and to describe mathematically population dynamics. Toxicity tests focused on as many endpoints as necessary to conduct population modelling (reproduction, survival and growth). Results were analyzed with DEBtox models, to describe the time and concentration dependence of the parameters involved in population models. Additional experiments were proposed to assess the physiological mode of action of the tested compounds, which is crucial to perform a relevant upscaling. Finally, population endpoints were estimated and a threshold for significant effects on the population was derived, once the distribution of control population endpoints had been characterized.

## Modelling population responses of freshwater invertebrates to radionuclides with different toxic effects on organisms

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*Keywords: ecotoxicology, radionuclides, population dynamics, energy budget, daphnids*

**Abstract:** In order to assess the ecological risk of ionising radiation in aquatic ecosystems, a series of exposure experiments was conducted in recent years with the microcrustacean *Daphnia magna*, a representative wildlife species, widely-used for investigating potential toxicity of contaminants in freshwater invertebrates. Tested exposure conditions included chronic low doses of natural U, Am-241 and Cs-137, representing respectively dominant chemotoxicity, internal alpha contamination and external gamma irradiation. Although radionuclide effects on life history and physiological traits of daphnids has been increasingly well described at the organism-level under controlled laboratory conditions, consequences at the population level remained poorly documented. A previous modelling approach using Leslie matrices examined how decrease in survival, fecundity or delay in reproductive maturity affected population growth. Simulations showed that impacts on population growth strongly differed, according to which life history trait was affected. However, these simple population models do not integrate perturbations in physiological functions (nutrition, respiration, growth in mass and storage of energy reserves). Consequences of physiological changes observed under optimal laboratory conditions were more difficult to evaluate in a broader ecological context, notably because populations in natural biota are constantly subject to variable environmental conditions, including food resources, which influence their capacity to survive, grow and cope with toxic contaminants.

In this study, we present a model which simulates population dynamics of *Daphnia* exposed to different radionuclides. The model is individual-based and describes the acquisition of energy from food and its allocation towards survival, growth and reproduction (based on our results and data from the literature). Further exposure experiments conducted at different food levels aim to test how natural constraints, such as variable food conditions, might influence responses of organisms and populations to radiological and chemical pollutants.

## **A dynamic and mechanistic model of PCB bioaccumulation in the European hake (*Merluccius merluccius*)**

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*Keywords: Merluccius merluccius, demersal fish, Polychlorinated biphenyls (PCB), Bioaccumulation model, Dynamic Energy Budget (DEB).*

**Abstract:** We use the DEB theory to relate the growth and energy expenditure of a fish to its food consumption and to study the accumulation of organic pollutants. The bioaccumulation model proposed is a comprehensive approach that relates physiological information about the fish, such as diet, metabolism, age, reserve and reproduction status, to environmental conditions. The species studied is the European hake (*Merluccius merluccius*, L. 1758). The model is applied to study the total concentration 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). Outputs of the model compare consistently to measurements over the life span of fish. Observations 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. The variation of growth rate between males and females explains observed sex-specific PCB concentration differences. Finally, PCB losses during spawning is mechanistically simulated by mobilisation of lipids and PCB associated from reserves to eggs.

## Bioaccumulation of organic contaminant in the common sole (*Solea solea*): an investigation coupling experimentation, *in situ* sampling and modelling

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*Keywords: Solea solea, Polychlorinated biphenyls (PCB), Bioaccumulation model, Dynamic Energy Budget (DEB)*

**Abstract:** We used the dynamic energy budget (DEB) theory to model the growth of common sole (*Solea solea* L., 1758) and to study the accumulation of organic pollutants. The model has been calibrated and validated on data sets on juveniles based on *in situ* measurements and on experiments gathered under controlled conditions (Fig. 1). In parallel, experiments were realised to study the effects of polychlorinated biphenyls (PCB) on sole growth. Consequently, a model of PCB kinetics has been established, coupled to the growth one. We first focused on persistent PCB congener to characterise the bioaccumulation process. Due to its lipophilic character and as fish energetic reserves are mainly constituted of reserve lipids, PCBs contained in fish are considered bound to storage lipids after assimilation. Thus, we assumed in the model that fish contamination by PCBs is exclusively due to food consumption. The bioaccumulation model has been calibrated on experimental data exhibiting PCB kinetics of lipids from liver and muscles. Then, the model has been applied on less persistent PCB congeners, in order to estimate their constants of metabolism. Ultimately, this approach, coupling experimental work, *in situ* sampling and modelling, should allow the evaluation of contaminants effects on the physiological functions of wild fish.

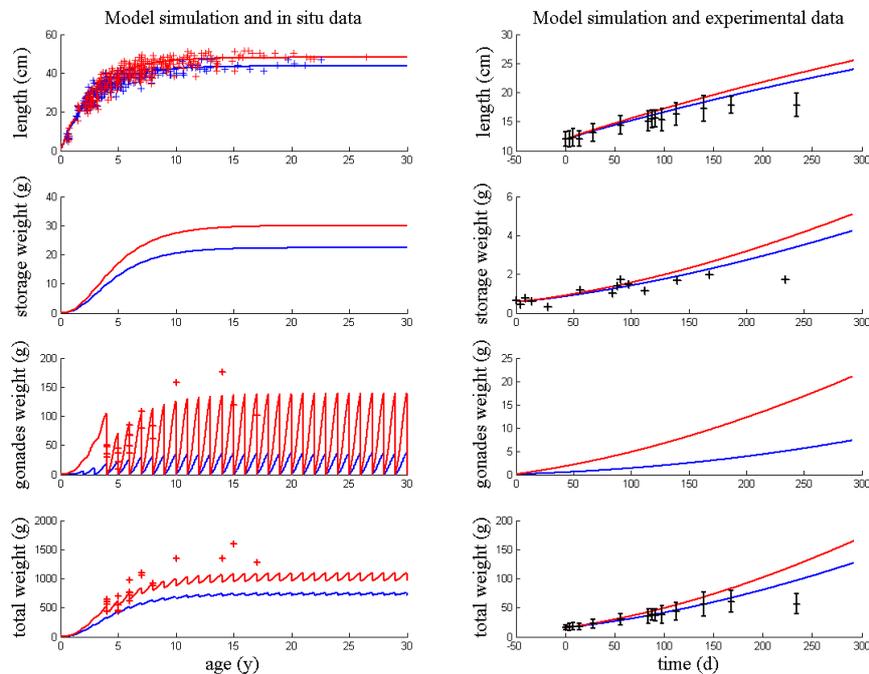


Figure 1: Left part: comparison between DEB model outputs (red lines for female and blue lines for male) and *in situ* data from the Douarnenez Bay (Deniel 1981) for length, storage, gonad and total wet weight. Right part: comparison between DEB model outputs (red lines for female and blue lines for male) and experimental data based on juvenile soles (black crosses  $\pm$  sd) for length, storage, gonad and total wet weight. Parameter values are exactly the same for both simulations.

## Towards the implementation of a DEB mussel model for B and vB screening of new chemicals

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*Keywords: prioritization exercises, bioaccumulative, WFD, bivalves*

**Abstract:** The daughter Directive of the WFD (Water Framework Directive) on Environmental quality standards in the field of water policy (COM (2006) 397) has been approved by the European Parliament (EP) on 17<sup>th</sup> June 2008. The document states that quality standards have to be developed in surface water, sediments and biota. The contaminants considered in the legislation are subdivided in priority substances (PS) and priority hazardous substances (PHS) and the European Commission (EC) has requested measures to control and reduce point and diffuse sources for the progressive reduction of PS and the cessation of PHS within 20 years after the adoption of the Directive. Furthermore for 2010 the EC has to propose a new list of PS and PHS as well as their associated EQS (water, sediment or biota concentrations that can not be exceeded to protect human health and the environment). In addition, a new prioritization exercise is being conducted.

At the moment the prioritization methodology is based on monitoring data. However, there is a serious risk in relying heavily on monitoring data because substances that are not subject to monitoring would be missed. For this reason an *in silico* / computational approach for prioritization is being developed. Within this approach an automated PBT and vBvT (Persistent, Bioaccumulative and Toxic) screening is being implemented for the HPVs (High Production Volume Chemicals, >1000 t/y) and the LPVs (Low Production Volume) lists. In addition to the estimation of the BCF using QSAR (Quantitative Structure Activity Relationships), it was decided to implement a DEB mussel bioaccumulation model (van Haren et al., 1994) and validate it with experimental data from Thau lagoon (France) for several POPs (Persistent Organic Pollutants) families (Castro-Jimenez *et al.*, 2008) and with forcing provided by an integrated 3D fate-biogeochemical model (Dueri *et al.*, 2009; Marinov *et al.* 2009). The final objective is to develop an open-source tool able to predict the BCF in mussels based on the physico-chemical properties of the compound and environmental conditions.

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## A combination of DEBtox and Leslie models to quantify ivermectin impacts on cladoceran species

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*Keywords: chronic toxicity, aquatic invertebrates, Bayesian inference, matrix population model*

**Abstract:** The parasiticide ivermectin has been widely used since 1980s due to its high efficiency and its wide spectrum of activity against endo- and ecto-parasites in livestock and pets. Livestock treatments introduce ivermectin into the environment through direct input from pasture animals and through the application of manure to agricultural land. So, local aquatic ecosystems can particularly be contaminated due to direct excretion into surface waters. Many studies showed drastic effects of ivermectin on non-target organisms like dung-inhabiting beetles and flies, but very few data are available to deal with chronic effects of ivermectin on aquatic organisms. Nevertheless the parasiticide was recently pointed out to be locally hazardous for soil and water organisms and of high priority for further environmental monitoring and risk assessment (Garric *et al.* 2007).

Based on the Dynamics Energy Budget theory, DEBtox models allow a mechanistic biology-based approach to understand, at the individual level, how contaminants disrupt the energy balance between various physiological processes. At the population level, matrix population models provide the finite rate of population increase,  $\lambda$ , as a robust endpoint to measure population sensitivity to contaminant as well as a confidence band added to predict critical exposure concentrations for population health. Thus the study we present aims (1) through DEBtox models to determine how ivermectin acts on vital processes (survival, growth and reproduction) of two cladoceran species (*Daphnia magna* and *Ceriodaphnia dubia*); and (2) to combine DEBtox and matrix population models to predict ivermectin impacts on daphnid population dynamics.

With this purpose, bioassays were led with adults exposed to different concentrations of ivermectin (from 0 to 1 ng/L according to the species). Survivor and newborns were daily recorded, while length of adults was only measured at the end of the test. DEBtox parameters were estimated using Bayesian inference allowing simultaneous fittings on these reproduction, growth and survival data. Bayesian inference also permitted to calculate both marginal and joint distributions of the parameters leading to ponctual estimates and credible intervals for each parameter, just as correlations between parameters. Then, we move to the population level by combining such individual effect models into a Leslie type matrix population model.

Results first showed the noteworthy efficacy of Bayesian inference to estimate DEBtox model parameters on various kind of experimental data. Different modes of action were observed for ivermectin according to the species. At the population scale, results showed that daphnid populations were strongly affected by ivermectin, with a very low critical exposure concentration. The new toxicity threshold proposed at the population level (called  $NEC_{pop}$  for No Effect Concentration at the Population level) appeared as a promising alternative to the more classical approaches involving individual toxicity indices.

**Reference:** Garric, J., Vollat, B., Duis, K., Péry, A., Junker, T., Ramil, M., Fink, G., Ternes, T.A., 2007. Effects of the parasiticide ivermectin on the cladoceran *Daphnia magna* and the green alga *Pseudokirchneriella subcapitata*. Chemosphere 69, 903-910.

## Extrapolation of chronic effects of toxicants based on short-term test data using DEBtox models

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*Keywords: Toxicity tests, extrapolation methods, chemical risk assessment.*

**Abstract:** Ecotoxicity tests results greatly depend on test design, and particularly on test duration and concentration range. Therefore, uncertainty is high when extrapolating effects from one exposure scenario to another. This constitutes a crucial issue in chemical risk assessment procedures. Current research on modelling can help to solve this extrapolation problem.

DEBtox models allow estimating relevant biological endpoints (survival, growth and fecundity) and toxicological endpoints (no-effect concentration, tolerance concentration, killing rate) continuously against toxicant concentrations. They also include time explicitly, so that parameter values do not depend on exposure duration. Therefore, it is assumed that short-term tests, which are the most frequently implemented tests in ecotoxicology, provide adequate data to assess long-term effects of toxicants using DEBtox models.

This study aimed at testing the relevance of DEBtox models to extrapolate between short-term and long-term effects of toxicants. Both short-term tests and life-cycle tests were implemented for differing concentration ranges in two long-lived freshwater invertebrate species (*Valvata piscinalis* and *Branchiura sowerbyi*) exposed to zinc contaminated sediments. Short-term test data were used to parameterize DEBtox models. These models were then used to assess long-term survival, growth and fecundity. Obtained predictions were lastly compared to life-cycle test data. Both frequency and margin of error were used as indicators of fittings quality. Furthermore, the relevance of parameter values was discussed in the light of biological and toxicological data. Conclusions were drawn regarding the use of DEBtox models as an extrapolation tool for risk assessment of chemicals.



### **Session 3. Ecophysiology at the individual level**

***Chairwoman/man (1<sup>st</sup> part): . M. Alunno-Bruscia  
& J. Flye Sainte Marie***

***Chairwoman/man (2<sup>nd</sup> part): . L. Pecquerie & F. Jean***

## What the Dynamic Energy Budget theory can tell us about filter feeders eco-physiology?

*Keynote speaker:*

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*Keywords: DEB theory, eco-physiology, bivalve, bio-energetics, Pacific oyster*

**Abstract:** Marine filter feeders and especially bivalves are extensively and world-wide studied due to their key-role in the functioning of coastal ecosystems regarding ecological, fishery or aquaculture issues. Bivalves' physiology, growth, reproduction and survival strongly rely on environmental factors, especially food abundance and temperature. In this context and since more than 30 years, many authors have focused on the effect of both factors on growth and reproduction performances of bivalves: from Bayne (1976) to Riisgard (2001), knowledge on bivalve ecophysiology has undoubtedly gained in details, especially about feeding and particles selection mechanisms. Meanwhile, other multidisciplinary approaches have tried to catch the diversity of bivalve ecophysiology through bioenergetics' models. Most of these models are based on the Scope For Growth (SFG) concept and are built on empirical allometric relationships. They constitute useful tools to describe the multifactorial effects of food and temperature on growth performances of bivalves. But this generation of models exhibits some major limitations: (1) they are not dynamic since SFG describes only a state in the energy budget; (2) each model has its own set of equation and consequently is strongly species-specific and even site-specific; (3) a great part of them are largely over-parameterised and rely on weak mechanistic explanation underlying the various equations and parameters.

With a hope for generality in quantifying the bioenergetic of living organisms, recent applications of Kooijman's DEB theory to bivalves help to overcome these limitations by providing a generic and mechanistic framework to model with one unique set of rules the effects of environment on bivalves life traits (growth, reproduction and survival). As an illustration, this presentation will show successful applications of the DEB theory to filter feeders bioenergetics, from controlled experiments to field conditions. Results of simulating growth and reproduction of the Pacific oyster (*Crassostrea gigas*) will be presented by using data from several French sites and for many years (e.g. Fig. 1). A particular attention will be paid also on what we learn from DEB theory about the oyster physiology in natural environment, especially concerning its food preferences or its spawning strategy. Application of the DEB oyster model to other filter-feeders will be also addressed to demonstrate how far the DEB theory is generic. Finally, potential DEB applications in operational scientific projects at Ifremer will be shown especially in the domain of climate-induced variability in marine resources.

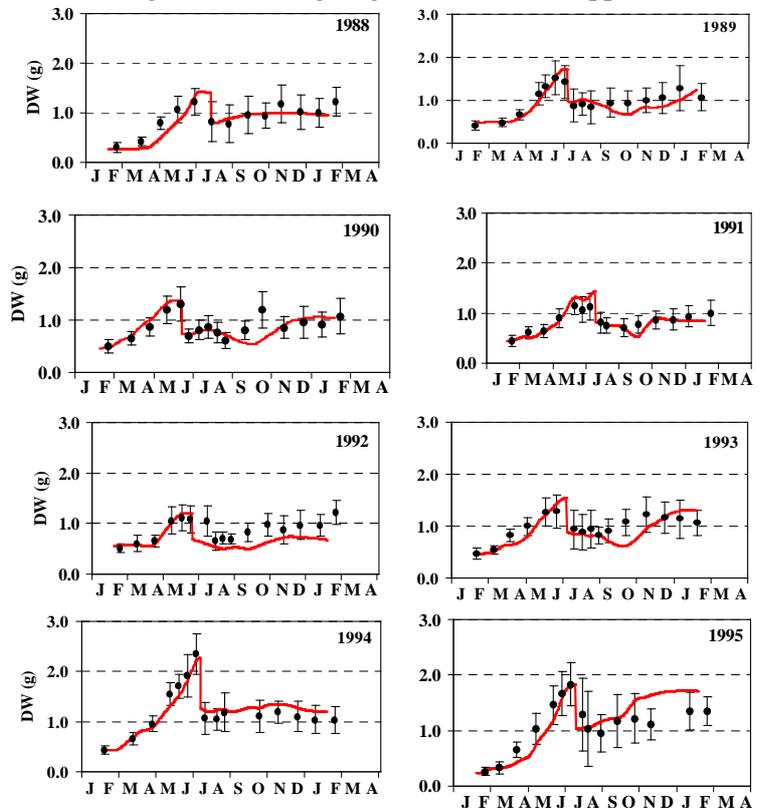


Figure 1 : Application of the DEB theory to model the growth and the reproduction of the Pacific oyster model in the Bay of Arcachon (France): more than eight years of data. Black dots are mean individual oyster flesh weight observation (in dry weight g +/- 1C), red curves are simulation obtained each year from the model under real environmental forcing (sea temperature and phytoplankton concentration). The sharp decrease corresponds to the spawning event simulated by the model and also observed in data.

## Discovering and learning the DEB through the Growth DEB equation

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*Keywords: teaching, DEB theory, Growth, von Bertalanffy*

**Abstract:** The DEB theory allows to model a wide diversity of biological situations. This great ambition has also a cost as counterpart : a well built formalism using a large amount of parameters. Thus the DEB theory is often felt as an efficient, but rather complex and abstract theory which required a long and hard learning before considering a first actual application.

In order to make the DEB learning easier, I propose to come back to one of the more important inspirations of the DEB: the observation of the von Bertalanffy Growth in biological systems. The DEB can be understood as an extension of the classical von Bertalanffy growth to varying environments. I propose a Growth DEB equation which fits this idea. It contains the strictly necessary parameters to model the DEB growth in the synthetic form of a single equation (see frame below). The Growth DEB equation is an intermediate step between the classical von Bertalanffy growth and a whole complete DEB model. Thus the DEB learning can be split into two parts: (i) a simple extension of the von Bertalanffy growth, *i.e.* the DEB restricted to the growth, followed by (ii) a progressive enrichment leading to the entire DEB. As an example, the Growth DEB equation allows to follow the reserves or catabolic dynamics: these central concepts of the DEB can be introduced smoothly through well chosen examples of the food environment.

*The Growth DEB equation*

$$\begin{aligned}
 & -9Lg'^2 + 3LgLg'' - f\dot{v}_\delta \dot{k}_M Lg_m + 6f\dot{k}_M Lg_m Lg' + 3\dot{v}_\delta Lg' \\
 & + \dot{v}_\delta \dot{k}_M Lg - 2\dot{k}_M Lg Lg' - 9f \frac{\dot{k}_M Lg_m}{\dot{v}_\delta} Lg'^2 - 3 \frac{\dot{k}_M}{\dot{v}_\delta} Lg Lg'^2 + 3 \frac{\dot{k}_M}{\dot{v}_\delta} Lg^2 Lg'' = 0
 \end{aligned}$$

where  $\dot{v}_\delta = \frac{\dot{v}}{\delta}$ ,  $\dot{k}_M = \frac{[\dot{p}_M]}{[E_G]}$ , and  $Lg_m = \frac{L_m}{\delta}$ .

## A DEB-based framework for analyzing individual life traits recorded by fish otoliths

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*Keywords: fish otolith, otolith growth, otolith opacity, bioenergetics, otolith biomineralization, numerical modelling*

**Abstract:** Fish otoliths, calcified structures located in the inner ear, are actual biological and environmental archives. Their accretionary growth results from a strict physiological control of the organism, but is influenced by the environmental conditions in which the fish lives. For instance, environmental variables such as temperature and salinity, as well as season-based or age-based metabolic variations are known to influence the deposit rate and the incorporation of chemical elements. This accretionary process often leads to the formation of a sequence of structures (rings), whose periodicity goes from the day to the season. Otolith analysis then offers a unique potential to reconstruct, at a daily and/or yearly scale, environmental parameters as well as individual life traits (age, growth and migration patterns) and population features (age structure, spatio-temporal distribution). Although otolith analysis is now recognized as an invaluable source of information, the extraction of the metabolic and environmental information archived in the otolith remains critical in numerous cases due to a lack of understanding of the mechanisms driving the biomineralization of the otoliths.

The DEB theory opens new avenues to address these issues. A 2D DEB-based model of otolith formation, supported by experimental evidences, is presented. Stating otolith formation as a DEB product, otolith growth and opacity result of elementary metabolic fluxes (i.e., somatic growth and maintenance fluxes). In addition to this direct metabolic modulation, a biomineralization-specific temperature effect is considered as calcium carbonate precipitation is known to be temperature-dependent. From these two elementary components, the model conforms to the relationships observed empirically in different experiments regarding the effects of metabolism and environmental conditions (i.e., food availability and temperature) on global otolith characteristics (growth and opacity) and provide a clear interpretation of the interactions between these two (opposite in some cases) effects.

The relevance and the potential of this DEB-based otolith model for the analysis of individual life traits is illustrated through the comparisons of real and simulated otolith patterns of North Sea and Barents Sea cod

otoliths (Figure 1). These two cod stocks are associated with different environmental cycles both in terms of food availability and temperature, which make their comparison particularly illustrative. Besides, an application to the reconstruction of feeding conditions from observed otolith patterns is presented and discussed as one of the many potential applications of the model.

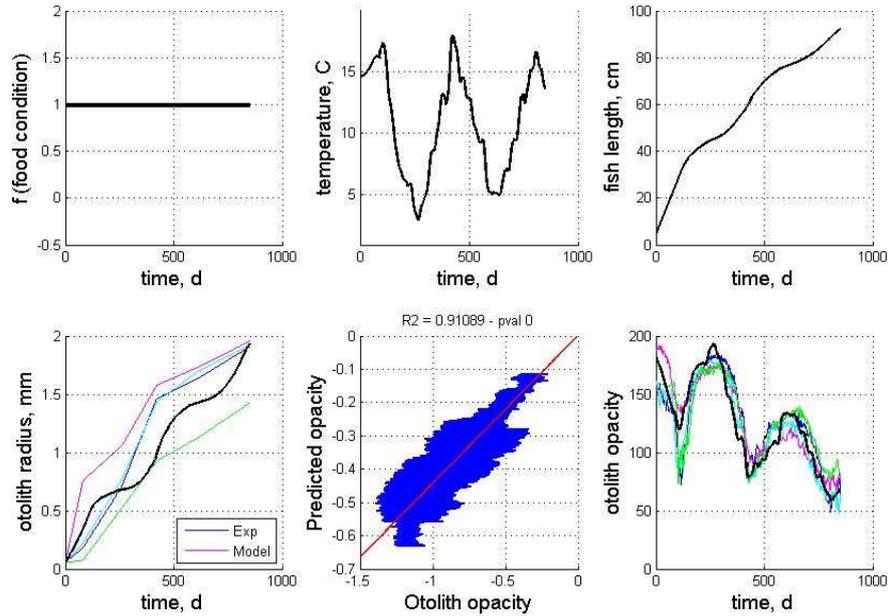


Figure 1: numerical DEB-based simulation of the formation of a cod otolith for known rearing conditions (temperature and feeding conditions): from left to right, feeding conditions, temperature series, simulated somatic growth, simulated otolith growth, predicted opacity vs. measured opacity, opacity signals. The model simulation (black line) is compared to four otoliths of cod (coloured lines) reared in the considered feeding and temperature conditions. In opacity plots, the greater the opacity value, the more opaque the otolith.

## Dynamics of stable isotopes in fluctuating environments

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*Keywords: stable isotopes, bioenergetics, seasonal environment, food availability, ontogeny*

**Abstract:** Stable isotopes analysis is a powerful tool used for the identification of trophic web structures, the reconstruction of individual life histories, and tracking the flow of elemental matter through ecosystems. Such studies often make the assumption that isotopes within the organism are in equilibrium with the environment. However this equilibrium might not be reached as natural environments typically fluctuate and individuals themselves evolve through ontogeny. Yet it is a challenge to take account of isotope dynamics because of the limited understanding of isotope fractionation processes and how they relate to metabolism. DEB theory provides a particularly suitable conceptual and quantitative framework to couple isotope dynamics to metabolism, as all mass fluxes are specified.

Here we present a new set of assumptions, based on DEB theory, to study isotope fractionation within an organism in a fluctuating environment. This introduces some new issues for DEB theory regarding turn-over processes, as the latter are critical to understand isotope fractionation. The model is generic to any chemical element. We focus here on the dynamics of  $^{13}\text{C}$  and  $^{15}\text{N}$ . We examine how organism size and food availability impact isotope signature within the organism when the isotopic signature of the food is fluctuating (Figure 1). We discuss the implications of our findings for interpretation of sampled isotope data. To our knowledge, this is the first model that couples bioenergetic processes and isotope dynamics in a causal way throughout the life cycle of an individual. This model provides a new basis for analyzing and interpreting variations in isotopic fractionations and increases our ability to extract much of the information from isotopic studies.

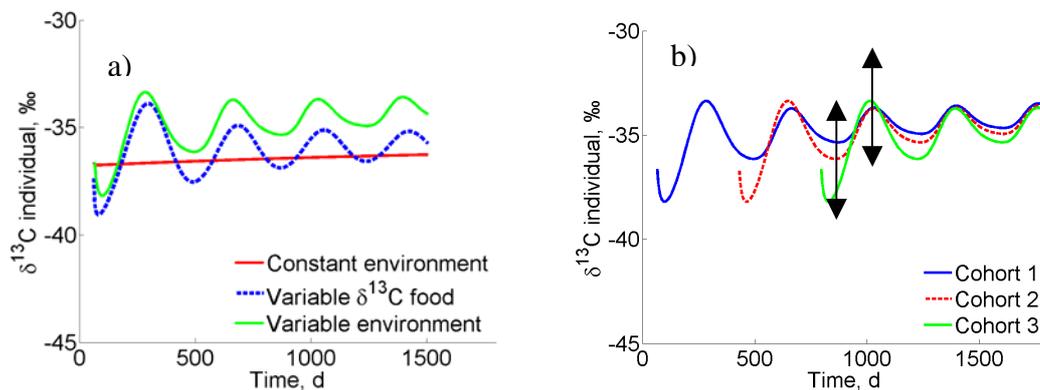


Figure 1: Model simulations of the isotope ratio  $\delta^{13}\text{C}$  within the individual: a) for 3 individuals born the same year (same cohort) but that lived in different environments and b) for individuals of 3 different cohorts that lived in the same seasonal environment. Left panel shows an enrichment of  $^{13}\text{C}$  through ontogeny (constant environment). It also shows how the isotopic signal in the organism can vary if food availability is fluctuating or not during the season (green vs blue lines) in combination with a fluctuating isotopic signature of the food. Right panel shows that variability of  $\delta^{13}\text{C}$  among individuals can vary according to the timing of the sampling (arrows) as individual of different sizes (different cohorts) have different dynamics when the environment is fluctuating.

## Differentiated growth of organs in gulls

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*Keywords: growth, Herring gull, Dynamic Energy Budget theory*

**Abstract:** Many animals do not show isomorphic growth, but the various body parts may show differentiated growth. Wing growth in birds for example occurs much later than growth of the head (Fig. 1). Following Kooijman (2006, *J. Sea Res.* 56: 103-106, Special DEBIB issue) we generalize the kappa-rule to cope with this phenomenon within the context of DEB theory. Model predictions are related to observed data. Various alternative generalizations of the kappa-rule are compared.

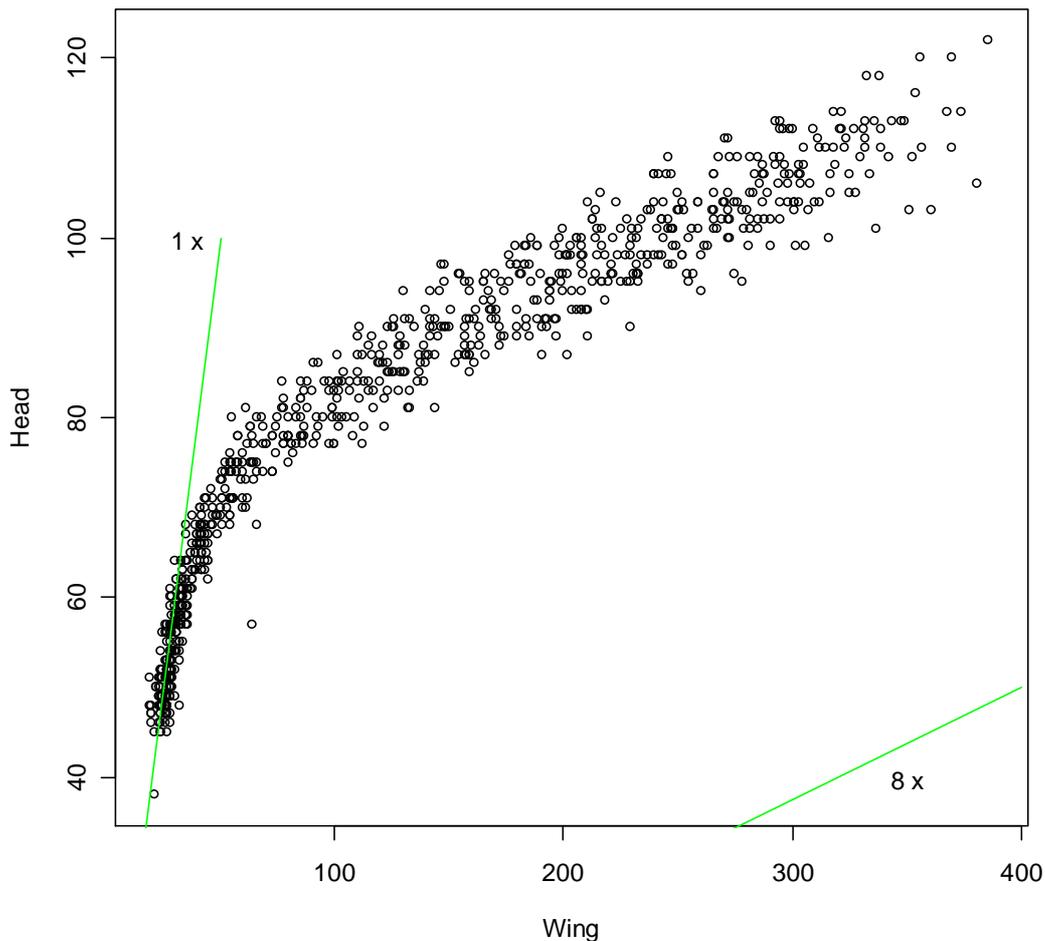


Figure 1. Head length (in mm) versus wing length (in mm) for growing Herring gulls, *Larus argentatus*. Initially, head and wing show a similar length growth rate, but when the animal reaches a certain size, wing growth accelerates.

## **Physiological performance of plaice *Pleuronectes platessa* (L.): from Static to Dynamic Energy Budgets**

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**Keywords:** allometric relationship, Dynamic Energy Budget, physiology, plaice, Static Energy Budget

**Abstract:** In the present study, various body size scaling relationships, which describe physiological performance of plaice *Pleuronectes platessa* (L.), were derived using a dynamic energy budget (DEB) model and compared with allometric relationships derived from a static energy budget (SEB) model. Results indicated that DEB models can more correctly predict the physiological performance of plaice within variable environments. Dynamic energy budgets are preferred over static energy budgets because they are not descriptive but based on first principles, they are not species-specific, and they can be used for extrapolations beyond the range of experimental data. Nevertheless, some aspects of the DEB model can still be improved. These include: [1] processes underlying the temperature tolerance range, temperature acclimation and the relationship between optimal temperature and body size; [2] the contribution of various processes to metabolism; and [3] the incorporation and quantification of Fry's scheme of the environment, especially of masking factors (e.g., sub-optimal salinity conditions which load the minimum metabolism) and limiting factors (e.g., low oxygen conditions that constrain the maximum metabolic rate). These improvements would offer a wide range of opportunities for further application, such as the reconstruction of food and growth conditions; the validation of age determination by means of otolith readings; the analysis of intraspecific genetic variability versus non-genetic phenotypic adaptations; and the interspecific comparison of energy flows by means of variability in the various DEB model parameters.

## Bio-energetic modelling of growth of the European sea bass in aquaculture, based on Dynamic Energy Budget theory

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*Keywords : Sea bass, parameter estimation, least square method*

**Abstract:** The European sea bass (*Dicentrarchus labrax*) represent 13% of the economical production of Mediterranean aquaculture. Optimization of *D. labrax* aquaculture involves various criteria including selecting traits of commercial interest for *e.g.* fish welfare or for waste management, which would benefit from a better understanding of the fish energetic budget. In this context, we applied the Dynamic Energy Budget (DEB) theory to the sea bass and estimated a set of DEB parameters for this species by using different data sets from Ifremer teams and from the literature. We developed a methodological approach to calibrate accurately parameters using minimization of the Least Squared Error. To overcome some biases due to auto-correlation of the repeated measures and to heterogeneity in the fish size, the data were weighed. We also developed a method for quantifying the variability in the estimated DEB parameters considering the data used for calibration. This innovative method allowed us to evaluate the precision of estimation for each parameter, but also the covariance between each couple of parameters. This information could be of great interest to determine the reliability of the estimation of each parameter, but also to evaluate the quality of the data used for estimating parameters. We obtained a set of reliable DEB parameters and we showed that the estimation of the maintenance costs [ $p_M$ ] was quite imprecise because of its minor influence on growth, and so was the estimation of the influence of temperature on this parameter ( $T_A$ ). The evaluation of kappa ( $\kappa$ ) was much more precise, though we worked with immature fish implying that  $\kappa$  represents only the maturation. Finally, we proposed a measurement of the energetic reserve  $E$  using calorimetric data. From the set of parameters we estimated, we obtained a bio-energetic model which allowed us to study the difference of growth in different rearing conditions.

## **DOC consumption and release by marine bacteria in transient environment: from experiments to modelling**

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*Key words: bacterial dynamics – DOC degradation – DOC release – mechanistic model – DEB theory*

**Abstract:** We developed a new model for the degradation of dissolved organic compounds by marine bacteria. This model has been compared to a data set from an experiment designed with pulsed supply of substrate. Indeed, experiments realised to determine the bacterial growth efficiency are usually performed in batch cultures without any perturbation during the time course experiment. Typical models of bacterial growth, such as Monod or Marr-Pirt models, are based on this condition. However, the ecosystem is much more complex and dynamic compared to these *in vitro* experiments and the bacterial carbon demand is fuelled by episodic input of dissolved organic matter. We therefore realised experiments with a monospecific culture of a marine bacterial strain (*Alteromonas infernus*) and pyruvate as single source of labile dissolved organic carbon (L-DOC). Pyruvate was periodically added in the culture (every 48 hours) to reproduce environmental variability. We measured DOC and bacterial biomass, determined from the particulate organic carbon (POC) values, four times a day. We demonstrated that bacteria consumed the DOC source very rapidly (about 24 hours) after its addition, but they also produced unlabile-DOC that accumulated in the batch between two subsequent pulses of substrate. Bacterial growth occurred in parallel to substrate decrease whereas bacterial shrinking occurred in parallel to DOC release.

We applied the Dynamic Energy Budget (DEB) theory to develop a mechanistic model able to reproduce the experimental dynamics. The model takes into consideration one reserve compartment and two maintenance fluxes: the maintenance is paid from reserve when food is abundant enough and from reserve plus structure when starvation occurs. The typical DEB growth model for bacteria has so been improved by the addition of one variable (released DOC) and two parameters describing the production by bacteria. The model has so far 4 state variables and 7 parameters and adequately matches the experimental data. These results suggest that during starvation period, bacterial degradation of labile organic matter might be a source of semi-labile or refractory DOC in the ocean. We also compared DEB model outputs with those of the typical bacterial growth models. Because of the release of DOC by bacteria, the Monod model was unable to reproduce experimental dynamics. The Marr-Pirt model showed a quite good agreement with data but less plasticity than the DEB model. Moreover, DEB model is constructed on mechanistic basis and can therefore explain the production of DOC, whereas Marr-Pirt model can not.

## **Inter-annual variability of individual growth of the great scallop *Pecten maximus***

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*Keywords: parameter estimation, ecophysiology, bivalve, individual growth*

**Abstract:** Many studies have evidenced the influence of natural environmental variability on the shell growth of the great scallop *Pecten maximus*. We used a time series on the growth of *P. maximu* in a coastal embayment (the Bay of Brest) and another time series describing the environmental variability of the area (temperature at the bottom interface, phytoplankton communities composition) to identify « standard » and « non standard » years of growth. We build a model based on the Dynamic Energy Budget theory to simulate and study the variability of the individual growth of *P. maximus* in the natural environment of the Bay of Brest among those years. Data sets used for calibration and for validation of the model were independent.

We will present results showing the ability of the model to describe dynamically the general patterns of the ecophysiology of the great scallop and to simulate the inter-annual variability of the shell and body mass growth of *P. maximus* as environmental conditions vary. We will also show results of simulations of the effect of natural sedimentation of phytoplankton blooms on the bivalve's growth dynamics.

## Choice of food quantifiers in shellfish DEB modelling

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*Keywords: food quantifiers, half-saturation coefficient*

**Abstract:** DEB modelling has been increasingly popular in studies with marine filtering feeders, especially shellfish. However, the common difficulty in the application of these models in these studies is uncertainty of half-saturation coefficient which governs the functional response of energy uptake to food density. This is mainly resulted from the correct choice of food quantifiers. The present study is to investigate the appropriate choice of food quantifiers for greenshell mussel. Data of food indicators were collected from mussel growth experiments at five sites including chlorophyll, size-fractioned chlorophyll, phytoplankton carbon, carbon of selected phytoplankton groups, particle carbon and particle nitrogen etc. Each of the food indicators at one site was used to obtain the half-saturation coefficient. The calibrated set of parameters was then applied to other sites. The goodness of fits was compared between model simulations using different food quantifiers. The results will be analysed to get better understanding of the choice among the food quantifiers.

## The effect of food composition on feeding, growth and reproduction of bivalves

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*Keywords: growth, feeding processes, food composition, bivalves, Dynamic Energy Budget theory*

**Abstract:** Bivalve species living in coastal and intertidal habitats experience highly dynamic physical environmental changes, resulting in a large variability in terms of food quantity and quality. In some systems, temporal and spatial variability of suspended particles (phytoplankton, zooplankton, particulate organic matter and sediments) induced by tidal flow due to advective processes, resuspension and wind-induced wave action, can be as important as those induced by seasonal changes. Thus, the food variability in these ecological systems enhance the importance of food selection (separate nutritious from non-nutritious particles) due to the abundance of less-digestible particles. In this study, filtration and ingestion in bivalves are assumed as two different steps of the feeding process and formulations for its descriptions are presented and discussed, considering the existence of several types of food. For each type of food, different ingestion and assimilation efficiencies can be included, for example. A direct consequence of this approach is that the production of pseudofaeces depends on the amount of particles in the water column. All model formulations required to simulate the life cycle of an organism followed the Dynamic Energy Budget theory. The specific example of *Mytilus edulis* was used and several scenarios were performed in order to further understand the feeding processes and the role of food composition in growth and reproduction.

## Modelling *Crassostrea gigas* growth and reproduction: Application of the oyster-DEB model to various shellfish areas in France

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*Keywords* : DEB model, Pacific oyster *C. gigas*, growth, reproduction, bio-energetic

**Abstract:** Oyster farming is the main aquaculture activity in France, where Pacific oyster (*Crassostrea gigas*) is spatially cultured from the English Channel to the Mediterranean coasts. Oyster growth performance monitored along French coasts are widely heterogeneous among culture sites and over years. Many studies have been carried out to understand the effects of environmental factors on oyster growth and physiology, by using bioenergetics growth models. However, most of these studies were site-specific. As an example, the model developed by Barillé *et al.* (1997), which was extensively specified with more than 50 parameters, was validated in the Marennes-Oléron Bay, but cannot be successfully applied to other culture sites without re-estimating parameters or re-formulating some processes.

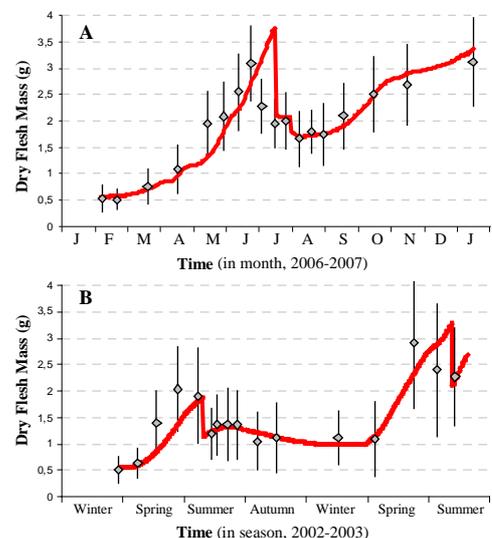
In that context, our study aims to develop a generic growth model, *i.e.* a model than can be applied in various contrasted environments with a constant set of parameters. Such a model will allow us to assess directly the links between oyster growth and environmental parameters in each culture site.

We use the DEB model designed for the Pacific oyster *C. gigas* (Pouvreau *et al.*, 2006; Bourlès *et al.*, *subm.*) based on the DEB theory (Kooijman, 2000). The resulting oyster-DEB model is built on 10 main DEB parameters with some extra parameters to consider specific bioenergetics of *C. gigas*.

The results of simulating oyster growth are presented herein by using the oyster-DEB model in several French ecosystems: Arcachon, Marennes-Oléron (Fig.1.A) and Quiberon bays along the Atlantic coastline, Thau Lagoon in Méditerranée, and the Baie du Mont-Saint-Michel and the Baie des Veys (Fig.1.B) in the English Channel. Applying DEB model in contrasted environments allows to explain oyster growth variability among rearing areas according to food quantity (*e.g.* chlorophyll a, phytoplankton abundances) and quality (phytoplankton species), as well as seawater temperature. The variability of spawning events among sites is also successfully simulated according to the spawning processes implemented in the oyster-DEB model.

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**Figure 1:** Comparison between observed (dots) and simulated (red line) dry flesh mass (in g) of *C. gigas* reared in Marennes-Oléron Bay (A) and in Baie des Veys (B, East Normandy).

**Session 4: Population, ecosystem, and evolutionary aspects**

***Chairmen (1<sup>st</sup> part): S.A.L.M. Kooijman & P. Pondaven***

***Chairmen (2<sup>nd</sup> part): C. Bacher & O. Maury***

## **Dynamic energy budget theory and ecology; learning from *Daphnia***

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*Keywords: DEB theory, Daphnia*

**Abstract:** Major themes in ecology include population persistence and regulation, the origins and maintenance of biodiversity, and regulation of the flows of energy and elemental matter. There is a currently a formidable body of sophisticated (non-DEB) theory addressing each of these themes. DEB theory offers a perspective on ecology whose starting point is energy utilization by, and homeostasis within, *individual* organisms. It is natural to ask what it adds to existing ecological theory. I shall show that simplifications of DEB models lead to the widely used “size structured” models that have produced important recent conceptual advances in population and community ecology. Furthermore, DEB theory is the natural framework for modelling ecological stoichiometry and constitutes a distinctive “metabolic theory of ecology”. I shall illustrate these themes drawing on recent studies of zooplankton.

## Reaching consensus between marine ecological models and metabolic theories in ecology

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*Keywords: marine ecological models, ERSEM model, DEB theory, modelling strategies*

**Abstract:** The last decades have witnessed an explosion in marine modelling efforts, both at the development and application level. Several models with different degrees of complexity have been created, mostly to address the increasing problems of nutrient enrichment in marine systems. Model applications now range from simple hydrodynamic settings with coupled physical-ecological processes, to more complex applications with biogeochemical model for the regional scale. The ERSEM model, originally conceived to address the pelagic food web in the North Sea, is considered to be the state of the art in marine biogeochemical modelling. ERSEM has been widely accepted among marine ecologists and modellers that have adopted and developed its basic original setup.

Metabolic theories in ecology aspire at achieve a general theory of energy and mass budgets in organisms and communities. These theories, based on the energy conservation law, rely on simple mechanistic description of how individual organism take up and use energy and material. Since it was proposed, DEB theory has been calling the attention of the scientific community, and used as a paradigm in different research fields. Both theories have growth models containing fundamental energy budget parameters and describe energy supply rate and maintenance rate as function of body size.

Metabolic theories focus on the basic physiologic processes known to be identical to all living organisms, providing a model that accounts for processes at all levels of organization. As such, they address detailed physiological cellular processes and trace their influence to the ecosystem scale, through matter and energy fluxes. Apparently, marine ecological models follow the same rationale and try to achieve a similar purpose. However, these models are used to study specific features of a system at an ecosystem scale and, most recently, as tools of management support and human activity impact assessment. To avoid detailed parameterisation of processes, minimize computer requirements and simplify result interpretation, they rely on a number of assumptions and simplifications.

Apparently, a general agreement is expected between ecological models and metabolic theories, and one should be able to use ideas and principles from both views. Nevertheless, there are marked differences that can vary from differences in formulation of processes to baseline assumptions. So far, efforts to conciliate both models of the natural systems have been limited. Here we critically compare both models, highlighting similarities and show where the approaches differ. This study focuses on primary producers and is drive by two main questions: (1) Is it possible to harmonize the philosophy and structure of models like ERSEM with the general scope of unifying metabolic theories such as DEB? (2) Can we bring the current paradigms in ecological modelling for marine communities to consensus with metabolic theories? Finally, we show that ERSEM model can be seen as a special case of DEB theory.

## Dynamic energy budgets in syntrophic symbiotic relationships between heterotrophic hosts and photoautotrophic symbionts

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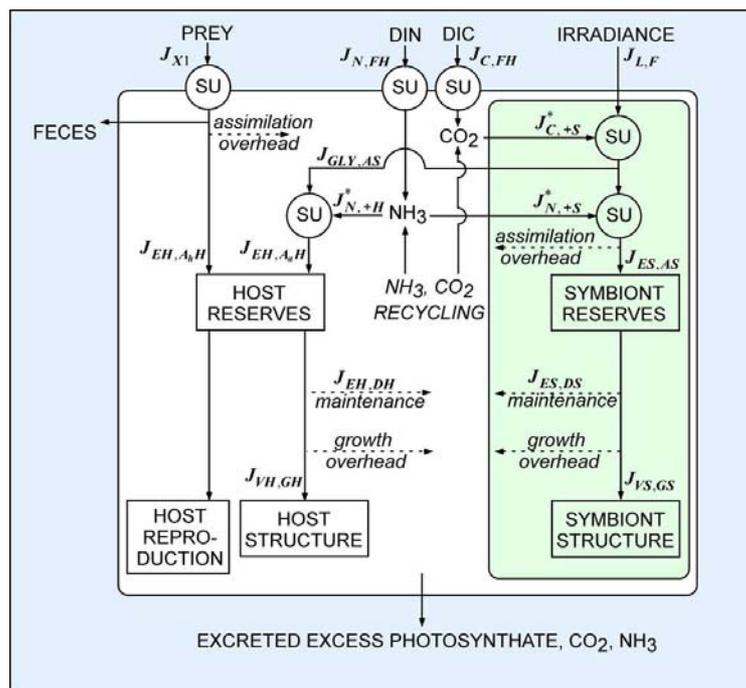
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*Keywords: dynamic energy budget theory, syntrophy, endosymbiosis, scleractinian coral, mutualism*

**Abstract:** We investigate a Dynamic Energy Budget (DEB) model describing the syntrophic symbiotic relationship between a heterotrophic host and an internal photoautotrophic symbiont; the Figure shows the matter and energy flows among host (clear), symbiont (green) and environment (blue). The model is of minimal complexity, e.g. the symbiont lacks nutrient reserves, and uses the concept of synthesizing units to describe smoothly the assimilation of the potentially limiting factors inorganic carbon, nitrogen, and irradiance. The model has two passive regulation mechanisms: the symbiont shares only photosynthate that it can not use itself, and the host delivers only excess nutrients to the symbiont. With parameter values plausible for scleractinian corals, we show that these two regulation mechanisms suffice to obtain a stable symbiotic relationship under constant ambient conditions, provided those conditions support sustenance of host and symbiont. Furthermore, the symbiont density in the host varies relatively little as a function of ambient food density, inorganic nitrogen and irradiance. This symbiont density tends to increase with light deprivation or nitrogen enrichment, either directly or via food. We also investigate the relative benefit each partner derives from the relationship and conclude that this relationship may shift from mutualism to parasitism as environmental conditions change.



## **Mechanistic formulations of kinetics absorption with multi-limitation consequences on community dynamics**

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*Keywords: multi-limitation, population dynamics, models complexity, mechanistic formulations*

**Abstract:** Biogeochemical models aim to describe the spatio – temporal dynamics of nutrients and primary producers in natural environments. There are often based on a functional group splitting of the phytoplanktonic community. Various limiting nutrients are involved, leading to a description of the different ratios C:N:P for each functional groups for instance. These models also include zooplankton populations in order to better describe the death rate of the primary producers.

In these models, the absorption rates of nutrient by phytoplankton populations are often based on the same kind of formulations, namely the product of hyperbolic functions (each of them describing the absorption of a given nutrient) or the Liebig law, which is the minimum absorption rate that is the absorption rate of the most limiting nutrient. These formulations are mainly empirical.

DEB theory provides the tools for describing the mechanisms underlying the absorption rates and their consequences on population dynamics. In the DEB theory, multi-limitation is explicitly linked with physiological constraints.

In this work, we compare multi-limiting nutrients formulations obtained from DEB theory with empirical ones and some data are used, which validate the DEB formulation. Then we compare the effects of the mechanistic approach on population and community dynamics by comparing population models based on different absorption formulations (mechanistic and empirical) fitting the same set of data. By introducing physiological details for the mechanistic description of absorption, we obtain more complex models. In order to reduce the resulting mathematical complexity, we use time scale separation techniques which permit to deal with models exhibiting the same level of complexity. This facilitates the models comparison.

## **A DEB-based model of marine ecosystem size-spectrum with life history diversity.**

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*Keywords: size spectrum; biodiversity; life history traits; predation; Dynamic Energy Budget (DEB) theory;*

**Abstract:** This talk presents a DEB-based size-structured mathematical model of marine ecosystem dynamics. The model represents the transfer of energy in both time and body weight (size) in marine ecosystems. The processes taken into account include size-based opportunistic trophic interactions, competition for food, allocation of energy between growth and reproduction, somatic and maturity maintenance, predatory and starvation mortality as well as ageing mortality. Using some of the body-size scaling relationships of the DEB theory, the diversity of life-history traits (*i.e.* the biodiversity) is integrated explicitly into the model without resolving explicitly the dynamics of individual species. The effects of biodiversity on the bottom-up and top-down propagation of environmental signals (*e.g.* variability of primary production, temperature and fishing) is studied using simulations, comparing the model with and without inclusion of life-history traits diversity.

## **An adaptive model of marine biogeochemistry in the Archaeon**

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*Keywords: Archaeon, ecosystem modelling, adaptive dynamics, biogeochemistry*

**Abstract:** The potential importance of resolving different phytoplankton functional types within marine ecosystem models has been reflected in many recent modelling studies. However, several key challenges still face such efforts. In particular, quantitative information on metabolic rates used to constrain physiological parameterizations is extremely limited, while the ability of such models to address questions of long term climate change, where organisms may potentially adapt to changing environmental conditions, is uncertain. Here we present a new individual-based model of a marine ecosystem. The model simulates the adaptation of microbial organisms based on selection pressures from both the environmental conditions and competition between species. Organisms within the model are grouped into several guilds depending upon their metabolic function. Parameterizations of metabolic rates and nutrient sensitivities are genetically defined, supplying handles upon which selection may act. Successful organisms grow and reproduce, while unsuccessful ones may starve and perish. Using the Archaeon as a starting point, we demonstrate the model's ability to generate diverse, self-sustaining microbial communities with realistic nutrient distributions. Further to this, with the inclusion of a simple trade off between resource assimilation and the organism's affinity for that resource, simulations have shown clear instances of community succession, without any unrecoverable loss in ecosystem diversity. This work demonstrates the first step in a larger program of study that will seek to examine evolutionary adaptation in microbial communities, as well as trade-offs in physiological parameterisations.

## Modelling microalgal growth with DEB Theory

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*Key words: microalgae, Dynamic Energy Budget Theory, carbon capture*

**Abstract:** Strategies to address global warming involve the reduction of greenhouse gas emissions. This can be accomplished through reduction on fossil fuel consumption and carbon capture, among other actions. Microalgae can potentially play a key role in both strategies. One of the most studied applications consists in the use of the flue gas from industrial and energy plants in the cultivation of microalgae, thus removing the carbon dioxide. The high energetic content of these organisms make them also valuable for biofuel production.

We developed a model based on the Dynamic Energy Budget Theory that describes the evolution of the state variables of a microalgal population, namely structural mass and reserves densities, and of the environment, namely nutrient concentration in a photobioreactor. Almost all microalgae models in the literature consider only one limiting factor, usually light. In our DEB model we considered 3 reserves, one for nitrogen, one for phosphorous and one for carbon whose assimilation depends on light intensity. Thus, we are able to simulate both light and nutrient limited growth, providing a new approach among the models presented in the microalgae literature. The microalgae DEB model also takes into account photoinhibition and temperature predicting the combined effects of light and temperature on the microalgae growth. In the DEB model photoinhibition is simulated by adapting the synthesizing units mechanism to an existing photoinhibition model.

We used published data on *Pavlova lutheri* to adjust the microalgae DEB parameters. Preliminary tests and results are coherent with expected observations.

Additionally, we coupled to the DEB growth model a module for the optimization of carbon capture, based in genetic algorithms. Results provide the optimal time schedule and the quantity that should be removed each time allowing for an optimal management of a photobioreactor.

## **Potential spawning of anchovy in the Bay of Biscay: use of a bio-energetic model with an environmental long time-series**

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*Keywords: Engraulis encrasicolus, reproduction, environmental forcing, DEB theory, climate change*

**Abstract:** The aim of this work is to estimate the variations of the spawning season of a small pelagic species, the Bay of Biscay anchovy (*Engraulis encrasicolus*), according to the environmental conditions encountered by the individuals. Fecundity and length of the spawning season adults are recruitment processes. Recruitment forecast is a major stake for anchovy population in the Bay of Biscay of which abundance is critic since 2005. We use a bioenergetic model of anchovy based on the Dynamic Energy Budget (DEB) theory and forced by a 25-year time-series of temperature and primary production to simulate individual spawning patterns. This species is able to spawn 20 times per season in average but the variability of this number of spawnings according due to environmental variability is hardly known. To simulate individual growth and spawnings, we use realistic environmental conditions for the period 1973 – 1998 built from the outputs of an environmental model of the Bay of Biscay (ECO-MARS3D). Length of individual and maturity date influenced the spawning windows. Environment have an effect on growth and development of individual, but on available reserves for reproduction too. Spawning seasonality and total fecundity are influenced by environmental conditions distant in time - accumulation of reserves during the last autumn, use of these reserves during the winter - and by proximate conditions - nutrition during the spawning period. The influence of distant and proximate conditions is study for spawning and no-spawning years. We show that the bioenergetic approach is essential to integrate the different environmental effects on the annual cycle. It's a normal approach to constitute long time-series of hydro-climatic parameters to study impacts of climate change. Here, the proposed approach allows constituting a long time-series of a biological function, *i.e.* reproduction.

## Local effects of blue mussels around turbine foundations in an ecosystem model of Nysted off-shore wind farm, Denmark

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*Keywords: blue mussels, carrying capacity, DEB-model, depletion, reef effect*

**Abstract:** The development of off-shore wind farms along the coastline of north-west Europe is rapidly increasing and it is therefore important to study how this will affect the marine environment. The present study modelled 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 dynamic energy budget (DEB) model to a small-scale 3D hydrodynamic-biogeochemical model. The model results showed 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. The model results was supported by field measurements of chl *a* concentrations and biomasses of the fauna community around foundations. Our study emphasised that OWF's seem to be particularly favourable for blue mussels in the western Baltic Sea and that the functioning of the OWF's as artificial reef ecosystems depends upon how the blue mussels interact with their local pelagic and benthic environment.

## **Modelling the ecophysiological response of the Pacific oyster *Crassostrea gigas* to the spatial variability in environmental factors: Application to the Baie des Veys ecosystem**

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*Keywords* : *Crassostrea gigas*, phytoplankton carbon concentration, hydrodynamic model, biogeochemical model, Dynamic Energy Budget model

**Abstract:** Baie des Veys is an open estuary and intertidal ecosystem (37 km<sup>2</sup>) influenced by four rivers, with an important oyster farming activity (10 500 tons produced per year). At the bay scale, some spatial differences in the structure of phytoplanktonic and microphytobenthic communities and in the biological performances of cultivated oysters were observed. It is assumed that a trophic heterogeneity may exist without further evidence on the mechanisms controlling it. In order to assess whether spatial interactions between oysters and the ecosystem may affect phytoplankton availability and oyster growth, a three-dimensional (3D) hydrodynamic model was coupled to an ecosystem model. The ecosystem model simulates the Baie des Veys nutrient-phytoplankton-oyster food web. The method consists of coupling a biogeochemical sub-model which simulates trophic resources of oysters (i.e. phytoplankton biomass via chlorophyll *a*) and a Dynamic Energy Budget sub-model which simulates growth and reproduction (i.e. gametogenesis and spawning) using mechanistic bases. The biogeochemical sub-model successfully simulates phytoplankton dynamics using river nutrient inputs and meteorological factors as forcing functions. An adequate simulation of oyster growth dynamics needed to find a relevant food quantifier compatible with outputs of the biogeochemical sub-model (i.e. chlorophyll *a* concentration). We decided to use the phytoplankton carbon concentration as quantifier for food, because it is a better estimator of energy really available to oysters. As no measurements of carbon concentration were available, we used an empirical formulation of the chlorophyll *a* to carbon ratio in order to transform chlorophyll *a* concentration in carbon concentration. Seasonal variations of the chlorophyll *a* to carbon ratio allowed to reproduce seasonal patterns in phytoplankton carbon dynamics which improved the simulation of oyster growth. The integration of this coupled model in the hydrodynamic model provided a suitable tool to better understand the observed spatial differences in oyster biological performances in relation to the effect of water circulation on food production and availability for filter-feeders.

## **DEB model of the growth of Pacific oysters in the Marennes-Oléron Bay: implications of life cycle closure and density-dependent feedback**

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*Keywords: Crassostrea gigas, recruitment, harvesting, time series, phytoplankton population dynamics, density dependent growth, environmental factors*

**Abstract:** We present a model that studies the dynamics of a Pacific oyster population in Marennes-Oléron Bay and the interaction with its environment over a period of almost 30 years. Growth and reproduction of individual oysters are modelled within the framework of Dynamic Energy Budget theory, using a modification of a previously developed model, parameterized for the stock. We extend the model by explicitly modelling density dependence in individual growth and recruitment.

We use two key measures of the environment, water temperature and food availability (chlorophyll a concentrations). They are described by 1980-2006 time series of data from Marennes-Oléron Bay. We implement two different methods to investigate the effect of food availability on oyster growth and population dynamics. Firstly, we use the time series of food concentration ‘as is’ and run simulations to find the values of the half-saturation coefficient in food intake and parameter  $\kappa$  describing energy allocation of individual oysters that together provide the best fit for the observed oyster growth and population biomass over the entire observation period.

Secondly, we use a simple model that describes the impact of oyster grazing on the concentration of phytoplankton and thereby accounts for density-dependent growth of individual oysters. Our approach allows us to express the density-dependent feeding rates of individual oysters without the need to explicitly model the full feedback loop between the oysters and phytoplankton. We then use the time series of food concentration as a relative measure of intra- and inter-annual fluctuations in phytoplankton levels and run simulations to find the value of the half-saturation coefficient in the food intake, parameter  $\kappa$  describing energy allocation, phytoplankton carrying capacity and phytoplankton growth rate that together provide the best fit for the observed oyster growth and population biomass.

## A DEB model for cockles in the Oosterschelde

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*Keywords: Cerastoderma edule, population dynamics, sensitivity analysis, functional response*

**Abstract:** The natural and cultured shellfish populations in the Oosterschelde are of considerable biological and economical interest. The hydromorphology of the Oosterschelde is continuously changing and adapting in response to natural anthropological and climatological changes. In view of these changes and of possible future developments in the region, questions arise with regard to the impact on the system's carrying capacity for shellfish populations. Dynamic shellfish models can help to answer these questions.

As a first step, a Dynamic Energy Budget (DEB) model for cockles (*Cerastoderma edule*) has been developed and validated with long-time field observations from the Oosterschelde. The field observations cover the population dynamics of cockles in the intertidal areas of the Oosterschelde since 1992 as well as the environmental conditions. This dataset gives a good overview of the development of the cockle population in relation to the environmental conditions (food availability and ambient temperature). A functional response has been formulated and calibrated to translate the field measurements of food quality parameters such as chlorophyll-a, POM, POC and TPM into ingestion rate for the cockles. The model performance is validated by relating the model output to field observations. A sensitivity analysis has been applied to display the sensitivity of the model output to the parameters related to the functional response.

The DEB model for individual cockle growth is scaled up into a simple population model and has been incorporated as a grazer module into a 3D hydrodynamic and water quality model for the Oosterschelde. This model allows for a direct coupling between water quality processes and population dynamics of the cockles. The performance of the model has been evaluated with field observations from the Oosterschelde.



**Abstracts of Posters  
(by alphabetic order)**

## Effects of uranium on zebrafish, *Danio rerio*: relationships between biomarkers and history life traits using a Dynamic Energy Budget model.

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*Keywords: Danio rerio, oxidative stress, gene expression, DEB model, radionuclides.*

**Abstract:** Aquatic ecosystems are submitted to chronic rejections of pollutants coming from different anthropic sources (industry, agriculture, etc). Radionuclides are among the different kinds of stressors occurring in the environment and can directly interact with aquatic organisms especially fish. The alteration of one or several biological functions can modify the fish's homeostasis and potentially affect their reproduction, their growth, and their survival thus endangering the whole population (Van der Oost et al. 2003).

*Danio rerio* exposed to waterborne uranium show signs of oxidative stress associated with membrane lipid peroxidation and the inhibition of several enzymes involved in anti-oxidative defence (Cooley et al. 2000; Labrot et al. 1999). Several studies conducted within the Laboratory of Radioecology and Ecotoxicology (LRE) on uranium effects have comforted these results on *Danio rerio* using biochemical (catalase, superoxide dismutase, glutathione peroxidase activities) (Barillet et al. 2007) and molecular markers (expression of genes involved in anti-oxidative stress) (Lerebours et al., accepted). Studies are currently in progress in our laboratory to develop immunological biomarkers as well (phagocytosis, production of reactive oxygen species involved in oxidative stress).

Studies conducted within the LRE at the individual level showed that uranium could modify *Danio rerio* life traits in both early stages (delays in hatching and development/growth in larvae, larvae mortality at high concentrations) (Bourrachot et al., pers. comm.) and in adults (decrease of fecundity).

One way to extrapolate effects induced by pollutant toxicity on physiological and life history traits to population dynamics is to measure how such a stress impacts the overall energy budget of an organism (Kooijman and Bedaux 1996; Kooijman 2000). Dynamic Energy Budget (DEB) models describe the acquisition of energy by food uptake and its distribution to the major physiological functions of an organism (maintenance, growth and reproduction) considered at different stages of its development.

This PhD project takes place within the context of pollution to the environment by radionuclides (i.e. uranium) in environmentally relevant conditions. The main aim of this project is to study eventual links between the early responses of the immune and the oxidative stress systems (measured at molecular and cellular levels) and responses measured at higher levels of biological organisation (such as the individual or the population). First it will be necessary to synthesize all the data already available in the literature pertaining to DEB models as well as the data obtained from the previous three thesis in the LRE on how uranium interacts with *Danio rerio* (S. Barillet, A. Lerebours in progress, S. Bourrachot, in progress). The main focus of this work is on linking different levels of biological organisation through the DEB theory and understanding the mechanisms at stake. Then it will be possible to obtain supplementary data in laboratory-controlled experiments in order to develop and parameterize the model. These experiments should enable us to evaluate how toxic stress (measured indirectly by the perturbations of immune and anti-oxidative systems) impacts the energy budget of *Danio rerio*.

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## Effects of uranium on carbon assimilation and energy budget of *Daphnia magna*

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*Keywords: ecotoxicology, radionuclides, energy budget, carbon assimilation, daphnids*

**Abstract:** In natural biota, populations are constantly subject to variable environmental conditions, including food resources which influence their capacity to survive, grow and cope with toxic contaminants. This is why it is difficult to evaluate the consequences of toxic effects observed in the laboratory under optimal food conditions in a broader ecological context.

In this study we investigate effects of natural uranium, a radioactive heavy metal whose chemotoxicity dominates over its alpha radiotoxicity, on biological responses of the microcrustacean *Daphnia magna* at different food levels. Under controlled conditions, we measure food ingestion, carbon assimilation, and energy allocation towards reserves, survival, growth and reproduction. Results will be used to model the combined consequences of natural and toxic stresses for population dynamics in freshwater invertebrates.

## Studying the trophic ecology of the Pacific oyster (*Crassostrea gigas*) at large spatial scale by coupling isotopes and DEB modeling

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*Keywords: Pacific oyster, trophic resources, isotopes tracers, Dynamic Energy Budget (DEB) model, shellfish ecosystems.*

**Abstract:** Biological performances (growth and reproduction) of intertidal bivalves mainly rely on environmental factors such as water temperature and food sources. Both quality and quantity of bivalve food sources, however, are not easy to determine because of complex features of coastal ecosystem functioning, such as high spatial heterogeneity. This is particularly critical for oyster (*Crassostrea gigas*) culture in France when quantifying and explaining the variability in growth performances of oysters among culture sites at a large spatial scale. In this context, insights for new operational tools to characterise trophic features of coastal ecosystems are needed. The aim of the present study is to couple natural isotope tracers and DEB modeling to describe and quantify bioenergetic processes and isotope dynamics in oyster tissues under varying environmental conditions (temperature, food sources). The model will be tested and validated on carbon and nitrogen isotope data of oyster tissues measured in experimental controlled mesocosms. Once validated, the resulting DEB-isotopes model will be used in inverse method to provide biological indicators (e.g. nutrition level, food sources, availability of reserves, maintenance, growth rate) about oysters cultured in different shellfish areas and to allow comparison of yields among culture sites.

## Effect of photoinhibition and photodamage on the stability of syntrophic symbiotic relationships in scleractinian corals

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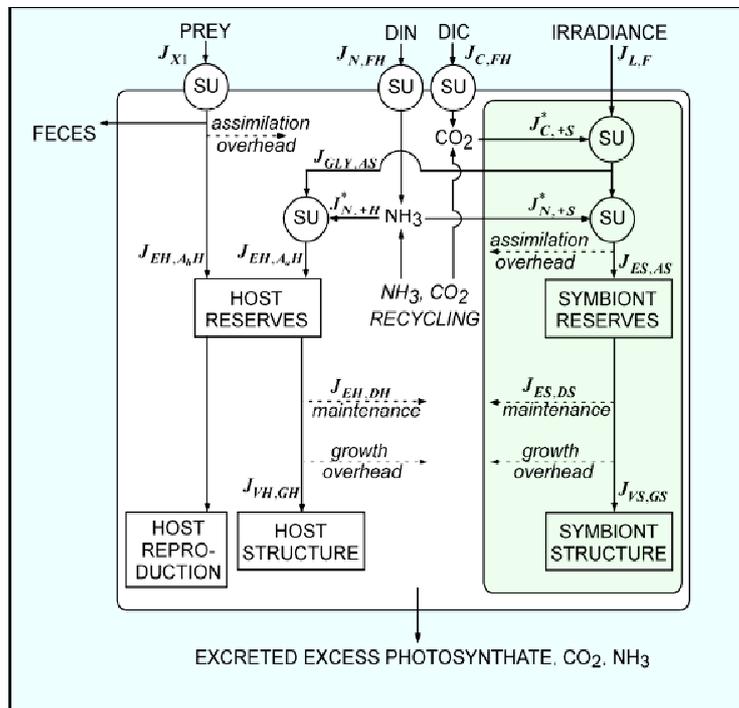
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*Keywords: photoinhibition, photodamage, coral bleaching, syntrophic symbiosis*

**Abstract:** Since coral bleaching is a major issue in coral reef systems, understanding its causes is a major research subject. DEB theory allows us to represent the complex relationship of host and symbiont in corals in a relatively simple way. We consider the effect of photoinhibition as a slowing effect on carbon assimilation by the symbiont caused by an excess of photons, and the effect of photo-damage as an increase in the maintenance requirements of the symbiont. We investigate the impact of photoinhibition and photo-damage on the metabolic fluxes in both symbiotic partners, specifically with the goal to determine the impacts of these effects on the stability of symbiotic assemblage. Our tentative results show that photoinhibition and/ or photo-damage alone can not cause coral bleaching, but these impacts can significantly increase the vulnerability of the assemblage to other sources of environmental stress. Photoinhibition and photo-damage have qualitatively different effects on metabolic fluxes, notably the dynamics of energy reserves.



## **Bioenergetic, life-history modelling of sprat (*Sprattus sprattus*) in the Baltic Sea and the North Sea**

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*Keywords: Bioenergetic model, environmental forcing, life-history optimization, parameterisation*

**Abstract:** Recruitment in Baltic and North Sea sprat stocks has a strong and seemingly unpredictable year-to-year variations due to fluctuations in the physical environment as a response to atmospheric forcing and longer term climate trends. Because sprat is short-lived the fluctuations in year class strength generate large alterations in stock abundance, thereby reinforcing the unpredictability of the forthcoming recruitment.

Therefore, the aim is to develop a bioenergetic model framework with life-history optimization to conduct detailed recruitment studies, with an emphasis on the timing and spatial patterns of egg production and implication for recruitment success. Reproductive success in the sprat stock is most likely linked to the interplay between food supply and temperature. The bioenergetic life cycle model will be coupled to a hydrodynamic model to include the importance of the abiotic environment on the recruitment of sprat. Zooplankton concentrations, i.e. the prey fields, will be tested both in accordance to available data as well as output from ecosystem models. The combined life cycle and hydrodynamic model frameworks will further be used for improving the understanding of climate effects on recruitment.

The research will provide detailed information on processes important for recruitment of sprat under different climate scenarios. This improved understanding will hopefully enhance our predictive capabilities of the year-to-year variability in sprat recruitment. The poster will present an overview of the work which has been made and obtained results.

## **Assessing trophic carrying capacity of the Baie des Veys (Normandy, France) with a biological model**

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**Abstract:** The Baie des Veys is an important site of shellfish culture in Normandy. The Pacific oyster, *Crassostrea gigas*, is the main species in culture with a standing stock of ca. 10 200 tons. Regularly, oyster culture had to face to several mortality crisis and oystermen wish to optimise organisation of the activity in the bay. They wish to optimise rearing densities as a function of ecosystem capacity but also to protect the bay from an ecological point of view. In this context, a first step was to develop a biological deterministic model to assess the trophic carrying capacity. The model takes into account nutrients, phytoplankton and oysters compartments as well as inputs from the watershed which are known to have a major influence on this ecosystem. This model was coupled with an ecophysiological model simulating oyster growth and based on the Dynamic Energy Budget theory. A first set of scenarios was undertaken with different values of standing stock in order to test the effect of density on oyster growth and to assess the trophic capacity of the bay. A growth indicator was then developed where growth is given as a function of the oyster number. Oyster growth also varies according to environmental conditions. A second set of scenarios was then undertaken in order to examine the effect of environmental variability (e.g. water temperature, residence time, watershed inputs) on oyster growth. A second step was to use the model to study the ecological carrying capacity of the bay. This topic was addressed in another communication.

## Estimation of DEB parameters in *Carcinus maenas*

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*Keywords: Dynamic Energy Budget theory, parameter estimation, Carcinus maenas*

**Abstract:** The theory of Dynamic Energy Budgets (DEB) link physiological processes of individual organisms. It describes an organism as two state variables: the structural body volume (volume that requires maintenance) and energy reserves (from where energy is allocated).

The present study provides measured values for ingestion and assimilation in relation to body size (Fig 1.) and describes energy allocation towards maintenance, growth and reproduction. Experiments to assess structural body volume and reserve density (reserves per unit body volume) were performed. The common shore crab *Carcinus maenas* (L.) was used as organism of study. Crabs were fed *ad libitum* with blue mussels (*Mytilus edulis* (L.)) to measure food intake rate, were starved to measure maximum energy density and received intermediate diets to measure energetic costs of growth and maintenance.

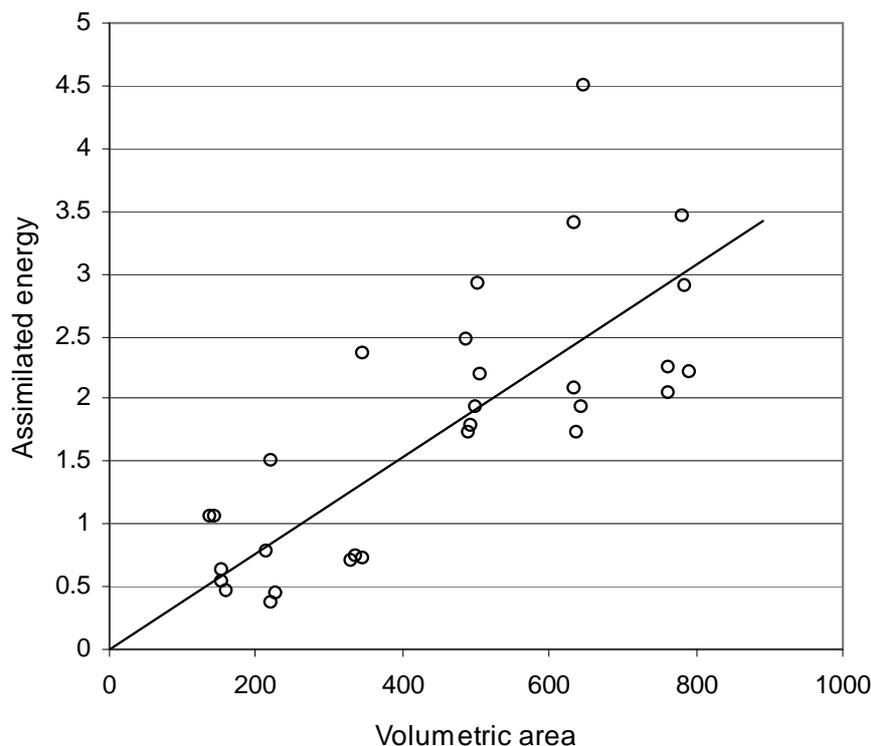


Figure 1. Assimilated energy (in  $\text{kJ day}^{-1}$ ) versus volumetric area (in  $\text{mm}^2$ ) for Common shore crabs *Carcinus maenas* of 28 to 64 mm in carapace width. There is a linear relationship between assimilated energy and volumetric length.

## Uncertainty analysis and validation of a C-flux model of the Atlantic vent mussel *Bathymodiolus azoricus* and its endosymbionts

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**Abstract:** *Bathymodiolus azoricus* is a mussel from the vent fields located at the Azores Triple Junction (Mid-Atlantic Ridge). Experimental evidence indicates that *B. azoricus* is a mixotrophic organism, which obtains energy from a dual endosymbiosis and filter-feeding. Recently, we have developed a size-dependent carbon flux model of *B. azoricus* and its endosymbionts. Predicted mussel productivity was tested against empirical data and the fitting level between the two sets was highly significant (ANOVA,  $F_{1,4}=2 \times 10^8$ ,  $P < 0.001$ ,  $r^2=1$ ). Model results indicate that the dominant nutritional strategy of *B. azoricus* varies with body size and external conditions. Small and presumably young mytilids can not derive enough energy from endosymbiosis to account for their energetic needs and, thus, filter-feeding must play an important role in their nutrition. Gradually, as the mussel grows, the amount of energy derived from microbial oxidations increases and, potentially, *B. azoricus* is able to increase the ratio endosymbiosis: filter-feeding. Under non-limiting conditions, average size mytilids at the Menez Gwen vent site (60 mm shell-length) can obtain 58% of their energy from endosymbiosis and the rest from filter-feeding. In the present work, we attempt to validate the previously developed model with a data set obtained in the lab, where *B. azoricus* was kept for several months under different feeding regimes. Moreover, we perform uncertainty analysis of the parameters previously detected as most sensitive. Using these methodologies, we reinforce the idea that bio-energetic models represent a valuable tool in the study and understanding of extreme ecosystems such as deep-sea hydrothermal vents.

## Current Problems in Stoichiometric Ecology: A Unified Approach

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**Abstract:** The flow of mass and energy has a foundational role in Ecology. The fact that energy transformations always imply energy loss, led Lindeman (1942) to advance an explanation for the relations between the biomasses of successive trophic levels. The core of ecological theory has been focused on overall food supply, emphasizing energy demands in the Lindeman's tradition. However, Ecology has itself not made a too substantial progress in the energy analysis itself. In particular, this means that when papers address energy and energetic balances in organisms or ecosystems, it is not even clear exactly what is being discussed: internal energy, enthalpy, Gibbs free energy, exergy, etc. Energy has become a rather transcendent property in Life sciences.

The coupling of population dynamics to fluxes of nutrient elements has led to the development of stoichiometric models. Until recently, most of these ecological models have frequently rested on the assumption of constant proportions of elements in organisms' biomass. Recent modelling approaches, however, rest on the fact that the crucial elements cycles in marine systems (i.e. carbon and nitrogen) are explicitly addressed. So, variable stoichiometry presupposes that nutrient content variation is in part controlled by processes controlling the carbon dynamic.

The study of the balance of multiple chemical substances has been extended to ecological interactions and processes. This new conceptual framework, ecological stoichiometry, can improve our understanding of the organization of populations and communities. However, it is also important to consider energy constraints, and to be able to relate the two. In fact, stoichiometry is frequently also meant to include both mass and energy constraints.

Here we show how, starting from the currently usual formulation of Droop dynamics for multiple nutrient limitation and variable stoichiometry, it is possible to arrive at a special case of the Dynamic Energy Budget theory, where stoichiometric and energy constraints can be combined. We discuss that the conventional models in aquatic ecology can in fact be seen as particular cases of DEB models. This implies that parameter values from these models can be carried over to DEB, significantly reducing the problem presented above. Additionally, we show that these conventional models have several shortcomings, which are in fact removed by the DEB model.

## **A new approach for estimation of DEB parameter values estimation, the Growth DEB equation, illustrated by the common Sole (*Solea solea*) case**

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*Keywords: DEB theory, Growth, parameter estimation, Solea solea*

**Abstract:** We developed a new equation describing growth based on the DEB theory. This equation (described below, here only for isomorphic and ectotherm organisms) represents an alternative to the utilisation of the von Bertalanffy growth equation and offers advantages for the estimation of DEB parameter values. The Growth DEB equation (GDE) contains strictly the necessary DEB parameters to simulate the DEB growth in a synthetic form : a unique equation for length growth.

We demonstrated that the use of this equation provides three main advantages :

1. It only requires data on the most widely used observable to quantify the size of an organism : the unidimensional length, named  $L_g$  here. This length relates to the structural length by an appropriate shape coefficient. The GDE involves three DEB parameters: the energy conductance and the maximal length, which both are expressed in physical length, and the maintenance rate coefficient. Parameters of the von Bertalanffy equation are functions of these parameters.

2. The GDE is a DEB equation with all possibilities and potentialities allowed by the DEB theory. Contrary to the von Bertalanffy equation, the GDE allows working with variable environments, *i.e.* variable temperatures and food densities.

3. This equation eliminates the sequence of successive approximations made when we use the von Bertalanffy growth equation in order to estimate the DEB parameters values. Indeed, this latter process approximates the DEB trajectory by a von Bertalanffy growth which required a constant environment and an appropriate initial condition on the energy density. The von Bertalanffy growth is itself approximated by a constant when the ultimate length is gauged.

We applied this equation on growth data of the common sole (*Solea solea*). Our equation has been calibrated, by accounting for variable environment, on *in situ* data for males and females. This equation showed a very good agreement with these data sets. We compared these simulations to those of the von Bertalanffy growth equation. We demonstrated that the fact of accounting for a variable environment in the calibration process has a non negligible effect on the resulting dynamics. By using parameters estimated with the von Bertalanffy equation and by simulating growth with these parameters and the GDE, the agreement between model outputs and data was less betterworse than when the model was calibrated and simulated with the GDE.

## Dynamic Energy Budget (DEB) growth model for *Crassostrea gigas* larvae

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*Keywords: Dynamic Energy Budget; Crassostrea gigas; Bivalve larvae; Ecophysiology; Growth*

**Abstract:** Dynamic Energy Budget (DEB) theory aims to quantify the energetic framework of an individual organism as a dynamic model from the uptake of food to the utilisation for metabolic processes (maintenance, growth, development and reproduction). The purpose of the present work is to extend the existing DEB model for adult of Pacific oyster *Crassostrea gigas* to its larval life stage. For this, we introduced DEB theory applied to larval stage and we formulated specific assumptions on the basis of physiological processes. We focused on the methodological procedure to calculate the primary parameters values from available laboratory data in terms of ingestion and growth for larvae related to phytoplankton density and temperature as forcing variables in the model. Calculated parameters for oyster larvae followed the physiologic statements of the DEB theory. The simulations of the DEB larval model allowed to predict properly length growth at controlled conditions providing a more extensive description of the energetic costs in the *C. gigas* larvae. A food density of  $1200 \mu\text{m}^3 \mu\text{l}^{-1}$  around the larvae must be maintained throughout the whole larval development to maximise growth and metamorphosis success. Timing of metamorphosis decreases exponentially with increasing temperature. This model however is not specific to a larval stage of species and can thus be applied to other bivalve larvae. Moreover, several promising perspectives of application of this model in post larval life stage for this species are proposed.

## **Applying DEB model to simulate mussel growth variability in long-line farms as a function of stocking density and farm design**

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*Keywords: mussel culture, DEB modeling, long-line design*

**Abstract:** The mussel (*Mytilus edulis*) is cultured on ropes suspended from long-lines arranged in parallel to maximize growth and facilitate farming operations. High mussel culture densities due to short distance between long-lines and length of farms may cause seston depletion, which results in low mussel growth or tissue wasting due to reduced feeding and negative net energy balance. In this paper we combine a mussel DEB model with a water flow reduction model in long-line farms to simulate seston depletion and mussel growth as a function of stocking density and farm design. The mussel DEB model has been implemented and tested in several contrasted ecosystems prior to the coupling with the farm scale model. The farm scale model is based on assumptions that the frictional forces on water flow are a function of the geometric shape of the channel delimited by the suspended mussel ropes. The model simulates growth variability as a function of farm length, spacing between long lines, and background seston concentration and current speed. Estimates of how farm structure and stocking density in mussel farming can be optimized in relation to prevailing currents and seston concentrations (*i.e.* carrying capacity) are crucial to production management decisions, and the model may provide predictors for decisions regarding new site selection or redesign of existing operations.

## **Application of a dynamic energetic budget model to the pearl oyster (*Pinctada margaritifera*) larvae**

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*Keywords* : larvae, ingestion rate, food limitation, *Pinctada margaritifera*

**Abstract:** Pearl oyster (*Pinctada margaritifera*) farming in French Polynesia depends entirely on the wild spat recruitment. In that context, the success of larval development in lagoons plays a key role to supply spat needs. With the objective to better understand the space-time variability of spat yield, a dynamic energetic budget (DEB) model has been adapted to pearl oyster larvae in order to evaluate the potential effect of environmental factors (*i.e.* trophic state and temperature) to larval development success.

Most of the DEB model parameters were estimated on previously published data except for the ingestion rate. Concerning ingestion parameterisation, laboratory and *in situ* experimental protocols have been conducted aiming at (i) estimate the maximum ingestion rate and half-saturation concentration for monospecific algal cultures and (ii) evaluate the relative contribution of natural plankton communities in the larval diet.

To test and validate the model, growth data have been collected with both, cultured algae and lagoon plankton. Finally, the DEB model will be applied with environmental forcing (*i.e.* trophic state and temperature) recorded in one atoll lagoon and the potential success of larval development will be linked to the pearl oyster settlement observed.

## Development of a DEB model of the coldwater coral *Lophelia pertusa* for the quantification of sedimentation stress

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*Keywords: coldwater corals, experiment, DEB parameter, physiology, stress*

**Abstract:** One of the most spectacular ecosystems on continental margins is formed by cold-water corals (CWC). CWC thrive in dark, cold and mostly deep oceanic waters and can form complex reef structures with abundant species diversity and biomass. In contrast to tropical corals, CWC do not contain symbiotic algae and rely on heterotrophy by filtering particles from the water column. One potential threat for CWC ecosystems reported in the literature is oil and gas exploitation; in particular the smothering effect of drill cuttings, i.e. particles produced during exploration drilling and clay-like weighing agents, when released near the reefs. However, there is almost no information on how cold-water corals respond to being exposed to sediment and people have to rely on parallel work carried out on tropical coral species.

The possible adverse impacts of smothering on CWC relate to their physiology: 1) tentacle clogging with particles may interfere with the feeding process, 2) active excretion of so-called mucus sheets to free the coral surface from particles and 3) a thin sediment layer on the tissue surface may lead to oxygen shortage of the coral. To quantify the possible negative effects of smothering of CWC by drill cuttings we are developing a physiological model of CWC based on DEB theory in the frame of the CORAMM project (funded by the Norwegian oil company StatoilHydro). The reef-building species *Lophelia pertusa* is selected as model species, because it is the dominant reef-building species and it is possible to maintain this species in the laboratory for prolonged periods of time. A series of experimental studies on feeding, respiration and mucus excretion are carried out on laboratory contained specimens. The results from the experimental studies will be used to infer primary DEB parameters and parameterize the DEB model. Subsequently, the abovementioned impacts will be included in the model and be used to simulate the impact of drill cuttings on growth and reproductive output by the CWC from realistic drilling discharge scenarios.

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