Intensive DEB workshop

21 – 31 May 2017 Tromsø, Norway

This is an advanced training course on Dynamic Energy Budget theory. The objective is to train participants in estimating DEB model parameters for their species during 8 days. Trainees will come together in Tromsø and interact with skilled scientists actively involved in applying DEB to their own research. The teaching team will present exciting lectures on applications of the theory in a variety of fields: environmental quality management, ecology, fisheries, population dynamics .... It is also the ideal format for networking and strengthening international cooperation. We further expect this training to generate many new high quality entries in the online AmP (Add-my-Pet) database of DEB models and parameters. AmP is an initiative in the context of much wider aims: find the simplest organisation principles for metabolism upon which all life is based & understand taxon-specific patterns as variations on this common theme.

1 Course schedule

8 day practical course on DEB theory (Tromsø, MAY 2017)

	Sun 21 May	Mon 22 May	Tues 23 May	Wed 24 May	Thurs 25 May	Fri 26 May	Sat 27 May	Sun 28 May	Mon 29 May	Tues 30 may
9:00-09:30		"Summary tele-course" (S. A.)	"Alternative Approaches" (S.K.)	"Trajectory reconstruction" (L.P.)	"Accelerations and evolution of acceleration" (S. K.)	"Biophysical Ecology" (M. K.)	"Multivariate DEB models" (G. M.)	"Individuals to populations to community" B. K.	"Thermodynamics of Organisms" (T. S.)	"Ecosystem Dynamics" (R. N.)
09:30 - 10:00				DEB in practice II						
10:00 - 10:30		Break	Break	Break	Break	DEB in practice IV (M. K.)	Break	Break	Break	Break
10:30-11:00		AmP: guided example (K. L.)	DEB in practice I	DEB in practice II	"Individual Based Models" (R. N.)		AmP	AmP	AmP	"Sensitivity Analysis" (K. L.)
11:00-11:30						Break				
11:30-12:00					"Impact assessment" (EZ)					Plenary discussion (M. K.)
12:00-12:30		Lunch				AmP		Lunch		
12:30 - 13:00										Sandwiches & personnal time
13:00-13:30		"Overview of the AmP procedure" (G. M.)	DEB in practice I	DEB in practice II	DEB in practice III (J-C. P. & B. K.)		"Simple versus Complex" (J-C. P.)	"Evolution: adaptive dynamics" B. K.	Group discussion	
13:30-14:00	Arrivals and settling in									
14:00 - 14h30		"The metabolic theories of ecology" (M.K.)		AmP		Excursion (sandwiches & Tromsø museum 13H - walk from hotel 15h00 - BBQ Charlottenlund recreational park 18H00	Group discussion	Group discussion	AmP presentations	Tour of Polar Museum (with some talks) - be there at 14h00
14:30-15:00			"Empirical Population Dynamics" (J. M.)							
15:00-15:30		Break			Break		Break	Break	Break	
15:30-16:00		"Covariation of parameter values" (K. L.)	Break	Break	Group discussion		"Organization levels and scales" (J-C. P.)		AmP presentations	
16:00-16:30				"Unstructured population models" (J. M.)				AmP		Personal time
16:30-17:00			AmP		Plenary discussion (R. N.)				Break	
17:00-17:30		AmP		Group discussion			AmP		AmP presentations	
17:30-18:00										
18:00-18:30		Personal time	Personal time	Personal time	Personal time		Personal time	Personal time	Personal time	
18:30- 19:00										
19:00-20:30	Welcome and Dinner	Dinner	Dinner	Dinner	Dinner	night out - no dinner provided		Dinner	Dinner	Dinner
20:30 - 21h30		Group discussion	Group discussion	Wonderful nature (S. K. slide show)				Group discussion	Wonderful nature (S. K. slide show)	

2 Learning objectives

- Estimate DEB parameters for animals and more specifically an animal you are interested in for your research
- Formulate a research question
- Apply DEB parameter estimation to support your own research and address contemporary problems in conservation, environmental impacts and resource management
- Step from individuals to populations: Explain principles of structured and unstructured populations models, methods for analysis of model dynamics and applications.

3 Contents of the 57-hour course

AmP workshop	16h
DEB in practice guided exercises	9h
Lectures	19h
Group discussions	8h
Plenary discussions	2h
Pet presentations	3h
Total:	57h

4 Items to bring to Tromsø

You can read online how to get from the airport to the Sydspissen hotel where the course takes place. You will find on the same page some information about things to do in your spare time, as well as practical information.

Please bring with you :
- Walking shoes
- Laptop with matlab 2006 or higher
- Recent version of DEBtool
- A well prepared mydata file for your pet
- MathCont (JC, Bob)
- Netlogo
- NichMapperR (DEB in practice IV)
- List of participants (we skip introductions) :

If you don't have a Matlab license, there are two viable options:
- Download the free 30-day trial version from mathworks.com. Organize it so that these 30 days includes your visit to Tromsø
- Buy the Student version of Matlab if you are a student at a university. The student version apparently has all the capabilities of Matlab and is cheap (35 Euro excl. VAT for the basic program).

5 DEB2017 Team

The teaching team (starting from top left: Bob, Roger, Dina, Jaap, Elke, Bas, Jean-Christophe, Goncalo, Laure, Tânia, Nina, Starrlight, Mike)

5.1 Leaders discussion groups
Jean-Christophe, Elke, Jaap, Laure, Nina, Bob

5.2 Assistants exercise groups
Gonçalo Marques; Dina Lika; Laure Pecquerie; Starrlight Augustine; 'Bas' Kooijman; Elke Zimmer; Nina Marn

5.3 Lecturers
Michael Kearney (M. K.), Bob Kooi (B. K.), Elke Zimmer (E.Z.), Sebastiaan 'Bas' A. L. M. Kooijman (S. K.) Konstadia 'Dina' Lika (K. L.), Gonçalo Marques (G. M.) Jaap van der Meer (J. M.), Roger Nisbet (R. N.), Starrlight Augustine (S. A.), Laure Pecquerie (L. P.), Jean-Christophe Poggiale (J-C. P.), Tânia Sousa (T. S.)

5.4 Leaders plenary discussions
Michael Kearney; Roger Nisbet

5.5   Leader Add-my-pet presentations
Elke Zimmer

5.6   Onsite support crew for Symposium
Starrlight Augustine; Nina Marn; Cristina Wood

6   AmP workshop (16h)
Objective: Parameter estimation on the basis of the submitted mydata- file in small groups.

Each group will be assisted by the team. In addition to the task and learning objectives outlined below, the AmP workshop will also be used to provide Matlab and DEBtool training and basics in statistical and numerical methods for those who have an interest in it.

6.1   Tasks:
- compose a predict_my_pet file for your pet
- estimate parameters values using run_my_pet
- compute over 100 implied properties of your pet

6.2   Learning objectives:
- Create user defined predictions for length, weight, reproduction and/or respiration data with the help of the DEBwiki, DEBtool and AmP websites
- Control parameter estimation by setting options in run_my_pet and/or setting weight coefficients in mydata_my_pet
- Saving results and choosing starting values for parameter estimation by setting options in run_my_pet
- Computing goodness of fit
- Discussing goodness of fit in (biological) context

6.3   Assessment:
Pet presentation of main findings.

6.4   Pets

First Name	Pet (Latin Name)	Pet (English Name)
Andre	*Notonecta maculata*	Backswimmer
ANDREA	*Serranus scriba*	Painted comber
Antonio	*Eriphia verrucosa, Chromis chromis*	Warty Crab, Damselfish
Catalina	*Salmo salar*	Atlantic salmon
Cheryl	Salvelinus namaycush	lake trout
Chiara	*Oncorhynchus clarkii stomias*	greenback cutthroat
Christina	*Amphiura filiformis*	the long-armed burrowing brittlestar
Claudia		
David	*Phoca vitulina*	Harbour seal
Felix	*Salmo Salar*	Salmon
Flor	*Rhizoglyphus robini*	Bulb mite
Inês	*Ruditapes decussatus*	Grooved Carpet shell
Irene	*Arctica islandica*	Ocean quahog
Jean-Pierre	*Ursus maritimus*	Polar bear
Jessica	*Chelonia mydas*	Green turtle

Jéssica	*Archilochus alexandri*	Black-chinned hummingbird
Joany	*Thyasira gouldi*	Northern hatchet-shell
Josef	*Nitocra spinipes*	(A copepod)
Kim	*Chaoborus crystallinus*	Glassworm / phantom midge
Liz	*Liocarcinus depurator*	Swimming crab
Nathanaël	*Pinctada margaritifera*	Black-lip pearl oyster
Nicola	*Natator depressus*	Flatback turtle
Nicolas	*Mastigias papua, Cephea cephea, Linuche unguiculata*	
Nigel	*Extatosoma tiaratum,* Onthophagus taurus	Spiny Leaf Insect, Bull Headed Dung Beetle
Nikos	*Argyrosomus regius*	meagre
Quentin		Anchovy
Reid	*Litoria raniformis*	Growling grass frog
Roland	*Pimephales promelas*	Fathead minnow
Romain	*Daphnia pulex*	Waterflea
Rose	*Psammechinus miliaris*	Purple-tipped sea urchin
Salomé	*Sterechinus neumayeri*	Antarctic sea urchin
Shu-Ping	*Takydromus hsuehshanensis*	snow mountain lizard
Starrlight	*Boreaogadus saida*	polar cod
Vaskar	*Ictalurus punctatus*	Channel catfish

7   DEB in practice (9 H)

Download here Matlab files for running simulations with state varibles of the DEB model:
http://deb.akvaplan.com/debschool/DEB2017_std_simulation.zip

7.1   DEB in practice I: Estimation in Context (3 H)

Leader: Starrlight
Assistants: Gonçalo, Laure, Dina, Bas, Jaap, Elke, Nina

7.2   Material

http://deb.akvaplan.com/debschool/DEB_in_practice_I.docx
http://deb.akvaplan.com/debschool/DEB2017_PPT_DEB_in_practice_I.pdf

7.2.1   Summary

Deep-sea fishing started without much knowledge of the life-history characteristics of the newly exploited stocks. Is it possible to say something at all about growth and age at maturity without being able to age specimens, know anything about their reproduction or being able to raise them in the laboratory?
We will work with the Greenland shark *(Somniosus microcephalus).*
Results will be discussed in a wider context of eesource management (deep sea fisheries) and with respect to published work by from van der Meer et al 2014 [1] on the Atlantic hagfish.

7.3   **DEB in practice II "Reconstruction of food intake from growth data" (2H)**

Leader: Starrlight
Assistants: Gonçalo, Laure, Starrlight, Dina, Elke, Bas, Nina

Chap 4. Univariate DEB models [2] presents 4 examples of "Trajectory reconstructions": reconstruction of food intake and body temperature from growth data, reconstruction of food intake from reproduction data and last reconstruction work from otolith data.

Trajectory reconstructions are useful and creative applications of the DEB theory, as many data sets (on growth or reproduction) do not provide adequate information about food intake and this information is often very hard to quantify experimentally.

In this guided exercise we will conduct the reconstruction of food intake from growth data for the great scallop *P. maximus* which is a real case study carried out by Romain Lavaud and co-workers in the context of his doctoral thesis [3].

Slides available here: http://deb.akvaplan.com/debschool/DEB2017_PPT_DEB_in_practice_II.pdf

7.3.1 Material you will need:
Fully completed files for doing the trajectories in three sites:
- http://deb.akvaplan.com/debschool/reconstruction_traena.zip
- http://deb.akvaplan.com/debschool/reconstruction_celtic.zip
- http://deb.akvaplan.com/debschool/reconstruction_brest.zip

Raw data for reconstruction in excel: http://deb.akvaplan.com/downloads/Reconstruction_pecten_maximus.xlsx

Parameter values for *Pecten maximus*

http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Pecten_maximus_res.html

Romain Lavaud's Thesis http://www.bio.vu.nl/thb/research/bib/Lava2014.html

7.3.2 Summary
Romain Lavaud [3], chap. 6, developed and applied a modelling approach consisting of the inversion of the DEB model in order to reconstruct the functional response of food assimilation from growth data (obtained from the sclerochronological study of the shell) and temperature.

P. maximus shell grows by sequential increments and the analysis of the striae allows an accurate measurement of daily growth dynamics. These high frequency data are used in order to reconstruct the history of functional response along the growth trajectory.

The process relies on writing out the equation for growth as function of food (for the standard DEB model) and then inverting the equation in order to estimate the scaled functional response as function of time.

Length at time for individual *P. maximus* is recorded at three separate sites: Bay of Brest, the Celtic sea, Traena. Temperature is recorded continuously but the shells only start growing in spring when phytoplankton blooms. Temperature is a constant 12deg C in the Celtic sea at the depth the biometric measurements were made.

R. Lavaud will be present during the last 30 min via Skype. We will discuss his method and approach from his thesis [3].

7.4 DEB in practice III " From individuals to populations: an introduction" (Thurs 25 May 2H)
Leaders: Jean-Christophe Poggiale and Bob Kooi
- Course document: http://deb.akvaplan.com/debschool/IBM_DEB2017.pdf
- Slides: http://deb.akvaplan.com/debschool/lezingIBMdeb5.pdf , http://deb.akvaplan.com/debschool/DEB2017_Kooi_DEB_in_practice.pdf
- Html of published code: http://deb.akvaplan.com/debschool/V1morphDividers.html
- Matlab code that you will need: http://deb.akvaplan.com/debschool/WithReproduction.zip

7.5 DEB in practice IV "Biophysical Ecology with NicheMapR " (Fri 26 May 1 H)
Guided exercise/lecture lead: Mike R Kearney

http://deb.akvaplan.com/debschool/DEB_in_practice_IV.zip

Presentation of niche mapR
Demo
- follow the Setup Instructions for NicheMapR downloadable here
- Standard DEB model in excel

8   Lectures (19 H)

8.1   Lecture 1 "Summary of the DEB-tele course" (Starrlight Augustine 1 H)
Learning objectives:
- Define strong homeostasis (chemical indexes, chemical potential)
- Define structural homeostasis
- Compare differences in how chemical composition changes with growth rate between (a) an individual over its ontogeny subject to constant food and (b) between two individuals where one is subject to constant high food and the other is subject to constant low (but sufficient) food. Explain the roles of weak and strong homeostasis to capture (a) and (b)
- List the processes of the standard DEB model and write out the macro-chemical reaction equations for each process
- Convert an equation from an energy-length-time framework to a mass-length-time framework.
- Provide at least one reason that it is more complex to perform a mass balance than an energy balance.

8.2   Guided AmP example (Konstadia Lika 2H)
Step by step guided example of estimating parameters for the spurdog *Squalus acanthias*.

8.3   Lecture 2 "Overview of the AmP procedure" (Gonçalo Marques 1 H)
Topics:
- Short history/introduction to AmP
- Purpose of estimation, start from bijection
- Data: zero-variate and uni-variate
- Parameters: core and auxiliary
- Understanding of the several components of the estimation: Nelder-Mead method, filters, pseudodata
- Evaluation of the estimation: assessment criteria MRE & SMSE
- Code architecture
- AmP Collection

Reading: Lika et al. [4], Lika et al. [5]

8.4   Lecture 3 "The Metabolic Theories of Ecology" (Michael Kearney, 1 H):
- Role of budgets in ecology: theoretic vs empirical
- Comparison of existing approaches: bryozoans
- Long-term perspective for bio-energetics

8.5   Lecture 4 "Covariation of parameter values" (Konstadia Lika, 1H)
- Scales of life in time & space
- Primary vs compound parameters
- Covariation of parameter values
   - Intensive & extensive parameters
   - Primary and secondary scaling relationships
- Comparisons of intra- and inter-specific scaling relationships
- AmP – patterns in covariation of primary parameters

Primary Reading: chapter 8 [2].
Additional Reading: Kooijman et al. [6], Lika et al. [7]

8.6   Lecture 5 "Alternative approaches to modelling metabolism" (Sebastiaan Kooijman 1 H)
Metabolism is the set of chemical transformations in living cells to maintain and propagate life. Life originated as prokaryotes, so their metabolism might reveal aspects of metabolic organisation that is at basic to metabolism in general. I briefly discuss a possible evolutionary scenario for the evolution of central metabolism and the metabolic organisation of eukaryotes.

Models for metabolism can generally be classified as the biochemical (bottom-up) approach, where a (small) number of particular chemical compounds are followed, and the pool (top-down) approach, where pools of metabolites are followed, which do not change in composition (strong homeostasis). Both approaches have strengths and weaknesses. Mixtures of both approaches suffer from the problem of the huge range in time and spatial scales even for unicellulars. An intermediate one, however, which deals with the a few interacting biochemical modules might possibly link both approaches and serve as communication channel.

Among the pool models, single pool (called "biomass") models are most frequently used, and especially what became known as production (or scope for growth) models. Losses of acquired resources are first subtracted from inputs and the remaining part is allocated to growth and/or reproduction. This approach will be compared with assimilation models, of which the DEB model is an example. The interpretation of respiration, which is generally seen as a quantification of metabolic rate, and the use of allometric functions will be discussed in the context of all possible internal organisation schemes.

This type of presentation cannot be done without my views on the various alternatives. I don't ask you to agree with my views, but invite you to think about the arguments that will be presented.

Background material: Kearney et al 2010 [8], Kooijman 2010 [2], Kooijman & Hengeveld 2005 [9], Kooijman & Segel 2005 [10], Kooijman & Troost 2007 [11], Lika & Kooijman 2011 [12]

8.7 Lecture 6 "Unstructured population dynamics" (Jaap van der Meer, 1H)
Most unstructured population models are coupled sets of non-linear differential equations, that describe the rate of change of the size of the populations.
Various classical models are discussed, including a DEB model for a
substrate eating V1-morph in a chemostat

8.8 Lecture 7 "An introduction to Trajectory Reconstruction" (Laure Pecquerie 1 H)
- Otoliths
- Reconstructing environmental conditions

8.9 Lecture 8 "Unstructured Population Behaviour" (Jaap van der Meer 1 H)
- classic models: potential & problems
- DEB approach in comparison with other approaches: weak-strength evaluation

8.10 Lecture 9 "Accelerations and evolution of accelerations"(Sebastiaan Kooijman 1 H)
Application of the standard DEB model to a large number of animal species learned that quite a few species did not fit that model over their full life cycle. Deviations allowed a classification in 5 modes of acceleration, which is defined as a long-term increase in metabolic rate during ontogeny, compared to expectations of the standard DEB model. I first briefly review some properties of the standard DEB model to introduce deviations from it. The 5 modes are an increase in maturation, assimilation, body temperature and changes in diet and morphy-type (temporary V1-morphy, as opposed to continued iso-morphy). I will discuss examples for each of these modes, and discuss ecological and evolutionary contexts where possible.

Background material: Kooijman 2010 [2], Kooijman 2014 [13], Kooijman et al 2011 [14], Lika et al 2014 [15], Mueller et al 2012 [16]

8.11 Lecture 10 "Individual-based and structured population models of interacting species" (Roger Nisbet 1 H)
- Concepts for individual-based and structured population models
- Daphnia as model organism
- DEB-IBM – with demonstration
- testing an IBM
- applications to ecotoxicology
- future challenges

Primary Reading: section 9.2. [2]
Additional Reading: Martin et al. [17], Martin et al. [18], Martin et al. [19]

8.12 Lecture 11 "Impact assessment for effects of a power plant on a mussel population" (Elke Zimmer 30 min)
Introduction:
- Context: DEB modelling in risk assessment (chemical or environmental stress)
- DEB-IBM in netlogo – what is netlogo and how is DEB implemented?
- Example: Daphnia population effects (Martin et al)

Main part:
- Case study:
- O impact assessment; additional power plant; impact of cooling water on mussel population
- O Data availability: deal with what you get
- O Existing stress: reconstruction of food level as stress indicator?

- Model application and results

Discussion

8.13 Lecture 12 "Biophysical Ecology" (Michael Kearney 1 H)
- Thermodynamic constraints
- Endotherm body temperature
- Predicting endotherm energy and water requirements
- Predicting climate niches

8.14 Lecture 13 "Multivariate DEB models" (Gonçalo Marques 1H)
- Synthesizing units: complementary compounds DEB2017_Marques_2.pdf
- Multiple reserves: excretion, damming up
- Nutrient limitation
- Multiple structures: static and dynamic
- Plants
- Multiple maturities?

8.15 Lecture 14 "Simple versus Complex" (Jean-Christophe Poggiale 1 H)
- Why do we need to simplify (introduction)?
- Some elements of dynamical systems theory (equilibrium, stability, stable, unstable and centre manifolds, structural stability, ...)
- Slow - fast systems, reduction of dimension and time scale separation
- Some examples

8.16 Lecture 15 "Organization levels and scales" (Jean-Christophe Poggiale 1 H)
- Individuals level : general comments on modelling individuals in ecology, Synthesising units (how are there defined, how do we use them, ...)
- Linking individuals and population levels : how to formulate models? How time scale separation may help when it is valid?
- Some examples

8.17 Lecture 16 "Individuals to populations to community" (Bob Kooi 1H)
Introduction and discussion of the following types of population models:
- Densities vs numbers
- Processes vs events
- Deterministic vs stochastic
- Continuous time vs discrete time
- Continuous state vs discrete state
- Ordinary differential equations vs Markov chain
- Population mean vs population variability
- Spatially homogeneous vs heterogeneous environment

Study of a simple predator-prey system. The classical model is the Rosenzweig-MacAthur model where the prey grows logistically. We formulate and analyse a mass balance model where the law of mass conservation is obeyed. In this model nutrients are modelled explicitly. A detailed analysis of the different model types illustrates their specific features with respect to dynamical behavior.

In case of deterministic models we will use the populations existence and a stability analysis showing dependence of the dynamical behavior on parameter values.

In case of stochastic models we use a stochastic simulation algorithm to obtain realizations in order to study the population variability.

8.18 Lecture 17 "Evolution: adaptive dynamics" (Bob Kooi 1 H)
Modelling evolution of species via (indirect) competition for food between a resident and an invader population, see Troost et al 2007 [20]:
- Adaptive dynamics vs optimization theory
- Adaptive dynamics vs game theory
- Adaptive dynamics vs replicator dynamics

Study of evolution in populations under different environmental conditions

- Toy model
- Lotka-Volterra competition model
- DEB model
- Population in spatially homogeneous environment
- Population in water column
- Population in spatially homogeneous environment with seasonality
- Population with discrete annual reproduction

8.19 Lecture 18 "Thermodynamics of Organisms" (Tânia Sousa 1 H)

Topics
- First and second law of thermodynamics for open systems
- Entropy production in organisms

8.20 Lecture 19 " Ecosystem Dynamics" (Roger Nisbet 1 H)

Topics:
- Energy flow and material cycling in ecosystems
- Stoichiometry in DEB
- Simplest DEB ecosystem model (canonical community)
- From molecules to ecosystems with DEB

8.21 Lecture 20 "Sensitivity Analysis" (Konstadia Lika 1 H)

Topics:
- Parameter identification
- Confidence intervals
- Sensitivity
- Monte Carlo simulations

9 Group discussions

6-8 people per group discussion

The chair(wo)man appoints a reporter, who will summarize the discussion during 5 min in the plenary discussions. In each hour, 2 participants have a 10 min presentation on the problem that they submitted in 0.5 A4 at the end of the tele-part, followed by a 10 min discussion per presentation.

The remaining time (some 10 min per hour) we discuss:
- TOPIC 1 (22/05 – 25/05, first four discussion groups sessions): Theories vs. models: What is the difference between them and how are they related, particularly in the context of DEB theory? Sub questions could be: Can you have theory-free models, and when would they be useful? Can you use theories without models? Can you have mechanistic models without formal theory? How are parameters interpreted in theoretical and empirical models? When is it ok to modify models from theoretical expectation?
- TOPIC2 (27, 28 29/05): Future developments – Starting points could be to read some of the comments to "Physics of Metabolic Organisation" by Jusup et al [21]. Patricia Holden – Galik & Forbes – Bas Kooijman - Pecquerie & Lika (but there are others). You can also look at the DEB research program, developments, applications pages from the DEB wiki.
- TOPIC3: evaluation of tele- and practical course with respect to learning objectives

The reporters will summarize the findings of these discussions in the plenary discussion. The chairmen reports the conclusions of the last evaluation discussion to the organizer. The composition of the groups will be a matter of self-organization, but we reshuffle after the first plenary discussion, again by self-organization.

10 Plenary discussions

The reporters of the discussion groups report at the plenary session for 5 min each, leaving some 30 min for discussion with all of the participants simultaneously.

11 Pet presentations (2H)

We ask successful participants to present their results briefly; experts giving comments. If time allows we will compare the parameter values and give a short presentation of the findings.

12   Discussion topics

12.1   André Gergs

Weight loss and reproduction under fluctuating food conditions

Individual-based model designs based on metabolic theories such as the dynamic energy budget (DEB) theory or the metabolic theory of ecology are increasingly be used to describe individual and population level performance under environmental perturbation and fluctuading conditions such as food availability. However, for reasons outlined below, Johnston et al. (2014) argued that due to the the kappa rule which assumes fixed fractions of assimilated energy being allocated to growth and reproduction, the standard DEB model is not applicable to earthworm life cycles. In this regard, the objective of one of my current studies is to explore if (or to what extent) the standard DEB model needs to be adjusted to appropriately describe growth and reproduction patterns in Eisenia fetida.

Johnston and coworkers (2014) presented an energy budget model for E. fetida based on formulations provided by Sibly et al (2013) and tested the model along data on growth and reproduction of individual or cohorts of worms. The authors dismissed DEB models for being not applicable to earthworms, mainly based on the observation that E. fetida specimens to some extent continue reproduction during periods of weight loss under limiting feeding conditions (Reinecke and Viljoen 1990). Johnston et al. (2014) interpreted the weight loss as shrinking during starvation; however, as long as the energy reserve is above a threshold of 50% of the maximum energy reserve, the individual continues reproduction. A few model assumptions are key to understand the implicit interpretation of the above observations by the authors: In their model, energy assimilated from ingested food is hierarchically allocated to 1) maintenance, 2) reproduction (in adults only), 3) to growth and 4) energy reserves. As a consequence, the individual grows in terms of mass if sufficient energy is assimilated from the environmental and the remaining energy is stored in the reserves with some efficiency. However, the reserve energy does not contribute to mass, and changes in mass are only due to growth (increase in mass) or the catabolization of tissue (decrease in mass) during starvation.

I follow an alternative hypothesis regarding the observations by Reinecke and Viljoen (1990), which would not lead to a violation of the 'kappa-rule': Weight loss under limited feeding conditions (or the absence of food) is initially due to the utilization of the reserve (which contributes to weight), and, in turn, the reserve allows continued reproduction for a limited period until starvation strikes. However, under prolonged starvation, the individual stops reproduction and starts shrinking in structure.

In the published experiments only wet weight and cumulative cocoon production (reproduction) have been measured which makes it difficult to distinguish between structure, reserve and water replacement during reserve utilization (which might also depend on environmental moisture conditions). Moreover, in E. fetida, experiments are usually done by providing the animals with food such as sludge or cattle solids, and soil is added as a medium. After the food has been depleted by the worms, soil (which might have some nutritional value) could serve as alternative food source, and thus, might slow down reserve utilization and the concurrent loss in wet weight, which complicates the data analysis.

Johnston A.S.A., Hodson M.E., Thorbek P., Alvarez T., Sibly R.M. (2014). Ecological Modelling 280, 5-17.
Reinecke A.J., Viljoen S.A. (1990). Biology and Fertility of Soils 10, 184-187.
Sibly R.S.; Grimm V., Johnston A.S.A., et al. (2013) Methodss in Ecology and Evolution 4: 151-161.

12.2   Quentin Queiros

The aim of my thesis is to study the mechanisms of the bottom-up control exerted on sardines and anchovies in the Gulf of Lions (France). Thus, the first part of my PhD consists in an experimental approach investigating the effects of food (size, quantity, quality) on body condition, growth, reproduction, locomotion and immunity.

Then we would like to use the DEB theory to model the same life-history traits and compare both experimental and modeling results with the current situation in the wild.

Moreover, we would like to test for a possible 'cocktail effect' mixing various environmental parameters such as water temperature, quality or quantity of food. In fact, all these parameters could imply different consequences themselves but studying them together should give insight on potential synergistic implications (processes vs. group of processes).

As food seems to be the main trigger of the current situation in the Gulf of Lions, we would like to improve the functional response f in the DEB to take into account effects of food size, quantity, quality, or foraging strategy.

Eventually, we hope to combine the DEB model with a population dynamics model to investigate population responses rather than individual ones and be able to account for other sources of variability such as fishing mortality.

12.3 Nathanael

Changing sex ability of the black-lip pearl oyster (Pinctada margaritifera) in stressful environmental conditions, a DEB approach.

Pearl oyster P. margaritifera is a hermaphrodite protandrous species (Tranter 1958) (consecutive change in sex). Indeed, at the first maturity all oysters are male and then the female sex appears gradually from about 2 years to reach an equilibrium with a sex ratio close to 1 : 1 for older populations of 8 years old individuals (Chávez-Villalba et al., 2011). However, Thielley (1993) showed that female-to-male sex changes can occur when natural conditions (temperature and food) or artificial conditions (manipulation and cleaning) were stressful. Bisexual individuals (sexual inversion in progress) or undifferentiated individuals are rarely observed, suggesting that these processes of sex change or stopping gametes production occur very quickly. Despite a lack of knowledge regarding processes behind these observations, DEB theory that deal with energetics flux and content of an individual seems appropriate to describe such concepts as a physiological adaptations. Since females and males have different bioenergetic functioning (Chávez-Villalba et al., 2013), modify standard energetics as a result of stressful environmental conditions might change basic concept of the reproduction buffer handling rules for species-specific concept (Kooijman, 2010).

Female gametes are supposed to be more energetically costly than the production of male gametes, estimated at 50% more energy (Russell-Hunter, 1979). Bayne, (1976) indicated that gametogenesis only begins when energetic reserves are sufficient. Poorly fed pearl oysters probably might not have enough energy from the diet and reserves to initiate gametogenesis and therefore change sex. Describe these observations with DEB theory might lead for example to change the kappa value or reduce the costs of a gamete (E0) in order to keep growth and reproduction performance high as possible when energetic storage become low.

Describe such concepts with a DEB model might lead to get insights on the mechanisms underlying changing sex behavior. However it appears that DEB basic concepts like kappa rule are able to well fit with Von Bertalanffy growth rate despite the fact that it might not be realistic for some species. The challenge lies in the selection of the most relevant hypotheses and thus tests them according to various environmental scenarios.

Bayne, B. L. (1976). Aspects of reproduction in bivalve molluscs. Estuarine processes, 1, 432-448.

Chávez-Villalba, J., Soyez, C., Aurentz, H., & Le Moullac, G. (2013). Physiological responses of female and male black-lip pearl oysters (Pinctada margaritifera) to different temperatures and concentrations of food. Aquatic Living Resources, 26(3), 263-271.

Chávez-Villalba, J., Soyez, C., Huvet, A., Gueguen, Y., Lo, C., & Le Moullac, G. (2011). Determination of gender in the pearl oyster Pinctada margaritifera. Journal of Shellfish Research, 30(2), 231-240.

Kooijman, S. A. L. M. (2010). Dynamic energy budget theory for metabolic organisation. Cambridge university press.

Russell-Hunter, W. D. (1979). The evolution of filter-feeding bivalves. A life of invertebrates. New York: MacMillan Publishing.

Thielley, M. (1993). Etude cytologique de la gamétogenèse, de la sex-ratio et du cycle de reproduction chez l'huître perlière Pinctada margaritifera (L) var. cummingi (Jameson),(mollusques, bivalves): comparaison avec le cycle de Pinctada maculata (Gould). Comparaison avec le cycle de Pinctada maculata (Gould). Université française du pacifique, 233.

Tranter, D. J. (1958). Reproduction in Australian pearl oysters (Lamellibranchia). IV. Pinctada margaritifera (Linnaeus). Marine and Freshwater Research, 9(4), 509-525.

12.4 Romain Richard

Energy budgets under fluctuating food conditions

I was wondering about the possible effects of fluctuating food conditions on patterns of individual production (e.g. growth, reproduction, respiration…).

For example, under constant food conditions, both fecundity and respiration rates are predicted to be a weighted sum of individual surface and volume. Do fluctuations in food density fundamentally affect those relationships, or do they only cause small deviations?

My motivation in asking that question is that in DEB theory, energy utilization does not depend on the state of the environment at all, but only on the state of the individual. Nonetheless, if the environment fluctuates strongly enough, the ratio between reserves and structure may never (or rarely) approach their ratio under steady state conditions. How does all this translates to the life history expressed by an individual?

Also, is that possible / likely that strongly fluctuating food conditions can affect rules of energy use? I'm for example thinking of consumer-resource cycles. In those cycles, food density varies to quite a substantial extent and the dynamics

may be fast enough to occur on the same time scale than physiological processes. In these circumstances, the current state of an individual may correspond to high food conditions (e.g. high reserve density) whereas it actually experiences low and decreasing food conditions. From an evolutionary point of view, if a species evolved in such kind of environment, it seems to me that it would be poorly adaptive to maintain the same allocation strategy under both increasing and decreasing food conditions. Is there any branch of DEB theory that accommodates for changes in energy use under changing food conditions? Is that even possible to integrate such a rule to the standard DEB given the way energy mobilization rule is derived?

12.5 Flor Rhebergen

A major goal in evolutionary biology is to understand how traits evolve by natural selection. In order to gain insight in how selection acts on trait expression, it is common practice to compare fitness statistics between individuals expressing trait X and individuals that do not (or to a lesser extent) express trait X. The difference in fitness represents selection.

However, fitness (defined as an individual's expected contribution to the growth of the population) is notoriously hard to operationalize. In practice, evolutionary biologists often use fitness approximations (depending on personal preference, context and logistic constraints) such as the number of offspring during a breeding season, the instantaneous rate of offspring production, lifetime reproductive success, or even physiological performance. The implicit assumption here is that the fitness proxy correlates well with 'true' fitness. However, this is not obviously true. For example, the number of offspring during breeding season 1 may negatively affect the number of offspring in breeding season 2, if the production of offspring is energetically costly. Alternatively, expression of a seemingly favourable trait may indeed increase the rate of offspring production, but at a longevity decrease or an increase in development time. Therefore, the 'true' direction and strength of selection may not correspond to the direction and strength of selection estimated by comparing fitness proxies.

It seems that this problem could be solved if we had a mechanistic theory of the individual life cycle, that would predict an individual's net contribution to the population in terms of somatic growth, timing of reproduction, number of offspring, and longevity (in short: fitness). DEB theory seems promising. Could DEB theory estimate fitness differences between classes of individuals? Should evolutionary biologists start to measure DEB parameters rather than fitness proxies, in order to understand trait evolution? In other words, should evolutionary biology move a little bit away from purely statistical descriptions of populations towards a mechanistic understanding of individuals, in order to understand how traits evolve?

I guess the main issue would be the problem of time scale. DEB theory predicts the life cycle at the scale of an individual's life time, but evolutionary biology needs predictions on selection over multiple generations. However, it seems that this is not so much a problem of the application of DEB theory to evolutionary questions, but more a problem of evolutionary biology in general. After all, statistical estimates of fitness proxies also need to be constant over multiple generations in order to be evolutionarily relevant, but are commonly only measured once. Therefore, it seems that using DEB theory to predict fitness could still be an improvement over current practice.

12.6 Joany Marino

Among symbiotic relationships, the association between chemosynthetic bacteria and invertebrate animals is a prominent example because of its prevalence in diverse habitats and within multiple phyla of hosts, especially within the Bivalvia. One particular family of bivalves, the Thyasiridae, is notable for containing symbiotic as well as asymbiotic members. Within this family, the genus Thyasira and the cryptic complex of Thyasira cf. gouldi contain species with and without symbionts; this is a unique example of extreme variation at species and genus taxonomic levels. Representatives of this intriguing group can be found in various sites within the fjord of Bonne Bay (Newfoundland, Canada), and they form a subject of active research. Recent studies provide evidence that these populations constitute an early evolutionary stage of the symbiosis between bivalves and chemosynthetic bacteria, and it is likely that speciation is occurring within them. Hence, this group represents an outstanding opportunity as a model system to study the evolution of chemosymbiotic associations. The characteristics inherent to the chemoautotrophic symbioses allow addressing general issues, such as how does endosymbiosis affect patterns of speciation in the associated organisms. The particular features of chemosymbiosis in the Thyasiridae also permit evaluating more specific matters with respect to the variability of the symbiotic association —i.e. a transition in the interaction towards the loss of the symbionts or a greater reliance upon them—, which could arise as a consequence of selection pressures that affect the abundance of free-living bacterial symbionts. My research links optimal foraging to population dynamics and evolutionary ecology, I'm particularly interested in gaining ideas for experimental design and measures that could be made to parameterize

the deb model and adjust it for its application to chemosymbiosis, as well as extending it to an agent-based model in order to study the population dynamics.

12.7 Josef Koch

In my research I try to use DEB theory to investigate effects of chemical stressors (individually and in mixtures) to aquatic invertebrates in terms or their mode of action (MoA). Despite the fact that copepods are estimated to form the largest animal biomass on earth and are of fundamental importance for the global ecosystems they have only been scarcely investigated in a DEB framework. With life cycle data of temperature and food effects on the harpacticoid species Nitocra spinipes, it is my aim to calibrate a DEB model for this species. In previous works, copepods have been treated as V1-morphs (abp typified model). During the course I want to get deeper insights into the typified models and investigate which model can describe the life cycle of N. spinipes best.

Furthermore, I want to interpret effect data of the antidepressant citalopram on N. spinipes's development and reproduction in terms of the present MoA on energy.

12.8 Catalina Chaparro

Several species experience a habitat switch and often the two habitats differ in the abundance of resources, resulting in a discrete change in nutritional conditions. For instance, salmonid species spend their early life stages in a freshwater habitat with strong density–dependence and high competition for food, while later on they migrate to the sea where density–dependence is low and food is more abundant (Jonsson, Jonsson, & Hansen, 1998). This change in food abundance changes, among others, the energy allocation and consequently the body composition (i.e. energy density) of individuals (Johansen, Ekli, Stangnes, & Jobling, 2001; Morgan & Metcalfe, 2001; Rasmussen & Ostenfeld, 2000; Stoks, Block, & Mcpeek, 2011). In the case of salmonid species, the discrete increase in food availability experienced during the habitat switch from freshwater to seawater leads to an increase in growth rates but a decrease in energy density (MacFarlane, 2010). Thus, the increase in food makes individuals allocate more energy to growth and less to energy reserves (Johansen et al., 2001). This bias toward increased somatic growth at the expense of energy reserves occurs more generally in response to an increase in food levels following a phase of food limitation: vertebrate (Auer, Arendt, Chandramouli, & Reznick, 2010; Sinervo & Doughty, 1996; Taborsky, 2006) and invertebrate (Kleinteich, Wilder, & Schneider, 2015; Zeller & Koella, 2016) species have been documented to compensate their growth and reach similar sizes as individuals that continuously experience high food levels, at the expense of a lower fecundity.

- Auer, S. K., Arendt, J. D., Chandramouli, R., & Reznick, D. N. (2010). Juvenile compensatory growth has negative consequences for reproduction in Trinidadian guppies (Poecilia reticulata). Ecology Letters, 13(8), 998–1007. http://doi.org/10.1111/j.1461-0248.2010.01491.x
- Johansen, S. J. S., Ekli, M., Stangnes, B., & Jobling, M. (2001). Weight gain and lipid deposition in Atlantic salmon, Salmo salar, during compensatory growth: Evidence for lipostatic regulation? Aquaculture Research, 32(12), 963–974. http://doi.org/10.1046/j.1365-2109.2001.00632.x
- Jonsson, N., Jonsson, B., & Hansen, L. P. (1998). The relative role of density-dependent and density-independent survival in the life cycle of atlantic salmon Salmo salar. Journal of Animal Ecology, 67(5), 751–762. http://doi.org/10.1046/j.1365-2656.1998.00237.x
- Kleinteich, A., Wilder, S. M., & Schneider, J. M. (2015). Contributions of juvenile and adult diet to the lifetime reproductive success and lifespan of a spider. Oikos, 124(2), 130–138. http://doi.org/10.1111/oik.01421
- MacFarlane, R. B. (2010). Energy dynamics and growth of Chinook salmon (Oncorhynchus tshawytscha) from the Central Valley of California during the estuarine phase and first ocean year. Canadian Journal of Fisheries and Aquatic Sciences, 67(10), 1549–1565. http://doi.org/10.1139/F10-080
- Morgan, I. J., & Metcalfe, N. B. (2001). Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. Proceedings. Biological Sciences / The Royal Society, 268(1464), 295–301. http://doi.org/10.1098/rspb.2000.1365
- Rasmussen, R. S., & Ostenfeld, T. H. (2000). Effect of growth rate on quality traits and feed utilisation of rainbow trout (Oncorhynchus mykiss) and brook trout (Salvelinus fontinalis). Aquaculture, 184(3-4), 327–337. http://doi.org/10.1016/S0044-8486(99)00324-5
- Sinervo, B., & Doughty, P. (1996). Interactive Effects of Offspring Size and Timing of Reproduction on Offspring Reproduction : Experimental , Maternal , and Quantitative Genetic Aspects, 50(3), 1314–1327.
- Stoks, R., Block, M. De, & Mcpeek, M. A. (2011). Physiological Costs of Compensatory Growth in a Damselfly Published by : Ecological Society of America Stable URL : http://www.jstor.org/stable/20069107 . America, 87(6), 1566–1574.
- Taborsky, B. (2006). The influence of juvenile and adult environments on life-history trajectories. Proceedings. Biological Sciences / The Royal Society, 273(1587), 741–750. http://doi.org/10.1098/rspb.2005.3347

- Zeller, M., & Koella, J. C. (2016). Effects of food variability on growth and reproduction of Aedes aegyptiZeller, M., & Koella, J. C. (2016). Effects of food variability on growth and reproduction of Aedes aegypti. Ecology and Evolution, 6(2), 552–559. http://doi.org/10.1002/ece3.1888. Ecology and Evolution, 6(2), 552–559. http://doi.org/10.1002/ece3.1888

12.9 Chiara Accolla

DEB and Ecotoxicology

My purpose is to parametrize a model for an endangered trout species (Oncorhynchus clarkii stomias) using DEB theory and then write an IBM taking into account:

- the life cycle of the trout;

- the mortality linked to environmental factors and/or inter-species competition.

The goal is to understand why this trout is endangered and to find the right combination of parameters that represents its population dynamics.

In a second time, I will study the effects on population dynamics caused by chemical stressors.

I think I will have to deal with a metabolic acceleration DEB-model and this will be my first concern.

Then, I expect to spend a lot of time on finding the right set of parameters representing the different causes of mortality and eventually leading to trout extinction. In particular, it seems that feeding success of juveniles is compromised both by competition with other trouts species and by temperature. So, expressing temperature-age-dependence in feeding behavior will be another discussion point.

12.10 Jean-Pierre Desforges

Ecotoxicology deals with the interaction of environmental processes and toxic substances. A current focus within this field is to expand on traditional toxicity approaches looking at individual stressors and move towards risk assessment of multiple stressors and to include chronic sub-lethal effects. DEB theory is an ideal tool to address multiple stressors; by using the common currency of 'energy' we can compare and combine stress effects in the same model of individual fitness. My research is specifically focused on marine mammals and chronic sub-lethal effects of environmental contaminants on health, including immune and endocrine effects. It is well established that contaminants modulate the immune system of mammals and increase the susceptibility to and mortality of disease. Endocrine disrupting compounds are known to affect steroid hormones, thyroid hormones and sperm quality in mammals, which likely influence growth, development and reproductive success. While these aspects of toxicology are well studied at the molecular level, much less is known about how these stressors play out at the individual and population level. I hope to use DEB theory to address some of these issues. However, I foresee many problems/obstacles to this type of analysis. The first and largest hurdle is to model the physiological processes associated with immunity and endocrine function and then to estimate the effects of contaminants. DEB models to date have been used to generalize physiological processes, but to model the effects of contaminants on immune function will necessitate a further development of general maturity maintenance costs as these relate to immunity. I am not currently sure how one would incorporate endocrine dysfunction within DEB theory. A second and associated hurdle is to estimate these physiological processes in non-model organisms such as marine mammals. Marine mammal science is plagued with this problem generally since it is difficult to perform controlled studies in these species, such that stressor effects are often extrapolated from studies in other animal species. This leads to the question of how easily can stressors be extrapolated between species in DEB theory? For instance, can stress functions described in one species (eg. no-effect concentration and tolerance) be directly applied to another? There is likely species differences in the effects of contaminants, but to what level does this apply in DEB? Lastly, energy allocation to thermoregulation and movement may be important in Arctic mammals like polar bears that live in harsh environments and roam large distances to find food. Adding these aspect to DEB models may be difficult.

12.11 Vasker Nepal

1) Can we modify the framework with growth at different temperatures to growth at growing degree days? This would simplify things a lot from an applied (data collection) perspective, though might be too much from a mathematical view.

2) What does DEB theory have to say about Bergmann's rule?

3) What about life history theory? At different stages of invasion, the growth rate and size at maturity definitely change. Plenty of evidence for this, including my own research work.

4) How can I include the effect of salinity stress in fish? Most likely goes to surface area specific maintenance rates (Page 42 DEB3), right? But, how do I actually include this in the model?

5) DEB theory seems to let you assess the fundamental niche. For invasive species, which I am interested in, fundamental niche is interesting in the worst-case-scenario sort of way. More interest would be in truncating this fundamental niche

into the realized niche. How would one go about that? NicheMapR seems interesting in this regard, but can it be applied to aquatic animals?

6) Biphasic growth models in fisheries applications suggest that growth changes allometrically, with declines in growth rates typically observed after maturation. Lester's biphasic model even says that the model is based on (an extension of) the DEB theory. Is it a valid approach based on the standard DEB theory?

12.12 Shu-Ping Huang

Topic: Is the condition in winter hibernation a crucial factor setting altitudinal boundary of a high mountain lizard, Takydromus hsuehshanensis? Application of Niche Mapper/DEB model on simulation of the life history traits

Research question

Environmental temperature affects elevational distribution of reptiles by affecting physiological function and ultimately ecological performance. To survive cold weather, many high-mountain reptiles often thermoregulate, such as by basking in the sun, to elevate their body temperatures to meet physiological requirements. This raises the question of why some lizard species are restricted to high mountains since they require high body temperature during their activity seasons.

Rationale

When a suite of physiological/behavioral traits of high-mountain lizards have evolved in order to survive the cold weather, it on the other hand may incur energetically disadvantages to survive in a warm climate. For example, a high mountain lizard is capable of being active a much lower body temperature range and having a low set-point body temperature to trigger winter hibernation. When exposed to the winter condition lower than its native elevation, it may not undergo winter hibernation and therefore may incur a higher energetic cost during winter, which causes disadvantage for maintaining a population.

Hypothesis

I will use Takydromus hsuehshanensis (2000– approximately 3500 m in elevation distribution) as a study animal. I hypothesize that this lizard is able to have a positive population growth as a result of the thermal consequence on annual energetics. The temperatures outside its native area could be energetically very costly, which can outweigh the benefit gained during the activity season. Especially when combined with winter food shortage, it many lead to high mortality to some life stages and a difficulty to maintain population size.

Supporting evidence

1.   A transplant study in the lowland area (Chen et al., 2010):
A high growth rate in the summer but high mortality beginning autumn-winter season (food ad libitum) were detected in lowland areas. The adults reproduced and laid eggs in the summer but were active and suffered from illness in the winter. Also, T. hsuehshanensis remained active in the winter, while its lowland counterparts went winter hibernation in general.

2.   A winter hibernation study in the laboratory (Huang, unpublished data):
Treatment of a winter hibernation at 15oC caused a higher body weight loss, compared to those at cool temperatures (5, 10oC).

3.   Other observations: A. T. hsuehshanensis matures in 2 years at a bigger size while its lowland counterparts mature in 1 year at a smaller size.

Methodology

In order to investigate the effects of environmental factors (temperature, food availability) on life history traits and simulate the potential yearly energy budget and reproduction output of T. hsuehshanensis, I will use Niche Mapper to simulate the body temperature in an altitude gradient. Then, I will use the simulated Tb as a parameter in the DEB model to simulate the energy budget/population dynamics in an array of temperature and food availability scenarios.

12.13 Jess Stubbs & Nicki Mitchell

Using DEB theory to compare sympatric species of sea turtle with different life history patterns.

My research focuses on the foraging ecology and energetics of green turtles in the Ningaloo World Heritage area in Western Australia. I am using stable isotope analysis to quantify their diet, and satellite tagging to investigate their movement between foraging grounds. I am interested in using DEB theory to explore how environmental change (increased water temperatures, altered food abundance) would impact upon the energy dynamics of this population. I am also interested in the applications of isotope dynamics within the DEB framework. Can DEB theory help to understand observed differences in stable isotope values? Can the theory account for differences in metabolic processes and isotope accumulation or depletion between juveniles and adults thereby identifying whether differences in stable isotope values are due to differences in energetics or in diet?

There is a huge volume of literature on green turtles from around the world. As I was gathering data for my DEB model I noticed differences in many parameters from different population (e.g. maximum size, number of clutches per season). In contrast, there is little data available from my study population, aside from data that I have generated on embryonic stages myself. I wonder whether it is better when building a DEB model to use more data (and more types of data) from different populations or to only use the limited amount of data available for my study population.

Additionally, my PhD supervisor Nicki Mitchell and other members of our lab are working on Flatback turtles that use similar nesting locations and nearshore environments to green turtles, but have different diets and life histories. Post-hatchling green turtles disperse great distances from nesting beaches and display a pelagic developmental phase whereas flatback turtles remain on the continental shelf during this life-stage. Green turtles produce clutches of approximately 100 small eggs, whereas flatback turtles produce smaller clutches (approx. 50) of larger eggs, and the size at birth of flatback turtles is around 2-3 times that of most other sea turtle species.

Another potential problem in modelling these species is that post-hatchlings of both species show allometric growth rather than isometric growth in this life stage. They grow wide faster than they grow long, which is likely to make them less vulnerable to gape-limited predators at a younger age. How would this be incorporated into a DEB model? Is this short period of allometric growth important or could these species still be modelled using the standard model? Loggerhead sea turtles also show this allometric growth, and as DEB models have recently been developed for the North Atlantic and Meditterean stocks by Nina Marn and her collaborators, Nicki and I hope to learn from Nina's experience and to shortly add two more sea turtle species to the DEB collection.

12.14 Jessica Morais
The growth pattern of the Black-Chinned Hummingbird (Archilochus alexandri)
The Black-Chinned Hummingbird (Archilochus alexandri) and other hummingbird species exhibit a growing pattern that includes a period of body mass decrease before and after fledging, which is consistent with the growth pattern of some species group such as Falconiformes or Suliformes [1]. In this case, the fledglings weighed 149% of the mean body mass of adult [2].

Numerous hypotheses have been considered to explain this type of behaviour in other bird species like the Wandering Albatross: i) energy is stored for later use; ii) stored energy provides a kind of insurance against changes in the environment; iii) Stored energy provides a quicker development before fledging so that adults may migrate sooner and iv) stored energy provides a smooth transition to the post-fledging period [3].

Beside this, after fledging, the locomotion is responsible for the daily energy expenditure in the hummingbirds (1260beats/min), which can affect their energy needs.

Based on these hypotheses, how can I apply the DEB model to modulate the Hummingbird's growth and to compute the DEB parameters?

I propose the application of the DEB standard model to the period before fledging and to the period after fledging separately, with the purpose of understand the growing pattern presented.

[1] H. F Greeney, E. R. Hough, C. E. Hamilton, and S. M. Wethington, "Nestling growth and plumage development of the Black-chinned Hummingbird (Archilochus alexandri) in southeastern Arizona", Huitzil, 2008, Vol. 9, pp.35–42. [2] G.D. Constantz, "Growth of nestling Rufous Hummingbirds", Auk , 1980, Vol. 97, pp. 622-624.
[3] C.M.G.L. Teixeira, T.Sousa, G.M.Marques, T.Domingos, and S.A.L.M Kooijman, "A new perspective on the growth pattern of the Wandering Albatross (Diomedea exulans) through DEB theory, " J. Sea Res., Vol. 94, pp.117-127, 2014.

12.15 Roland Kuhl
While working on a project for modelling mortality in Gammarus pulex with the General Unified Threshold model for Survival (GUTS), I encountered problems when trying to fit multiple tests and different exposure regimes.
-        Constant exposure scenarios and pulse exposure scenarios seem to be problematic to represent with one set of parameters
-        Tests conducted at different points in time seem to be difficult to fit together.
While the long term tests (10 days) could be fitted nicely, the prediction graphs for the short term experiments (4 days) showed that the toxicity was extremely overestimated. This was true for different substances.
The tests were conducted with collected Gammarus from the wild and at different time points of the year. So there could be variability in the sensitivity of the organisms throughout the year affecting the outcome of the studies.

The idea to discuss is if there is a possibility to achieve a more flexible model using the dynamic energy budged to better address this problem than with a simple GUTS model and to simulate different Energy distributions throughout the year. Detailed information about the live cycle Gammarus goes through every year would be necessary to estimate different energy allocations in different seasons.

A lower metabolic rate in the spring due to colder conditions could reduce the influence of toxicity in experiments due to slower intake. So a temperature dependent elimination could be helpful.

Another option would be different NEC due to a change in the feeding status over the year. Different food levels available to Gammarus could cause different sensitivity.

12.16 Kim Ladermann
STARVATION

The dynamic energy budged (DEB) theory deals with the uptake of energy from the environment by an organism and the use of this energy for maintenance, development, growth and reproduction. It follows the changes of fluxes during the lifecycle of the organism.

My question is: What happens, if no food is available? How do organisms cope with that and how does DEB theory manage these changes.

In the handbook for the DEB telecourse starvation is explained in detail.

At the beginning of starvation growth can continue although at decreasing rate. If starvation continues, somatic maintenance costs cannot be paid via reserve. The structure of an organism undergoes constant reorganisation which means a mobilization of structure at a constant rate. This flux is used to pay somatic maintenance costs if necessary. This mobilized flux normally equals the synthesized flux, as part of the turnover process, but not during starvation. The resynthesis during starvation is not complete and leads to shrinking which results in reduced maintenance costs. Shrinking occurs at a rate. The respiration during starvation is proportional to the use of reserve and should decrease exponentially. If maturity costs cannot be paid anymore the maturity level decreases and rejuvenation occurs. At this state the organism is more vulnerable towards environmental changes or chemicals.

Strategies/ways to cope with starving conditions:

1)   Shrinking in structural mass during starvation as a way to pay somatic maintenance costs. Also animals with a skeleton use shrinking: shrews of the genus Sorex reduce their braincase during the year (shrinks in the winter, expands in the spring (Dehnel phenomenon)). Also mussels seem to be able to reduce shell size.

2)   Reducing body temperature saves a lot of energy

3)   Switching to a torpor state in which growth and reproduction cease, while maintenance (and heating) costs greatly diminish

4)   Hibernation: not only body temperature is lowered, but other maintenance costs are reduced as well. Some reserve has to be present, if maintenance costs cannot be reduced completely.

5)   Emergency reproduction: winter eggs in daphnids, switch to sexual reproduction as a reaction to adverse feeding conditions

6)   Long-distance migration: requires physiological preparation

7)   Dormancy: Freshly laid eggs can frequently survive adverse conditions, because the infinitesimally small embryo requires little maintenance; it only has to delay development. The pupal stage in holometabolic insects is also very suitable for inserting a diapause.

These various strategies were observed to be used by organisms to escape adverse feeding conditions. The further question is: How is this implemented in DEB theory and which parameters have to be changed or adapted? In DEB theory the scaled functional response f represents different feeding conditions. If f is set to 1 (f=1) that means 100% food availability/quality, for "food-reduced" or "starving" datasets f can be lower than 1 or even 0. The species list in add-my-pet includes also species with higher values than 1, means that this food quality was outstanding good?

Survival under mild starvation was longer than under ad libitum food availability, is this because metabolic activity is reduced and linked with aging?

Are more parameters involved in starvation than f?

12.17 Inês Lopes
Aquaculture has been growing at remarkable rates in the last decades, it contributes to increase fish productions and keeping the overall fish price down. As the world population increases the pressure to feed everyone has challenged researchers all over the world to develop this sector, improve technologies and increase knowledge so that we can supply more fish in a sustainable way.

DEB theory aims to quantify the metabolism of an individual organism as a dynamic model, accounting for the uptake of food, assimilation into reserves, maintenance, growth, increasing maturity and reproduction. The work I have been developing focuses on applying this model to aquaculture, firstly to mussels, the gilt-head seabream and also to the carpet shell clam.

So, it is interesting to discuss how to go from an individual model to a population model that it can be coupled to hydrodynamic and atmospheric models. Focusing firstly in parameters, is it a good assumption that individuals have the same DEB parameters, and are therefore equal? Or should a variation be accounted for, for instances stating that a certain parameter varies between its value plus the standard deviation and its symmetric? Also, related with model parameters, a problem arises with large scale simulations, to compare two populations of a species for example, should two set of parameters be used?

Population dynamics has also an influence on the individual behavior and fate, how should intra and inter species relationships be included in order to follow the DEB theory?

12.18 Orestis Stavrakidis

Under the ClimeFish project, we are investigating the impact of climate change in European aquaculture in order to ensure sustainable fish production and for that we are creating an imaginary fish farm that runs under various climatic scenarios. Our current focus is to improve the existing fish models by increasing their accuracy across a wider range of sizes, especially up to market size, and temperatures. Making predictions at higher temperatures and therefore calculating the lower and upper values of the Arrhenius temperature at TL and TH is vital for our work. So far, we have been unable to calculate these values with the covariation method and TL and TH tend to progressively diverge reaching unrealistic values which forces us to use fixed values found in literature. Is this caused by insufficient temperature-related data and is there a better way to deal with the lower and upper ends of the temperature tolerance range of our species?

In addition, our future challenge regarding the imaginary farm is to introduce variability when we extrapolate from individual to population level. Stocking density and interactions between individuals could mean different access to food and therefore different functional responses, how could we model that realistically? Another approach would be to assume that there is some small genetic variability within the population and that genetic traits (which correspond to DEB parameters) follow a distribution, therefore each individual comes with a slightly different set of parameter values. DEB parameters however don't fluctuate independently but co-vary and some tend to be more conservative than others (eg κR, v), how can we account for that and what would be a recommended approach to introduce individual variability in general?

12.19 Liz Talbot

Liocarcinus depurator (swimming crab)

I am particularly interested in using DEB to capture the dynamics of the moult in crustaceans. Rather than working as if growth is continuous and using DEB to predict size/wet mass after a given amount of time (and so having a linear growth curve), I use it to predict size/wet mass at each time point to produce a stepwise growth curve, which is what we actually measure in relatively slow growing crustaceans. As carapace width only increases at a moult, even though the crab is adding structure inside it, I have been focussing on wet mass and carbon mass in my experiments, and using the ratio of the two (carbon mass/wet mass) to predict the timing of the moult and the magnitude of the increase in wet mass post moult. My supervisor and I made the assumption that carbon mass (and so the CMWM ratio) will increase between moults, and this would be simple tool to use to capture the energetics of moult dynamics. I have a (very) simple DEB model running in R using this assumption and it does capture moult timing and wet mass increase, so I end up with a stepwise growth curve for wet mass and a linear curve for carbon mass, which is what I'd hoped for. I also think that it should be possible to link changes in O2 consumption over the course of the moult cycle (it increase immediately before a moult and stays high for ~24 hours afterwards) to the CMWM ratio, in order to get a DEB model that better describes the physiological changes that occur during the crustacean moult cycle.

12.20 Nigel Andrew

My lab is currently focussed on identifying if behavioural, ecological and physiological traits of insect species are predictable across environmental gradients, and whether these traits can then be scaled up to predict changes within and between ecological communities:. The broader aim to understand biotic adaptations to a rapidly changing climate and develop predictive models in how interactions will change in a warmer and more variable climate.

We are starting to get together datasets on ants, dung beetles, and stick insect species: primarily thermolimit respirometry, life history, community assemblage data, both in the lab and the field. I am attempting to determine how using a DEB framework, as well as Individual Based Models can help me to develop a framework for predicting impacts of increased temperature and moisture variability on populations across different parts of their range.

12.21 Nicki Mitchel

Can DEB theory explain divergent patterns of growth and reproduction within a single population of Australian dragon lizards?

I work on reptiles with temperature-dependent sex determination (TSD) and it strikes me that DEB theory could be a powerful framework for exploring the adaptive significance of TSD. For example, in reptiles with a type II (FMF) pattern of TSD, does the production of females at the two extremes of tolerable incubation temperatures influence their life history traits (e.g. fecundity), or is the energy allocated to lifetime reproduction relatively unaffected by differences in their early development? As DEB models already exist for two reptiles with TSD that I have worked on (tuatara and loggerhead sea turtles) I decided to develop a DEB model for a short-lived Western Australian agamid (dragon lizard) that also has TSD and for which a large amount of growth and physiological data are available. The earliest studies (from the 1960s) of field growth rates in this species (the ornate dragon, Ctenophorus (=Amphibolorus) ornatus) reported an unusual phenomenon of fast growing and slow growing lizards coexisting in a single population. Fast growers reach sexual maturity (puberty) in less than one year, while slow growers reach puberty after more than three years. Dragons with intermediate growth rates also exist, and in all cases puberty is reached at the same length of 6.8 cm snout-to-vent length. Two PhD theses on the ecophysiology of ornate dragons (by Don Bradshaw and later by his student Peter Baverstock) focused on understanding if the growth morphs differed intrinsically in their physiological traits. The first researcher (Bradshaw) found that fast growers were more cold tolerant but less drought tolerant than slow growers in their first year. Conversely, slow growers were less tolerant of winter frosts, but were tolerant of drought. One explanation was that as the ant-based diet of the dragons becomes sodium-loaded under drought conditions, one morph (slow growers) was better able to tolerate high plasma and tissue sodium than the other. The second researcher identified few differences in the physiological tolerances of the two growth morphs under standard laboratory conditions, but showed that fast growers grew much faster than slow growers when fed identical diets and kept at identical temperatures. The mechanistic basis of this variation in growth rate and reproductive age appears ripe for exploration with DEB theory (the TSD element notwithstanding) but it is difficult to understand how to parameterise a generalised DEB model for this species when growth rates (and consequently age at birth, puberty and death) can be so different, and have not been measured under the ideal conditions of constant temperature and food.

Using DEB to estimate developmental strategies of anuran tadpoles

12.22 Reid Tingley

The goal of my project is to characterise geographic variation in developmental strategies of growling grass frog (*Litoria aurea*) tadpoles in south-eastern Australia. Specifically, this project has the following aims:
1. 	Empirically characterise among-population variation in how tadpoles respond to temperature and hydroperiod;
2. 	Estimate among-population variation in DEB parameters;
3. 	Determine the extent to which we can use DEB theory to predict how a given population of tadpoles allocates energy to growth vs maturity from the microclimates it experiences during development in the wild .

To achieve these aims, I will study 6 populations spanning environmental gradients across the species' range. I will breed adult frogs in captivity shortly after capture, and raise their tadpoles in a 'common garden' design. Each population will be raised at one of three temperatures, and will be allocated to one of two hydroperiod treatments (constant vs declining water level).

I will empirically assess effects of temperature and hydroperiod on metabolic rate, larval period, and growth rate (using length and wet weight). I will then parameterise a standard (?) DEB model for each population, to examine intraspecific variation in DEB parameters (with a particular interest in variation in Kappa).

Examples of questions that I hope to clarify:

(1) 	How would I parameterise a DEB model only for the tadpole stage?
(2) 	Is the isomorphy assumption of the standard DEB model justified across the tadpole stage?
a. 	What about across the entire 'juvenile' stage (i.e., tadpoles + metamorphs)?
(3) 	How do I account for the fact that decreasing water levels might accelerate development?

(4)   How do I best account for accelerated development once tadpoles reach a particular maturity level, if found (e.g., Mueller et al. 2012 allowed κ to decrease at a constant rate after hatching until birth)?

(5)   Which typified DEB model is most appropriate as a starting point, given the considerations above?

(6)   More prosaic; do I include the tail in measures of length over time?

12.23 Salomé Fabri-Ruiz

Correlative species distribution models (SDM) are used in many ecological studies define prioritized places for sustainable management, or evaluate the impact of climate change on species distribution (Elith and Leathwick, 2009). However, many criticisms were produced in the literature about the equilibrium assumption made in correlative SDM, which implies that organisms must be at the equilibrium with their environment.

Such an assumption can be violated when dynamic predictions are modeled, such as range shifts during climate change. Correlative SDM are unable to consider the full range of processes determining species. To go further with my PhD project, my objectives are to take into account biological processes in models and build mechanistic models based on Dynamic Energy Budget (DEB) theories. Mechanistic SDM will give information about physiological constraints that determine the boundaries of species distribution. This approach allows getting a better idea about fitness components like survival, development, growth and reproduction period. This will be applied to two common and closely related echinoid species of the Southern Ocean, Sterechinus diadema and Sterechinus neumayeri, for which correlative SDM have been produced.

Sterechinus neumayeri has been already done for parametrization. For S. diadema I don't have the data to do DEB models now.

12.24 Antonio Giacoletti

The DEB model as a tool to predict the effects of Multiple Stressors on marine environments

My current research is about the effects of Multiple Stressors such as microplastics, oil, acidification, hypoxia and the increasing sea surface temperatures on functional and behavioural traits of marine organisms, through the application of bioenergetic predictive models (DEB models). In our laboratory (EEB Lab) we usually collect physiological rates and behavioural observation on model species at natural condition and under treatments. During my Ph.D. thesis I collected a large series of experimental data, such as respiration rates, thermal tolerances and functional responses of different intertidal and subtidal species. In particular I worked on the mussel Mytilus galloprovincialis, by exposing it to various treatments (pH, oil, hypoxia, different food concentrations). Mytilus is a well parametrized species, so we didn't had problems in simulating the effects of multiple stressors on growth and fecundity of this species. I am also exploring the role of a foundation species, the Mediterranean damselfish Chromis chromis, in providing Ecosystem Services through the potential fertilization of habitats and the trophic by-pass of energy and matter from pelagic to benthic habitats. Although the species was already present in the add-my-pet collection I calculated the specific Arrhenius temperature for the juveniles, and soon I'm going to verify the correspondence with the TA of the adults. I collected also feeding-related (Hmax and Xk) and biometric (shape coefficient) parameters to complete the routine. During this course I want to learn how to implement the existing routine with my collected data, in order to figure out how to carry on the next experiments and simulate the effects of Multiple Stressors on this species, that is the most abundant fish in the Mediterranean basin. I further collected data on the intertidal predator crab Eriphia verrucosa by studying its feeding behaviour and its metabolic response to temperature. The bigger problem is the lack of data that translates in a lack of knowledge about age, weight and length at each morphological stage. My next model species will probably be the purple sea urchin Paracentrotus lividus (Lamarck, 1816).

12.25 Nicolas Djeghri

My pet(s): Zooxanthellate jellyfish (Mastigias papua, Cephea cephea, Linuche unguiculata...)

There is two point I would like to discuss:

First (and I think it is the easiest); How to integrate complex life cycles in DEB modelling? Jellyfish have a rather complex life cycle involving a planctonic medusa phase which reproduce sexually and a benthic polyp phase which reproduce asexually in at least two ways: budding (producing new polyps) and strobilation (producing medusa).

I think one could represent the two phases as distinct DEB individuals. The DEB stages, embryo, juvenile and adult would correspond to planula/bud, young polyp, mature polyp for the polyp phase while they would correspond to strobila, ephyra/young medusa and adult medusa for the medusa phase.

Budding and strobilation could be treated in a similar way foetuses work.

I wonder if it would be necessary to consider the change from ephyra to medusa as a metamorphosis?

Secondly: How to include photosymbiosis? Zooxanthellate jellyfish display a wide variety of relation to their symbionts. For instance, some keep their symbionts all their life, some expell them at some point. It challenges the classical view of photosymbiosis as a mutually beneficial relationship. If jellyfish expell their symbionts in normal conditions (unlike coral bleaching) it could suggest that they are a cost for them. I propose to include costs of the photosymbiosis for the host (such as transport of CO_2 to the symbiont).

13 Funding

14 References

1. van der Meer, J. and S.A.L.M. Kooijman, *Inference on energetics of deep-sea fish that cannot be aged: The case of the hagfish.* Journal of Sea Research, 2014. **94**: p. 138-143.
2. Kooijman, S.A.L.M., *Dynamic Energy Budget Theory for Metabolic Organisation*. 2010: Cambridge.
3. Lavaud, R., *Environmental variability and energetic adaptability of the great scallop, Pecten maximus, facing climate change*. 2014, Vrije Universiteit.
4. Lika, K., et al., *The "covariation method" for estimating the parameters of the standard Dynamic Energy Budget model I: Philosophy and approach.* Journal of Sea Research, 2011. **66**(4): p. 270-277.
5. Lika, K., M.R. Kearney, and S.A.L.M. Kooijman, *The "covariation method" for estimating the parameters of the standard Dynamic Energy Budget model II: Properties and preliminary patterns.* Journal of Sea Research, 2011. **66**(4): p. 278-288.
6. Kooijman, S.A.L.M., et al., *From food-dependent statistics to metabolic parameters, a practical guide to the use of dynamic energy budget theory.* Biol Rev Camb Philos Soc, 2008. **83**(4): p. 533-52.
7. Lika, K., et al., *The bijection from data to parameter space with the standard DEB model quantifies the supply-demand spectrum.* J Theor Biol, 2014. **354**: p. 35-47.
8. Kearney, M., et al., *Modelling the ecological niche from functional traits.* Philosophical Transactions of the Royal Society B: Biological Sciences, 2010. **365**(1557): p. 3469-3483.
9. Kooijman, S.A.L.M. and R. Hengeveld, *The symbiontic nature of metabolic evolution*, in *Current Themes in Theoretical Biology: A Dutch perspective* T.A.C. Reydon and L. Hemerik, Editors. 2005, Springer: Dordrecht. p. 159-202.
10. Kooijman, S.A.L.M. and L.A. Segel, *How growth affects the fate of cellular metabolites.* Bulletin of Mathematical Biology, 2005. **67**(1): p. 57-77.
11. Kooijman, S.A.L.M. and T.A. Troost, *Quantitative steps in the evolution of metabolic organisation as specified by the dynamic energy budget theory.* Biological Reviews, 2007. **83**: p. 1-30.
12. Lika, K. and S.A.L.M. Kooijman, *The comparative topology of energy allocation in budget models.* Journal of Sea Research, 2011. **66**(4): p. 381-391.
13. Kooijman, S.A.L.M., *Metabolic acceleration in animal ontogeny: An evolutionary perspective.* Journal of Sea Research, 2014. **94**: p. 128-137.
14. Kooijman, S.A.L.M., et al., *Scenarios for acceleration in fish development and the role of metamorphosis.* Journal of Sea Research, 2011. **66**(4): p. 419-423.
15. Lika, K., S.A.L.M. Kooijman, and N. Papandroulakis, *Metabolic acceleration in Mediterranean Perciformes.* Journal of Sea Research, 2014. **94**: p. 37-46.
16. Mueller, C.A., et al., *The trade-off between maturation and growth during accelerated development in frogs.* Comp Biochem Physiol A Mol Integr Physiol, 2012. **163**(1): p. 95-102.
17. Martin, B.T., et al., *Dynamic Energy Budget theory meets individual-based modelling: a generic and accessible implementation.* Methods in Ecology and Evolution, 2012. **3**(2): p. 445-449.
18. Martin, B.T., et al., *Predicting Population Dynamics from the Properties of Individuals: A Cross-Level Test of Dynamic Energy Budget Theory.* The American Naturalist, 2013. **181**(4): p. 506-519.
19. Martin, B., et al., *Limitations of extrapolating toxic effects on reproduction to the population level.* Ecological Applications, 2014. **24**(8): p. 1972-1983.

20.   Troost, T.A., B.W. Kooi, and S.A.L.M. Kooijman, *Bifurcation analysis can unify ecological and evolutionary aspects of ecosystems.* Ecological modelling, 2007. **204**: p. 253-268.
21.   Jusup, M., et al., *Physics of metabolic organization.* Physics of Life Reviews.