Towards an adaptive model for simulating growth of marine mesozooplankton: A macromolecular perspective

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ABSTRACT

Ultimately, the structure and functioning of marine ecosystems is defined by the transfer of autotrophic production to higher trophic levels and selective consumption of these autotrophs by predators. Hence, feeding regulation via modification of grazing and food incorporation by predators is critical for understanding and predicting the dynamics of ecosystems. In marine ecosystem and biogeochemical models, feeding regulation by consumers is assumed to be mainly dictated by food quality (Q), which is determined using food quality modules (FQMs) that mimic a consumers' ability to anticipate fitness consequences for feeding on specific prey items. Current FQMs are based on frameworks that *a priori* identify specific food components, usually nitrogen (N), and/or phosphorus, as limiting. This negates the importance of consumer physiology, and ignores biochemical constrains on the limiting role of chemical elements in animal production. To help address these problems, we propose a new adaptive approach that bases Q on consumers' capacity for food uptake and metabolic physiology. Uniquely, it (i) has separate pathways for the utilisation of carbon (C) associated with proteins, lipids and carbohydrates, (ii) considers stage-specific structural biochemical requirement of animals, and (iii) does not treat consumers' structural demand for carbon as a "unitary requirement" but discriminates among the required biochemical forms of carbon. The approach is applicable to all heterotrophs. In the example given here the model has been configured to represent the calanoid copepod *Acartia tonsa*. Consistent with experimental observation, but unlike previous models, our model predicts the relationship between Q and food C:N to be unimodal with a maximum Q only at the threshold C:N for biomass production. Results suggest that prey C:N ratios may be irrelevant for food quality due to macromolecular biochemical constrains on the utilisation of chemical elements. This result emphasizes the importance of biochemical substances in animal nutrition and production as well as the necessity of developing food quality models able to adapt to the biochemical needs of the consumer.

1. Introduction

Mesozooplankton require a number of different nutrients simultaneously at varying optimal levels for their metabolic growth. However, the nutrient composition of the available food items can vary substantially between the different prey species and also within a single prey species (Thompson et al., 1992; Dunstan et al., 1993; Søreide et al., 2010). In order to compensate for the lack of sufficient nutrients in a specific prey type, animals demonstrate varying feeding regulation mechanisms in order to satisfy their demands for energy and chemical substances (Illius et al., 2002; Mitra and Flynn, 2005). This involves behavioural and/or physiological adjustments to prey biochemical composition, and occurs before, during and/or after food ingestion by consumers. For example, even in simple systems where there may be single prey species the functional feeding response of the consumer has been shown to be variable (Houde and Roman, 1987; Tirelli and Mayzaud, 2005). Thus, animals can and do ingest high quantities of nutritionally poor diets (Cruz-Rivera and Hay, 2000; Mitra and Flynn, 2007) and/or differentially assimilate prey constituents (Logan et al., 2004; Mitra and Flynn, 2007) in order to obtain the required balance of nutrients for optimal growth. Such an acclimation via modification of feeding and incorporation by consumers would thereby influence food web structures (Kondoh, 2003) and contribute to the complexity of ecological communities (Levin, 2005). Furthermore, adaptive changes in behaviour would determine the fate as well as the ecological transfer efficiency of biomass (carbon) within foodwebs.

Acclimative behaviour is typically ignored or poorly represented in aquatic ecosystem models in part because a realistic framework, for addressing feeding behaviour, is lacking (Raubenheimer et al., 2009). Models for investigating aquatic ecosystems incorporate feeding acclimatization by employing parameters that optimize trade-off between feeding behaviour and the fitness (e.g. growth, reproductive success) of individual organisms (e.g. Taghon, 1981; Merico et al., 2009). Such parameters are usually built into functions which could collectively be referred to as food quality modules (FQMs) that mimic consumers' "internal mechanism for anticipating" (sensu Holland, 1998) the fitness consequences for feeding on specific prey items. This information is then employed as the basis for modelling species interactions, total food intake, how intake is derived from various resources, etc. Although the approach is heuristically important (Mitra and Flynn, 2005, 2007), a framework for food quality that is capable of providing a general, mechanistic understanding of prey nutritional value is lacking (John et al., 2010).

The emergence of ecological stoichiometry, as the 'biology of elements' (Sterner and Elser, 2002) has brought to the attention of many scientists the importance of the balance of chemical elements within organisms and their environment (Reiners, 1986; Elser, 2006). Stoichiometry refers to ratios of chemicals in reactions. In biology and ecology it is, if only for simplicity, usually related to elements. Thus, with the exception of very few examples (e.g. Anderson and Pond, 2000), elements are the preferred nutritional currencies in models for studying aquatic systems (Loladze et al., 2004; Andersen et al., 2004a; Darchambeau, 2005). Such models typically divide the chemical constituents of both prey and predators into two major categories: C (for both structure and energy) and a nutrient 'X' (where X is mostly nitrogen, and/or phosphorus). They then employ a variant of Eq. (1) as the base parameter for food quality.

$$Q = \min\left(\frac{\beta_{CX}}{\alpha_{CX}}, 1\right) \qquad (1)$$

where β_{CX} and α_{CX} are predator and prey C:X ratios, respectively. Other food component, such as toxins and structure are typically not represented within food quality modules. Rather, they are coded as separate constraints within which a consumer has to work in order to achieve its required nutrition.

While the merits for emphasizing elements are widely recognized, the conceptual assumptions for this approach to determining prey nutritional value are subject to vigorous debate. Tang and Dam (1999), for example, argued that the emphasis on elements glosses over the fact that most animals depend on complex organic molecules for nutrition. Thus, food quality predictions based on C:X ratios may be reliable only when elemental composition approximates the bio-molecular composition of organisms. In some cases such correlations exist. For example, nitrogen has been successfully used in many studies as a proxy for protein content of organisms (Kuijper et al., 2004). However in other contexts, elements may not be appropriate proxies for bio-molecules as functionally distinct molecular complexes can contain similar elements. Phosphorus for instance occurs both in phospholipids that have mainly structural roles in organisms, and in nucleic acid structures (DNA, RNA, ATP) that serves as a carrier of energy and information. The form of C in protein and polysaccharide is also a clear example. Boersma and Elser (2006) further suggested that the simple stoichiometric approach to determining prey nutritional value (implicitly) assumes that a prey containing more X is better (or at least never worse) for the fitness of consumers. This is not supported by experimental observation. There are for instance several observations of growth reduction in animals such as Acartia tonsa (Augustin and Boersma, 2006), Daphnia magna (DeMott et al., 1998)

and Penaeus monodon (Plath and Boersma, 2001) that feed on relatively X-rich diets. Similarly, animals grow poorly when they feed on diet containing excess C (Checkley, 1980; Kiørboe, 1989; DeMott et al., 1998). A more holistic food quality model, capable of capturing the cost for the consumption of excesses nutrients (not C), is therefore a major challenge of aquatic ecosystem model parameterisation (John et al., 2010).

Finally, Eq. (1) negates the importance of consumers' physiology in relation to food quality, as it does not consider consumers' physiological capabilities. Contrary, results from both modelling (Anderson and Hessen, 2005) and experimental studies (McGoogan and Gatlin, 1999) suggest that the nutritional value of prey items may be contingent on consumers' maximum capacity for food ingestion and assimilation as well as physiology. For example, many animals show plasticity in their preference for respiratory substrates, thus allowing preferential catabolism of only food components that occur in excess of their structural requirements. This enables animals to spare limiting substances for vital life processes such as growth and reproduction (McGoogan and Gatlin, 1999; Arnould et al., 2001). Consequently, consumers can maximize the usefulness of prey organisms by catabolising only excess substances. However, the stoichiometric approach to evaluating prey organisms ignores the gain(s) consumers might derive from substances supplied in excess of consumers' structural requirements. Hence, the biological foundation of this approach to modelling food quality needs to be modified to reflect these rather critical issues.

To help address these problems, we propose a new model that extents the concept of food quality a step further, to include consumers' maximum capacity for food uptake as well as plastic preference for respiratory substrates. The basis for the model is the food quality model of Anderson et al. (2005). However, we distinguish between stage-specific structural biochemical requirements of consumers. This is in keeping with experimental data demonstrating that structural biochemical requirement of zooplankton varies with their stage of development (Evjemo et al., 2003; Brucet et al., 2005). We also do not treat consumers' structural demand for carbon as a "unitary requirement" but discriminate among the needed biochemical forms of carbon. As a result, the respiratory physiology of our model consumer is not dependent on fixed substrates. Rather, substances are respiration based on the balance between their availability and the requirements (both energy and structural) of consumers. This is in keeping with findings demonstrating that zooplankton exhibit plastic preference for respiratory substrate (Roman, 1983; Anderson, 1992). In addition, the utilisation of chemical elements in our model follows three different macromolecular pathways, i.e. protein, lipid and carbohydrate utilisation pathways. Consequently, chemical elements impact the fitness of our model consumer via the different compound utilisation pathways, and not on the basis of elemental ratios as in simple stoichiometric models. Using net efficiency at which a prey biomass is converted into that of a consumer as the yardstick for food quality, we have currently configured the model to represent the calanoid copepod Acartia tonsa, and the results discussed in context of biochemical constrains on food quality.

2. Model description

2.1. Overview

Animals require diverse chemical substances (e.g. cholesterol, polyunsaturated fatty acids, amino acids, etc.) for survival and successful reproduction. However here, all substances are assumed to belong to one of three major macromolecules: proteins, lipids and carbohydrates. This ensures a simple model structure by decreasing the number of molecules that would otherwise be needed, and