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Qualitative use of Dynamic Energy Budget theory in ecotoxicology Case study on oil contamination and Arctic copepods

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ABSTRACT

The Dynamic Energy Budget (DEB) theory provides a logic and consistent framework to evaluate ecotoxicological test results. Currently this framework is not regularly applied in ecotoxicology given perceived complexity and data needs. However, even in the case of low data availability the DEB theory is already useful. In this paper we apply the DEB theory to evaluate the results in three previously published papers on the effects of PAHs on Arctic copepods. Since these results do not allow for a quantitative application we used DEB qualitatively. The ecotoxicological results were thereby set in a wider ecological context and we found a logical explanation for an unexpected decline in hatching success described in one of these papers. Moreover, the DEB evaluation helped to derive relevant ecological questions that can guide future experimental work on this subject.

1. Introduction

Reliable and replicable test results are important for management in risk evaluation of toxic substances and therefore follow guidelines like those set by the OECD (1984). These experiments are generally conducted with homogeneous cohorts of test organisms from a single life stage (usually adults), on which a single vital rate (e.g. survival, reproduction) is tested under standardized laboratory conditions for a relative short duration as seen from the perspective of the longevity of most tested species. Since risk evaluation of toxic substances is at the population level, an extrapolation method is needed that can be used to infer the population consequences of the test results on individuals, and that integrates the effects on different single vital rates to summarize the overall population impact. For such an extrapolation and integration the Dynamic Energy Budget (DEB) theory can be used (Jager and Klok, 2010). This theory developed by Kooijman (2010) is based on the principle that mass and energy are conservative quantities (one of the few hard laws available in biology), energy conversion process leads to dissipation, and mass and energy transport occur across surfaces. The DEB theory is developed as a non-species-specific metabolic theory that allows species differences to be reduced to differences in the set of parameter values (Sousa et al., 2008). The DEB theory has been tested for many species and deviations are rare (Kooijman, 2010). Test results on different vital rates such as survival, reproduction and growth can be interpreted by DEB as a change in the energy flow within the organism, and DEB gives mechanistic insight in how a change in growth infers a change in reproduction, treating these as dependent (Klok, 2007). Furthermore, the mechanistic insight makes it possible to extrapolate results beyond the range of tested conditions (Jager and Klok, 2010), and include effects of other factors such as temperature (Álvarez et al., 2006), food conditions (Jager et al., 2004; Klok, 2008), and mixtures of toxicants (Jager et al., 2010).

Application of DEB in toxicology started with the seminal paper of Kooijman and Metz (1984), followed by a simplified version of DEB named DEBTox to analyse standard toxicity tests (Kooijman and Bedaux, 1996a,b). The last was recently updated and improved by Jager and Zimmer (2012). More comprehensive models, such as DEB3 (Jager and Klok, 2010) that are fully consistent and have a superior explanatory value, do not always perform better than the simplified model given available experimental data (Jager and Klok, 2010).

If experimental data do not allow a quantitative evaluation with DEB the mechanistic philosophy of DEB still can be helpful to scrutinise the results of experiments. In this paper we extend the use of DEB in ecotoxicology by using its concept to evaluate test results qualitatively. Given the mechanistic philosophy of DEB such an evaluation can identify relations resulting in logic explanations for test results not delved into by standard reporting of ecotoxicological tests. Moreover, such an evaluation can result in new ecologically more relevant research questions. Here we give an example from studies on impacts of oil components like polycyclic aromatic hydrocarbons (PAHs) on Arctic copepods.

1.1. Case study

Global warming is expected to result in thinning and earlier retreat of sea ice, greatly facilitating shipment and mining of minerals,

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gas and oil in the Arctic. These activities will increase the risk of environmental disasters like oil spills and wide-spread contamination which may have profound impacts on the Arctic food chain.

The Arctic marine food chain is fuelled by a short summer pelagic algal bloom which is grazed by zooplankton, mainly *Calanus* spp. like *Calanus glacialis* and *Calanus finmarchicus*. These species play a key role in the food chain as they are fed upon by fish, seabirds and whales. *Calanus* spp. have a complex life cycle; they spend a limited time in surface waters, during the algal bloom where they feed and conserve energy in oil sacs, mainly wax esters (Sargent and Falk-Petersen, 1988). Afterwards they migrate to deep water to overwinter in a dormant phase, respiration rates are 20–50% lower compared to spring (Ingvarsdóttir et al., 1999), and surface the next spring to reproduce. Lipid rich reserves may fuel reproduction before the spring bloom (Niehoff et al., 2002) and sustain the organism in periods of food shortage (Falk-Petersen et al., 2009). Timing of the upward migration of adults is important such that the peak in their offspring coincides with the pelagic algal bloom.

Toxicants like oil components can impact *Calanus* spp. abundance not only by reducing survival and reproduction but also by delaying development which may have a dramatic impact on the timing of surfacing in adults. Polycyclic aromatic hydrocarbons enter marine ecosystems (Dachs et al., 1996) and are considered the most toxic oil components (Hylland, 2006). Experiments with PAHs on *C. glacialis* and *C. finmarchicus* have been conducted under different temperatures and food conditions (Hjorth and Nielsen, 2011; Jensen and Carroll, 2010; Jensen et al., 2008). The general understanding of these experiments is that *C. finmarchicus* is more sensitive to oil pollution than *C. glacialis*. The studies, however, were relatively short term (less than two weeks for species with a longevity of one year and longer) and focus on effects during the reproductive stage of the life cycle only. These data therefore do not allow a quantitative evaluation with DEB. In this paper we review the results of these experiments and assess their possible ecological consequences using the DEB theory qualitatively.

2. Methods

2.1. Introduction to the use of DEB in ecotoxicology

Dynamic Energy Budget theory describes the energy pathways in individuals (Fig. 1). When food is assimilated, energy is first transported to a reserve compartment. These reserves introduce metabolic memory and can explain many biological phenomena such as reproduction taking place during starvation (Sousa et al., 2008). From the reserves, energy is allocated in a fixed ratio to maintenance and growth of structural elements and investment in reproduction. Maintenance of structural elements always takes precedence over growth, likewise for maturity maintenance.

According to the DEB theory, allocation to reproduction depends on reserves, which depends on feeding rate, which depends on body size, which in turn depends on growth. The law of conservation for energy implies that toxicants that reduce assimilation (process of feeding and digestion) (1 in Fig. 1), or maintenance costs (2 in Fig. 1), or growth costs (3 in Fig. 1), therefore have an indirect effect on reproduction. Toxicants can also have a direct effect on reproduction by an increase in the costs to produce eggs (4 in Fig. 1), and by affecting the survival of eggs (5 in Fig. 1).

2.2. General description of the life-history of C. finmarchicus and C. glacialis

The distribution range of *C. glacialis* is confined to the Arctic waters, whereas *C. finmarchicus* distribution ranges from temperate to Artic, and is more abundant in the Atlantic Waters of the Norwegian and Barents Sea, than in their Arctic waters (Loeng and Drinkwater, 2007). Both *C. glacialis* and *C. finmarchicus* reproduce during the late spring and early summer pelagic phytoplankton bloom. *C. glacialis* has a one to three-year life cycle (Arnkværn et al., 2005; Conover, 1988; Scott et al., 2000) and overwinters in deep waters as copepodite stage III (CIII), CIV or CV in its first year of life, and as CV its second (Hirche, 1991). In the Arctic *C. finmarchicus* has an annual life cycle and overwinters as CV in deep waters up to 500 m (Hirche, 1996). Timing of surfacing and descent is very important in these species. The timing of surfacing is important such that the feeding stages of the offspring coincide with the peak in the pelagic algal bloom (Madsen et al., 2001), and the timing of descent to diapause depth must be before the onset of the winter convective mixed layer (CML) to conserve energy (Irigoien, 2004). Copepods can overwinter, and may survive to the next spring above this layer where they are regularly transported to the surface (Hirche et al., 2001; Irigoien, 2004). They, however, generally have lower lipid levels (Jónasdóttir, 1999; Leu et al., 2011; Miller et al., 2000; Søreide et al., 2010) and with less reserves available maturation is retarded and production of offspring is reduced (Hirche et al., 2001; Irigoien, 2004).

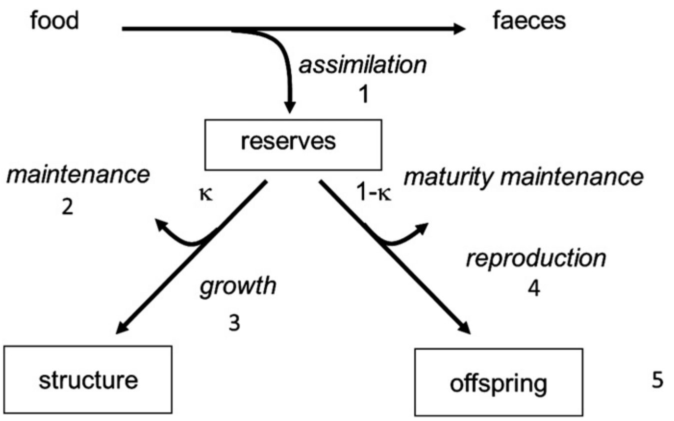

Fig. 1. Schematic representation of the Dynamic Energy Budget model after (Kooijman, 2010). Assimilated food is transferred to the reserves and divided over two fractions; κ into somatic growth and maintenance and 1-κ to reproduction. Numbers indicate where the energy allocation may influence by toxicants.

Reproduction in *C. glacialis* starts earlier than in *C. finmarchicus* (Madsen et al., 2008). The first relies on lipid rich reserves and ice algae, which develop before the phytoplankton bloom, to fuel reproduction and the peak in offspring nauplii can coincide with the phytoplankton bloom. *C. glacialis* can even spawn using only their reserves (Hirche and Kattner, 1993), but with algal food, egg production is higher (Hirche, 1989). *C. finmarchicus* adults on the other hand need the algal bloom to fuel reproduction. Egg production is therefore highly dependent on the phytoplankton concentration (Madsen et al., 2001; Niehoff et al., 2002).

Development by moulting to the next stage in copepods is weight dependent and moulting only takes place if a critical structural weight, life weight minus reserves, has been reached (Carlotti et al., 1993).

2.3. Description of ecotoxicological tests on oil components under Arctic conditions on C. finmarchicus and C. glacialis

Jensen et al. (2008) tested the PAH pyrene in five concentrations increasing in order of magnitude (0.01, 0.1 … 100 nM) on adult females of *C. finmarchicus* and *C. glacialis* collected in the field. Grazing (measured by the proxi faecal pellet production) and egg production of exposed *C. glacialis* and *C. finmarchicus* females were measured daily over a period of 9 days. Hatching success (the percentage hatched in 4 days) of eggs produced by mothers kept under abundant food exposed over a period of 3, 6 or 9 days was also assessed. Experiments were conducted at 0 °C, under starvation and abundant food. Pyrene significantly reduced