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Mechanisms behind the metabolic flexibility of an invasive comb jelly

Starrlight Augustine [a,b,c,*], Cornelia Jaspers [a,d], Sebastiaan A.L.M. Kooijman [e], François Carlotti [b,c], Jean-Christophe Poggiale [b,c], Vânia Freitas [f,g], Henk van der Veer [g], Lodewijk van Walraven [g]

[a] *Center for Ocean Life, DTU AQUA, Charlottenlund Castle, 2920 Charlottenlund, Denmark*
[b] *Aix Marseille Université, Mediterranean Institute of Oceanography CNRS/INSU, IRD, UM 110, 13288 Marseille, France*
[c] *Université de Toulon, Mediterranean Institute of Oceanography, CNRS/INSU, IRD, UM 110, 83957 La Garde, France*
[d] *Helmholtz Centre for Ocean Research Kiel, Düsternbrooker Weg 20, 24105 Kiel, Germany*
[e] *Department of Theoretical Biology, Vrije Universiteit, de Boelelaan 1087, 1081 HV Amsterdam, The Netherlands*
[f] *CIMAR/CIIMAR — Centro Interdisciplinar de Investigação Marinha e Ambiental, Universidade do Porto, Rua dos Bragas 289, 4050-123 Porto, Portugal*
[g] *Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg Texel, The Netherlands*

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ABSTRACT

Mnemiopsis leidyi is an invasive comb jelly which has successfully established itself in European seas. The species is known to produce spectacular blooms yet it is holoplanktonic and not much is known about its population dynamics in between. One way to gain insight on how *M. leidyi* might survive between blooms and how it can bloom so fast is to study how the metabolism of this species actually responds to environmental changes in food and temperature over its different life-stages. To this end we combined modelling and data analysis to study the energy budget of *M. leidyi* over its full life-cycle using Dynamic Energy Budget (DEB) theory and literature data.

An analysis of data obtained at temperatures ranging from 8 to 30 °C suggests that the optimum thermal tolerance range of *M. leidyi* is higher than 12 °C. Furthermore *M. leidyi* seems to undergo a so-called metabolic acceleration after hatching. Intriguingly, the onset of the acceleration appears to be delayed and the data do not yet exist which allows determining what actually triggers it. It is hypothesised that this delay confers a lot of metabolic flexibility by controlling generation time.

We compared the DEB model parameters for this species with those of another holoplanktonic gelatinous zooplankton species (*Pelagia noctiluca*). After accounting for differences in water content, the comparison shows just how fundamentally different the two energy allocation strategies are. *P. noctiluca* has an extremely high reserve capacity, low turnover times of reserve compounds and high resistance to shrinking. *M. leidyi* adopts the opposite strategy: it has a low reserve capacity, high turnover rates of reserve compounds and fast shrinking.

1. Introduction

The comb jelly *Mnemiopsis leidyi* (A. Agassiz 1865) is native to the Atlantic coast of the United States of America (USA) and invasive in Europe (Costello et al., 2012). It was first accidentally introduced to the Black Sea in the 1980s from the Gulf of Mexico population. Then it was accidentally introduced to the North Sea from the north-east coast of the USA (Reusch et al., 2010).

At present, this species seems to be well established in European waters and its potential predatory effects on fish recruits and competition with zooplanktivorous fish species are of major concern. Thus there is a continued interest to elucidate its impact on local community structure and functioning. A rather essential problem in this context is to understand and predict size and maturity structure of populations throughout the season because this relates to recruitment dynamics, timing of blooms and strategies to wait out bleak periods.

The first step is to understand individual energy budgets which can later be used for extrapolations to the population level. Reeve et al. (1989) proposed a first carbon budget for this species, but many new datasets have since been acquired. And importantly, more advanced methods exist now to perform mass and energy balancing on different types of field and laboratory data, namely the Dynamic Energy Budget (DEB) theory. In this study we combine modelling and data analysis to study in depth the energy budget of *M. leidyi* over its full life-cycle using the DEB theory and literature data.

The DEB theory is a theoretical framework which specifies metabolic organisation of all living organisms from uni-cellular bacteria to whales. The theory offers a precise formulation of which metabolic processes need to be represented in order to fully quantify the energy/mass

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* Corresponding author at: Center for Ocean Life, DTU AQUA, Charlottenlund Castle, 2920 Charlottenlund, Denmark.

E-mail addresses: staug@aqua.dtu.dk (S. Augustine), coja@aqua.dtu.dk (C. Jaspers), bas.kooijman@vu.nl (S.A.L.M. Kooijman), francois.carlotti@univ-amu.fr (F. Carlotti), jean-christophe.poggiale@univ-amu.fr (J.-C. Poggiale), vania.freitas@nioz.nl (V. Freitas), henk.van.der.veer@nioz.nl (H. van der Veer), lodewijk.van.walraven@nioz.nl (L. van Walraven).

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budget of an animal (Kooijman, 2001; Sousa et al., 2008). The formulation of these processes and how they interact make up the standard DEB model which applies to animals (Kooijman, 2010, 2012). Parameters for this model have been estimated for many different animal species (see e.g. Kooijman and Lika, 2014, for a recent overview). A number of those species seem to accelerate their metabolism after birth (Kooijman, 2014), i.e. they seem to increase metabolic rates in connection with their development. This metabolic, or type $\mathcal{M}$, acceleration is newly introduced to the eco-physiological literature but might well concern a large number of animal species which warrants us mentioning it here.

In this study we estimate a set of DEB model parameters on the basis of available literature data. The data all originate from different geographical locations (US and Europe) and years (1976–2014), were obtained at different temperatures (8–31 °C) and were measured in different ways (different types of weight or length measurements). By comparing the different data to a same reference (DEB model predictions) we provide an overview of this species' energy budget. We further obtain a set of DEB model parameter values based on a sub-set of the data. Last, the new findings are discussed relative to our current understanding of the biology and ecology of *M. leidyi* and compared with that of another gelatinous holoplanktonic species, the purple mauve stinger *Pelagia noctiluca* (Forskål, 1775).

2. Setup of the DEB model

We herein briefly outline the setup of the standard DEB model extended to deal with the type $\mathcal{M}$ metabolic acceleration introduced in the precedent section. The way metabolism is conceptualized according to this model is presented in Fig. 1A. Arrows represent energy fluxes expressed in J d^{-1}. The energy fluxes are functions of the DEB model parameters which are listed in Table 1. The equations are listed in Section A.1, Online Appendix. Boxes represent variables: energy in food E_X (J), energy in faeces E_P (J), energy in reserve E (J), structural volume V (cm^3), cumulated energy invested in maturation E_H (J) and in reproduction E_R (J). The state variables of the individual are E, V, E_H and E_R. The total mass of the individual is the sum of the mass of reserve and of structure respectively. We assume that energy invested into reproduction is immediately released into the environment in the form of gametes and so neglect its potential contribution to the total mass. Furthermore maturity itself has no mass or energy: the investment dissipates into the environment.

The model specifies energy allocation to all of the processes over the full life-cycle as shown in Fig. 1B where we illustrate how important metabolic events are situated along a maturity gradient (thick black line). Maturity is quantified as the cumulated amount of energy in joules invested into the process of maturation. Age zero is defined as the start of development (conception) and, by definition, $E_H = 0$ J. Energy investment into maturation encompasses any expenses linked to tissue differentiation, i.e. re-organisation of body structure from tentaculate to lobate form. This is different from growth which can be conceptualized as synthesis of more of the same.

Energy invested into growth is fixed into the biomass of the organism (with some overheads), but energy invested in maturation is oxidized as metabolic work making it more difficult to quantify in practice. Nonetheless it can be quantified and it can even represent a substantial part of the energy budget (Augustine et al., 2011; Mueller et al., 2012).

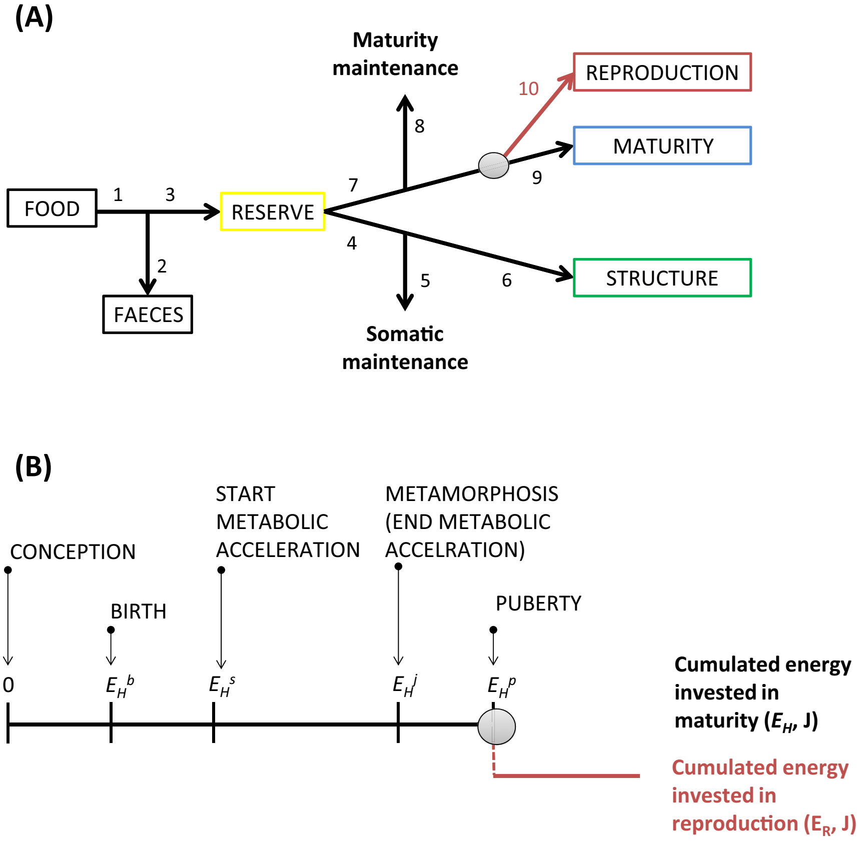

Fig. 1. Full life-cycle DEB model of the invasive comb jelly, *Mnemiopsis leidyi*. (A) DEB model scheme. Boxes: variables; arrows: energy fluxes J d^{-1}. The numbers correspond to equations given in Section A.1, Online Appendix. The state variables are food (E_X, J), faeces (E_P, J), structure (V, cm^3), reserve (E, J), maturity (quantified by the cumulated energy invested in maturation, E_H, J), and investment into reproduction (quantified as cumulated energy invested into reproduction E_R, J). Maturity and somatic maintenance costs are energy sinks. Grey circle: metabolic switch between the processes of maturation and of reproduction. (B) Definition of the different life stages in the DEB model. Between conception ($E_H = 0$) and birth ($E_H = E_H^b$) there is no external assimilation. Assimilation is switched on after birth. After birth at maturity level $E_H = E_H^s$ the organism starts metabolic acceleration which ends at metamorphosis ($E_H = E_H^j$). After puberty ($E_H = E_H^p$), i.e. the lobate adult stage, allocation towards maturation stops and allocation towards reproduction starts.