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A model for the description of feeding regulation by mesozooplankton under different conditions of temperature and prey nutritional status

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Abstract:

Ecosystem modelling studies that consider mesozooplankton feeding regulation have primarily focused on the impact of prey nutritional status and temperature separately, despite experimental evidence for strong links between these two factors. Here, we propose a method based on optimal feeding behaviour of individual mesozooplankton that can be used to derive acclimative food ingestion, assimilation, and respiration under different temperature and food conditions. In the model, animals first evaluate the nutritional value of prey organisms based on their temperature-specific demand for energy and structural biochemical substances. They then regulate their feeding behaviour as well as metabolic physiology in order to satisfy their specific biochemical requirements for maintenance and growth. The approach is applicable to all heterotrophic plankton. In the example presented here the model has been configured to simulate egg production by the calanoid copepod *Acartia tonsa*. The model realistically reproduces the observed rates for egg production, as well as carbon (C) and nitrogen (N) gross growth efficiencies of egg production by *Acartia* in response to changes in both algal C:N-ratio and temperature. Results suggest that enhanced temperature accelerates respiratory consumption of the N assimilated by mesozooplankton, and thus decreases the rates for reproduction at higher temperatures. They also show that the optimum temperature for maximum egg production increases with algal C:N-ratio. These findings support and extend conclusions previously obtained for mesozooplankton and indicate that ocean warming could alter the role of *Acartia spp.* in planktonic food webs.

Highlights

► An adaptive model for temperature dependence of zooplankton growth is proposed. ► Rates and gross efficiencies for *Acartia* reproduction are realistically predicted. ► Results show warming accelerates respiratory consumption of assimilated nitrogen. ► They show that optimum temperature for egg production increases with algal C:N.

Keywords: Temperature ; Algal C:N-ratio ; Mesozooplankton ; Feeding regulation ; Respiration ; Egg production

1. Introduction

Temperature and prey nutritional status are perhaps the most important variables that affect the performance of mesozooplankton. Virtually all aspects of mesozooplankton physiology, including grazing (Kiørboe et al., 1982 and Houde and Roman, 1987), respiration (Ikeda, 1985 and Thor et al., 2002), timing of reproduction and ontogenic development (Dell et al., 2011), are impacted by ambient prey nutritional status and temperature.

Not surprisingly, mesozooplankton have evolved a range of acclimative strategies for dealing with sub-optimal temperature and food conditions. Physiological response to prey nutritional status by mesozooplankton has been reviewed by Mitra and Flynn (2005). This review highlighted that mesozooplankton can preferentially ingest nutrient-rich food or modify grazing rate to optimize nutrient intake for growth and other vital life processes (Houde and Roman, 1987). Furthermore, they can adjust their metabolism to some extent to compensate for insufficient nutrient supply (cf. Roman, 1983 and Anderson, 1992). Similarly, there is also a large body of evidence to show that ectothermic organisms, such as mesozooplankton, can respond to changes in temperature in several ways. Hertz (1981) characterized these responses by the time-scale over which they enable organisms to cope with variation in environmental temperature. At the most rapid extreme, an individual may use behaviour (e.g., alter food ingestion), physiology (e.g., modify tissue metabolism), or both to regulate the effect of sub-optimal temperature conditions (see reviews by Angilletta et al., 2002 and Lagerpetz and Vainio, 2006). Acclimative shifts in the physiological behaviour of mesozooplankton can also occur over longer time scales. For example, within the lifetime of an individual, acclimative response to temperature variability may involve the expression of allozymes (Somero et al., 1996), modifications of cell membranes (Farkas, 1979 and Hasset and Crockett, 2009), or alterations of the intracellular environment that may or may not be reversible (Somero et al., 1996).

However, the physiological controls for dealing with sub-optimal conditions of food and temperature may not be mutually exclusive (cf. Clarke, 1993). This is because in the pelagic environment, variations in temperature and nutrient supply for mesozooplankton production are often linked. For example, during winter and early spring, small diatoms and cryptophytes, which are known to be rich in essential nutrients for mesozooplankton production (Ahlgren et al., 1990 and Mayzaud et al., 1989), usually dominate the composition of phytoplankton in temperate seas (Ahlgren et al., 1990, Reid et al., 1990 and Marshall and Nesius, 1996). In contrast, prymnesiophytes and cyanobacteria, that are generally poorer in nutrition, dominate the phytoplankton composition in summer (Malin et al., 1993). Thus, depending on the season, mesozooplankton may be confronted with low concentrations of nutrient-rich food or, conversely, with a large quantity of potentially unfavourable food. Furthermore, short-term changes in ambient temperature may alter the biochemical composition of microalgae (Thompson et al., 1992 and Maazouzi et al., 2008), which could potentially impact mesozooplankton growth and reproduction.

The combined effect of temperature and food is, however, ignored or poorly represented in ecosystem models. Existing mesozooplankton feeding models primarily consider the impact of prey nutritional status when determining the regulation of food ingestion, assimilation and metabolism (e.g., Kuijper et al., 2004 and Mitra, 2006). Typically in these models, temperature effects on biological processes are not considered explicitly, if at all. Conversely, models that consider the effect of temperature typically describe biological rates by using an Arrhenius function, whose shape is controlled by the Boltzmann factor, $\exp^{-\partial/\kappa T}$, where T is temperature, ∂ is activation energy of metabolism and k is Boltzmann's constant. Some studies use the Arrhenius equation without modification (Savage et al., 2004), while others modify the equation to allow for thermal denaturation of rate-limiting enzymes (Schoolfield et al., 1981) as well as allometric constraints on the biological rates (Brown et al., 2004). These models however provide no opportunity or mechanism for acclimation (for a more complete discussion on this problem, see Clarke, 2004 and O'Connor et al., 2007). We consider this an important limitation that could hinder the ability of ecosystem models to reflect possible changes in mesozooplankton dynamics under future global climate change.

Considering that thermal sensitivity is variable, and not fixed as in current models, we propose a method based on optimal behaviour of heterotrophic plankton that can be used to derive, for example, acclimative food ingestion, assimilation, and respiration under different temperature and food conditions. In our model,

temperature impacts physiological rates through its effect on the energetic cost of metabolism (cf. Clarke and Fraser, 2004), while prey nutritional status serves as a separate constraint on thermal acclimation by mesozooplankton at the level of food ingestion, assimilation and respiration. This method provides a simple physiologically based approach to incorporate some aspects of physiological plasticity into existing marine ecosystem models. Here, the model has been configured to simulate egg production by the calanoid copepod *Acartia tonsa* a key copepod species in many coastal ecosystems under variable food C:N-ratio and temperature conditions. We discuss our results in the context of previous findings and present possible consequences for the pelagic ecosystem under global warming.

2. Model description

2.1. Overview

The method we suggest is shown schematically in Fig. 1. Mesozooplankton feeding behaviour, in terms of ingestion, assimilation and metabolism, influences and is in turn influenced by the physiological state of the animals. Physiological state here means the state of mesozooplankton body function. Naturally, this may depend on many variables including body temperature and the levels of lipid stores. Body function may also depend on the animal's extent of maturity and the various phases of the reproductive cycle. Therefore, a complete description of the physiological state is likely to be complex. However, in order to predict feeding behaviour, we focus on the most important variables previously identified in earlier models (e.g., Anderson et al., 2005 and Mitra, 2006).

Furthermore, we assume that the physiological state of mesozooplankton depends on two main groups of variables. The first group of variables is the energetic costs for basal metabolism (b) and growth (d). We posit that the magnitude of these variables is influenced by temperature in a deterministic manner (cf. Gillooly et al., 2001). The second set of determinants for mesozooplankton physiological state within the model are the structural biochemical requirements for the maintenance (β_i) and growth (δ_i) of the animals. These parameters are likely to change as the mesozooplankton grows or moves through the various phases of its life history. For the sake of simplicity, the values of β_i and δ_i are fixed in the present model.

Given these assumptions, we expect temperature to influence the feeding behaviour of mesozooplankton via its effect on the energetic cost for metabolism; this assumption corresponds with previous proposition on the effect of temperature on the physiological behaviour of organisms (Clarke, 2004).

In addition to temperature, another component of the environment which is considered in our model to influence the feeding behaviour of mesozooplankton is food. In our approach we propose that food is represented by the “macronutrients” associated with algal bulk properties, i.e., protein, lipid and carbohydrate, that are major determinants of feeding behaviour (Houde and Roman, 1987 and Cruz-Rivera and Hay, 2000) and nutrient utilization efficiency among mesozooplankton (Kuijper et al., 2004).

Drawing from optimum foraging theory (Pyke, 1984) and from the stoichiometric modulation of predation approach (Mitra, 2006), our approach for evaluating the rates of physiological processes under different temperature and food conditions is composed of three steps: (1) determining the energetic requirement for basal metabolism and growth of the mesozooplankton at different temperatures, (2) evaluating the potential cost/benefit (in terms of growth) for the ingestion of different food items, considering both the energetic and structural biochemical requirements for the maintenance and growth of the mesozooplankton, and (3) the regulation of food ingestion, assimilation and metabolism to optimize the net rate of new biomass production under different temperature and food conditions based on the information derived from the second step.

In our model, ingested substrates are first subject to variable assimilation efficiencies based on their potential to limit the growth of the mesozooplankton, with unassimilated material egested in faeces. Assimilated substrates are next used to meet the cost of basal metabolism, which leads to respiration and release of C (and N if the respiratory substrate contains N). After basal metabolism is accounted for, remaining substrates are

used for growth. Thus, growth in our model can be described using Eq. (1), where ingestion minus egestion equals assimilation.

Growth=(food ingestion−egestion)−respiratory lossGrowth=(food ingestion−egestion)−respiratory loss

Model variables and parameters are listed in Table 1 and Table 2 respectively. Further arguments for the model structure are provided in the following sections (see also Appendix A for details on the model formulation).

2.2. Temperature effect on the energetic cost of metabolism

Traditionally, the cost in terms of energy for metabolism is measured as the rate of oxygen uptake (Kiørboe et al., 1985 and Thor, 2000). This is because in many animals including mesozooplankton, the energy (i.e., ATP) for powering metabolism is generated aerobically using oxygen as the final electron acceptor. Experiments have shown that the rate of oxygen consumption, and hence ATP production, increases exponentially with temperature (Blier and Guderley, 1993), but in simple ecological terms, it is suggested that the process is driven by energy demand for physiological work (Clarke and Fraser, 2004). Based on these observations, we assume that temperature influences mesozooplankton physiological behaviour through its effect on the energetic cost for metabolism.

We, therefore, quantify temperature effect on mesozooplankton growth by using a series of equations (Appendix A) that link physiological behaviour (i.e., food ingestion, assimilation and utilization) of the animals to their energetic costs of metabolism at different temperatures.

For any organism, the cost of metabolism per unit of body mass may vary depending on many factors including protein synthesis (cf. Thor, 2000), and requirement for ion gradients within tissues (Preedy et al., 1988). In common with previous studies (e.g., Anderson et al., 2005), we differentiate energetic cost of metabolism into two types: a basal metabolic cost b (J $(gC)^{-1}$ d^{-1}), and biomass production cost d (J $(gC)^{-1}$). The term b represents the cost of living; it is the summation of the costs for all processes that preserve cellular and organismal integrity, and important components include ion pump activity (Milligan and McBride, 1985), protein/biomass turnover and basal neural activity (Rolfe and Brown, 1997 and Clarke and Fraser, 2004). Conversely, d represents the summation of all the energetic costs associated with the production of new biomass; an important component of d may include specific dynamic action (Kiørboe et al., 1985) and the cost for protein synthesis (Thor, 2000). Both b and d are described based on the assumption that the cost of metabolism vary with temperature according to the Boltzmann factor, $\exp^{-\partial/kT}$ (cf. Gillooly et al., 2001), where T is the absolute temperature (K), ∂ is the activation energy of metabolism (J), and k is Boltzmann's constant (J $(K)^{-1}$).

Previous studies have shown that the combination of the Boltzmann's constant together with the concept of activation energy introduced by Arrhenius (1915) provides a powerful mechanistic explanation of the thermal dependence of metabolic rates, where nothing in the system changes apart from temperature (see Brown et al., 2004). We now know, however, that metabolic rate is also influenced by the availability of metabolic substrates, which depends on the quantity and biochemical composition of the prevailing ambient food conditions (Thor et al., 2002). Hence, in our model, the production of energy to satisfy the demand for metabolism is linked to the availability metabolic substrates via food ingestion and assimilation.

2.3. Food ingestion and assimilation

As discussed above, there is a large body of evidence to show that mesozooplankton can regulate their behaviour and metabolic physiology in order to satisfy their demand for energy and chemical substances. Limits on this reversible changes in phenotypes are set by complex interplay between external drivers (e.g., temperature, nutrient supply) and genetically prescribed features such as thermoregulation and chemo-receptive abilities that enable mesozooplankton to respond to changes in their temperature – food environments; they are thus difficult to fully parameterize.

We assume that the ability of mesozooplankton to capture (w, L gC^{-1}), ingest (I_c, [gC (gC)$^{-1}$ d^{-1}]) and assimilate (λ_i dimensionless) the nutritional constituents of a prey is bounded within two limits (Fig. 2). The first limit (w_{mg} for prey capture efficiency, I_{mg} for ingestion, λ_{mg} for assimilation efficiency) define the highest sustainable rate of material flow through the mesozooplankton. This can be considered as representing the phenotypic limit on food intake that is associated with specific feeding appendages, gut size, structure of feeding vacuoles, etc. The parameters for the first limit are fixed in the present model, but they could be made a function of animals' ontogeny (or allometry) if required. The second limit on mesozooplankton feeding behaviour (w_m for prey capture efficiency, I_m for ingestion, λ_m for assimilation efficiency) describes the parameters needed for feeding to satisfy only the cost for basal metabolism. This limit can vary with ambient conditions as well as with the developmental stage of mesozooplankton. Hence in our model, the actual rates for food ingestion and assimilation efficiency are regulated within the two limits, with the aim of satisfying the energetic costs and material demand for metabolism at different temperatures.

Previous studies on the chemosensory capabilities of mesozooplankton have shown that the animals can detect odour of food patches (Poulet and Marsot, 1978). Other behavioural studies have demonstrated that mesozooplankton alter their body position or increase the velocity of their feeding currents in response to biochemicals associated with individual prey items (Busky, 1984 and Poulet and Oullet, 1982). In these studies, the probability for encountering and capturing a prey is improved by chemo-receptive ability of the animals. Furthermore, high-speed films have revealed that prey items captured by mesozooplankton are "tasted" at the mouth before being either ingested or rejected, with nutrient-poor particles (e.g., faecal pellets) being more likely to be rejected after capture than nutritious particles (Paffenhöfer and Van Sant, 1985 and Vanderploeg et al., 1990). Based on these observations, we assume that (i) mesozooplankton evaluate prey nutritional quality (defined as the degree to which the quantity and nutritional composition of a prey meets consumers' nutritional needs: Müller-Navarra, 2008) before ingestion, and (ii) both capture efficiency and ingestion rate increase with the quality of the prey; this assumption is consistent with the optimum behaviour hypothesis of Mariani and Visser (2010).

We determine prey nutritional quality following the approach described by Acheampong et al. (2012), considering temperature effect on the cost of metabolism. This approach first evaluates the growth-limiting potential L_i ($0 \le L_i \le 1$) of individual food constituents based on the differences between prey biochemical composition (of proteins, lipids and carbohydrates) and the metabolic requirements (both in terms of energy and tissue materials) of mesozooplankton. It then determines prey quality Q ($0 \le Q \le 1$) by assuming that quality is controlled not by the amount of resources available, but by the resource with the least potential to limit the growth of the mesozooplankton. Hence, we implicitly ensure that limiting biochemical compounds that are usually utilized for growth with high efficiency contribute positively towards the quality of prey items, while unwanted or excess compounds decrease prey quality. The consequence is high quality values for prey with a low content of excess substances and vice versa.

During prey quality evaluation, mesozooplankton are assumed to assimilate food at a constant maximum rate and make metabolic adjustments based on their energetic and structural biochemical requirements (Anderson et al., 2005). Following this approach, the value of Q will be 1 ($\equiv$good quality food, which is possible only theoretically) when food composition exactly balances the nutritional requirements of mesozooplankton at different temperatures. Conversely, $Q = 0$ ($\equiv$bad quality food) when a prey has no nutritional value for the growth of mesozooplankton. Similarly, the limiting potentials of substances supplied in excess of the animals' requirement will be lower than those supplied in lower amounts, and that for individual food substrates, the value of L_i lies between 0 and 1. L_i equals 1 means a chemical occurs below consumer's structural composition requirement. Conversely, $0 < L_i < 1$ means a chemical occurs in excess of consumer's requirement.

After assigning nutritional value to individual prey items and their chemical constituents, mesozooplankton then regulate food ingestion and assimilation in order to satisfy their nutritional requirements at different temperatures.

We describe ingestion rate as a hyperbolic function [Holling Type II according to Ivlev (1955)] of prey concentration (V, [gC (L)$^{-1}$]) with the operational parameters, i.e., prey capture efficiency (w, L gC^{-1}) and intake threshold (I_{td}, [gC (gC)$^{-1}$ d^{-1}]), configured to increase with Q within the confines of the two feeding limits

described above. The intensity of the grazing response to food quality is defined by new parameters Z_{ing} (for I_{td}) and Z_{ce} (for w) (Fig. 2a).

After the mesozooplankton ingests the prey, assimilation of the food takes place. Again, we follow the "optimum behaviour approach" by assuming that the assimilation efficiency (λ_i, dimensionless) for individual food chemicals increases with their respective potential to limit the growth of the mesozooplankton; this assumption is also consistent with previous studies (e.g., Mitra, 2006). As for food ingestion, the intensity of the response was defined by a new parameter η (dimensionless) as well as bounded within the two limits for assimilation as described above (Fig. 2b).

After assimilation, the compounds are utilized for basal metabolism and growth as described below.

2.4. Basal metabolism and growth

Our approach for determining substrate utilization is described in detail elsewhere (Acheampong et al., 2012). Hence, it is only briefly described here.

Substrates assimilated by mesozooplankton are used first for basal metabolism, with growth being possible only when the amount of assimilated food exceeds the needs required to cover the costs of maintenance. In our model, basal metabolism occurs in order to (i) satisfy the cost, in terms of energy, for staying alive (b, [J $(gC)^{-1}$ d^{-1}]), and (ii) maintain a fixed biochemical composition (β_i, [gC $(gC)^{-1}$]) of the mesozooplankton biomass. We thus introduced a new variable ρ_i (dimensionless), which determines the fraction and thereby the mass (m_i, [gC $(gC)^{-1}$ d^{-1}]) of each assimilate that could be used for basal respiration without adversely affecting the chemical composition requirements of the organism. As a consequence, respiratory consumption (m_c, [gC $(gC)^{-1}$ d^{-1}]) of assimilated food for basal metabolism is determined by the value of ρ_i and the energy content (E_i, [J $(gC)^{-1}$]) of the different assimilates.

Once basal metabolism is completed, the remaining substrates are used for growth. Similar to basal metabolism, the process of growth is required to (i) satisfy the energy cost (d, [J $(gC)^{-1}$]) for growth, and (ii) maintain a fixed biochemical composition (δ_i, [gC $(gC)^{-1}$]) within the structure of new biomass. As described above, d covers temperature-specific costs for producing a unit C of new biomass. Conversely, δ_i represents the fraction of the new biomass constituted by a specific substance. In common with previous biochemical models (e.g., Anderson et al., 2005), we assume that only substrates assimilated in excess of the specific structural needs of the animals are catabolized for energy to power growth. The rate (g_c, [gC $(gC)^{-1}$ d^{-1}]) at which food is converted into energy to power growth is thus regulated to ensure that the structural requirements of mesozooplankton for specific substances are not compromised during catabolism. As for maintenance, we introduced a new variable γ_i (dimensionless), which determines the fraction and thereby the mass (g_i, [gC $(gC)^{-1}$ d^{-1}]) of each assimilate that could be respired to power growth without adversely affecting the required biochemical composition of the new biomass.

So at each temperature in our model, the process of growth runs as long as mesozooplankton can satisfy their energy and structural requirement for metabolic growth; otherwise, growth ceases, leaving some proportion (x_i) of the assimilated food unutilized within the gut of consumers. Within the mesozooplankton community, the fate of these nutritional excesses varies widely (for detail discussions, see Hessen and Anderson, 2008). Following Anderson et al. (2005), we assume that excess food as perceived by the mesozooplankton is voided via respiration decoupled from biochemical/mechanical work.

2.5. Parameter determination and model implementation

The model is parameterized to simulate egg production by *A. tonsa* under different temperature and food conditions. Consequently, the biochemical composition β_i is calibrated to represent that of an adult female *Acartia*, while δ_i represents that of *Acartia* eggs. Experimental studies show that *Acartia* adults do not undergo significant structural (exoskeleton) growth (Miller et al., 1977), thus justifying our assumption of egg production as the only form of growth. Unlike other copepods (e.g., *Calanus hyperboreus*), *Acartia* adults have considerably less capacity for substrate storage (Lee et al., 2006). Furthermore, the biochemical (e.g.,

cholesterol) content of eggs produced by *Acartia* does not change with ambient temperature (Hasset and Crockett, 2009). We therefore choose a fixed biochemical composition for the copepod.

The majority of model constants were determined directly from previous studies involving *A. tonsa* (Table 2; Appendix B presents details on how the remaining parameter values were calculated). We set the food concentration, V, at an unlimited level of 1E−3 gC L^{-1} based on the experimental data of Kiørboe et al. (1985), and applied our model assuming other abiotic factors (e.g., salinity) to be constant. The activation energy for metabolism (∂) was determined by fitting the model to experimental observation (we advise that ∂ could also be determined from the slope of an Arrhenius plot of oxygen uptake versus temperatures: Gillooly et al., 2001). Similarly, constants representing feeding for only basal metabolism (i.e., w_m, I_m and λ_m) by mesozooplankton were determined by fitting the model to experimental data. The justification for this approach is that empirical studies on the maintenance requirement of copepods are typically starvation experiments, with no measurements of feeding rates (e.g., Tsuda, 1994 and Thor, 2003). As a consequence, the intensity of the feeding response to food quality (i.e., Z_{ce}, Z_{ing} and η) was also determined by fitting the model to experimental data. First, the model was fitted to observations from Kiørboe (1989) demonstrating the effect of algal C:N status on *Acartia* egg production. For this simulation, temperature was set constant at 18 °C as in the laboratory experiment of Kiørboe (1989). Furthermore, the algal biomass was divided into protein-, lipid- and carbohydrate-specific fractions (α_i) based on empirical relationships (i.e., Eqs. (2a)–(2d) of Kuijper et al., 2004) between algal C:N and macromolecular biochemical composition. Using the parameter values obtained from the simulation, the model was then compared to data from experiments (e.g., Fernandez, 1978, Deason, 1980, Ikeda, 1985 and Sullivan and McManus, 1986; Holste and Peck, 2006) demonstrating temperature effect on the physiology of *Acartia*. Parameters were accepted if they gave good model – data agreement based on the Q_{10} for food ingestion, assimilation, and respiration and gross growth efficiency for egg production at different temperatures.

In our model, uptake and subsequent utilization of ingested food depends on that of protein, lipid and carbohydrate macromolecules. The rates for these processes are calculated based on carbon. This is because carbon is closely related to energy content of food items (Sterner and Robinson, 1994) and occurs in every organic compound. Hence, carbon assimilation, respiration and conversion into eggs were simply the sum of the respective rates for the individual compounds. Within the modelling community, N uptake and utilization by marine copepods is typically assumed to depend on that of proteins (Kuijper et al., 2004). For our results to be comparable, we assumed that N occurs only in proteins. Thus, N-specific assimilation, respiration and growth rates were determined by dividing the respective rates for protein by protein C:N mass ratio (assumed to 3.2; Vollenweider, 1985).

3. Results

The main focus of our study was on understanding the combined impact of ambient prey biochemical composition and temperature on the growth of mesozooplankton, using egg production by *A. tonsa* as a test case. First, however, we will demonstrate the validity of the assumptions underlying our model as well as the realism in its predictions by comparing our results with observed values from previous studies.

3.1. Effect of algal C:N

Fig. 3 shows the comparison between model and laboratory observation (Kiørboe, 1989) of egg production rate, as well as C and N gross growth efficiencies of egg production in response to changes in algal C:N-ratio. In general, there is a good agreement between model and observations. In particular, the model is able to reflect the high egg production rate under a low algal C:N-ratio and vice versa (low egg production rate under a high algal C:N-ratio); almost 68% of the observed variation in egg production rate at 17 °C can be explained by the model output (i.e., R^2 was 0.6753 for the linear regression between model prediction and laboratory observation). Both the model output and the experimental observation suggest that the carbon based gross growth efficiency of mesozooplankton strongly depends on the C:N-ratio of the food. Here, almost 72% of the observed variation in C gross growth efficiency (K_C) for egg production can be explained by the model output (i.e., R^2 = 0.7213). The agreement between the predicted and observed variation in nitrogen based gross

growth efficiency (K_N) was moderate (R^2 = 0.4215). The model predicts that K_N declines at low and high algal C:N because some proportion of the food N has to be catabolized for basal metabolism (see Fig. 4). These predictions compare with results from previous models (e.g., Kuijper et al., 2004) and demonstrate the ability of our model to address the effect of algal C:N on the reproduction of *Acartia*.

Nitrogen in food is assumed to be solely in the form of proteins which are assimilated with a high efficiency of ~90% (cf. Head, 1992 and Harvey et al., 1987), so the fraction of ingested N released as pellets was predicted to be constant at ~10% (Fig. 4). Unlike N, much of the C present in food items is often presented in forms that are not readily assimilated by mesozooplankton. The fraction of C egested as pellets increased with increasing food C:N-ratio because of increasing proportion of carbohydrate in the algae which were difficult to assimilate. Typically in algae, carbohydrate occurs in structural and so-called "reserve" forms, which are assimilated at different efficiencies by copepods (Anderson, 1994). In our approach prey structural or reserve components were not considered. Therefore, the predicted impact of algal carbohydrate on C egestion typifies copepods feeding on algae with high indigestible components such as cellulose and mucus. These compounds accumulate within N-deficient algae and impact C assimilation (see, for example, Van Donk et al., 1997). Our model prediction is therefore consistent with existing observation.

Perhaps the most striking asymmetry in the modelled fates of C and N is in the fractions allocated to basal metabolism. *Acartia* was predicted to catabolize mainly non-nitrogenous compounds (e.g., carbohydrates) during basal metabolism (Fig. 4). The copepod was thus able to spare most of the ingested protein/N for growth as observed in laboratory experiments (Roman, 1983 and McGoogan and Gatlin, 1999).

Due to the regulation of protein assimilation and sparing over lipids and carbohydrates, the copepod supplied excess proteins for egg production when the available food was protein-rich (i.e., low C:N algae); the copepod incurred a deficit in energy-rich substrates when the ingested food was poor in proteins (i.e., high C:N algae). In both these cases, the use of protein for energy production was predicted to be relatively high and constant, while the respiration of lipids and carbohydrates varied substantially. The results show that >40% of the ingested N was voided or respired to power egg production (Fig. 4). The fraction of C allocated for the production of energy to power egg production increased with food C:N-ratio because of increasing proportion of proteins in the substrates. As a result, both the rate and carbon gross growth efficiencies (K_C) for egg production were predicted to decrease with increasing food C:N, agreeing closely with the data of Kiørboe (1989).

3.2. Effect of temperature

We will now evaluate our model considering temperature effect on the physiological behaviour of Acartia on constant diet. For this simulation, a prey with a C:N ratio of 5, representing high-quality algae in this study (see Fig. 3a), was used as food source. Fig. 5 shows the results. Energy demand for basal metabolism and growth increased with temperature as prescribed within the model (Fig. 5a and b). Such increases in energetic requirement induce higher food ingestion by the mesozooplankton. Within the temperature intervals studied (0–32 °C), food ingestion rate increased exponentially with temperature approaching a maximum rate equal to ~632% of body C $(day)^{-1}$ at 26 °C. The predicted increase in the ingestion rate corresponds to a Q_{10} of 1.6, which is within the Q_{10} range of 1.2–3.7 determined by Fernandez (1978) for a variety of mesozooplankton at 10–25 °C. Strong dependence of food ingestion on temperature has been also reported for individual copepod species such as *Centropages hamatus*: Q_{10} of 3.9 (between 1 and 15 °C: Kiørboe et al., 1982) and *Eurytemora velox*: Q_{10} of 2.4 (between 10 and 15 °C; Pagano and Gaudy, 1986). Our result is therefore consistent with the existing observation. The maximum ingestion rate predicted in the present study is also realistic [cf. 660% of body C d^{-1} observed by Deason (1980) for *Acartia hudsonica* at 15 °C].

The model shows that the proportion of ingested C released as faeces at low temperature did not markedly differ from that at the higher temperatures (Fig. 5e and f). On average, ~8% of the ingested C was released as faeces; the proportion of ingested N released as faeces was ~10%. These egestion values compare with the rates calculated from the previous simulation involving N-rich algae (i.e., egestion at algal C:N = 5 in Fig. 4). They also suggest that C and N assimilation for egg production by *Acartia* ingesting N-rich algae does not vary with ambient temperatures. Unfortunately, we have not found any publication demonstrating temperature effect on food assimilation by *Acartia*. Our results though compare with data on other copepods (Conover,

1966). We could therefore relate the metabolic fate of the chemicals assimilated at different temperatures directly to their respective amount within the ingested food.

Unsurprisingly, temperature had a major influence on the partitioning of ingested food resources between the various metabolic requirements of model copepods (Fig. 5e and f). Relative allocation of food C to respiration increased with increasing temperature with basal metabolism consuming most (>60%) of the carbon at higher temperatures (>17 °C). Between the temperature intervals studied (0–32 °C), the Q_{10} for total C respiration was 1.7. This prediction compares with observed Q_{10} (1.63–1.89) for oxygen uptake by epipelagic mesozooplankton (Ikeda, 1985), assuming a fixed respiratory quotient for C catabolism (cf. Al-Mutairi and Landry, 2001). A similar Q_{10} value has been reported also for individual species: 1.5–2.2 and 1.9–2.3, respectively, for *A. tonsa* and *Acartia clausi* at 10° to 20 °C (Gaudy et al., 2000); *Eurytemora hirundoides*: at 6° to 16 °C: 1–2.7 (Gyllenberg and Lundqvist, 1979); *Brachionus plicatilis* at 20° to 28 °C: 1.9–2.4 (Epp and Lewis, 1980).

The results show that N respiration during basal metabolism was only limited to higher temperatures (>12 °C). As previously noted, assimilation and subsequent utilization of food N depends on protein. Protein constitutes 53% of the food used in the experiment (results not shown). As this is less than the protein composition assumed for the structure of the copepod (Table 2), protein and hence N was not catabolized for basal metabolism when the cost for metabolism was low. This occurred at temperatures below 12 °C (Fig. 5f). In contrast, at temperatures above 12 °C, the copepod catabolized proteins, and hence released N during basal metabolism. As a consequence, new biomass production and hence C gross growth efficiency of the copepod decreased with increasing temperature (Fig. 5e). This prediction agrees with experimental observations (Sullivan and McManus, 1986). It also demonstrates that our model can resolve the effect of temperature on food uptake and utilization by *Acartia*.

3.3. Combined effect of temperature and food composition

Based on the foregoing results we applied our model to investigate the combined effect of ambient temperature and prey biochemical composition on egg production rate based on two indices: (i) the temperature for maximum egg production at each prey nutritional status (we refer to this as “optimum temperature”, T_{opt}, below), and (ii) the maximum rate of egg production (G_{max}) at T_{opt}. For this simulation, the model run conformed to a 7×32 experimental factorial design (food C:N: 5, 7, 9, 11, 13, 15, 17 gC gC^{-1}; temperature: from 0 to 32 over unit steps of 1 °C).

Fig. 6 shows the model results considering the interplay between the effects of food C:N ratio and temperature. When considered alone, both temperature and food C:N impacted egg production by *A. tonsa*. Egg production decreased with increasing food C:N-ratio, and under N-rich food, egg production response to increasing temperature was roughly unimodal with G_{max} at ~25 °C. The predicted response and optimum temperature compare with earlier observation obtained for the same copepod species (Kiørboe, 1989; Holste and Peck, 2006). However, when both temperature and food C:N were combined, the rate for egg production did not follow the trends indicated by previous studies using only single stressors.

The temperature for G_{max} increased from 25° to 29 °C with increasing food C:N ratio. This shift in T_{opt} also impacted the rates for egg production (Fig. 6): G_{max} was high at low food C:N-ratio but decreased with increasing food C:N-ratio. At extremely high food C:N ratios (>8), the relationship between temperature and egg production deviated from unimodality; egg production increased gradually with increasing temperature, reached a first maximum at an intermediate temperature below T_{opt}, and then declined to a relatively stable but lower rates at temperatures ranging from 20° to 24 °C (Fig. 3a). In fact, at temperatures ranging from 20° to 24 °C, egg production was barely possible. Here, most of the substrates remaining after basal metabolism were not incorporated into eggs as they were constrained by the assumed structural requirement for egg production. These findings follow intuitively from the observation that dietary biochemical limitation of somatic growth and reproduction among mesozooplankton can be intensified at higher temperatures (cf. Masclaux et al., 2009 and Sperfeld and Wacker, 2009). In our simulation experiment, copepods ingesting N-rich algae could maximize egg production as the C associated with “low C:N algae” could easily be assimilated for metabolism (Fig. 4a). C assimilation efficiency however decreased with the N content of the algae. As a consequence, copepods ingesting N-poor food could only achieve maximum egg production at higher temperatures when food ingestion and hence energy intake was high (Fig. 5d).

4. Discussion and conclusions

It has long been known that animals' physiological response to changes in ambient temperature is contingent on food conditions (Clarke, 1993 and Coles et al., 2002). This mechanism has been ignored or given a cursory coverage in ecosystem models, partly because a simple physiological framework for describing the interplay between the effects of ambient temperature and prey nutritional status is lacking. To help address this problem, this paper proposes a model for describing changes in mesozooplankton feeding behaviour (i.e., food ingestion, assimilation, and respiration) when confronted with sub-optimal temperature and food conditions. Below, we discuss how the implementation of the approach we have suggested contributes to our understanding of ecological processes.

Marine copepods use N for egg production with an efficiency of only 40% even when supplied with high C:N food (Checkley, 1980 and Kiørboe, 1989), and it has been hypothesized for many years that one determinant of the phenomenon is limited intake of energy-rich substrates such as lipids and carbohydrates (Kuijper et al., 2004). Kuijper et al., (2004) posit that in the event of a shortage of lipid and carbohydrate in the pool of assimilated food, mesozooplankton use protein for energy production, and thus decrease the utilization efficiency of the N in protein. Furthermore, the regulation of protein intake over lipids and carbohydrates by animals can lead to superfluous protein supply for metabolism, which can limit the role of N in egg production; this is akin to the "protein leverage" effect proposed by Simpson and Raubenheimer (2005).

Our simulation provides another explanation why copepods may use protein for energy production even when they assimilate high amounts of lipids and carbohydrates.

Our results suggest that copepods, like many marine invertebrates (Roman, 1983), conserve assimilated proteins for egg production by preferentially catabolizing non-protein compounds (e.g., carbohydrates) for basal metabolism. They also suggest that the use of non-protein compounds for basal metabolism leads to superfluous supply of proteins for new biomass production and thus forces copepods into respiring most of the compound for energy to power egg production. As a result of this mechanism, N gross growth efficiency is predicted to be low, at about 0.46 on average, which agrees closely with the efficiency of 0.4 observed by Kiørboe (1989). Hence it is clear from our simulation that the regulation of protein sparing over other substrates provides a possible explanation for the low N gross growth efficiency observed among marine copepods. There is therefore the need to consider the post-ingestive physiology of mesozooplankton when undertaking stoichiometric studies of nutrient transfer from phytoplankton to higher trophic levels via mesozooplankton.

In our model, nutrient utilization for egg production depends not only on food C:N, but also the cost for metabolism at different temperatures. The results show that at lower temperatures (<12 °C) where the cost for metabolism is low, copepods do not respire N for energy to power basal metabolism. Here, most of the N ingested by copepods was incorporated into eggs or voided without any production. In contrast, at higher temperatures (>15 °C) where the cost for metabolism was high, most of the N ingested by copepods was respired for energy. Based on these results, and as supported by observations demonstrating temperature-related increase in the excretion of N/ammonia (Gophen, 1976, Stickle and Bayne, 1982, Dabrowski, 1986 and Robertson et al., 2001), we conclude that copepods may require nitrogen-rich food for successful reproduction at higher temperatures.

This feature could exacerbate the impact of global climate change on the dynamics of marine ecosystems by modifying prey preference by mesozooplankton. Based on the results of this study and as supported by laboratory observations (Masclaux et al., 2009 and Sperfeld and Wacker, 2009), we anticipate that the effect of warming could be beneficial for the growth of *Acartia* in winter and early spring, when small diatoms and cryptophytes, which are known to be rich in essential nutrients for mesozooplankton production (Mayzaud et al., 1989), usually dominate the composition of phytoplankton in temperate seas (Reid et al., 1990 and Marshall and Nesius, 1996). Conversely, warming would have a negative impact on the growth of the copepod in summer, when nutritionally poor prymnesiophytes and cyanobacteria dominate the composition of phytoplankton (Malin et al., 1993). Consequently, warming in summer would have a negative impact on the growth of *Acartia*. However, it must be noted that the actual impact of warming on copepod production will

also depend on the response of other components of the ecosystem, e.g., development of predator populations and competition from other herbivores. Clearly, further research is required to understand the importance of diet – temperature interactions in marine ecosystems.

The classical understanding in ecology holds that at the level of individual ectotherms, fitness (e.g., growth, reproduction) increases gradually with increasing temperature, reaches a maximum at the optimal temperature, T_{opt}, and then declines rapidly with further increases in temperature (Huey and Stevenson, 1979, Huey and Hertz, 1984 and Huey and Kingsolver, 1989; Holste and Peck, 2006). The initial rise in fitness that occurs with increasing temperature is attributed to Arrhenius kinetics, in which rates of reaction exponentially increase with increasing temperature (Arrhenius, 1915). The decrease in fitness that occurs above T_{opt} is attributed to thermal denaturation of proteins (Fields, 2001 and Hochachka and Somero, 2002). Here we show that the classical understanding is theoretically sound if and only if the C:N ratio of the food available to the mesozooplankton is low (<6). Our model, which explicitly incorporates animals' ability to regulate feeding to offset energetic demand for metabolism at different temperatures, predicts that (1) the optimum temperatures for maximum egg production increases with algal C:N, and (2) below T_{opt}, the rate for egg production can sometimes decrease with temperature, especially when copepods are fed with algae containing high C:N ratio (>8). Food C:N ratios in the pelagic zone of marine systems tend to be relatively high (>5; Geider and Roche, 2002); our results therefore indicate that the classical unimodal relationship between temperature and mesozooplankton fitness should be uncommon.

To adequately describe the reaction of organisms to thermal challenges requires an understanding of their compensatory, acclimation response to food. The model in our present study assumes that temperature influences acclimation response of mesozooplankton to ambient food conditions through its effect on the energetic cost of metabolism. This effect is included through the Boltzmann's factor for predicting the kinetic energy of simple systems such as molecules in solution. Such an approach has a long and useful history in the physiological explanation of ecological processes (e.g., Brown et al., 2004). Still, the extent to which the Boltzmann's factor relates to acclimative physiological behaviour of organisms is an open question in ecology, particularly in systems in which dynamics result from multiple, interacting factors (see, discussions in O'Connor et al., 2007). We assume that the Boltzmann's factor is related to the generation of metabolic energy (see Section 2.2). Hence in our model, an organism living at a higher temperature has no option but to synthesize more energy by consuming more food, as well as vice versa. There are clear ecological benefits to be gained from such a behaviour, notably the ability to power membrane function at higher temperatures and conserve food at low temperatures (cf. Clarke, 2004). In reality, however, the synthesis of energy, and hence consumption of food, occurs under complex and subtle feedback control. For example, it has been suggested that one important control on the synthesis of metabolic energy stems from the concentration of ATP within the cells of organisms (Clarke and Fraser, 2004): when ATP concentration is high, synthesis of ATP from ADP slows, and when ATP concentration drops because it is being utilized rapidly, synthesis of ATP is stimulated. There are also many other feedback mechanisms, such as inhibition of glycolysis by increase in the concentration of citric acid cycle intermediates (Clarke and Fraser, 2004). The parameterization of such feedback mechanisms goes beyond the scope of the present study, thus here, the assumption of the synthesis of energy, and hence the utilization of metabolic substrates (food macromolecules), is driven by energy demand for physiological work of new biomass production and maintenance.

Ultimately mesozooplankton models need to reflect the broad pattern of acclimative behaviour that we observe, and yet are simple enough in their structure to find wide applicability. To that end, the physiological framework we have proposed requires no more parameters than previously documented models (e.g., Kuijper et al., 2004 and Mitra, 2006). We recognize that the framework does not incorporate all acclimative responses demonstrated by mesozooplankton under different temperature – food conditions. We view our model as preliminary work that needs to be extended to include other acclimative processes vital for the development of mesozooplankton. For example, during poor food conditions, species capable of storing lipids rely mostly on accumulated reserves for reproduction (Lee et al., 2006). This adaptive strategy, where trophic history plays a key role, removes the lipid requirement for egg production from the immediate nutritional needs of females, and thus could buffer the dependence of metabolism on the prevailing ambient food conditions. Furthermore, mesozooplankton may modulate the lipid content of their membranes in order to maintain fitness at different temperature conditions (Farkas, 1979 and Sperfeld and Wacker, 2009).

The animals can also avoid nutritional excesses by balancing how they assimilate substrates from ingested materials against their requirements (for example, see (DeMott et al., 1998). This can be achieved by regulating digestive enzymatic activity (Darchambeau, 2005) and/or the retention time of food in the gut (Santer and Van Den Bosch, 1994; Darchambeau, 2005). We have to consider the catabolic physiology of the animals to ensure the removal of excess chemical substances. Hence, in our model, the ingestion and assimilation of food increase with the energetic cost of metabolism, independent of the structural biochemical composition requirements of the animals. Several experimental studies support the assumption we employ in our approach (see, for example, discussions in Anderson et al., 2005 and Acheampong et al., 2012). Moreover, the approach lays the foundation upon which the model could be improved to allow consumers the option of either storing excess assimilates or using them as substrates for biosynthesis.

So, by explicitly considering the interplay between ambient temperature, prey nutritional status and mesozooplankton metabolic processes, the model presented here provides an improved means of studying mesozooplankton growth under changing environmental conditions. The model indicates that the constraints exerted by prey nutritional status on the production of new biomass, at least by generalist consumers such as *Acartia*, increases with increasing temperature.

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Appendix

Appendix A. Model formulation

Justifications for the model structure are provided within the manuscript. Hence, only the model formulation would be described here.

A.1. Temperature effect on the energetic cost of metabolism

We differentiate energetic demand for metabolism into two types: a basal metabolic cost (b, [J $(gC)^{-1}$ d^{-1}]) and biomass production cost (d, [J $(gC)^{-1}$]). Here, b covers the costs for all processes that are essential for organisms to remain alive. Conversely, d is the energetic costs associated with new biomass production. At any temperature T (K), b was described using Eq. (A1), adapted from the universal temperature dependence function of Gillooly et al. (2001):

$$b = b_0 \times \exp\left(\frac{\partial(T - T_0)}{kTT_0}\right) \quad \text{equation(A1)}$$

where ∂ is the activation energy (J) for metabolism, and k is Boltzmann's constant (J $(K)^{-1}$), whereas b_0 denotes the cost (J $(gC)^{-1}$ d^{-1}) for basal metabolism at a standard temperature T_0 (assumed here to be 273.15 K). Similarly, d (J $(gC)^{-1}$) was determined using Eq. (A1) but with b and b_0, respectively replaced by d and the cost d_0 (J $(gC)^{-1}$) for new biomass production at a standard temperature.

A.2. Food ingestion

As discussed above, mesozooplankton can and do alter the rate of food ingestion, and assimilation in order to obtain the required balance of nutrients for optimal growth. In our model, food ingestion (I_c, [gC (gC)$^{-1}$ d^{-1}]) increases with nutritional quality (Q, dimensionless) of the available food. For an animal consuming a prey containing i to n different macromolecules, Q was determined using Eq. (A2) (Acheampong et al., 2012):

$$Q = \min(U_i, U_j, \ldots, \ldots, U_n, 1) \quad \text{equation(A2)}$$

with U_i (dimensionless) representing the potential net efficiency for converting a food chemical into that of the consumer:

$$U_i = \frac{G\delta_i}{I_{mg}\lambda_{mg}\alpha_i(1-\rho_i)(1-\gamma_i)} \quad \text{equation(A3)}$$

where I_{mg} and λ_{mg} respectively represents maximum food ingestion (gC (gC)$^{-1}$ d^{-1}) and assimilation efficiency (dimensionless), δ_i (gC (gC)$^{-1}$) is structural requirement of chemical i for growth (G, [gC (gC)$^{-1}$ d^{-1}]), α_i (gC (gC)$^{-1}$) is prey composition of the same chemical, ρ_i (dimensionless) represents the fraction of each assimilate that could be respired to satisfy the cost b for basal metabolism, while γ_i (dimensionless) specifies the fraction that could be respired to satisfy the cost d for growth.

Food ingestion (I_c, [gC (gC)$^{-1}$ d^{-1}]) was described using Ivlev (1955) function:

$$I_c = I_{td} \times (1 - \exp^{-w \times V}) \quad \text{equation(A4)}$$

where I_{td} is the threshold for food ingestion (gC (gC)$^{-1}$ d^{-1}), ω is prey capture efficiency (L (gC)$^{-1}$), and V is prey concentration (gC (L)$^{-1}$). We then incorporated feeding regulation by assuming that both w and I_{td} increases with the quality of food. So within the model, the operational threshold for food intake equals the maximum food ingestion rate when food quality is good (i.e., $I_{td} = I_{mg}$ when $Q = 1$); otherwise, I_{td} increases with the quality of food as described by Eq. (A5):

$$I_{td} = I_m + (I_{mg} - I_m) \times Q^{Z_{ing}} \quad \text{equation(A5)}$$

where I_m represents minimum intake required for basal metabolism, and Z_{ing} (dimensionless) defines the slope (or intensity) of the ingestion response to food quality (Fig. 2). Setting $I = I_{mg}$ makes grazing independent of ambient temperature.

Similarly, prey capture efficiency, w, was configured to vary between a minimum value (w_m, [L (gC)$^{-1}$]) required for grazing to only satisfy the requirements for basal metabolism, and a maximum (w_{mg}, [L (gC)$^{-1}$]) needed for grazing to satisfy both maintenance and maximum growth requirements of the animal using Eq. (A6):

$$w = w_m + (w_{mg} - w_m) \times Q^{Z_{ce}} \quad \text{equation(A6)}$$

where Z_{ce} (dimensionless) defines the intensity of prey capture response to food quality. Here too, we could makes prey capture efficiency independent of ambient temperature by setting $w_m = w_{mg}$.

Many copepods are omnivorous (e.g., Poulet and Marsot, 1978) and hence may derive a significant part of their nutrition from multiple sources. Obviously, our method for describing grazing is only suited for a single prey system. Hence for describing ingestion within a multiple prey system, a different approach would be needed (for example, see Mitra, 2006).

A.3. Food assimilation

After the mesozooplankton ingests the prey, assimilation of the food takes place. We assume that the assimilation efficiency λ_i for individual food chemicals varies with their respective potential to limit the growth of the mesozooplankton. Growth limiting potential (L_i, dimensionless) for each food chemical was calculated using Eq. (A7) (Acheampong et al., 2012):

$$L_i = \min(U_i, 1) \quad \text{equation(A7)}$$

Here too, we follow the optimum behaviour approach by assuming that mesozooplankton regulate feeding in order to maximize the uptake of limiting compounds. λ_i was thus described as a hyperbolic function of the limiting potential for individual compounds using Eq. (A8) (Mitra, 2006):

$$\lambda_i = \lambda_m + (\lambda_{mg} - \lambda_m) \times (1 + \eta) \times \frac{L_i}{L_i + \eta} \quad \text{equation(A8)}$$

where λ_{mg} represents maximum threshold for the assimilation of chemicals, while λ_m is the assimilation efficiency required for basal metabolism. η defines the intensity of the response; the higher the η value, the stronger the intensity of the response and vice versa (Fig. 2b); setting $\lambda_m = \lambda_{mg}$ makes assimilation efficiency independent of L_i.

The rates for the assimilation of individual substrates (A_i, gC gC^{-1} d^{-1}) and total food carbon (A_c, gC gC^{-1} d^{-1}) were thus calculated as follows:

$$A_i = I_c \alpha_i \lambda_i \quad \text{equation(A9)}$$

$$A_c = I_c \sum_{i=1}^{n} [\alpha_i \lambda_i] \quad \text{equation(A10)}$$

Unassimilated fraction of each substance is egested as faecal pellets. The egestion rate for individual substrates (F_i, [gC $(gC)^{-1}$ d^{-1}]) and total carbon (F_c, [gC $(gC)^{-1}$ d^{-1}]) is calculated as follows:

$$F_i = I_c \alpha_i (1 - \lambda_i)$$

equation(A11)

$$F_c = I_c \sum_{i=1}^{n} [\alpha_i (1 - \lambda_i)]$$

equation(A12)

Dividing Eq. (A12) with I_c gives the fraction of total ingestion that is egested by the animal.

A.4. Metabolism

Substrates assimilated by mesozooplankton are used first for basal metabolism, with growth being possible only when the amount of assimilated food exceeds that required to cover the costs of maintenance. Our method for determining substrate utilization is described in detail elsewhere (Acheampong et al., 2012). A brief summary of it is therefore described here.

A.4.1. Basal metabolism

We consider that basal metabolism is required to satisfy two biochemical demands: the energetic costs *b* (J (gC)$^{-1}$ d^{-1}) for staying alive at different temperature, and a fixed biochemical requirement (θ_i, [gC (gC)$^{-1}$]) for the structure of the animal. Here, *b* covers the energetic costs associated all non-growth processes. θ_i represents carbon-specific fraction of different compounds constituting the biomass of the mesozooplankton. It was employed to ensure that structural demand by mesozooplankton for specific substances is not compromised during catabolism of assimilates. Hence for an animal requiring and ingesting *i* to *n* different compounds, we described basal metabolism using the following equations:

$$b = I_c \sum_{i=1}^{n} [\alpha_i \lambda_i \rho_i E_i]$$

equation(A13)

$$\beta = \frac{I_c \alpha_i \lambda_i (1 - \rho_i)}{I_c \sum_{i=1}^{n} [\alpha_i \lambda_i (1 - \rho_i)]} = \frac{\alpha_i \lambda_i (1 - \rho_i)}{\sum_{i=1}^{n} [\alpha_i \lambda_i (1 - \rho_i)]}$$

equation(A14)

where $\sum_{i=1}^{n} [\beta_i] = 1$ ∑i=1n[βi]=1, and ρ_i represents the fraction of each assimilate that could be respired for maintenance without adversely affecting the structural biochemical requirements of the mesozooplankton. E_i denotes energy content (J (gC)$^{-1}$) of each chemical.

So at any instance, energy demand, *b*, for survival is attained by catabolizing a specific mass (m_i, [gC (gC)$^{-1}$ d^{-1}]) of each chemical assimilate via the following equation:

$$m_i = I_c \alpha_i \lambda_i \rho_i$$

equation(A15)

Total food catabolism during basal metabolism is then described by Eq. (A16), as the sum of the solutions to Eq. (A15) for different chemicals.

$$m_c = I_c \sum_{i=1}^{n} [\alpha_i \lambda_i \rho_i]$$

equation(A16)

Dividing Eq. (A16) with I_c gives the total fraction of ingested food that is catabolized for maintenance. Similarly, dividing Eq. (A15) with $I_c\alpha_i$ gives the fraction of each ingested chemical that is catabolized for maintenance.

A.4.2. Growth

Once basal metabolism is completed, the remaining substrates are used for growth. As for basal metabolism, biochemical requirement for growth was separated into two components: (i) the energetic cost d (J $(gC)^{-1}$) of new biomass production at different temperatures, and (ii) a fixed biochemical requirement (δ_i, [gC $(gC)^{-1}$]) for the structure of the new mesozooplankton biomass. The parameter d covers all the energy costs for producing a unit C of new biomass. The parameter δ_i represents the fraction of the new biomass constituted by a specific substance. It was also employed to ensure that the specific structural biochemical requirement for new biomass formation is met during respiration to power anabolism. As a result, the process of growth within the model is described using the following equations:

$$G = I_c \sum_{i=1}^{n} [\alpha_i \lambda_i (1 - \rho_i)(1 - \gamma_i - x_i)]$$

equation(A17)

$$E_g = Gd = I_c \sum_{i=1}^{n} [\alpha_i \lambda_i (1 - \rho_i) \gamma_i E_i]$$

equation(A18)

$$\delta = \frac{I_c \alpha_i \lambda_i (1 - \rho_i)(1 - \gamma_i - x_i)}{I_c \sum_{i=1}^{n} [\alpha_i \lambda_i (1 - \rho_i)(1 - \gamma_i - x_i)]} = \frac{\alpha_i \lambda_i (1 - \rho_i)(1 - \gamma_i - x_i)}{\sum_{i=1}^{n} [\alpha_i \lambda_i (1 - \rho_i)(1 - \gamma_i - x_i)]}$$

equation(A19)

where G is total growth rate (gC $(gC)^{-1}$ d^{-1}), E_g is total energy requirement (J $(gC)^{-1}$ d^{-1}) for growth, γ_i represents the fraction of each chemical assimilate that could be respired to power growth without adversely affecting the required biochemical composition (i.e., δ_i) of the new biomass. x_i denotes the fraction of assimilates that may be in excess of mesozooplankton requirement for both maintenance and growth.

The rate at which each chemical substance is converted into energy to power growth (g_i, [gC $(gC)^{-1}$ d^{-1}]) and new mesozooplankton biomass (G_i, [gC $(gC)^{-1}$ d^{-1}]) is thus described using Eqs. (A20) and (A21) respectively:

$$g_i = I_c \alpha_i \lambda_i (1 - \rho) \gamma_i$$

equation(A20)

$$G_i = G\delta_i = I_c \alpha_i \lambda_i (1 - \rho_i)(1 - \gamma_i - x_i)$$

equation(A21)

Dividing Eq. (A17) by I_c gives carbon-specific gross growth efficiency (K_C). Similarly, dividing Eq. (A21) by $I_c\alpha_i$ gives the fraction of each ingested chemical that is catabolized to power growth and incorporated into new biomass respectively.

We do not currently consider the metabolic fate of excess food in our model. Hence, the excess fraction (x_i) of each chemical assimilate is discarded via respiration decoupled from biochemical/mechanical work (Anderson et al., 2005). Following this approach, the quantity (in carbon) of individual assimilates and total food that is voided by mesozooplankton was calculated using Eqs. (A22) and (A23) respectively:

$$X_i = I_c \alpha_i \lambda_i (1 - \rho_i) x_i$$

equation(A22)

$$X_c = I_c \sum_{i=1}^{n} [\alpha_i \lambda_i (1 - \rho_i) x_i]$$

equation(A23)

where X_i and X_c represent, respectively, the voiding rates (gC (gC)$^{-1}$ d^{-1}) for individual assimilate and total carbon. Dividing Eq. (A22) by $I_c\alpha_i$ gives the fraction of each ingested chemical that is voided by consumers, while dividing Eq. (A23) by I_c gives the voided fraction of the total ingestion.

The equation describing egg production rate (i.e., Eq. (A17)) is not linear as it can only be solved by simultaneously satisfying all the energy (i.e., Eqs. (A13) and (A18)) and structural biochemical requirements (i.e., Eqs. (A14) and (A19)) of the mesozooplankton. Therefore, substrate utilization for metabolism and/or voiding to maintain mass balance and biochemical homeostasis within animal tissues was determined using an iterative approach (methods described in, and as implemented by, Acheampong et al., 2012).

Appendix B. Derivation of parameter values

The majority of model constants were determined directly from previous studies involving *A. tonsa* (see Table 2). Below we present details on how the remaining parameter values were calculated.

We applied our model using the *Acartia* egg production data of Kiørboe (1989). In the Kiørboe's experiment, *Acartia* females were fed the diatom *Thalassiosira weissflogii* with C:N ratios manipulated through the concentration of nutrient in the algal growth medium. Protein (=α_P), lipid (=α_L) and carbohydrate (=α_H) compositions based on empirical relationships (i.e., Eqs. (2a)–(2d) of Kuijper et al., 2004) between algal C:N and composition of proteins, lipids, and carbohydrates. Typically in algae, carbohydrate occurs in structural and so-called “reserve” forms, which are assimilated at different efficiencies by copepods (Anderson, 1994). In our approach prey structural or reserve components were not considered, and so the carbohydrate composition of the algae was the sum of the two forms. The implication of this assumption is discussed within the main manuscript (Section 3.1).

B.1. Energy cost for metabolism at standard temperature

Energetic demand for basal metabolism at standard temperature was taken to be 2755.10 J gC^{-1} d^{-1}. This corresponds to the value calculated by Acheampong et al. (2012) based on the rate of oxygen consumption by starving copepods.

Following previous studies (Bämstedt et al., 1999 and Kiørboe et al., 1985), the cost for a unit egg production at standard temperature, d_0 (J $(gC)^{-1}$), was determined based on the macromolecular biochemical composition required for the eggs. In the calculations, we assumed an egg dry weight of 120 ng (62.64% protein, 35.12% lipid and 1.78% carbohydrates: Acheampong et al., 2012). Table B1 contains a summary of the calculations, assuming all monomers required for the synthesis of individual macromolecules within the egg are derived from dietary sources (Kiørboe et al., 1985). For the synthesis of protein and carbohydrates, we used the same monomer constituents as previously used by Kiørboe et al. (1985). Lipid, on the other hand, consists of a wide range of structurally different molecules with very different chemical properties, but no repeating unit or monomers as in the chemical sense of the word. Therefore the conversion factor for lipid was based on the average of all value for the different lipid groups in Table 5 of Kiørboe et al. (1985). A mole of ATP was assumed to contain 30569.48 J of energy (Campbell, 1993).

Using the above approach, energy needed for the formation an *Acartia* egg at standard temperature was determined to be 10.05E−5 J egg^{-1}. This converts into an energy requirement of 1377.96 J $(gC)^{-1}$; assuming C constitutes a fixed fraction of proteins (53%), lipids (76%) and carbohydrates (40%) (cf. Ventura, 2006).

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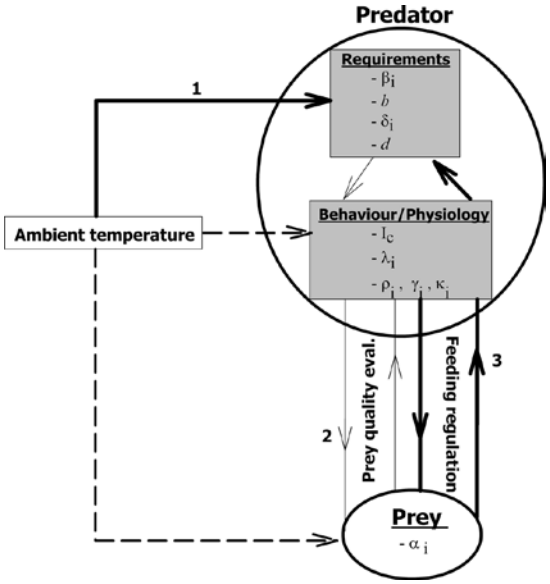

Fig. 1 Model flow diagram, with numbers identifying the order of events in the model. Temperature affects energy cost and structural biochemical requirements for maintenance (b, β_i) and growth (d, δ_i); thus influencing prey nutritional value, grazing rate (I_c), substrate assimilation (λ_i) and catabolism during maintenance (ρ_i), and growth (γ_i, x_i). The extent of these processes determines growth response of the animal to changes in ambient temperature. Subscript i represents proteins, lipids or carbohydrates; whereas α_i is the fraction of prey biomass made up of each macromolecule. Broken line represents known temperature effect (e.g., Thompson et al., 1992) not considered in the model. Symbols are defined within Table 1 and Table 2.

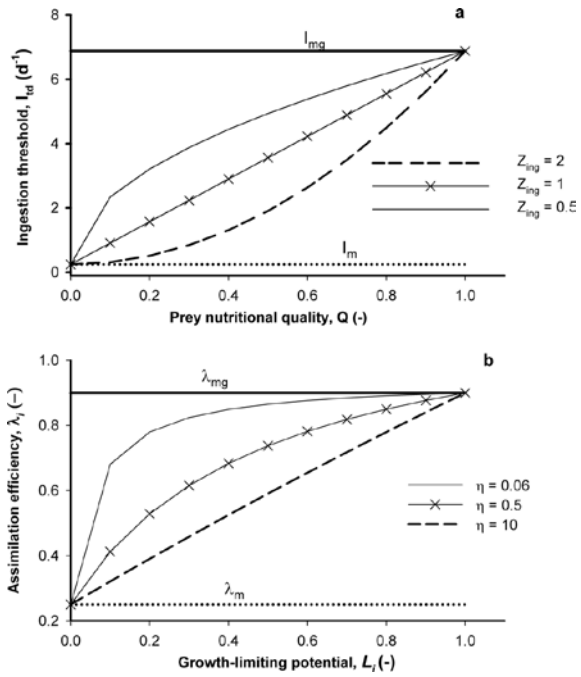

Fig. 2. The effect of auxiliary variables (Z_{ing} and η) on the functional form of (a) grazing parameters, and (b) chemical assimilation efficiency. I_{mg} and λ_{mg} represent maximum food ingestion rate and maximum assimilation efficiency respectively. Conversely, I_m and λ_m represent minimum food ingestion rate and minimum assimilation efficiency respectively. See text associated with Eqs. (A5) and (A6) for further explanation.

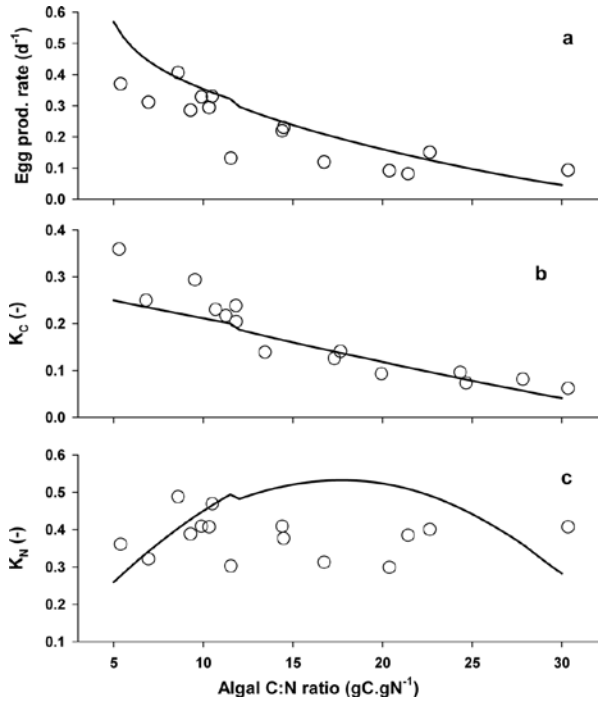

Fig. 3. Predicted (lines) and observed (open circles; Kiørboe, 1989) effect of algal nutritional status on the rate (gC gC^{-1} d^{-1}), carbon- (K_C) and nitrogen-specific (K_N) gross growth efficiency for egg production by *Acartia tonsa* at 18 °C.

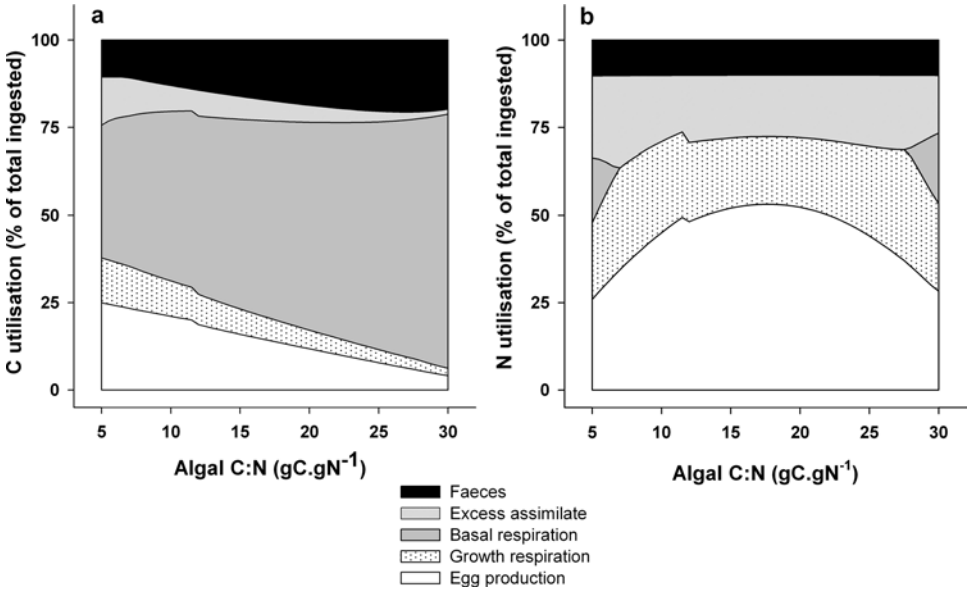

Fig. 4. Predicted metabolic fate of ingested carbon (C) and nitrogen (N) as influenced by algal nutritional status. Excess assimilates here represent the fraction of ingested chemical that is in surplus to that required for the maintenance and growth of the copepod. Unlike other copepods (e.g., *Calanus hyperboreus*), *Acartia* adults have considerably less capacity for substrate storage (Lee et al., 2006). Accordingly, excess assimilates are voided via “wastage respiration” (Anderson et al., 2005).

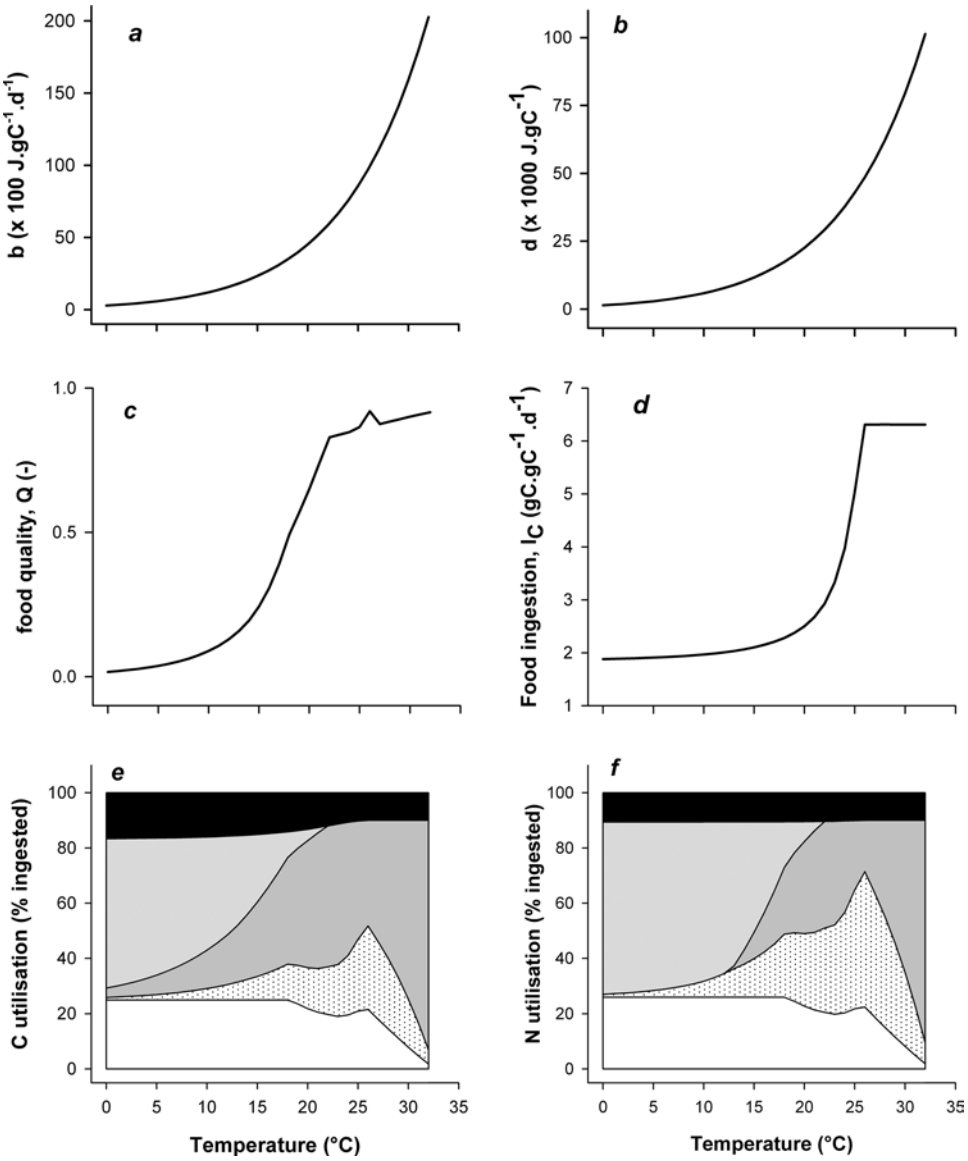

Fig. 5. Predicted impact of temperature on (a) the energetic requirement for basal metabolism, (b) the energetic requirement for growth, (c) prey nutritional quality, (d) ingestion rate, I_c, and (e and f) metabolic fate of ingested chemicals. Fractions of subplots “e” and “f” are the same as described under Fig. 4.

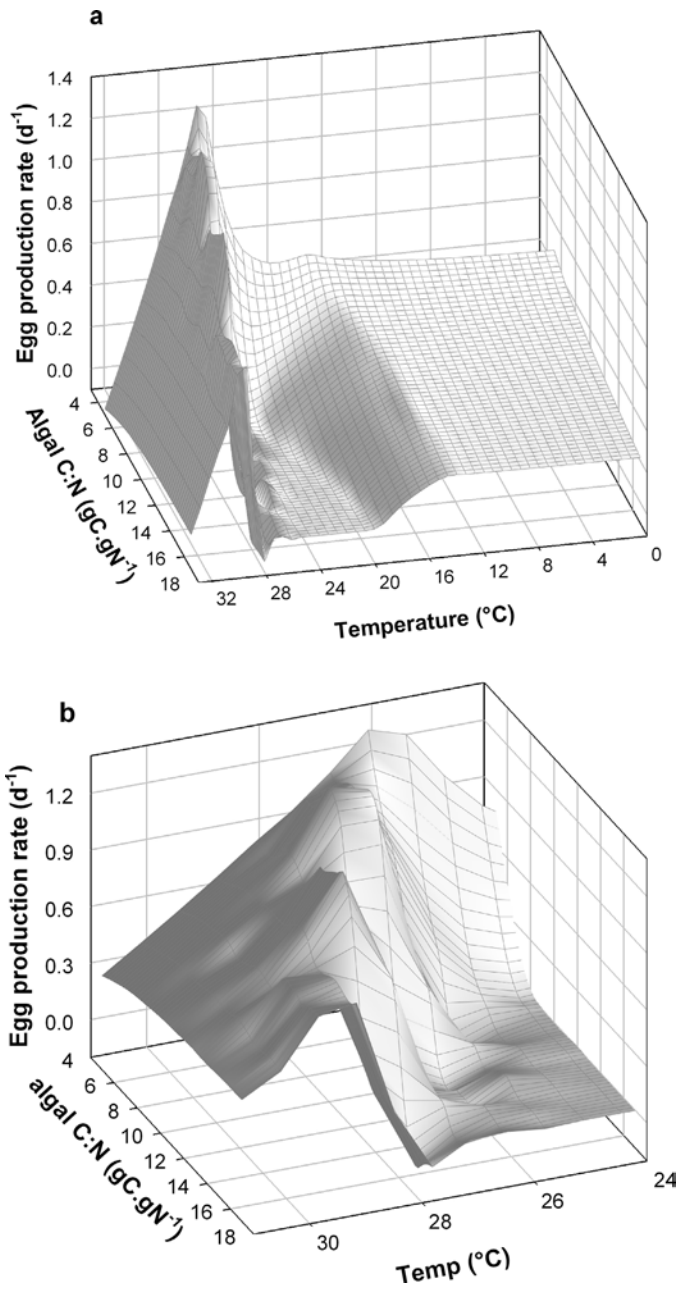

Fig. 6. (a) Egg production rate of *Acartia tonsa* under variable temperature and food conditions. Subplot "b" highlights the model output that the optimum temperatures for maximum egg production increases from ~25° to 29 °C with increasing algal C:N-ratio.

Table 1.

Short description and unit of measurement for each variable included in the model.

Variable	Description	Unit
T	Ambient temperature	K
b	Energy cost of basal metabolism	$J(gC)^{-1}\,d^{-1}$
d	Energy cost of biomass synthesis	$J(gC)^{-1}$
V	Prey concentration	$gC(L)^{-1}$
α_i	Chemical-specific fraction of total prey carbon. Subscript i represents protein, lipid or carbohydrate	$gC(gC)^{-1}$
L_i	Growth-limiting potential of each food chemical	dl[a]
Q	Prey nutritional quality	dl
I_{td}	Prey ingestion threshold	$gC(gC)^{-1}\,d^{-1}$
w	Prey capture efficiency	$L(gC)^{-1}$
I_c	Prey ingestion rate	$gC(gC)^{-1}\,d^{-1}$
λ_i	Chemical assimilation efficiency	dl
ρ_i	Fraction of assimilate respired to power basal metabolism	dl
γ_i	Fraction of assimilate respired to power growth	dl
x_i	Fraction of assimilate in excess of animal's maintenance and growth requirements	dl
F_c (or F_i)	Total carbon (or compound) defecation rate	$gC(gC)^{-1}\,d^{-1}$
A_c (or A_i)	C or compound-specific assimilation rate	$gC(gC)^{-1}\,d^{-1}$
M_c or M_i	Basal respiration rate of C or compound	$gC(gC)^{-1}\,d^{-1}$
g_c or g_i	Growth respiration rate of C or compound	$gC(gC)^{-1}\,d^{-1}$
X_c or X_i	Release rate of excess C or compound	$gC(gC)^{-1}\,d^{-1}$
G or G_i	C or compound-specific growth rate	$gC(gC)^{-1}\,d^{-1}$
K_C or K_i	C or compound-specific gross growth efficiency	dl

[a] dl: dimensionless.

Table 2.

Short description, unit of measurement, value and associated reference for each of the parameter that have been estimated or fixed within the model.

Parameter	Description	Unit	Value	Reference
I_{mg}	Maximum prey ingestion rate	$gC(gC)^{-1}\ d^{-1}$	6.88	Acheampong et al. (2012)
I_m	Minimum prey ingestion rate	$gC(gC)^{-1}\ d^{-1}$	0.01	Fitted
Z_{ing}	Prey ingestion control parameter	dl[a]	0.21	Fitted
w_{mg}	Maximum prey capture efficiency	$L(gC)^{-1}$	2500	Støttrup and Jensen (1990)
w_m	Minimum prey capture efficiency	$L(gC)^{-1}$	500	Fitted
Z_{ceff}	Prey capture control parameter	dl	0.30	Fitted
λ_{mg}	Maximum food assimilation efficiency	dl	0.90	Bämstedt et al. (1999)
λ_m	Minimum food assimilation efficiency	dl	0.25	Fitted
η	Half saturation constant for assimilation	dl	0.10	Fitted
E_p	Energy content of protein	$J(gC)^{-1}$	32312.64	Acheampong et al. (2012)
E_L	Energy content of lipid	$J(gC)^{-1}$	51439.43	Acheampong et al. (2012)
E_H	Energy content of carbohydrate	$J(gC)^{-1}$	42922.90	Acheampong et al. (2012)
k	Boltzmann's constant	$J(K)^{-1}$	1.38E−23	
∂	Activation energy for metabolism	J	1.50E−19	Fitted
d_0	Energy cost for basal metabolism at standard temperature	$J(gC)^{-1}\ d^{-1}$	2755.10	Acheampong et al. (2012)
b_0	Energy cost for growth at standard temperature	$J(gC)^{-1}$	1378.96	Calculated
β_P	Structural requirement for proteins by female copepods	$gC(gC)^{-1}$	0.7269	Acheampong et al. (2012)
β_L	Structural requirement for lipids by female copepods	$gC(gC)^{-1}$	0.2363	Acheampong et al. (2012)
β_L	Structural requirement for carbohydrates by female copepods	$gC(gC)^{-1}$	0.0367	Acheampong et al. (2012)
δ_P	Structural requirement for proteins by eggs	$gC(gC)^{-1}$	0.5478	Acheampong et al. (2012)
δ_L	Structural requirement for lipids by eggs	$gC(gC)^{-1}$	0.4404	Acheampong et al. (2012)
δ_H	Structural requirement for carbohydrates by eggs	$gC(gC)^{-1}$	0.0117	Acheampong et al. (2012)

[a] dl: dimensionless.

Table B1.

Bioenergetic costs for Acartia egg formation at standard temperature. Letters A–E show how calculations were done. E denotes energy per mol of ATP (assumed to be 30569.48 J; Campbell, 1993). See text for source of data on egg biochemical content and for further explanation.

Biochemical substance	ng egg^{-1} [a] A[a]	Monomer mol weight[b] B	Mol ATP mol^{-1} monomer[b] C	ATP egg^{-1} (mol × 10^{-10}) D = A·C/B	Cost egg^{-1} (J × 10^{-5}) D·E
Proteins	75.16	112	4	26.84	8.21
Carbohydrates	2.69	162	2	0.33	0.10
Lipid	42.14	535.75	7.25	5.70	1.74
Total	120	809.75	13.25	32.88	10.05

[a] Data extracted from Acheampong (2010).
[b] Data extracted from Table 5 of Kiørboe et al. (1985).