



Near-future ocean acidification impacts maintenance costs in sea-urchin larvae: Identification of stress factors and tipping points using a DEB modelling approach



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ABSTRACT

Ocean acidification (OA) affects the life-history traits of marine invertebrates. To understand the effects of OA on the life cycle, and to assess its ecological consequences, it is essential to look at bioenergetics. Dynamic Energy Budget (DEB) models are particularly useful to quantitatively assess the effects of (multiple) stressors on all life-history traits in an integrated manner. Here, we apply a simplified DEB model (DEBkiss) to previously published data on growth, feeding and respiration of larval green sea urchins (*Strongylocentrotus droebachiensis*), exposed to a range of pH values. Overall, the standard DEBkiss model provides a good explanation of the larval traits over its development from egg to the maximum larval body size. The observed effects of OA were best explained by the hypothesis that OA increases the maintenance costs of the larvae. This increase in maintenance is reflected in a slower development and increased respiration, but has no negative effects on feeding (when comparing animals of similar body sizes). However, it appears that older larvae are able to compensate to some extent for these increased costs by increased feeding and/or decreasing their maintenance rates. The stress factor on energetic processes (such as maintenance costs) is a useful measure of stress that aids the comparison of species, life stages and stressors, and also allows for multi-stress analyses. Interestingly, the stress factor for OA shows an apparent tipping point around a pH of 7.5, which corresponds to the extreme of the present-day natural variability. This result offers an interesting perspective on the potential relationship between natural variability in pH and species sensitivity to OA.

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1. Introduction

Since the beginning of the industrial revolution, atmospheric CO₂ concentrations have increased from 280 to 400 ppm and are expected to double by 2100, with well-described consequences for the climate (global warming, increase in extreme events frequency, etc.). The ocean represents a major sink for CO₂ and absorbs half of the excess of this gas. Continued uptake of CO₂ alters the carbonate chemistry of the ocean and increases the concentration of hydrogen ions, thereby reducing pH, a phenomenon called ocean acidification (Caldeira and Wickett, 2003). A growing body of evidence demonstrates that this ocean acidification can impact survival, growth, development and physiology in marine invertebrates (e.g., Wittmann and Pörtner, 2013). Building upon the large body of existing literature, the field of ocean acidification is now moving forward. It was argued that any large scale projection of future impacts requires understanding of the mechanisms

in action, how they are intertwined across levels of biological organization (molecular, cellular, systemic, ecosystem, all as a result of evolution), and their potential hierarchies (Dupont and Pörtner, 2013). To increase our predictive power, a mechanistic understanding of the physiological response of organisms exposed to ocean acidification is required (see e.g., Woodin et al., 2013).

Sea urchin larvae are excellent candidates to mechanistically investigate the physiological response to ocean acidification. Sea urchin development has been studied for over a century, and the complex nets of intercellular communications leading to each temporal developmental event and stage are well known. They are also sensitive, simple, and reliable tools for assessing and monitoring marine pollution (e.g., Shaw et al., 2009). Sea urchins were identified early on as a primary target for ocean acidification research, and are today one of the most studied models in this field (Dupont and Thorndyke, 2014). The green sea urchin (*Strongylocentrotus droebachiensis*) is a particularly popular test species; it is widely distributed and plays a key ecological and economical role in boreal coastal ecosystems. When exposed to ocean acidification, the planktotrophic pluteus larvae of the green sea urchin showed a high level of plasticity. Development of normal, although showing

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morphological plasticity, swimming larvae was possible as low as $\text{pH}_T \geq 7.0$. Within that range, decreasing pH increased mortality and asymmetry, and decreased growth rate. Respiration rates increased with decreasing pH suggesting changes in the energy budget. At the lowest pHs ($\text{pH}_T \leq 6.5$), development was arrested and no larva survived past 13 days post fertilisation (Dorey et al., 2013). Physiological studies revealed that pluteus larvae are unable to compensate for an extracellular acidosis (pHe) resulting from an exposure to ocean acidification. However, the calcifying primary mesenchyme cells are able to fully compensate an induced intracellular acidosis (pHi) using a bicarbonate buffer mechanism involving secondary active Na^+ -dependent membrane transport proteins (Stumpp et al., 2012). Additional energetic costs also derived from compensatory mechanisms associated with larval gastric pH changes (Stumpp et al., 2013). It was hypothesized that the associated cost of pHi regulation leads to a shift in energy budget, with less energy available for growth (Dupont and Thorndyke, 2014; Stumpp et al., 2011).

To quantitatively test this hypothesis, and to assess its ecological consequences, it is essential to look at all life-history traits of the sea-urchin larvae over its development in an integrated analysis. Dynamic Energy Budget (DEB) models are particularly useful for such quantitative assessments. DEB theory is one of the most comprehensive framework for bioenergetics (Kooijman, 2001; Nisbet et al., 2000), and models based on this theory have been extensively applied to understand the effects of chemical stress (see Jager and Zimmer, 2012; Jager et al., 2006) and environmental factors such as food and temperature (e.g., Freitas et al., 2009), including the ecological consequences of climate change (e.g., Teal et al., 2012). Recently, Muller and Nisbet (2014) presented a DEB model for the effects of ocean acidification on calcifying phytoplankton (coccolithophores). Here, we apply the simplified DEB-based model DEBkiss (Jager et al., 2013) to previously published data on the effects of ocean acidification on growth, feeding and respiration in sea-urchin larvae.

2. Materials and methods

2.1. Experimental data

Data were taken from the studies published in Dorey et al. (2013); Stumpp et al. (2013) and Chan et al. (2015), which used the same methodologies. Briefly, adult urchins were spawned and gametes fertilized. Embryos were then cultured in replicated 5 L culture vessels at a density of 10 embryos per mL. When reaching the pluteus stage, larvae were fed daily with algae (*Rhodomonas* sp.) at a constant concentration of $150 \mu\text{g C L}^{-1}$. Larval cultures were monitored regularly over several weeks. On each observation day, a subsample of > 10 larvae was taken, photographed with a digital camera mounted on a dissecting microscope, and body length (BL in μm) was determined. Larvae were cultured in pH_T ranging between 6.98 and 8.06 at 9°C . Data on respiration rates were extracted from Dorey et al. (2013), and data on feeding rates from Stumpp et al. (2013).

2.2. Basic model

We depart from the DEBkiss model, as presented in detail in Jager et al. (2013), and see supporting information. This model is a simplification of the standard DEB animal model (Sousa et al., 2010). The main difference with the standard model is that DEBkiss lacks a reserve compartment, which implies that energy assimilated from food is used directly for the energy-requiring processes (growth, maintenance, etc.) without buffering by a reserve. Storage of energy can be included in the form of a reproduction buffer; in the case of sea urchins, the gonads in adults are a typical example of such a reproduction buffer with a dual purpose of collecting energy for spawning events and energy storage to survive periods of food limitation (Russell, 1998). The DEBkiss model specifies growth, reproduction, feeding, and respiration. As we focus on larvae in this

study, the storage in the gonads and reproduction will not be discussed here. The energy flows in an individual embryo/larva are schematically shown in Fig. 1.

In a constant environment, the DEBkiss model for structural growth reduces to the von Bertalanffy curve. For any well-chosen measure of physical length (L_w , e.g., total body length or test diameter), the differential equation for growth is specified by:

$$\frac{d}{dt}L_w = r_B(fL_{wm} - L_w) \text{ with } L_w(0) = L_{w0} \quad (1)$$

where r_B is the von Bertalanffy growth rate constant (d^{-1}), L_{wm} is the maximum physical length (mm), L_{w0} the initial length, and f is the scaled functional response (dimensionless; $f = 1$ marks *ad libitum* feeding conditions, and $f = 0$ complete starvation). This equation can be used as long as there are no large changes in body shape with ontogeny, otherwise, a correction is needed (Jager et al., 2015, and see supp. info.). Eq. (1) can be solved to an explicit expression for body length as function of time, as long as all parameters are constant:

$$L_w = fL_{wm} - (fL_{wm} - L_{w0})e^{-r_B t}. \quad (2)$$

Within a DEB context, the model parameters r_B and L_{wm} relate to underlying primary parameters of the energy budget (see supp. info.). In DEBkiss (Jager et al., 2013), r_B is related to the volume-specific costs for maintenance (J_M^v in $\text{mg}/\text{mm}^3/\text{d}$) as follows:

$$r_B = \frac{y_{VA}}{3d_V} J_M^v \quad (3)$$

where y_{VA} is the yield of structural biomass on assimilated biomass from food ($\text{mg dwt}/\text{mg dwt}$), and d_V is the dry-matter density of structural biomass ($\text{mg dwt}/\text{mm}^3$). Both these parameters are expected to remain constant with ontogeny, and defaults are often used in practice.

The maximum length (L_{wm}) is determined by the volume-specific maintenance costs (J_M^v), but also by the maximum area-specific assimilation rate (J_{Am}^a in $\text{mg}/\text{mm}^2/\text{d}$), and the fraction of the assimilated mass that is allocated towards maintenance and growth (κ , dimensionless, see Fig. 1):

$$L_{wm} = \frac{\kappa}{\delta_M} \frac{J_{Am}^a}{J_M^v}. \quad (4)$$

The shape coefficient δ_M (dimensionless) translates the length measure that was used (e.g., total body length) to volumetric length (the cubic root of biomass volume).

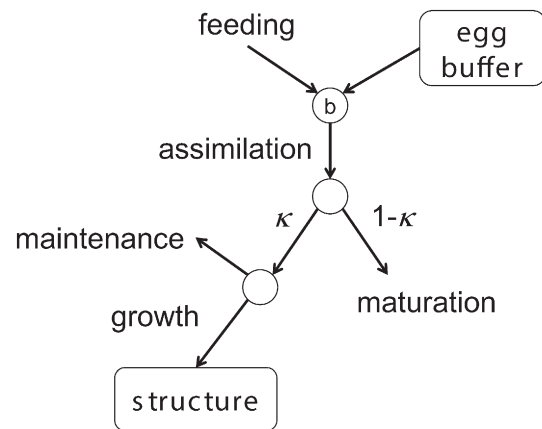


Fig. 1. Schematic representation of the energy flows in embryos and larvae. The node b marks 'birth', i.e., the start of external feeding. A constant fraction κ of the assimilation flux is allocated to maintenance and structural growth, where maintenance costs have to be paid first. The $1-\kappa$ flux is assumed to dissipate in the maturation process.

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