



Bridging the gap between marine biogeochemical and fisheries sciences; configuring the zooplankton link



Aditee Mitra^{a,*}, Claudia Castellani^b, Wendy C. Gentleman^c, Sigrún H. Jónasdóttir^d, Kevin J. Flynn^a, Antonio Bode^e, Claudia Halsband^f, Penelope Kuhn^c, Priscilla Licandro^b, Mette D. Agersted^d, Albert Calbet^g, Penelope K. Lindeque^h, Rolf Koppelmanⁱ, Eva F. Møller^j, Astthor Gislason^k, Torkel Gissel Nielsen^d, Michael St. John^d

^a Centre for Sustainable Aquatic Research (CSAR), Swansea University, Swansea SA2 8PP, UK

^b Sir Alister Hardy Foundation for Ocean Science (SAHFOS), The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

^c Department of Engineering Mathematics and Internetworking, Dalhousie University, Halifax, NS B3J 1Y9, Canada

^d National Institute of Aquatic Resources, Technical University of Denmark, Jagtvej 69, 2920 Charlottenlund, Denmark

^e Instituto Español de Oceanografía, Centro Oceanográfico de A Coruña, Apdo. 130, 15080 A Coruña, Spain

^f Akvaplan-niva AS, Fram Centre, N-9296 Tromsø, Norway

^g Institut de Ciències del Mar (CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain

^h Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth, Devon PL1 3DH, UK

ⁱ University of Hamburg, Center for Earth System Research and Sustainability (CEN), Institute for Hydrobiology and Fisheries Science, Grosse Elbstrasse 133, 22767 Hamburg, Germany

^j Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark

^k Marine Research Institute, Skulagata 4, P.O. Box 1390, 121 Reykjavik, Iceland

ARTICLE INFO

Article history:

Available online 6 May 2014

ABSTRACT

Exploring climate and anthropogenic impacts on marine ecosystems requires an understanding of how trophic components interact. However, integrative end-to-end ecosystem studies (experimental and/or modelling) are rare. Experimental investigations often concentrate on a particular group or individual species within a trophic level, while tropho-dynamic field studies typically employ either a bottom-up approach concentrating on the phytoplankton community or a top-down approach concentrating on the fish community. Likewise the emphasis within modelling studies is usually placed upon phytoplankton-dominated biogeochemistry or on aspects of fisheries regulation. In consequence the roles of zooplankton communities (protists and metazoans) linking phytoplankton and fish communities are typically under-represented if not (especially in fisheries models) ignored. Where represented in ecosystem models, zooplankton are usually incorporated in an extremely simplistic fashion, using empirical descriptions merging various interacting physiological functions governing zooplankton growth and development, and thence ignoring physiological feedback mechanisms. Here we demonstrate, within a modelled plankton food-web system, how trophic dynamics are sensitive to small changes in parameter values describing zooplankton vital rates and thus the importance of using appropriate zooplankton descriptors. Through a comprehensive review, we reveal the mismatch between empirical understanding and modelling activities identifying important issues that warrant further experimental and modelling investigation. These include: food selectivity, kinetics of prey consumption and interactions with assimilation and growth, form of voided material, mortality rates at different age-stages relative to prior nutrient history. In particular there is a need for dynamic data series in which predator and prey of known nutrient history are studied interacting under varied pH and temperature regimes.

© 2014 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/3.0/>).

Changing perspectives of zooplankton in marine ecosystems

Prior to the 1980s, the structure of the ecosystem in the pelagic marine waters was typically described through what is now

termed the “classical” food web (Steele, 1974; Cushing, 1975). Within this structure, primary production is attributed to photoautotrophic phytoplankton. These phytoplankton are then consumed by the “herbivorous” zooplankton (i.e., primary consumers) which are in turn ingested by carnivorous zooplankton and pelagic fish, which then serve as food for larger fish. Despite some earlier suggestions to modify this classic food web structure (e.g., Pomeroy,

* Corresponding author. Tel.: +44 1792 295036.

E-mail address: A.Mitra@swansea.ac.uk (A. Mitra).

1974), it was not until the early 1980s that the importance of microbial production gained recognition (Williams, 1981; Fenchel, 1982), and the planktonic food web concept was broadened towards a more integrated view (the microbial food web). In this new defined structure phytoplankton as well as bacteria are consumed by protozoan grazers (Sherr and Sherr, 1994; Calbet, 2008), thus providing an additional food source for copepods and higher trophic levels. Following such studies, Azam et al. (1983) proposed the “microbial loop” as an addition to the food web, within which dissolved organic carbon (DOC) is reincorporated into the food web, mediated by microbial activity.

The recognition of the importance of the microbial loop led to the “link-sink” debate (Gifford, 1991), questioning whether the activity of the protozoan grazers served as a “link” between the microbial loop and the classical food chain (Sanders and Porter, 1987), or as a “sink” for carbon (Ducklow et al., 1986). Various field studies, experimental results and modelling efforts have subsequently shown microzooplankton to be a link between the classical and microbial food webs in marine as well as fresh water bodies thus acting as conduits of energy and nutrients between the microbial level and higher trophic levels (Suttle et al., 1986; Frost, 1987; Cushing, 1995; Calbet and Saiz, 2005). Additionally, based on stoichiometric and biochemical grounds, microzooplankton, rather than phytoplankton, could be expected to be better prey for mesozooplankton (Klein Breteler et al., 1999; Broglia et al., 2003; Mitra and Flynn, 2005). The latest twist to this is the concept that much of the plankton community currently split between either phototrophic phytoplankton or heterotrophic microzooplankton should be recognised as mixotrophic (Flynn et al., 2013; Mitra et al., 2014).

Today, the construction, testing and deployment of mathematical descriptions of plankton dynamics are central planks in marine ecology and climate change research. Many of these studies are based on the classic ecosystem model of Fasham et al. (1990), or variations on that theme. However, while over the last half century our understanding of aquatic ecology has undergone a substantial change, models portraying these systems have not developed in line with field and laboratory observations. Model structure and complexity has not typically changed in ecosystem models to reflect improvements in our understanding of biological complexity with its attendant feedback mechanisms (Mitra and Davis, 2010; Rose et al., 2010). The dramatic increase in model complexity over this period has been almost wholly focussed on the phytoplankton–nutrient link, with regard to variables, processes and parameters. Very little, by comparison, has been done with the Z component, quite often employing only 2 classes (e.g., 78 P boxes vs. 2 Z boxes in Follows et al., 2007). Despite the plethora of mechanistic zooplankton models which have been developed over the past two decades (e.g., Carlotti and Hirche, 1997; Carlotti and Wolf, 1998; Mitra, 2006; Mitra and Flynn, 2007; Flynn and Irigoien, 2009), the Z-boxes within ecosystem models are still biologically extremely simplistic with little or no differences in the physiological descriptions between the different Z-boxes. This is despite the manifest difference in the ecophysiology of the protist microzooplankton and the metazoan zooplankton. Increased complexity has usually been in numerical rather than detailed structural complexity; for example, 1-box representing the entire zooplankton (Z) community vs. 3-boxes representing different zooplankton functional types (e.g., Franks, 2002 vs. Blackford et al., 2004).

The zooplankton community has thus been typically side-lined within ecosystem studies, not receiving the same level of importance as the phytoplankton and fish communities. Within biogeochemical models, zooplankton represent the top trophic level acting as a closure function, while within many fisheries models, zooplankton form the bottom level (see reviews by Plagányi (2007), Carlotti and Poggiale (2010), Fulton (2010)). However, there is a growing recognition of the need to bring together these

two strands of research (biogeochemical and fisheries) through development of end-to-end ecosystem models combining physico-chemical oceanographic descriptors with the biology of all trophic levels from microbes to higher-trophic-level, including humans, in a single modelling framework (Mitra and Davis, 2010; Rose et al., 2010). Fig. 1 presents a conceptual model of such an end-to-end food web ecosystem. The zooplankton community (Z) acts as the conduit for the transfer of energy and material from the primary producers to the higher trophic levels and has a pivotal role in recycling and export of nutrients. Thus the zooplankton community is the critical link between biogeochemistry and fisheries (Carlotti and Poggiale, 2010; Mitra and Davis, 2010).

Here, we demonstrate the need to ensure that the description of this Z-link is appropriate for the task at hand, identifying the mismatch between our biological understanding and mathematical descriptions and thence proposing a guide for future experimental (laboratory and field) as well as modelling efforts. As an additional justification for such work, we point to the need to find out how various environmental and climatic factors may impact on ecosystem services important to humans (e.g., fisheries). Key amongst those factors are the rather well studied affects of temperature and the far less well understood implications of ocean acidification (OA; Royal Society London, 2005). All of this requires a good understanding of the processes governing the functioning of the ecosystems. This can be best achieved through an iterative process involving observations, experimentation and modelling, in which enhancements in understanding in any one component prompts renewed emphasis in others.

We commence by investigating the influence different vital rates and physiological functions have on zooplankton dynamics. We then examine the experimental (field and laboratory) and modelling approaches which underpin zooplankton research (especially related to the Z-vital rates) with an aim to determine the level of mismatch in the two approaches. Using this information we provide a roadmap of how the gaps between these two research strands may be narrowed such that the Z-link in end-to-end studies can be configured more realistically. The findings from this work will act as a basis for the development of the next generation ecosystem models which will aid understanding of the ocean ecosystem dynamics under changing anthropogenic and climate events and thence inform various ocean management and policy formulations through, for example, the EURO-BASIN project.

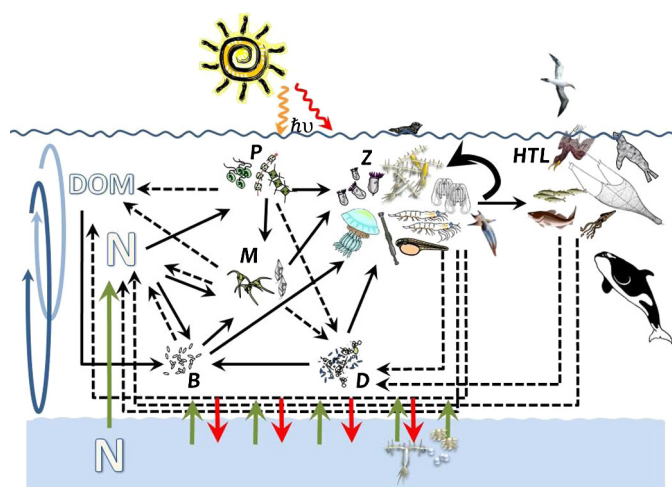


Fig. 1. Conceptual model of marine food web. P, phytoplankton, Z, zooplankton, N, nutrients, M, mixotroph, B, bacteria, D, detritus, HTL, higher trophic levels; solid arrows, inputs; dashed arrows, outputs; blue arrows, mixing; red and green arrows, exchange between the mixed surface layer and lower water. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Classification of zooplankton according to their physiological functionality.

Zooplankton type	Physiological functionality
Protist: (microzooplankton)	Single-celled organism without a gut, with relatively simple and rapid life cycle strategies (e.g., reproduction through binary fission with generation times typically 0.5–few days). Digestion period can equate to a large proportion of the life cycle. Potential for high efficiency for retention of ingested N and P especially in mixotrophic forms.
Non-mixotrophs	Purely heterotrophic protists (i.e., capable of only capturing food); e.g., <i>Oxyrrhis</i> , <i>Paraphysomonas</i> .
Mixotrophs	Protists that possess the capability to fix carbon (photosynthesis) as well as capture food (phagotrophy); e.g., plastidic ciliates.
Non-protists: (mesozooplankton)	Multicellular organisms typically with a gut, with relatively complex life cycle strategies (e.g., age structured populations). Often display swarming behavioural traits. Often maintain energy (oil) reserves; e.g., copepods, krill, cladocerans; some benthic forms release pelagic larvae (e.g., Nauplius, Zoa). Life cycle extending far beyond planktonic stages in larger crustaceans.
Crustaceans	
Non-crustaceans	
Cnidaria	Meroplankton and holoplankton encompassing a wide variety of sizes and life-cycle strategies (e.g., polyp, medusa, colonial siphonophores); may display swarming behavioural traits, due to asexual and sexual reproduction. Variable allometry in predation; most physiological studies focus on a few meroplankton species (e.g., <i>Aurelia</i> spp.); e.g., cnidarian jellyfish.
Ctenophore	Holoplankton, similar to Cnidarians but without stinging nematocysts; no gut per se; most physiological studies focus on a few species (e.g., <i>Mnemiopsis</i> and <i>Pleurobrachia</i> species); ctenophore jellyfish, commonly referred to as “comb jellies”.
Polychaetes	Meroplankton (Trochophora and Nectochaeta larvae), some holoplanktonic forms (e.g., Tomopteridae); carnivorous.
Pteropodes	Holoplanktonic; mainly oceanic; Thecosomata (shelled) feed on phytoplankton and seston, threatened by ocean acidification; Gymnosomata (unshelled) are carnivorous.
Chaetognaths	Mainly planktonic; carnivorous (including cannibalism); exclusively marine; e.g., <i>Sagitta</i> , <i>Eukhronia</i> .
Tunicates	Planktonic forms considered here; all are planktivores; with gut; wide (non-allometric) feeding range; e.g., salps, doliolids, appendicularia.
Other meroplankton	Different larvae of benthic organisms (e.g., echinoderm larvae).
Larval fish	Like crustaceans but with life cycle extending far beyond the planktonic phase (i.e., similar to larger crustaceans).

Zooplankton definitions and vital rates

In order to parameterise the activities of the zooplankton, the Z-link in Fig. 1, we need to establish a working definition for zooplankton functional types. Over the decades, zooplankton have been classified into different types according to size (nano, micro, meso or macro), taxonomy, feeding strategy (e.g., ambush vs. suspension feeders; “herbivores” vs. carnivores), distribution (e.g., vertical, horizontal, geographical) and life-history strategies (e.g., broadcaster spawners vs. sac spawners). In this review we classify zooplankton according to the aspects of their physiological functionality that are key for defining the link within end-to-end ecosystem studies, and how they are typically characterised in modern biogeochemical and ecosystem models (Table 1). The two main categories are the unicellular protists which we will refer to as microzooplankton (i.e., microbial zooplankton), and the multicellular zooplankton (i.e., all non-protists ranging from copepods to fish larvae), which we will refer to as mesozooplankton (i.e., all metazoans; thus this group includes the size classes of meso-, macro- and megalozooplankton).

Fig. 2 presents a schematic of the interrelationships between the vital rate processes of zooplankton. Many of these processes are common for both microzooplankton and mesozooplankton. One exception is food digestion; typically this occurs within a food vacuole in microzooplankton, and within a peristaltic gut for most mesozooplankton. However, one could argue that the digestive vacuole holding time in protists is analogous to gut transit time in, for example, copepods. The other clear exception is in the life cycle and reproductive process. In microzooplankton this is largely driven by cell growth and simple binary fission. In contrast, in mesozooplankton it involves a far more complex suite of processes, usually occurring over protracted temporal and spatial scales and across significant size-scales (thus interacting with different prey and predators).

Configuring the Z-box

Sensitivity of Z vital rates to changes in the environment

Models are deemed to be *in silico* representatives of the real world. Arguably an ideal way to capture the dynamics of the

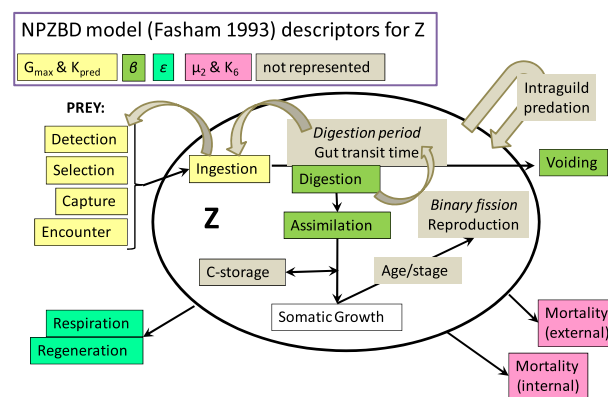


Fig. 2. Schematic of the inter-relationship between vital rates describing zooplankton growth. Almost all these features have equivalence in both protist microzooplankton and metazoan zooplankton; exceptions are indicated by *italic* script for microzooplankton. Colour coding indicates the parameter constants controlling these features of zooplankton physiology within classic NPZB models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

zooplankton community, within end-to-end ecosystem models, water quality models, fisheries models (where Z are prey), earth systems models, etc., is through incorporation of mechanistic descriptions of all the major physiological processes of the zooplankton functional types (Fig. 2; Table 1). In order to enable this, we would need a complete, biological and ecological, understanding of all those functions and how changes in the environment impact on the functionality of zooplankton as individuals as well as at the community level. This would be a Herculean task. Aside from economic and time constraints, there are numerous practical constraints which would hamper the attainment of the information (from experiments and observations) required to configure “perfect” zooplankton components. Even in instances where the physiological parameters can be determined through experimentation, external forcings (such as seasonality) make snap-shot datasets biased. Given all these challenges, there is a need to identify which zooplanktonic processes are the most significant (exert

greatest leverage on events) and warrant particular attention when linking the biogeochemical models to higher trophic level models within any and all ecosystem models.

One way to identify these key processes is through conducting sensitivity analyses of models. Sensitivity analyses of model structure are considered first at the level of the submodel (here, the zooplankton) when operated in a steady-state situation (e.g., fixed prey quality and quantity; Mitra, 2006). Having ensured that the zooplankton model structure (i.e., component equations) is not unduly sensitive, a dynamic sensitivity analyses can then be conducted. Dynamic sensitivity analysis of a model is carried out for the purpose of checking the behaviour of the model within its entire dynamic performance envelope. Thus dynamic sensitivity analyses of the Z-vital rate parameters used within food web and ecosystem models would demonstrate how robust the model outputs are to changes in the “input” parameter values (e.g., assimilation efficiency) and thence indicate the importance of ensuring the correct formulation and parameterization of these vital rate descriptors.

Various modelling studies have performed sensitivity analyses on different response curve formulations for a single process (e.g., Holling vs. Ivlev curves for grazing) to explore the impact on food web and ecosystem dynamics (e.g., Fulton et al., 2003; Anderson et al., 2010, 2013). Here, however, we present a dynamic sensitivity analyses on the zooplankton parameters (constants) which are used to formulate the response curves to describe the zooplankton vital rates (e.g., maximum growth rate, assimilation efficiency) within ecosystem and food web models. For this demonstration, we have used the Nutrient–Phytoplankton–Zooplankton–Bacteria–Detritus (NPZBD) model of Fasham (1993). One may argue that this model (Fasham, 1993) is a simplified representation of the planktonic ecosystem and thence question whether the results from the sensitivity analyses can be justifiably extrapolated to more complex ecosystem models. However, this simplified description of the nutrient–phytoplankton–zooplankton interactions is employed widely forming the basis of the plankton food web framework within ecosystems as well as fisheries models (e.g., Franks, 2002; Blackford et al., 2004; Follows et al., 2007; Plagányi, 2007; Rose et al., 2007, 2010; Anderson et al., 2013). While the descriptions of the physics, phytoplankton and fish populations have evolved to include varying levels of complexity (Fulton, 2010), the increase in complexity of the Z descriptor has mainly been achieved by adding more “Z” boxes, not by enhancing the description of each Z sub-model (Mitra and Davis, 2010). While some models include additional features such as temperature or movement (Blackford et al., 2004; Plagányi, 2007; Fulton, 2010), the main description of the core Z-vital rates accord with that of Fasham (1993). The vital rates of the Z box(es) in ecosystems models, are thus:

$$\frac{dZ}{dt} = \text{grazing} - \text{mortality} - \text{excretion}$$

In Fig. 2, parameters describing vital rates within the Z-box in NPZBD type models have been aligned with zooplankton physiological processes. It can be seen that each of the model parameters summarise a multitude of physiological processes. For example, all the processes associated with prey ingestion are summarised by two constants: the maximum grazing rate (G_{\max}) and associated half saturation constant (K_{pred}). The processes of prey encounter, detection, selection and capture are not considered explicitly (arguably, *de facto*, they are ignored). Likewise, the fate of incoming food (digestion, assimilation, voiding, implications of variable gut transit time and associated variability in assimilation efficiency) is summarised by a single fixed parameter, β (assimilation efficiency); in models with multiple Z-boxes each of the Z functional types maybe assigned different constant β , e.g., Blackford et al., 2004; Fulton et al., 2004; Anderson et al., 2010). Many feedback

processes, such as those between different vital rates and age-stage development, are rarely represented in these types of models at all (see review by Carlotti and Poggiale (2010)). Other important loss processes, such as zooplankton mortality, which links trophic levels, are described using a simplified closure function in which one fixed constant summarises mortality due to predation, cannibalism, diseases and senescence. Knowledge of how variable/sensitive these physiological processes are in reality to changes in conditions, and also how robust the model is to changes in parameter values is, thus, a useful first cut in gauging the importance of each zooplankton physiological processes within models.

Traditionally sensitivity analyses are first conducted using single-parameter, steady-state tests, which should identify overly-sensitive model components (Haefner, 1996). There are various studies which have been conducted under steady-state conditions to gauge the sensitivity of the model parameters. These can be broadly divided into two types, studies which investigate:

- (i) the sensitivity of the model structure; different empirical descriptors are employed to describe a single process (e.g., use of Holling Type II vs. Ivlev vs. Blackman response curves to describe grazing) to see how these affect the model outputs and thence stability of the steady-state system (e.g., Steele and Henderson, 1992; Edwards and Yool, 2000; Fulton et al., 2003; Anderson et al., 2010).
- (ii) the sensitivity of the zooplankton community to changes in physical factors such as turbulence (e.g., Fasham, 1995; Harms et al., 2000) or to non-linearity in trophic transfer efficiency (Flynn, 2009).

Dynamic (non-steady-state) sensitivity analyses are a more severe test of model behaviour, as the analyses indicate potential synergistic interactions within the range of inputs and outputs that a model is likely to encounter and generate. Such analyses can not only provide an indication of the relative sensitivity of each model parameter to fluctuations in the parameter value, but any and all parameters can be considered simultaneously. We have for the first time conducted sensitivity analyses of the zooplankton model vital rates parameters (Fig. 2 and Eq. (1)) under dynamic conditions. It should be noted that this analysis differs fundamentally from those contrasting different model components (referenced above). The results from our analysis are considered below.

Dynamic sensitivity analyses: the process and results

We conducted a dynamic (non-steady-state) sensitivity analysis of the zooplankton vital rate parameters in the classic NPZBD model framework (Fasham, 1993) over a year-long simulation period. Typically dynamic sensitivity analysis is conducted on the constants obtained from the process of fitting the model to data; NPZBD model was tuned to the BioTrans dataset of phytoplankton, zooplankton, bacteria, nitrate and ammonium for 47°N 20°W in the Atlantic (see Table 3 in Mitra, 2009 for the Z parameter values); a detailed description of the BioTrans dataset is given by Lochte et al. (1993). The dynamic sensitivity analyses were carried out using the “risk assessment” tool, in the modelling software, Powersim Studio, which employs a Latin Hypercube sampling method. The model was run 100 times with the values of the test parameters varied randomly around a mean value with an assigned distribution. The mean value for each test parameter was set as the value which gave the best fit to the data during the initial tuning process. All the parameters describing the zooplankton vital rates within the Z description in the NPZBD model were considered: grazing (G_{\max} , K_{pred}), assimilation efficiency (β), excretion (ε), and mortality (μ_2 and K_6) (see also, Eq. (1), and Fig. 2). Variation for each parameter was assumed to follow a normal distribution

around the optimal (tuned) value. In the absence of information to indicate the true variability of parameter values, in all instances, variation assumed a standard deviation of 10% of the mean (tuned) value. For the parameter describing assimilation efficiency (β), the variation was assumed to follow a truncated normal distribution (setting $\beta \leq 90\%$) since biologically it is not possible for the assimilation efficiency to approach 100%.

Fig. 3 shows the results from the dynamic sensitivity analyses on the modelled phytoplankton and zooplankton populations. From these plots can be gauged the sensitivity of the whole model behaviour (not just for zooplankton) to variation in the parameters controlling zooplankton vital rates. The parameters that have greatest potential for affecting the model behaviour were those describing grazing (G_{\max}), assimilation efficiency (β) and mortality (μ). The values for parameters setting the half-saturation for predation (K_{pred}), excretion (ε) and the half-saturation for mortality (K_6) had no significant effect. It is noteworthy that the effects of variation in the configuration of the zooplankton component of the whole model were broadly of equal significance for the phytoplankton as for the zooplankton (Fig. 3). When one considers the simplistic representation of the zooplankton vital rates in the NPZBD structure, that there is no consideration of prey quality and quantity and feedback processes on the vital rates, factors which have great impact upon zooplankton growth dynamics and thence on model output (Mitra and Flynn, 2005; Mitra, 2006; Mitra et al., 2007), then the need to improve our robust description of the functionality of models for zooplankton, as well as for parameter values is clear. Furthermore, here, and indeed in most plankton food-web models, the “Z” box encompasses all the different zooplankton functional types (Table 1), masking a range of ecologically important interactions (Mitra et al., 2007; Mitra, 2009).

In essence, the results of the dynamic sensitivity analysis (Figs. 2 and 3), together with studies of the importance of empirical forms used to describe the Z component (Steele and Henderson, 1992; Edwards and Yool, 2000; Fulton et al., 2003; Anderson et al., 2010, 2013), demonstrate the importance of behaviour of the zooplankton component in models, of getting the model descriptions right. This applies not only for the zooplankton, but also for the phytoplankton and, by inference, for higher trophic levels that may be simulated as well. Having established the critical importance of the modelled zooplankton vital rates, we now proceed to review the type and range of data available from experiments (field and laboratory) and also the extant modelling efforts with a view to identify gaps in our knowledge for proper configuration of zooplankton models.

Physiological attributes of zooplankton *in vivo* and *in silico*

Feeding: detection, selection, capture and ingestion

Zooplankton diets are diverse, and can include ranges of prey sizes and types. When faced with multiple prey types, especially at elevated prey concentrations, they typically demonstrate selective feeding. Feeding involves a series of processes that include prey (food) detection, encounter, selection, and capture leading to ingestion. Prey detection could be through usage of chemo- (“smell” and/or “taste”) and/or mechano- (“feel”) receptors and also depend on physico-spatial aspects such as swimming speed (of both prey and predator) and thence encounter rates and diffusion of chemical cues that in turn are affected by physical properties (e.g., turbulence).

Field and laboratory studies of feeding

Foraging takes place in a three-dimensional space with a patchy food distribution. Foraging effort comes at an energetic cost to

zooplankton and this must be balanced against food availability, its nutritional quality and predation risk. Most species have developed adaptive behaviours and ontogenetic routines such that their foraging strategies have emerged as an effort to optimise nutritional intake within their local environment. These include daily and seasonal vertical migrations, adapting different swimming modes in order to achieve a balance between avoiding mortality due to predation and enhancing encounter rates with prey items (Osgood and Frost, 1994; Hays, 2003; Titelman and Kjørboe, 2003; Pierson et al., 2005) and even jumping out of water (Gemmell et al., 2012). However, currently there are no available data to express the dependence of the total metabolism of zooplankton on their swimming velocity such as there is for fish (Brett, 1964).

In microzooplankton, although there are evidences of some sort of mechano-reception in ciliates (Jakobsen et al., 2006), prey detection is most likely associated with a combination of chemical cues, such as organics leaking from potential prey items, coupled with antibody–antigen type of surface recognition upon physical contact (Martel, 2006; Menden-Deuer and Grünbaum, 2006). It has been suggested that if a prey item turns out to be unpalatable, the protist predators can retain information about the physiological condition of the prey type for a short period and therefore avoid ingesting it (Flynn and Davidson, 1993; Roberts et al., 2011). Prey detection in non-protist mesozooplankton, such as copepods (Poulet and Ouellet, 1982), krill (Hamner et al., 1983), mussel larvae (Ward and Targett, 1989), siphonophores (Mackie et al., 1987) and fish larvae (e.g., turbot and sole; Knutsen, 1992), also occur in response to “smell” from leaked organics from the food item. Prey detection is further enhanced through physical perception using appendages specifically adapted for mechano-reception (e.g., for copepods: Gill, 1986; for jellyfish: Mackie et al., 1987; Haddock, 2007).

Following detection, the zooplankton may or may not elect to capture the item. Using the various combinations of prey detection mechanisms, most zooplankton (micro- and mesozooplankton) demonstrate active prey selection distinguishing prey of: different taxonomy (e.g., diatom vs. dinoflagellate; Tirelli and Mayzaud, 2005); varying stoichiometry (within same species, e.g., *Oxyrrhis marina*, Flynn and Davidson, 1993, and between different species, e.g., *Acartia tonsa*, Jones and Flynn, 2005); live vs. dead (e.g., *Paraphysomonas vestita*, Landry et al., 1991); natural vs. artificial (e.g., ciliate *Strombidium*, Christaki et al., 1998), and toxic vs. non-toxic (e.g., copepods, Leising et al., 2005a; appendicularian *Oikopleura dioica*, Lombard et al., 2011). Accordingly, zooplankton have been found to vary their feeding modes (suspension vs. ambush, Saiz and Kjørboe, 1995) switching between prey items, across different trophic levels, with changes in abundance (e.g., copepod, Castellani et al., 2005a; krill, Onsrud and Kaartvedt, 1998; Lass et al., 2001; Agersted et al., 2011) and prey nutritional status (Flynn and Davidson, 1993; Jones and Flynn, 2005).

Prey thus selected may still not be captured and ingested; indeed, all captured prey are not necessarily ingested. For example, Tong (1997) observed the microzooplankton *Paraphysomonas vestita* to capture prey and then either ingest them or reject them with a flicking action of its flagella; *Mesocyclops* has been observed to reject larger cladoceran prey such as *Bosmina longirostris* and *Scaopholeberis mucronata* post-capture and pre-ingestion (Chang and Hanazato, 2005). Copepods have been shown to “feel” captured prey before deciding whether to ingest or reject it (Paffenhöfer and Van Sant, 1985). Prey capture and ingestion may be influenced by allometrics (prey:predator size ratio), taxonomy and/or prey (chemical or elemental) stoichiometry (i.e., quality). Unsurprisingly, prey quantity has an overarching impact; the impact of allometrics and stoichiometrics on prey capture and ingestion is accentuated by extreme prey abundance (high and/or low).

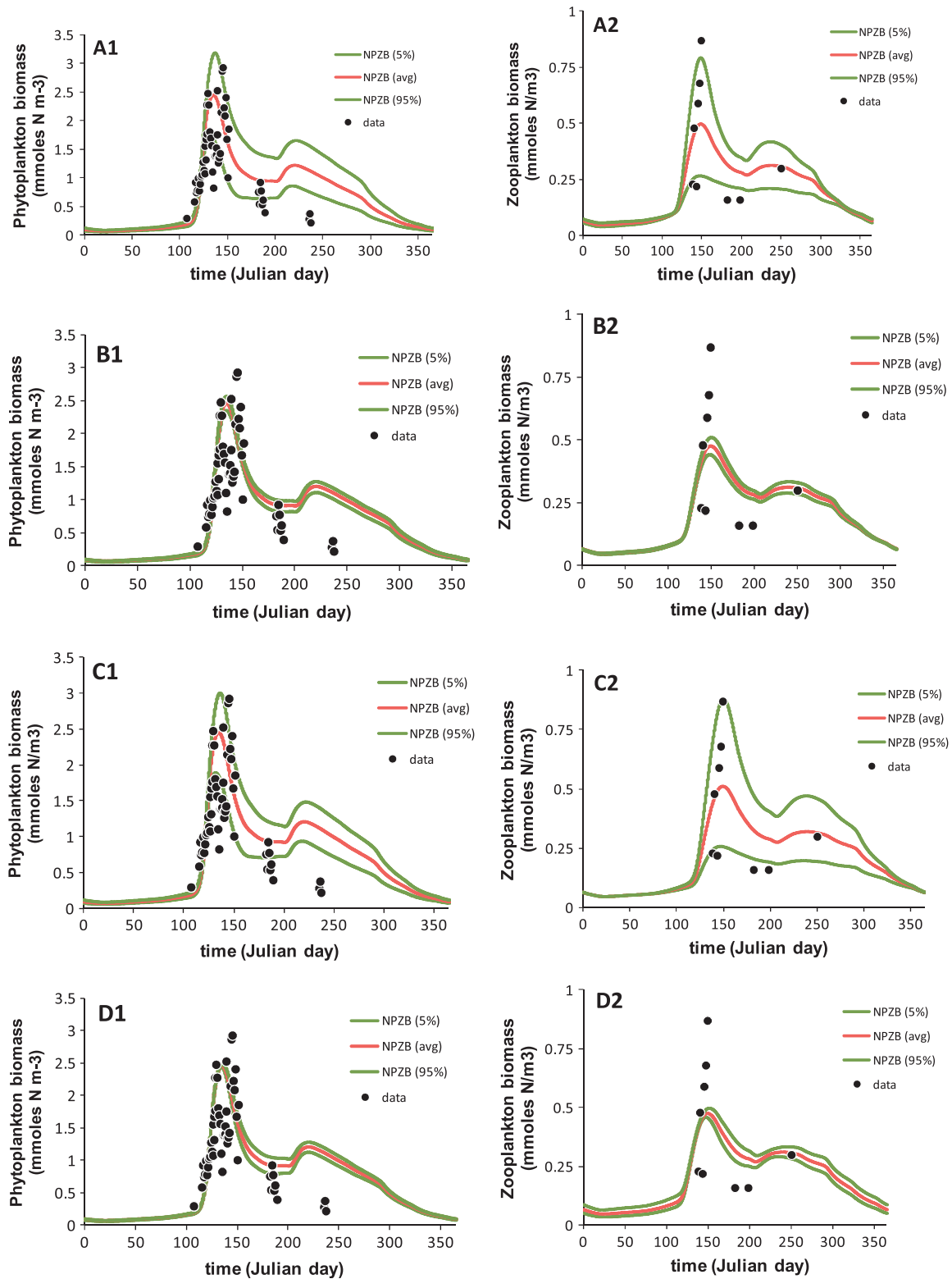


Fig. 3. Dynamic risk assessment outputs from running the NPZBD model (Fasham, 1993). Assessments were performed independently, utilising a Latin Hypercube routine applied to the feeding parameters (G_{\max} ; Panels A1 and A2 and K_{pred} ; Panels B1 and B2 for phytoplankton and zooplankton respectively), assimilation efficiency of the zooplankton (parameter β ; Panels C1 and C2 for phytoplankton and zooplankton respectively), nutrient regeneration (parameter ϵ ; Panels D1 and D2 for phytoplankton and zooplankton respectively), and loss parameters (μ , Panels E1 and E2, and K_G , Panels F1 and F2 for phytoplankton and zooplankton respectively). For the assessment, the mean values of G_{\max} , K_{pred} , β , ϵ , μ and K_G were set as equivalent to the optimal value established by tuning the model to the data. Standard deviations for the assessment were set as 10% of the optimal value. Red line shows the mean outputs, with the green lines showing the 5% and 95% confidence limits. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

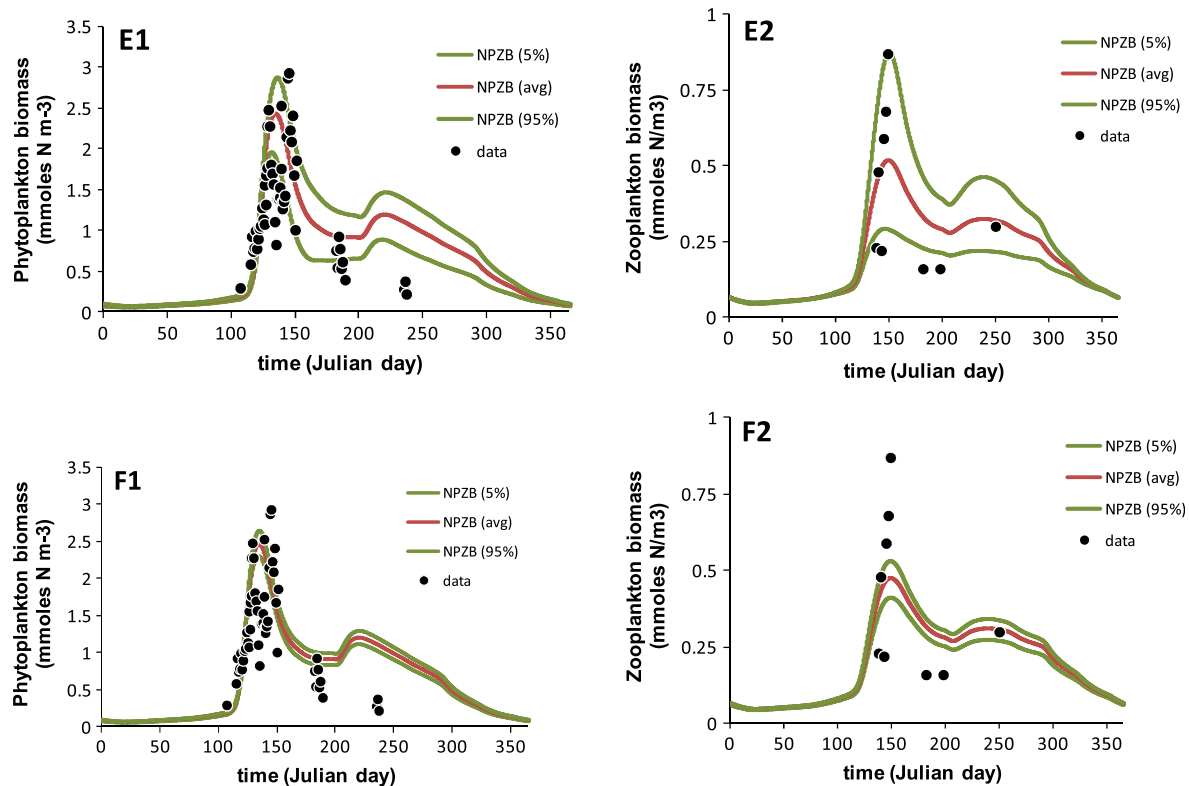


Fig. 3 (continued)

Copepods, when confronted with high prey: predator size ratios or with long diatom chains, have been found to be inefficient at the point of prey capture, demonstrating what is termed “sloppy (messy)” feeding (Corner et al., 1972; Møller, 2005, 2007). In contrast, zooplankton, such as pelagic tunicates, which are primarily filter feeders, appear to ingest food mainly as a function of numeric density and size, with typically no impact of food nutritional quality.

How zooplankton feed impacts on trophic dynamics in different ways. For example, superfluous feeding by mesozooplankton, resulting in the production of high densities of undigested faecal material subsequently lost from the pelagic waters, could support the benthic community (Beklemishev, 1957; Fig. 1). Sloppy feeding by copepods, releasing substantial amounts of dissolved organics into the pelagic waters (Cushing and Vučetić, 1963; Møller et al., 2003; Møller, 2005), and “messy feeding” by krill only ingesting part of copepod prey (e.g., limbs, copepod soft parts) leaving behind the entire copepod–carcass intact (Ohman, 1984; Båmstedt and Karlson, 1998), could be advantageous to the microbial community.

Furthermore, there is the issue of which prey types are being eaten and the allied consumption rates; this will have a direct effect on the prey community structure and abundance. For example, preferential grazing on certain phytoplankton species by zooplankton may promote production of algal, especially harmful or toxic, blooms on one hand (Pierson et al., 2005; Gismervik, 2006; Mitra and Flynn, 2006a; Ribalet et al., 2007) and on the other hand have been found to be capable of controlling established algal blooms (Calbet et al., 2003; Jeong et al., 2010). Certain zooplankton may continue feeding on toxic blooms (copepods, Halsband-Lenk et al., 2005; krill, Bargu et al., 2003) with deleterious effects on not only their own fitness but also that of the next generation (Colin and Dam, 2002; Halsband-Lenk et al., 2005). In contrast, intraguild grazing within the zooplankton community, releasing phytoplankton from grazing pressure, may induce trophic cascades

(e.g., copepods grazing on microzooplankton community, Leising et al., 2005b).

The available literature, thus, demonstrates the complexity and diversity in zooplankton feeding mechanisms and associated impacts from and on the environment. However, there are several caveats. The data available from experiments are for a limited range of zooplankton (often female copepods) and associated prey types (see Table 2). Also, often experiments are conducted under unnatural conditions (e.g., constant environments, high nutrient status). The data obtained are then typically fit with *a priori* functions that may not depict the correct relationship.

Modelling descriptions of feeding

Studying detection, capture and ingestion is non-trivial because of the rapidity of the interactions and the feedback from the accumulation (and then digestion) of ingested material. There is no single zooplankton model which encapsulates the full inter-relationship between the different mechanisms governing zooplankton feeding. Within ecosystem models (such as NPZBD, Fig. 2), zooplankton feeding is typically described through a single zooplankton functional response curve (e.g., the Holling II, Ivlev curve; Gentleman and Neuheimer, 2008; Anderson et al., 2010). The biological descriptors of the Z vital rates are thus lumped into a single process (typically defined through parameters akin to G_{\max} and K_{pred} in Fig. 2) and the feedback mechanisms between these processes, innate to biological systems, are ignored. This problem is analogous to that for nutrient transport and initial assimilation (collectively being “uptake”) in studies of phytoplankton nutrition (Flynn, 1998). However, what these models do demonstrate is that the incorporation of even biologically simplistic formulations of grazing have the potential to destabilize the system or predict very different population dynamics.

There are various modelling efforts investigating the different processes associated with zooplankton feeding. For example, there are a suite of models which explore the foraging strategies of

Table 2

Summary of empirical understanding and modelling activity for different zooplankton types. Good status ●, limited status ◐, minimal status ○. Data collated from field (F), laboratory (L) and modelling (M) studies.

	Mixotroph			Heterotroph μzooplankton			Copepod			Krill			Jellies			Tunicate			Chaetognath			Pteropod			Fish larvae		
	F	L	M	F	L	M	F	L	M	F	L	M	F	L	M	F	L	M	F	L	M	F	L	M	F	L	M
Prey detection and selection	●	●	●	●	●	●	●	●	●	●	●	○	●	●	○	●	●	●	●	○	○	●	○	○	●	●	●
Prey capture	○	●	○	○	●	●	●	●	●	○	●	○	●	●	○	●	●	●	●	○	○	●	○	○	●	●	●
Ingestion rate with prey quality	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Ingestion rate with prey quantity	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Gut transit time and digestion	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Assimilation	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Voiding	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Stoichiometry	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Respiration	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Regeneration	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Biomass specific growth rates	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Life cycle and reproduction	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Intrinsic mortality	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Predatory losses	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Temperature	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
pH	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Turbulence	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○

zooplankton (Leising and Franks, 2000; Leising et al., 2005c; Morozov et al., 2011); however, similar to the grazing descriptions in NPZ-type models, these models also focus on the impact of employing a single equation but of different mathematical form to describe the foraging strategies. Visser (2007) presented a detailed model describing the different physical chemical processes associated with zooplankton feeding and survival strategy highlighting the importance of considering these processes. There are various models describing prey detection and capture based on zooplanktonic swimming behaviour (e.g., Leising, 2001) and predator–prey encounter rates (e.g., linear swimming, Gerritsen and Strickler, 1977; random-walk swimming, Evans, 1989). These models tend to be dominated by theoretical considerations with little or no parameterisation to experimental data. However, Kjørboe and Saiz (1995) proposed mechanistic models describing the dynamics of mesozooplankton prey detection and capture efficiency; they constructed and parameterised their models using experimental data.

Selection between prey items is a complex biochemical/physiological suite of functions. In models this activity, which can be critical for system dynamics, has typically been modelled poorly. There are numerous ad-hoc prey selectivity functions which have been used as a front-end for zooplankton models (see review by Gentleman et al., 2003). Most of these selectivity functions group together the processes of prey detection, selection and switching using fixed constants to formulate the response curves. They typically do not take into account the singular or synergistic impact of prey quantity and quality on feeding as observed in reality. Nor do they enable adaptive prey switching or differentiate between contrasting ingestion kinetics of different prey types. Moreover, most of them result in modelled feeding behaviours that are contrary to biological knowledge, for example, ingestion rates that decrease when food availability increases with no change in assimilation (fixed assimilation efficiency, β in Fig. 2), rather than a continued high ingestion rate balanced by a declining assimilation efficiency (i.e., Stoichiometric Modulation of Predation, SMP; Mitra and Flynn, 2005). Clearly, there is a need to improve on such contrary model descriptions.

Mitra and Flynn (2006b) presented a selectivity function based on experimental findings that enables active prey selection allowing the zooplankton to switch to alternate prey types when there is a decline in prey (stoichiometric) quality and/or quantity; prey

preference can be made to vary with prey quality and quantity. The ultimate control within this function is not the external concentration of each or the total prey (as typically used in ecosystems models), but is a function of the rate of prey capture relative to predator demand and the amount of ingested prey within the predator gut. Hence, if required, any/all prey can be deselected, or the impact of inert materials or turbulence adversely affecting capture rates of any or all prey can be considered. Fig. 4 demonstrates the potential for this selectivity function to describe experimental results compared to traditional approaches.

Food processing: gut transit time, digestion, assimilation and voiding

Ingested material is either wholly or partially digested, and the unassimilated fraction is voided (Fig. 2). Digestion refers to the breakdown of ingested material for incorporation (assimilation) into the consumer body; digestion hence commences at the point of ingestion or during preliminary food crushing associated with prey handling. It terminates with defecation of undigested material, though some level of post voiding digestion associated with continued enzymatic activity and bacteria-mediated decay will likely occur. The processes of ingestion, digestion, assimilation and voiding are not independent of each other but are related through various internal feedback processes (Mayzaud et al., 1998) and depend on the quantity and quality of prey within the digestion vacuole or gut (Mitra and Flynn, 2005). Various studies have demonstrated that the stoichiometric (food quality) differences between the predator and ingested prey impacts on the digestion efficacy, the retention of the ingestate within the digestive tract (vacuole for protists) and therefore on assimilation efficiency (Tirelli and Mayzaud, 2005; Mitra and Flynn, 2007). The efficacy of these processes in turn impact on the trophic dynamics through the defecation and/or excretion (including regeneration) of material (Darchambeau et al., 2003). For example, the nature of the voided material affects not only the trophic levels above the zooplankton, but also those below. Thus, voided organic matter will drive the microbial loop (Landry, 1993; Ducklow et al., 2002; Calbet and Landry, 2004). Likewise, food quality has an impact on the size and density of faecal pellet production. *Acartia tonsa* when fed on ciliate and diatom diets have been observed to produce larger pellets resulting in faster estimated sinking rates (Feinberg and Dam, 1998) causing loss of material from the photic

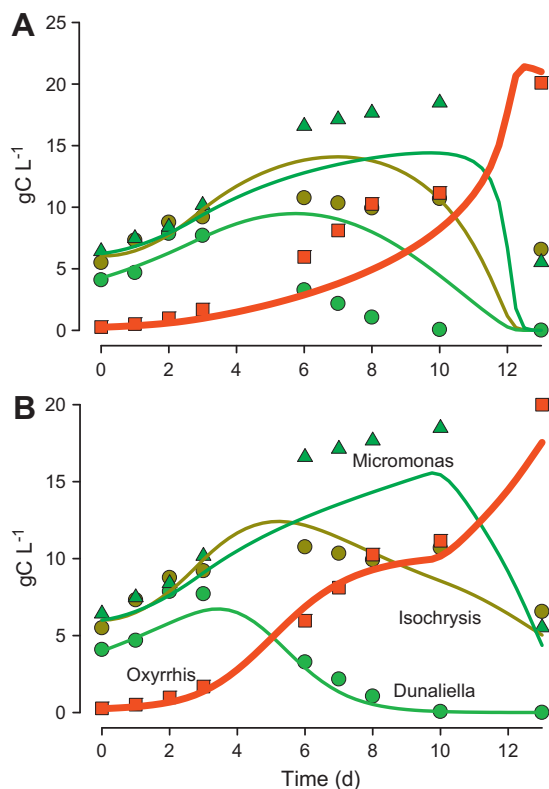


Fig. 4. Simulations of the grazing of the microzooplankton *Oxyrrhis marina* on the phytoplankters *Dunaliella primolecta*, *Isochrysis galbana* and *Micromonas pusilla*. Data (symbols) come from Fig. 5 in Flynn et al. (1996); model fits to data (lines) come from Fig. 5 in Mitra and Flynn (2006b). (A) Fits of the model using the prey selectivity function typically used in NPZ-type (e.g., Fasham et al., 1990) models. (B) Fits using the IS prey selectivity function proposed by Mitra and Flynn (2006b).

zone. As a result any inorganic nutrients ultimately liberated by microbial action on the voided organics will not necessarily be in the appropriate spatial or temporal frame to support algal growth as feed to the voiding zooplankton.

Field and laboratory studies of food processing

In protists, digestion occurs external to the main cell, or internally within digestive vacuoles (Öpik and Flynn, 1989; Hansen and Calado, 1999). External digestion may involve usage of a membranous feeding veil (e.g., thecate dinoflagellates, Jacobson and Anderson, 1986), or a peduncle to spear the prey and then withdraw the digestate back through the peduncle (Hansen and Calado, 1999); such adaptations enable microzooplankton to consume prey items that are bigger than themselves. Most non-protist zooplankton, in contrast, possess a digestive tract (gut) through which the ingested material passes and is digested by enzymes secreted by the different cell types lining different sections of the gut. A major advantage possessed by some protistan microzooplankton is their body plasticity. They have been found to accommodate food vacuoles throughout much of their volume (Öpik and Flynn, 1989; Roberts et al., 2011), increasing the initial cell volume several times (Calbet pers. obs.; Hansen, 1992), or to engulf large prey, such as diatom chains, several times their own body size (Nakamura et al., 1995; Saito et al., 2006; Calbet, 2008). The metazoan gut, in contrast, does not have such flexibility, though with some exceptions in the Cnidaria and Ctenophora phyla (Haddock, 2007; Pagès and Madin, 2010).

The period for retention of the ingested material within the digestive apparatus varies among microzooplankton. For example, *Oxyrrhis marina* has been observed to take as long as 3 days to

complete digestion of a single meal (Öpik and Flynn, 1989), while the digestion time of the heterotrichous marine ciliate *Fabrea salina* has been found to be ca. 70 min when presented with different prey concentrations (Capriulo and Degnan, 1991). In mesozooplankton the gut passage time (equivalent to the food vacuole processing time in a protist) is much faster in absolute terms (e.g., ~0.3 and 6 h, Besiktepe and Dam, 2002). The time it takes for the ingested material to pass through the gut is a function of the stoichiometric quality of the ingested prey as well as the quantity of food available in the environment. For example, the gut passage time of a mesozooplankton may increase (i.e., ingestate is held longer) in the presence of poor quality food to enable thorough digestion of the ingested material (e.g., Horn and Messer, 1992; Plath and Boersma, 2001). Alternatively, the gut passage time may decrease with low food quality or high food availability (Tirelli and Mayzaud, 2005; Dutz et al., 2008) and thence demonstrate density dependent inefficiency (Flynn, 2009). Such events are not unique to mesozooplankton, but occur across higher trophic levels such as yellow-rumped warblers and harbour seals (Afik and Karasov, 1995; Trumble and Castellini, 2005). In addition to the variability introduced by food quality and/or quantity, the gut transit time is also likely to be sensitive to incubation temperatures (Irigoien, 1998); one may expect protist food vacuole processing times to be similarly affected.

Even with optimal food quality, digestion and assimilation for any organism can never attain 100% efficiency. The assimilation efficiencies of micro- and meso-zooplankton have been found to vary widely from being as high as 60–95% to lower values of 10–20% (Landry, 1993; Thor and Wendt, 2010) dependent on food quality and quantity. At higher food concentrations, mesozooplankton are less efficient at assimilation (Corner et al., 1972; Head, 1992; Tirelli and Mayzaud, 2005; Thor and Wendt, 2010). The relatively lower assimilation efficiency observed in mesozooplankton compared with that of a microzooplankton may be attributed to the presence of a gut in the mesozooplankton and thus the inevitability of voiding material associated with the peristaltic gut functioning.

Low assimilation efficiency at high food availability does not adversely affect the individual grazer (though in time it may well affect the population). The critical issue is to maintain a high gradient of nutritional components across the gut wall or feeding vacuole membrane. That condition is best attained by having the gut or vacuole packed with only partly digested food, rather than retaining food and extracting every last useful molecule from it. Lehman (1976) reported that 95% of the demand could be met by a gut only 30% full. The activity does, however, have great potential for affecting ecosystem dynamics as the end product of the digestion/assimilation process would vary markedly (e.g., dense vs. loosely packed faecal pellets) depending on the rate of flow of ingested material through the gut (Mitra and Flynn, 2007; Flynn, 2009).

Due to biochemical constraints a consumer has to get rid of material in excess of what it requires for immediate use, for growth and (as applicable) for accumulating reserves such as oil. Thus food that is ingested and not assimilated is egested (voided). There is a suggestion that some zooplankton may “burn off” surplus ingested carbon (Darchambeau et al., 2003). However, this evidence comes from studies on *Daphnia*, which typically feed indiscriminately on phytoplankton species that accumulate excess carbon in the form of starch rather than lipid (such as in copepods feeding on diatoms). Lipid is less easily digested and metabolised compared to starch, so the respiration rate associated with “burning off” lipid will be relatively higher than when using starch. However, excess C (especially in the form of sugars) in the diet could conveniently compensate for the additional costs in hunting alternative, high quality, food.

Voided material includes particulate and dissolved organic components and their distribution depends on numerous factors including the balance of digestion and assimilation of ingested material, the gut/digestive vacuole transit rate, and the packaging of the faeces. For example, copepods may exhibit a short gut residence time coupled with high ingestion rates if food concentrations are high (Dagg and Walser, 1987) resulting in voiding of part-digested material. Such faecal pellets may sink and enter the benthic food web or may act as food for other copepods in the pelagic zone. Partly digested material has been found to act as food for mesozooplankton (Mauchline, 1998), as well as for microzooplankton (e.g., *Oxyrrhis marina*, Flynn and Davidson, 1993; *Gyrodinium dominans*, *Gyrodinium spirale*, *Diplopsalis lenticula*, *Protoperidinium depressum*, Poulsen et al., 2011), and some mixotrophic dinoflagellates in the absence of alternative prey items (Karlodinium armiger, and a gymnodinoid dinoflagellate, Poulsen et al., 2011). Some diatoms may pass through the gut of a zooplankton and upon defecation may still remain viable (Van Donk et al., 1997; Peterson and Jones, 2003); likewise cyanobacteria, such as *Synechococcus*, have also been found to be viable after passing through the gut of appendicularians (Gorsky et al., 1999). Subitaneous eggs and resting eggs of copepods have also been found to remain intact and viable after passage through fish guts (Bartholme et al., 2005).

Modelling descriptions of food processing

Traditionally consumer models are ingestion controlled for applications in ecology, or digestion controlled for use in aquaculture and animal husbandry (Mitra and Flynn, 2007). Rarely do they have an integrated representation of variable ingestion kinetics, digestion efficiency, and/or gut transit time with changes in food quality and/or quantity. Zooplankton models are typically ingestion controlled, with the primary, if not sole, kinetic interface being at feeding. Thus, for example, a fixed value for assimilation efficiency, irrespective of variations in food types, is typically assumed (akin to same maximum grazing rate assumed for all food types). Even where food quality is considered, this is related to stoichiometric differences between zooplankton and food at the point of assimilation and assimilation efficiency is typically assumed to be fixed (e.g., Sterner and Elser, 2002; Anderson et al., 2005).

If the food ingested is of poor nutritional value, a predator that possesses a gut has two options: (i) defecate it as fast as possible (with a high gut passage time), maintaining a high cross-gut membrane metabolite concentration and so increase the likelihood of absorption of compounds of value or, (ii) retain the food for a longer duration (with a low gut transit time) and thus ensure that digestion of the material is as complete as possible (Mitra and Flynn, 2005). In the former instance, the short gut residence time supports a high ingestion rate and a low assimilation efficiency. In the latter, the rate of assimilation would act as a feedback on ingestion slowing it down or even stopping it (Dagg and Walser, 1987) while assimilation efficiency is increased. These processes are modelled by Mitra and Flynn (2007), who presented a generic model for consumers with a gut describing the linkages between ingestion, digestion, assimilation and gut transit time as functions of food of varying quality and quantity. This model was validated against experimental data sets for marine copepods and freshwater cladocerans grazing on phytoplankton of different quality (i.e., N:C and P:C) and quantity. Ramifications for such events upon food web dynamics, as explored with models (Mitra and Flynn, 2007; Flynn, 2009), appear profound. In contrast to the broadly pro rata knock-on impact of increased primary production to higher trophic levels predicted by models with fixed assimilation efficiencies, these alternative simulations indicate a rapid conversion of excessive primary production to voided (waste, regenerated) material with a marked decrease in transfer efficiency.

In short, while experimental work shows the very real potential for variations in digestion dynamics to affect assimilation efficiency, these lines of evidence are not reflected by typical zooplankton models used in ecosystem studies. These continue to couple overly simple descriptions of feeding kinetics to, at best, stoichiometric-linked digestion functions with fixed assimilation efficiency. It is perhaps worth noting that possession of a high assimilation efficiency is not itself important to a consumer. The critical issue is the rate of transference of metabolites across the gut wall; there is in reality an important interaction between that driver, assimilation efficiency and ingestion rates (Mitra and Flynn, 2007) and thence to trophic dynamics (Flynn, 2009).

The form of voided material, the balance between POM and DOM, is typically either not modelled or assumed as a fixed ratio. In reality, it will vary with the nature of the food, with the predator type, and with gut transit time. This partitioning has important implications for trophic dynamics; POM may sink and represent food for other zooplankton while DOM is a resource for the microbial loop.

Excretion: respiration and nutrient regeneration

Respiration

Respiration is required to support the maintenance of homeostasis and to repair systems. Collectively these constitute basal, or resting, respiration. In addition there is respiration associated with anabolism, catabolism, growth and movement (e.g., swimming, vertical migration associated with prey capture and predator avoidance). Classically, interest in the respiratory rates of zooplanktonic organisms has been stimulated by interest in quantifying the energy requirements of copepods (as important representatives of the zooplankton community) and productivity of marine ecosystem and thence to gain a better understanding of ocean carbon cycling (Hernández-León and Ikeda, 2005). Overall, there is a substantial literature on respiration rates of planktonic copepods and crustacean in general, while very little is known about other zooplankton taxa (Ikeda et al., 2001; Hernández-León and Ikeda, 2005).

Field and experimental studies for respiration. In poikilothermic organisms, such as zooplankton, which have no thermal regulatory capacity, respiration rate is considered to vary mainly as a function of body size and external temperature (Peters, 1983; Ikeda et al., 2001) and a simple equation has been proposed to describe the metabolic rate of all organisms from “first principles”, using a combination of body mass scaling and classical statistical thermodynamics (Gillooly et al., 2001; Brown et al., 2004). The scaling of metabolic rate with body mass has long been a controversial topic (Gillooly et al., 2001; Brown et al., 2004; Glazier, 2006, 2010; Kolokotronis et al., 2010). Since the seminal work of Kleiber (1932) and Hemmingsen (1960) it has been generally assumed that the metabolic rate of most organisms, including animals, plants, and unicells increases as the body mass to the power $3/4$ (i.e. 0.75), intermediate proportionality between body weight and surface (Kleiber, 1932; Hemmingsen, 1960; Brown et al., 2004). The search for an explanation for this apparent universal exponent has led several authors to argue that the $3/4$ metabolic scaling is the result of the physical properties of internal resource–transport networks present in organisms, including the circulatory and respiratory systems (West et al., 1997; Banavar et al., 2010; West and Brown, 2005). However, recent theoretical and empirical research has questioned the $3/4$ -power law and the resource–transport network (RTN) models proposed to explain it, by showing that such models are based on questionable or unsubstantiated assumptions (Glazier, 2009; Kolokotronis et al., 2010; Agutter and Tuszyński, 2011). For instance, in a recent study, Kolokotronis et al. (2010)

have shown that the relationship between metabolic rate and body mass has a convex curvature on a logarithmic scale suggesting that this metabolic coefficient is highly sensitive to the body mass range used. Moreover, several comparative surveys of various animals and plants have demonstrated that intra- and interspecific values of the metabolic scaling often differ significantly from 3/4, varying from approximately 2/3 to 1 (e.g., Bokma, 2004; Glazier, 2005, 2010; White et al., 2006, 2007; Isaac and Carbone, 2010). Furthermore, recent studies suggest that the intraspecific metabolic-scaling exponent may be related to various ecological factors, including zooplankton activity, habitat, and temperature (Glazier, 2005, 2006, 2010). For instance Glazier (2006) reported that isometric scaling i.e. a metabolic scaling of 1, appears to be common in planktonic animals and argued that it probably represents an adaptation to the high-energy cost of continual swimming to stay afloat, rapid growth rates and reproductive rates in response to high levels of mortality in open water.

Other factors such as food availability, food quality and temperature acclimatisation also affect respiration (Conover and Corner, 1968; Butler et al., 1970; Kiørboe et al., 1985; Fenchel, 2005; Gaudy and Thibault-Botha, 2007; Castellani and Altunbaş, 2014). In addition, respiration rates vary between species and also within a species throughout the growth phase (Fenchel and Finlay, 1983; Kiørboe et al., 1985). Fig. 5 (recreated by transformation of data from Fenchel, 2005) demonstrates how the respiration rates of four different groups of microzooplankton change under food replete and deplete conditions. While under prey-replete conditions the “cell size” hypothesis appears to hold true, under prey deplete conditions, the respiration rates of the four groups appear to be more or less similar. Thus, it appears prudent to take into account the physiological state of the cell and environmental conditions and not just the cell size during measurement of respiration rates.

Respiration rates also depend on various physical factors such as swimming, turbulence and temperature in conjunction with the quantity of available food. At saturating food concentrations, zooplankton demonstrate high respiration rates a phenomenon known as Specific Dynamic Action (SDA) (Kiørboe et al., 1985). However, a decline in food availability often initially results in an increase in predatory activity; respiration increases with increasing swimming activity reaching a maximal value until starvation and fatigue sets in (Hernández-León and Ikeda, 2005). This increase may be further accentuated under high turbulence where the predator cannot easily find prey (Kiørboe and Saiz, 1995). Under starved conditions, zooplankton would be expected to only utilise energy necessary for survival resulting in low respiration rate values (Kiørboe et al., 1985). The increase in respiration rate of fed copepod, i.e. SDA,

has been shown to depend largely on protein biosynthesis (i.e. to growth and reproduction) and protein metabolism, rather than on the mechanical filtering and ingestion of the food (Kiørboe et al., 1985; Clarke and Fraser, 2004; Secor, 2009). Hence, several authors have proposed that seasonal changes in the oxygen consumption of poikilotherms including marine copepods could reflect seasonal changes in their growth and reproductive rates (Parry, 1983; Clarke, 1993; Castellani and Altunbaş, 2014). Results of a recent laboratory study have also shown that copepod respiration rate varies significantly with the quality of the food ingested probably as a result of changes in the biosynthetic activity of the organism (C. Castellani, personal communication).

Modelling descriptions for respiration. Steele and Mullin (1977) split respiration into three parts, (i) basal, (ii) foraging and/or capture cost, and, (iii) cost of transforming and assimilating food. The last two categories are often grouped as active respiration, and within models classed together as metabolic costs. Thus, typically respiration in (individual-based as well as ecosystem) models is considered as two components, basal and metabolic. Basal respiration is that part which is necessary for the survival of an organism; this includes all essential functions. Metabolic respiration costs occur in conjunction with metabolic functions (e.g., assimilation). It should be noted that what is usually measured experimentally is routine metabolism (i.e., basal + active) of starved organisms as it is physically difficult to separate these out. Models typically do not attempt to replicate changes in respiration rate with a downturn in food availability, as observed in nature (see above). A major impediment in the translation of empirical data to models is the basis of respiration measurements. Too often this relates oxygen consumption to animal size (length) while models typically require biomass-specific units, such as $C\ C^{-1}\ d^{-1}$.

The impacts of temperature on respiration rates are described further below (Section ‘External forcings: temperature, pH and turbulence’).

Nutrient regeneration

Zooplankton ingest food in the organic form, i.e., nutrients such as nitrogen and phosphorus, which are present in combination with carbon. A proportion, perhaps the bulk, of these elements is regenerated/excreted during catabolic respiration (Landry, 1993; Fenchel, 2005). We define the process of nutrient regeneration as the loss of nitrogen, phosphorus and others (notably iron, Fe) by the zooplankton in order to maintain its stoichiometric balance against the loss of carbon through respiration.

Field and experimental studies of nutrient regeneration. Regeneration of nitrogen (N) by the protist *Paraphysomonas* sp. has been observed to be low during starvation (Goldman and Dennett, 1992), consistent with the observed low (basal) respiration rates under similar conditions (Fenchel, 2005), while regeneration as well as respiration rates have been reported to be substantially higher during the active grazing phase. N, typically regenerated as ammonium (NH_4^+) during catabolism, cannot be accumulated in the zooplankton body (Hasegawa et al., 2001), but has to be excreted due to its toxic nature. This excreted NH_4^+ then supports primary production (Park et al., 1986; Bode et al., 2004). Phosphorus is typically released as phosphate (PO_4^{3-}) during catabolism, which unlike ammonium is not toxic, and can thus potentially be readily recycled internally.

Modelling descriptions of nutrient regeneration. Within classic N-based NPZ models (which do not describe carbon dynamics), nutrient regeneration is typically assigned a fixed constant; i.e., it is assumed that a fixed proportion of the ingested material is always excreted as ammonium (e.g., ϵ , Fig. 2). In multi-element models N

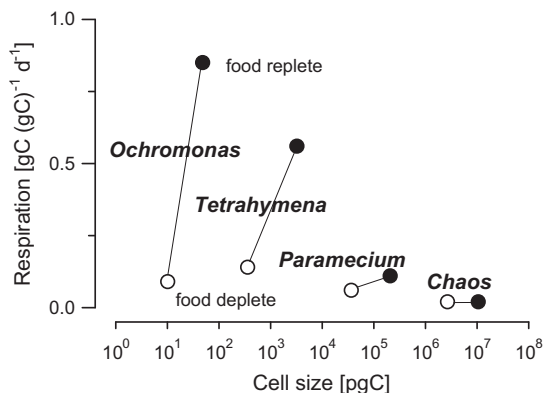


Fig. 5. Respiration rates ($gC\ (gC)^{-1}\ d^{-1}$) of microbial zooplankton of different cell size under starved conditions (open circle) and when presented with saturating food (closed circles); recreated by transformation of data in Fenchel (2005).

and P are regenerated to maintain (fixed) stoichiometric content of the zooplankton. Thus, for example, Mitra and Flynn (2007) describe nutrient regeneration as a function of the quality of ingested material. There are clear implications for trophic interactions if the prey stoichiometry is significantly poorer than that of the consumer (e.g., $N:C_{\text{prey}} < N:C_{\text{predator}}$). In such situations there is less release of N to support the next generations of phytoplankton, leading to a further deterioration in prey quality (i.e., low N:C) which in turn can lead to rejection of the low N:C phytoplankton by the zooplankton predator (Flynn and Davidson, 1993), resulting in a noxious phytoplankton and/or toxic algal bloom (Turner and Tester, 1997; Mitra and Flynn, 2006a). What is lacking in typical models of zooplankton, however, is a variable C:N:P ratio (e.g., for copepods storing lipids, Miller et al., 2000). Such events would affect nutrient regeneration both during lipid deposition and during consumption (respiration) of that lipid.

Zooplankton growth: growth and life cycles

Growth of the zooplankton is a function of ingestion, assimilation and the various loss processes. Life history strategies evolved as adaptive mechanisms to optimise zooplankton survival and proliferation and vary between constant environments and more variable, seasonal environments (Allan, 1976). Unique combinations of life history strategies, metabolic demands, and physiological performance determine the structure of pelagic food webs in an interplay of bottom-up processes (resource availability) and top-down control (predatory interactions) (Verity and Smetacek, 1996). During the life cycle of protist zooplankton allometric changes are limited to the approximate doubling and halving of cell volume (biomass). For non-protist zooplankton however, the range of organism size over the life cycle may cover many tens, hundreds, or even thousands of orders of magnitude. With this there are important allometric scaling events for every process mentioned previously (Atkinson and Hirst, 2007).

Associated with growth is development. The two processes of growth and development are decoupled on one hand but interdependent on the other. Thus, growth can be negative but development cannot. Likewise development can be arrested if growth is not at a critical level at that life stage.

Field and experimental studies of growth and life cycles

Because of the impracticability of measuring growth in the field over days and weeks, most field studies make snap-shot studies of individual growth rate (physiological) processes, and extrapolate these to estimate overall growth rates. The determination of growth rate from weight specific copepod egg production rate (i.e., egg gC female $\text{gC}^{-1} \text{d}^{-1}$; e.g., Kimmerer and McKinnon, 1987; Berggreen et al., 1988) or through an exponential model fit are prime examples. Even for microzooplankton, which may have generation times of around a day, growth rates are not determined by increases in whole organism biomass. Only in mesocosms may whole life cycles be followed. In consequence, there are remarkably few studies of zooplankton growth over a prolonged period where changes in C, N, P biomass has been followed, in addition to age and size-structure, as is required to properly test and validate models. Where growth rates have been estimated from experimentation, the methods of estimation (specifically for copepods) have received significant criticism (Hirst et al., 2005).

All organisms have a maximum possible growth rate at a specific temperature, and an absolute maximum possible growth rate, though for long-lived species the optimum temperature may differ for each/with age class. This maximum growth rate can be achieved when good quality food is present in high quantity in the environment such that there is an excess of nutritious ingestate within the zooplankton digestive vacuole/gut after accounting for all the losses

incurred by the predator (i.e., respiration, regeneration, etc.). A zooplankton may optimise its growth rate through enhancing its assimilation rate by altering its rates of ingestion, gut transit and/or voiding (Mitra and Flynn, 2005) depending on the quality and quantity of prey available (Section 'Food processing: gut transit time, digestion, assimilation and voiding'). However, in reality, typically it may not be possible to reach, let alone maintain, the absolute maximum rate due to: (i) the lack of sufficient food, (ii) competition for resources between different organisms, (iii) presence of unfavourable food in nature, and/or, (iv) unfavourable physical and/or chemical conditions (e.g., pH, temperature, salinity).

For survival under food limiting conditions, zooplankton may resort to consumption of storage lipids (Lee et al., 2006) or to different survival strategies such as formation of resting spores or cysts (microzooplankton: Rubino et al., 2000; hydrozoa: Boero et al., 2008) and diapause (copepods: Mauchline, 1998). During periods of food satiation, *Calanus* accumulates lipid, mostly in the form of wax esters along their prosome (Miller et al., 2000). These lipid reserves are thought to be used not only as an energy store throughout the non-feeding period, but also for gonad development and reproduction in spring (Tande, 1982; Richardson et al., 1999). More recent research proposes a new perspective on the role of lipids in zooplankton, suggesting that solid-liquid phase transitions of lipids are factors regulating their buoyancy and also controlling the life cycles of calanoid copepods that diapause (Pond and Tarling, 2011; Pond, 2012).

In the event of declining food availability zooplankton may decrease their respiration rate resulting in a decline in the carbon turnover preventing the organism from respiring itself to death (Fenchel, 2005). However, the respiration rate can only decline to a certain minimal value; if unfavourable conditions persist, the organism would form cysts and as there are no (or minimal) respiratory or excretory losses associated with cysts or diapause eggs they can thus remain viable for long periods of time. Excystment and hatching occurs in the advent of favourable conditions and, after a lag phase (required for revitalisation of the enzyme system), the organism starts to prepare for growth/division/reproduction (Mauchline, 1998; Fenchel, 2005).

Many species of the *Calanus* genus undergo a resting-phase, usually during the CV copepodite stage (Miller et al., 1991; Hirche, 1983; Heath and Jónasdóttir, 1999). When there is a shortage of food in the surface waters (typically in winter), the CV copepodites descend into deeper colder water (200–2000 m). Here it is believed they enter into a state of diapause where they cease to feed and have a decreased metabolic rate and respiration (Hallberg and Hirche, 1980; Ingvarsdóttir et al., 1999).

Diapause has been defined as a programme of arrested development or ontogeny coupled with physiological changes to ensure survival through adverse environmental conditions; this does not necessarily confer immunity from predation (Davies et al., 2013). It is not however an immediate response to the result of these unfavourable conditions, but rather, is cued by some factor that normally precedes the deterioration of these environmental factors, and is ultimately genetically determined. Many calanoid copepod species also produce diapause resting eggs that lie dormant in the benthos when the environmental conditions are unfavourable for development (Grice and Marcus, 1981; Engel and Hirche, 2004). While copepods typically form diapause eggs, encystment has also been observed in the marine copepod *Heteropsyllus nunni* (Coull and Grant, 1981).

To optimise the timing of life cycle traits, such as growth, reproduction and dormancy, many species synchronise their physiology to environmental clues. Many examples for polar and temperate settings are available, especially for copepods, and range from highly seasonally tuned ontogenetic cycles at high latitudes (e.g., Conover and Huntley, 1991; Schnack-Schiel, 2001) to continuous

life cycles with many generations per year (e.g., Halsband and Hirche, 2001; Halsband-Lenk et al., 2004).

Modelling descriptions of growth and life cycles

Growth rates, and specifically maximum growth rates, are key parameters in zooplankton models. However, in classic NPZ models (e.g., Fasham et al., 1990) as typically used in ecosystem studies, zooplankton growth is limited (fixed) by the parameter defining the maximum grazing rate (G_{\max} in Fig. 2). Maximum growth rate in these models is, therefore, a function of grazing kinetics, offset by a series of constants summarising assimilation, voiding and regeneration, with no recognition of any of the internal feedback processes that occur in reality. Often such descriptions are deployed, with common constant parameter values, across large sectors of the simulated ocean, with scant regard for biogeographic and seasonal variation.

Most models of zooplankton life cycles focus on calanoid copepods, including key species of the *Calanus* complex. They range from conceptual descriptions based on seasonal or multi-annual field sampling (Peterson, 1999; Halsband-Lenk et al., 2004) to individual- or stage-based models with or without coupling to oceanographic models or ecosystem models (Fiksen and Carlotti, 1998; Carlotti and Wolf, 1998; Zakardjian et al., 2003; Varpe et al., 2007). Descriptions of life cycle components with stage and allometric-linked implications are also rare. This is despite the importance of the dynamics of egg production, mortality-at-stage variations, etc. This can be seen clearly in the work of Flynn and Irigoien (2009), modelling the potential impact of polyunsaturated aldehyde (PUA) on copepod nauplii survival from consumption of diatoms.

Another notable oversimplification in zooplankton models which has various important ramifications, is the assumption that the zooplankton C:N:P ratios are constant. Clearly, in copepods that accumulate lipid that is not so. This then affects simulations of nutrient regeneration and also of mortality due to respiration in the absence of food (see above; Acheampong et al., 2012).

Zooplankton mortality

Zooplankton mortality is the death of individuals and loss of their associated biomass due to predation, starvation, inhospitable environments, or natural death from senescence, genetic malfunction, disease, viral attacks, etc. (Carlotti et al., 2000; ICES WKMOR Report, 2010). Whatever the mechanism, mortality is a key process that shapes zooplankton dynamics. Modelling studies have repeatedly illustrated how small changes in mortality translate to large changes in modelled abundance and production (e.g., Steele and Henderson, 1981, 1992, 1995; Twombly, 1994; Ohman and Wood, 1995; Lynch et al., 1998; Speirs et al., 2006; Neuheimer et al., 2009, 2010a,b; Skarðhamar et al., 2011). Further evidence of the importance of mortality is that various aspects of zooplankton migration behaviour (daily and seasonally), life history and reproductive strategies are believed to be adaptations that minimise mortality risk (Kaartvedt, 1996; Ohman et al., 1996; Hays, 2003; Leising et al., 2005c). For example, diel vertical migrations are believed to be a strategy for decreasing visual predation during the day light hours (Cohen and Forward, 2009); likewise, the egg-carrying strategy of cyclopoid copepods has been found to result in lower mortality rates of the eggs compared to suspended eggs spawned by the calanoid copepods (Kiørboe and Sabatini, 1994). During unfavourable periods when food resources are in short supply and the probability of survivorship is decreased, many species have developed adaptations such as production of resting eggs or a diapause in late developmental stages. Diapause itself is correlated with an ontogenic vertical migration, which similarly to diel migrations, is thought to be a mechanism to decrease visual

predation (Cf. Davies et al., 2013). For the most researched copepod, *C. finmarchicus*, studies indicate that mortality of the diapausing population during the overwintering period is much lower than during the growth period of the species (Bagøien et al., 2001; Gislason et al., 2007). The relatively low mortality at depth has been attributed to decreased predation; the dark habitat provides shelter from visually guided predators, and the non-mobile diapause stages minimise encounters with predators that rely upon mechano-reception (Kaartvedt, 1996; Hirche, 1997; Fiksen and Giske, 1995; Fiksen and Carlotti, 1998; Bagøien et al., 2001). It should be noted, however, that some predator species have adapted to exploit the diapausing zooplankton populations; for example, the North Atlantic right whales have been observed to feed on the diapausing *Calanus finmarchicus* (Baumgartner et al., 2003).

Causes of mortality

Predation. Predation, which includes cannibalism of copepod eggs and nauplii by older copepodites (Ohman and Hirche, 2001; Hirst and Kiørboe, 2002; Ohman et al., 2008; Neuheimer et al., 2009), typically dominates mortality losses (e.g., Hirst et al., 2010; ICES WKMOR Report, 2010), with estimated rates not uncommonly exceeding 100% per day. Predation is arguably the most complicated mortality mechanism to characterise as it depends on the abundance and consumption rates of the predator, both of which are synergistically coupled and influenced by various external (environmental) and internal (fitness) factors. Predator consumption rates depend on the ability of the predator to detect, attack and successfully capture their zooplankton prey which in turn varies with the type, size, age, quality and quantity of the zooplankton as well as other factors, such as the activity of competing members of the predator guild. All these dependencies are neither simple to measure nor easy to parameterize in models (see below). Predatory losses observed in the field are usually inter-specific. Examples include: copepods grazing on microzooplankton (Verity and Paffenhöfer, 1996), fish feeding on copepod eggs (Mauchline, 1998), various chaetognath and krill species feeding on copepods (Ohman, 1986; Båmstedt and Karlson, 1998; Tönnesson and Tiselius, 2005; Bonnet et al., 2010), jellyfish preying on zooplankton and fish (Mackie et al., 1987; Purcell and Arai, 2001), etc.

Cannibalism within a species has been noted to occur in both micro- and mesozooplankton, even in the presence of abundant potential prey alternatives. For example, in laboratory experiments, the microzooplankton *Oxyrrhis marina* has been found to demonstrate cannibalism whilst rejecting the phytoplankton *Isochrysis galbana* due to its poor quality (Flynn et al., 1996), while the adult copepod *Sinocalanus tenellus* has been found to cannibalise on its naupliar stages despite the presence of other palatable prey items (Hada and Uye, 1991). Ohman and Hirche (2001) found that egg mortality in the copepod species *Calanus finmarchicus* was directly related to the abundance of females in the population and concluded that this may be a self-regulating mechanism. However, *Temora longicornis* (copepod) have been reported to cannibalise on their naupliar stages only when alternative (algal) prey items are limiting (Daan et al., 1988). In some instances cannibalism has been found to occur simply as a reflection of high concentrations of the predator, as exhibited by the dinoflagellate *Prorocentrum* spp. (Jeong and Latz, 1994). Such intraguild predation may occur when the maximum carrying capacity of the ecosystem has been reached.

Predation of zooplankton is the process by which nutrients and energy are transferred to the higher trophic levels. Therefore, accurate estimates of mortality rates are essential for understanding zooplankton ecology, trophic links, ecosystem dynamics, and for predicting ecological responses to climate-related changes in the environment.

Non-predatory losses. Non-predatory losses can also be significant, accounting for as much as one third of copepod mortality globally (Hirst and Kiørboe, 2002). Starvation may be more important for smaller zooplankton that have limited ability to store reserves (e.g., copepod nauplii vs. copepodites; Elliott and Tang, 2011; Tsuda, 1994). Estimates of copepod egg mortality, also referred to as non-viability or non-hatching of eggs, is regularly on the order of 10–20% (Irigoien et al., 2002) but can sometimes be as high as 90% (Miralto et al., 1999). This is typically attributed to effects of poor female diet or condition (Jónasdóttir et al., 2009). Starvation is not relevant for non-feeding stages (e.g., *Calanus* N1–N2 and males). However, the first feeding stage (N3) and the first copepodite stage C1 are critical points in ontogeny (Peterson, 2001); and higher mortality for these critical stages has been observed (Eiane and Ohman, 2004). Lack of food or poor food quality can often affect ontogenetic growth and development (Koski et al., 1998) leading to higher mortality rates. To what extent these fatalities are due to bacterial or fungal infections, inborn errors in metabolism, intrinsic biochemical failures, or directly due to the lack of adequate food is not clear.

Mortality due to environmental factors. Environmental influences on mortality can be complicated and far-reaching. Their indirect influence affects predator guild size and composition, and behavioural factors related to predator consumption rates (e.g., predator and prey condition, prey motility, etc.). Higher water temperatures often correlate with increased mortality rates (Hirst and Kiørboe, 2002; Plourde et al., 2009); this may be a causal relationship (i.e., temperature tolerance is exceeded; the upper limits are unknown for most species). However, it is more generally believed that temperature serves as a proxy for other processes. Higher temperatures can cause or be associated with various factors, including increased disease and parasitism (Harvell et al., 2002), starvation risk (Tsuda, 1994), hypoxic conditions (Stalder and Marcus, 1997; Tiselius et al., 2008), decreased life span or changes in predator abundance and predation rate (Myers and Runge, 1983).

Estimating zooplankton mortality in the field and laboratory

Field estimates. Field estimates of zooplankton mortality are usually derived from observational data for zooplankton abundances and additional information about their population dynamics, such as reproduction and developmental rates. Most estimation methods are formulae that are based on an underlying conceptual model of zooplankton population dynamics, and therefore it is somewhat difficult to separate field studies from modelling studies. Furthermore, various errors associated with mortality estimation methods could arise due to (i) uncertainty in the values of input variables used in the formula and/or (ii) violations of the assumptions used to derive the formula. It is thus necessary to take into account both these issues in order to avoid introduction of unknown bias into the mortality estimates, or application of formulae that are inappropriate. In a comprehensive analyses using theoretical studies, field data, and individual-based population dynamics modelling, Gentleman et al. (2012) examined the importance of these issues for estimating stage-dependent mortality of copepods, identified limitations of certain existing methods, and made recommendations on how best to increase accuracy in the estimation of mortality rates under different conditions. Such information is important in order to provide realistic confidence intervals for estimates (e.g., Bi et al., 2011) as pooling data from different regions, time intervals and/or across life stages (such as is necessary when there are missing stages in the data) is likely to be inappropriate and limit mortality estimates due to differences in the population stage structure. Gentleman et al. (2012) concluded that there is a need to work towards development of new methods that are less restrictive and which could make use of

dynamic simulations, for example, to identify potential temperature and food variability as well as advective sources and losses.

Laboratory estimates. Field studies are based on observations of the survivors, and therefore, estimate losses due to multiple mortality mechanisms, as well as (often unintentionally) other losses including sinking, advection, etc. In contrast, laboratory studies are generally directed as quantifying mortality due to a single mechanism, typically predation by one predator species on one prey type. These experiments typically use a limited number of predators exposed to a restricted type of prey, and measure loss rates after a set period of time (Sell et al., 2001). Mortality is typically reported as a predator clearance rate; i.e., fraction of the prey population consumed per capita predator. Thus, in theory, laboratory studies provide a measure of predation losses when the size of the prey and predator populations in the field is known. The issue with such studies of course is that they have limited variability, and cannot usually account for any behavioural changes in the predator which could occur in the presence of mixtures of prey types, variable environmental conditions and/or competing predator species. Moreover, the laboratory estimates only typically account for predation, and not other mortality mechanisms (e.g., starvation). Thus it may not be appropriate to simply scale up laboratory measurements of predation to estimate field mortality.

In conclusion, it can be difficult to get realistic mortality estimates from field, laboratory or mesocosm studies; it is thus essential to use all the available approaches, field and laboratory based, in conjunction with modelling.

Modelling studies of zooplankton mortality

It is generally acknowledged that mortality rates are the most uncertain parameter in models, and as such, it is common practice to either (i) assign some particular value and perform the simulation, potentially including post hoc sensitivity analyses, or (ii) use observational data to constrain model abundances and biomass, and tune the mortality-related parameters such that the model results reasonably match the data. The latter practice is a form of parameter estimation (also called inverse modelling, data assimilation), which can either be done by trial and error or by a more automated approach using sophisticated modelling techniques (e.g., effectively creating a “shooting method” solution to the boundary value problem) that sometimes are designed to measure uncertainty (e.g., Monte-Carlo methods or genetic optimisation algorithms).

If described at all, intrinsic mortality (i.e., non-predatory losses, death due to environmental factors) within ecosystem models is typically applied at set rates at different age stages (e.g., Flynn and Irigoien, 2009). Modelling of predation on zooplankton is similar in scope, and thus in limitations, to approaches used to describe zooplankton predation on lower trophic levels. It is rare that the fate or activity of specific groups of zooplankton are modelled. More often whole groups, if not all zooplankton, are merged into what could be viewed as a closure term on the phytoplankton and bacteria (in biogeochemical models). By the same token, predation on zooplankton *per se* is not often modelled, rather a closure term is applied; closure implies some kind of functional response of the predators coupled with an assumed time-variation of the predators.

In ecosystems models where zooplankton mortality is explicitly considered (rather than resorting to a closure term), it is often represented as a loss term to zooplankton variables, Z , that represent the biomass or abundance of a particular group (e.g., age, stage, size-class of a population, or community/functional type), or as a probabilistic risk of death for individual-based population dynamics models. There is a disconnect between how models characterise these loss terms/risks and the zooplankton mortality mechanisms

outlined above (Section ‘Zooplankton mortality’) mainly due to the challenges of characterising predation-related mortality. It is impractical if not impossible for models to explicitly account for all the factors affecting zooplankton mortality. To do so would require realistic simulation of the dynamics of all higher predators in the predator guild as well as quantifying numerous dependencies and behaviours of both prey and predator and for which the functional relationships are generally unknown; in addition to quantifying all non-predation mortality mechanisms. Thus, representation of mortality in models is always a gross simplification, and is therefore always a source of uncertainty.

The choice of mathematical form for the mortality loss/risk term depends to some extent on the model structure. For models that explicitly include higher predator abundances, either as dynamic variables or forcings, predation mortality is described as the product of predator abundance and predator functional response using analogous formulations for zooplankton grazing. However, most zooplankton models (both population and lower trophic ecosystem) do not explicitly account for higher predators, and so must proxy the effects of predation along with other mortality mechanisms as part of the closure term. For models using differential equations, closure is usually characterised by an instantaneous loss rate that varies with Z , according to linear, quadratic, hyperbolic or sigmoidal relationships (Fig. 6). For models using differential equations, the mortality loss over the time step is typically defined by assuming a linear closure with constant mortality coefficient, such that survivorship at the end of the model time step is given by:

$$Z(t + \Delta t) = Z(t)e^{-\mu\Delta t}$$

where Δt denotes change in time and μ is the rate of loss.

The linear and quadratic variations are the two most common formulations and can be construed as predation mortality for a constant-biomass predator exhibiting non-satiating Type 1 vs. Type 3 functional response (Gentleman and Neuheimer, 2008). The quadratic formulation can also be argued to represent cannibalism or intraguild predation, for which the predator biomass that is proportional to Z , and the predators, exhibit a non-satiating Type 1 functional response. For individual based models, the probability of survival ($1 - \text{probability of dying}$) during the interval $[t, t + \Delta t]$ is similarly based on a constant mortality (Gentleman et al., 2012) described as:

$$P_{\text{survive}} = e^{-\mu\Delta t}$$

There are a number of issues related to the above approaches to modelling mortality. First, the choice of closure scheme is generally based on theoretical arguments rather than specific mechanisms or observations. Thus, the closure term typically lumps all the

processes leading to mortality (internal and external) into a single process; the interactions between mortality and other physiological processes as well as feedback mechanisms of these vital rates on mortality rates (Fig. 2), innate to biological systems, are ignored. However, there are many studies demonstrating how this unsupported choice has a pronounced effect on trophic dynamics and ecological stability (e.g., Steele and Henderson, 1981, 1992; Edwards and Yool, 2000; Fulton et al., 2003). Choice of value for the coefficients in any particular closure scheme can have similar effects on ecological stability (e.g., Neubert et al., 2004), yet parameter values are often taken from previous modelling studies without any observation support of these values (Plagányi, 2007). Moreover the influences of environmental factors (e.g., temperature, food, etc.) on mortality-related coefficients vary among modelling studies. Many ignore variation, and those that do consider environmental dependencies are typically limited to temperature, choosing to apply a similar Q_{10} to that applied to all other rates. However, evidence indicates that this is likely inappropriate as field estimates of Q_{10} for mortality have been observed to be significantly greater than for growth/development (e.g., Q_{10} growth/development Calanus = 2–3 vs. Q_{10} mortality = 8; Campbell et al., 2001; Plourde et al., 2009) (temperature is considered further in Section ‘Temperature’).

Another issue relates to the necessity of partitioning the total mortality loss into different components (e.g., natural death vs. predation), which itself is often done with an arbitrary parameter; despite this partitioning being critical for estimating the proportion of secondary production that is passed to trophic levels vs. that which is designated to detrital pools that sink from the surface waters (i.e. contributes to export production).

What these models do demonstrate though, similar to zooplankton feeding models, is that the incorporation of even biologically-simplistic formulations of mortality have the potential to destabilize the system or predict very different population dynamics. However, based on the very significant flow of energy and materials within the zooplankton component itself (Fig. 1; Table 1), one may question the validity of using these closure terms. The activity within the zooplanktonic community is so great that it may be more prudent to replace the traditional closure term applied to the zooplankton compartment (which is intended in large measure to summarise the top-down control levied by the higher trophic levels) with an intraguild cannibalism term (Mitra, 2009).

External forcings: temperature, pH and turbulence

Temperature

Temperature is probably the major external physical force affecting physiological processes of zooplankton growth. Typically the influence of temperature is characterised by a Q_{10} factor, which describes the relative change in a vital rate, r , due to a 10 degree increase in temperature; i.e., $\frac{r(T+10)}{r(T)} = Q_{10}$. For most physiological rates, a Q_{10} of ca. 2–3 is usually applicable. However, Q_{10} varies between organisms, and can also differ between physiological functions of the same organism. As noted above (Section ‘Modelling studies of zooplankton mortality’), Q_{10} for mortality rates can be higher than those for physiological rates, likely because these mortalities combine numerous factors that are each influenced by temperature.

Field and experimental studies of temperature. Impacts of temperature on zooplankton growth and respiration rates are relatively well studied (Ikeda et al., 2001; Hernández-León and Ikeda, 2005; Castellani et al., 2005b; Castellani and Altunbaş, 2014) although the physiological mechanisms through which temperature affects metabolism may not always be clear (Clarke and

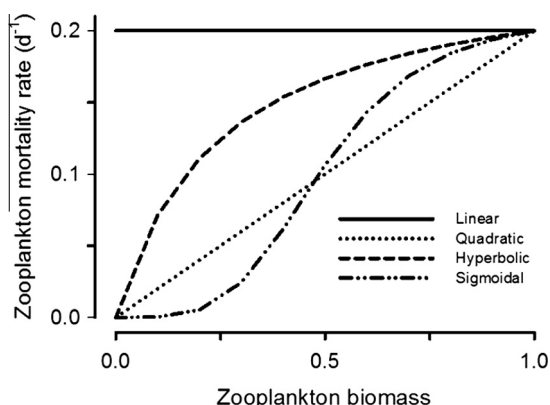


Fig. 6. Examples of the different curve forms of closure functions.

Fraser, 2004). Temperature affects all phases of zooplankton growth and life cycle; for example, feeding (Møller et al., 2012) and reproduction (Holste et al., 2008; Kjellerup et al., 2012) vary between and within species as well as between biogeographic locations. Increase in temperature typically implies an increase in the physiological processes, eventually reaching a maximum limit beyond which the zooplankton systems become damaged (e.g., respiration; Fenchel, 2005; Hernández-León and Ikeda, 2005). Increasing environmental temperatures induce decreasing body size due to differential responses of development rate vs. somatic growth, resulting in different potential reproductive output (Halsband and Hirche, 2001; Arendt et al., 2005; Jónasdóttir et al., 2005). Conspecifics tend to be smaller in warmer locations (Deevey, 1960) with shorter generation times and lower per capita reproduction rates, but in compensation produce more generations per year (Halsband-Lenk et al., 2002).

It has been suggested that a zooplankton species may acclimatise to varying seasonal temperatures (Carlotti et al., 2000) by altering their ingestion rates (Thébault, 1985; Saiz and Calbet, 2007; Møller et al., 2012), gut clearance rates (Dam and Peterson, 1988), and/or basal as well as metabolic respiration rates. A recent study by Castellani and Altunbaş (2014) reported that the seasonal changes in the acclimatised respiration rate of the copepod *T. longicornis* with *in situ* temperature was described by a sigmoid trend with Q_{10} ranging from 1 to 2.88; they attributed such variation to copepod nutritional and reproductive state. Saborowski et al. (2002) investigated temperature effects on respiration rates in the krill *Meganyctiphanes norvegica* from three geographically separate populations; Kattegat, the Clyde Sea and the Ligurian Sea. These three populations experienced differences in spatio-temporal temperature variation, together with differences in trophic conditions. It was found that the respiration rates among these three different populations were similar when incubated at their respective ambient temperature conditions (9 °C, 5 °C and 12 °C for Kattegat, the Clyde Sea and the Ligurian Sea, respectively). This suggests that krill are able to adjust their metabolic rate to the prevailing thermal conditions. On the other hand, certain vital rates seem to require specific temperatures, irrespective of location and temperature regime. For example, temperature responses of the female *Centropages typicus* for survival, embryonic and post-embryonic development vary between populations in the boreal North Sea and the sub-tropical Mediterranean, while the optimum temperature for egg production is the same in both regions and also in different seasons within the same region (Halsband-Lenk et al., 2002).

Ecologist and physiologists have long been interested in the way zooplankton metabolism (usually measured as oxygen uptake) reacts to the changing of the seasons and to the varying of ecological conditions at different latitudes (Cossins and Bowler, 1987). In particular numerous studies have looked at the effect of temperature by comparing the Metabolism–Temperature curve (i.e., M–T curve) of zooplankton for different seasons (Gaudy and Thibault-Botha, 2007) or from different latitudes (Ikeda, 1985). However, in the field zooplankton metabolism is also affected by changes in body size, nutritional history (food availability/quality), activity, growth and reproduction; seasonal and latitudinal fluctuations in respiration should thus not be interpreted simply as the effect of temperature (Clarke, 1993).

From the perspective of zooplankton communities, it has been argued that the effect of temperature on the growth of the total community *per se* may be negligible or even zero (Hirst and Lampitt, 1998); while specific species are adapted to live under specific temperature regimes, different species will dominate under different temperature conditions. Thus the specific populations may fluctuate, however, the community as a whole would not undergo any significant changes. It has been proposed that

the succession of zooplankton may be dependent on the variations in the temperature (Adrian and Deneke, 1996; Calbet et al., 2001). All this continuing effort on zooplankton temperature-related physiology contrasts with that on temperature relationships for phytoplankton, which typically refer back to classic papers such as Eppley (1972), or to the recent modification thereof (Bissinger et al., 2008). In consequence, the information about the impacts of subtle changes in temperature on zooplankton is probably more complete than that for their phytoplanktonic prey.

Modelling descriptions involving temperature. In modelling studies the impact of temperature on zooplankton is typically described through the use of an averaged Q_{10} value. However, it has been argued that the impact of temperature would vary for the different physiological functions (Carlotti and Poggiale, 2010) and also for the different developmental stages (Campbell et al., 2001); indeed some (very few) models do incorporate a non-linear function describing the relationship between zooplankton physiology and temperature (Travers et al., 2007). Moreover, Q_{10} values only apply for part of the range actually experienced by the organisms (Møller et al., 2012). Existing stoichiometric models of zooplankton could be configured to consider the effects of temperature on these processes. For example, within the model of Mitra and Flynn (2007), the maximum growth rate and respiration rates could be described as functions of temperature. However, as the different zooplankton physiological processes may not vary *pro rata* with alterations in the temperature, but show significant differences in the rates of changes, such an inclusion is not without dangers, especially as the lethal temperature is approached.

Various empirical models, specifically focussed on copepods, have been proposed to describe the relationships between temperature, development and growth (see Hirst and Lampitt, 1998 and references therein) as well as temperature and mortality (see Hirst and Kiørboe, 2002 and references therein). Embryonic and post-embryonic development generally is described with the Bělehrádek empirical equation that varies with the local temperature regime (McLaren, 1965, Table 47 in Mauchline, 1998) although it has been shown that this function is not drastically different from using a Q_{10} value (Gentleman et al., 2008). Vital rate descriptors incorporating Q_{10} or Bělehrádek's equation do not include a maximum temperature beyond which metabolic activities will stop (so the vital rates increase with increases in temperature). An additional concern is that egg production rates are often modelled using Q_{10} or Bělehrádek descriptors even when there is no clear evidence of temperature dependency, or when such dependency is observed, the relationships do not translate from one region to another for the same species (Gentleman pers obs).

Given that most zooplankton models in ecosystems describe whole Z communities, the Hirst and Lampitt (1998) view (see above) may be quite acceptable, that there is no significant impact of temperature. However, it is more difficult to accept such an argument in end-to-end models where specific fish are dependent on specific zooplankton, both/all of which will certainly respond differentially to temperature.

pH

Since the beginning of industrialisation, in ca. 1750, the CO_2 content in the atmosphere has increased from 280 ppm to 380 ppm early into the 21st century (Feely et al., 2004; IPCC, 2007), and has now exceeded 400 ppm. Approximately 1/3rd of the C released into the atmosphere by the burning of fossil fuels is absorbed into the oceans, and this dissolution decreases the pH of seawater. This effect is known as ocean acidification (OA; Royal Society London, 2005). Cellular homeostasis depends on the maintenance of proton (H^+) gradients and may thus be expected to be affected by OA, while under decreased pH conditions, the solubility of calcium and its

derivatives increases threatening organisms that contain calcite or aragonite.

Field and experimental studies of pH. In the pelagic zone, the most endangered zooplankton species appear to be the thecosomatic pteropods. Pteropods are holoplanktonic zooplankton which mainly live in the open ocean (Bé and Gilmer, 1977). Some groups of them build an aragonite shell. Experimental evidence has shown that the shells of these organisms are damaged under high CO₂ concentrations (Orr et al., 2005) and that physiological activities are enhanced to cope with such high CO₂ concentrations (Maas et al., 2012).

Zhang et al. (2011) have shown through a comparative study on toxicity of OA on several marine copepods that benthic copepods are more resilient than pelagic species, and that herbivores such as *Calanus sinicus* are more tolerant than omnivorous and carnivorous copepods. Low pH has been found to induce reproductive failure due to a decline in egg hatching success (Mayor et al., 2007; Kurihara and Ishimatsu, 2008). It has been suggested that zooplankton, such as jellyfish, may benefit from acidified conditions when competing with other, more sensitive species (Atrill et al., 2007). The impact of pH on the aquatic community and thence zooplankton is a new area of research; thus there are insufficient data (from observations and experiments) to enable the validation of such hypotheses (Richardson and Gibbons, 2008).

Modelling descriptions involving pH. While pH is increasingly included as a parameter in models of marine ecosystems (e.g., Artioli et al., 2012), models specifically relating changes in plankton physiology with pH are rare. Physiologically, the critical issue is not the pH of the bulk water (which is the parameter value reported in ecosystem models, and that typically measured in experimental studies), but of the water immediately surrounding the organism. In a recent modelling study, Flynn et al. (2012) show for plankton how the acidity (i.e., [H⁺]) next to the organism varies with particle size and metabolic activity, and also with the initial bulk water [H⁺]. The larger and more active the zooplankton the greater the [H⁺] increase over the bulk water values (i.e., large active organisms experience more extreme OA conditions). However, the consequences are likely mitigated by large animals having lower surface area to volume ratios so that external conditions have less leverage on internal homeostasis. Also, these zooplankton will have evolved to survive a more variable external [H⁺]. The real issue is that with OA the buffering capacity of the water decreases so that deviations in [H⁺] become larger for a given level of metabolic activity. As algal blooms (temporarily) raise local pH, clearly there is scope for differential impacts of OA on zooplankton of different size, activity and skeletal structure under different trophic interactions.

Aside from the effects of global change on pH, the consequences of natural increases of pH during dense phytoplankton blooms, promoted in many occasions by human activities (notably eutrophication), are seldom considered. In this regard, it has been suggested that high pH could be detrimental for many dinoflagellates and ciliates (Pedersen and Hansen, 2003a,b; Hansen et al., 2007).

Turbulence

Field and experimental studies of turbulence. The likelihood of a zooplankton encountering food or prey is a function of the water turbulence, irrespective of the quality and quantity of food available. While a low level of turbulence may increase the likelihood of encountering prey, a higher level of turbulence would be detrimental to the predator (Saiz et al., 1992; Havskum, 2003; Metcalfe et al., 2004). Turbulence may also set physical limits on the ability of copepods to be at a preferred depth, and hence may explain the presence of nauplii in areas with low levels of turbulence

(Maar et al., 2003) that would then impact upon transport, growth opportunities and thence trophic dynamics. The thresholds at which turbulence has effects on plankton are highly species specific, and respond to the feeding mechanisms involved in capture of prey. For instance, the feeding rates of the ambush copepods *Oithona davisae* appeared to be much more impaired by turbulence than other species (Saiz et al., 2003). This result agrees with field observations of *Oithona* sp. occurring deep in the water column under episodes of high surface turbulence (Incze et al., 2001; Visser et al., 2001).

Regarding protozoans, experiments with the ciliate *Strombidium sulcatum* suggest a negative effect of turbulence on growth and grazing rates. Conversely, *O. marina* decreased their size under turbulence, but increased their growth rates (Saiz et al., 2003), although Havskum (2003) found the effects of turbulence on this species were highly dependent on the turbulent intensity applied. Other dinoflagellates are more sensitive to turbulence, such as the case of *Pfiesteria piscicida* (Stoecker et al., 2006), and the primarily phototrophic *Ceratium tripos* (Havskum et al., 2005).

Modelling descriptions involving turbulence. There are various mathematical models exploring how turbulence impacts the potential of the zooplanktonic predator encountering another predator or a prey item (Rothschild and Osborn, 1988; Evans, 1989; Kiørboe and Saiz, 1995). These models focus on the physical aspects of predator–prey dynamics. Caparroy and Carlotti (1996) proposed an individual based model simulating the impacts of micro-scale turbulence on the physiological processes of the copepod *Acartia tonsa*. This was achieved by formulating ingestion to be a function of turbulence. Such an approach can be easily built into mechanistic stoichiometric models describing zooplankton population dynamics for use within end-to-end ecosystem models at the point of ingestion. Additionally the description of respiration rates would also need to be modified to take into account of environmental conditions on changes in respiration rates. For example, it has been observed that increase in suspended sediments in the water column are negatively correlated with egg production rates in *Temora longicornis* suggesting that sediment interferes with its feeding rate (Castellani and Altunbaş, 2006). Such a decrease in the egg production rate may be not just due to lower efficiency in the ingestion rate but instead a function of the high sediment load leading to an increase in energy (i.e., high respiration rates) diverted by the copepod to searching for food sources or sorting food from sediments, rather than reproduction.

Concluding discussion

Our primary aim in undertaking this review was to integrate disparate information about the physiology and functionality of the zooplankton community and to identify gaps between the two research practices (and thence philosophies) of experimentation/observation and modelling. In attempting to do so, we have come across various hurdles, not only between the two research strands but also within each research strand. Table 2 gives an overview of the current coverage of the topic in the literature. From this it is very apparent that large gaps exist in some groups in comparison with others, but that even for the best studied groups the extent of the knowledge base, and our modelling of it, is patchy. When one considers the importance of the description of zooplankton in even simple models (Fig. 3), the need to meet the challenges becomes all the more clear. We summarise these gaps below considering generic issues associated with zooplankton predator–prey status, and then according to the specific issues relating to micro- and then meso-zooplankton communities.

Finally we bring these issues together for considerations of challenges associated with modelling.

Prey status (quality plus quantity) and predator biomass

The importance of experiments in which the implications of prey (nutritional) quality as well quantity are studied needs to be recognised. Indeed prey quality should not be defined according to just differences in taxonomy but also according to the biochemical composition (nutritional history) of the individual. This is especially important for phytoplanktonic prey where the nutrient ratio varies widely over the life cycle depending on nutrient availability with lack of nutrients typically resulting in the accumulation of secondary metabolites (possibly toxins) within phytoplankton (Granéli et al., 1998). This in turn could result in predator avoidance of these prey types which would then form (harmful) algal blooms (Colin and Dam, 2003; Mitra and Flynn, 2006a). Very few experimental studies (e.g., Flynn and Davidson, 1993; Koski et al., 1998; Plath and Boersma, 2001; Jones and Flynn, 2005) have considered the effect of changes in elemental composition (either C:N or C:P) within a prey item on zooplankton population dynamics. And there are none which systematically look further at the changes in the elemental and biochemical composition in greater detail (e.g., C:N:P:fatty acids, etc., of prey and the zooplankton predator). To make use of such information in models requires a prey selectivity function that allows for deselection, for example according to prey quantity and quality (Mitra and Flynn, 2006b).

An additional problem associated with measuring phytoplanktonic prey biomass is that this is often measured in terms of chlorophyll and a crude conversion is used for derivation of the carbon biomass of the phytoplankton (e.g., Moloney and Gibbons, 1996). To improve the value of future phytoplankton–zooplankton experimental studies it is important not to use chlorophyll as the unit for phytoplankton biomass, because of the variability in chl:C with nutrient status and irradiance (Kruskopf and Flynn, 2006). Conversions from proxies such as length or diameter are better than nothing but they are no real substitute for data from elemental analysis, and especially not so for laboratory studies where direct measurements can be made.

Microzooplankton studies – strict heterotrophs vs. mixotrophs

Throughout the work that is summarised in this paper, a group of organisms was consistently under, or misrepresented; these are the mixotrophic protists. The term microzooplankton is typically used to imply strictly heterotrophic protists and thus ignores what are increasingly recognised as ecologically important components of this community – the mixotrophs (Flynn et al., 2013; Mitra et al., 2014). Studies on mixotrophs tend to be sidelined as a subject-area in itself rather than integrated as part of the microzooplankton community. The ability to photosynthesize, through acquired phototrophy, in organisms such as ciliates (Stoecker et al., 2009) provides an important additional nutritional route in addition to phagotrophy. That these processes occur within a single cell is a process which adds yet another degree of complexity to the already generally poorly understood physiology of microzooplankton. It is, nonetheless, an important topic that needs attention so that we may better understand the implications of phagotrophy plus phototrophy within the community as well on the lower and upper trophic levels (Mitra and Flynn, 2010; Mitra et al., 2014).

Mesozooplankton studies – “copepod-heavy”

Copepods are typically considered as the representative of the mesozooplankton community, if not of zooplankton in general.

This is evident from the various national and international research programmes which have focussed on copepods, the availability of abundant experimental data and indeed the presence of numerous copepod-focussed models (See also Table 2). While copepods undoubtedly do play an important role in the food-web interactions globally, equally important are other members of the mesozooplankton community such as krill, jellyfish, chaetognaths and the larval stages of fish.

To exacerbate the situation further, experimental studies on copepods often focus on the adult female. There is a need for parametric information on the activity of the entire life cycle rather than on just one event in a particular life stage (e.g., egg production, Campbell et al., 2001; pH, Cripps et al., 2014). Not only will the prey items vary for different life stages, but ingestion rates and assimilation efficiencies and thence growth rates and loss processes would also be expected to be markedly different. Differential mortality during moult stages is factor one may suspect as being particularly important (Gentleman et al., 2012).

Modelling challenges

If one was to argue that our ability to model zooplankton should give an indication of our understanding of the real organisms then we could conclude that we know frighteningly little with any surer. In reality, we know much, but we lack holistic integration of that knowledge in models due to the old issues of data (in)adequacy and model complexity. Those excuses aside, there are clear opportunities for relatively easy improvements in zooplankton models. Below we highlight some key areas for investigation.

1. Food selectivity: Even simple models usually contain some level of food selectivity, but field workers, including those investigating long-term changes in plankton succession, often identify detailed links between prey and predator species composition and the production cycle. It would help to have information especially concerning the consumption of phototrophs such as diatoms and coccolithophorids, vs. consumption of mixotrophs (the latter may have a more constrained stoichiometry, and are often classed within the microzooplankton). Food selectivity affects ingested food quality. These interactions may be considered between plankton functional types (e.g., diatoms vs. mixotroph consumption; effects of climate change, ocean acidification), and within types (e.g., impacts of nutrient status, which may be affected by climate change impacts on water column stability). Food selectivity affects the operational value of G_{\max} , a parameter of key importance (Fig. 3) and usually set as a constant (Fasham et al., 1990; Gentleman et al., 2003), but which in the context of responding to quality and quantity is not constant (Mitra and Flynn, 2007). We need to be able to better describe these interactions. For this we need more extensive knowledge on what the different zooplankton functional types eat in the field, and how they select prey especially in environments where a wide range of prey are available; i.e., we need more experimental studies of mixed diets which, in addition to zooplankton vital rates, record changes in prey physiology (e.g., C:N:P status) over time.
2. Kinetics of prey consumption and growth: While simple models relate zooplankton growth to prey availability using a rectangular hyperbolic function and fixed assimilation efficiencies (assimilation efficiency), there is more than ample evidence to show a biphasic interaction, complicated by feedback from satiation to ingestion, and from satiation to throughput and hence to variable assimilation efficiency. The implied density-dependent inefficiency (Mitra and Flynn, 2007; Flynn, 2009), perhaps with sloppy feeding (Møller et al., 2003), has important implications for system dynamics (Flynn, 2009), which urgently need

- to be established or refuted. Both G_{\max} and assimilation efficiency are known to be critical parameters affecting models of trophic dynamics (Fig. 3). Although our analysis suggests that model behaviour is rather less sensitive to the value of K_{pred} than to G_{\max} , the deployment of a single K_{pred} to cover all prey types encountered by a range of predator types, covering several orders of magnitude in size, appears at best questionable. Usage of such a value within ratio-based prey selectivity functions have been suggested to be better replaced with a function that can account for encounters and selectivity of individual prey types, though with a common (biomass) based satiation term (Mitra and Flynn, 2006b).
3. Form of voided excess ingested material: The fate of excess ingested material has important implications for system dynamics. If excess C is “burnt off” through respiration then there is a direct and rapid concurrent regeneration of inorganic N and P to support primary production. Release of DOM would support bacteria, and thence microzooplankton and mixotrophic production (Mitra et al., 2014). Release of POM as rapidly sinking pellets, however, supports production below the ergocline, in a very different system.
 4. Sensitivity of mortality at different age-stages to prior nutrient history: It is clear that different mortality rates at different stages of mesozooplankton life histories have potential for important implications on trophic dynamics. This is seen in the studies of the effects of polyunsaturated aldehydes upon nauplii stages of copepods on consumption of diatoms by the adults (Miralto et al., 1999; Flynn and Irigoien, 2009). Aside from that specific example, mortality in juveniles is likely to be a combination of inborn errors in metabolism, together with nutritional issues related to the health of the egg-laying adults and food availability (quality and quantity) to satisfy respiration and growth for the early stages. This component of the system dynamics warrants investigation so as to enable its consideration in modelling.
 5. Steady state vs. dynamic studies: For verification of models used in ecosystem scenarios, dynamic time series data are required; steady state data are of little relevance in studies of dynamic ecological processes not least because of the importance of nutrient history. It is of vital importance to have complete datasets for the different components (predator, prey, nutrients) of the total system.

It is noteworthy that in the much-cited work of Follows et al. (2007), trait selection in the description of the planktonic food web was developed entirely within the phytoplankton; there were many dozens of phytoplankton grazed by two zooplankton types (each of which had simple model structures). Given that prey selection, and grazing resistance can have such powerful effects on succession, easily overriding bottom-up autecology traits, one may wonder how the results of that study may have developed if the traits of the zooplankton models had been accorded the same level of investigation as had the phytoplankton. To do that would have required the type of extensive consideration of model development that phytoplankton have received over the last decade (Allen and Polimene, 2011).

The time has come for zooplankton models to rise in their status within marine biogeochemical and fisheries models. We have shown that the behaviour of the zooplankton model is pivotal, and that various empirical studies are required to enhance our understanding so that models can be better constructed and tested. Studies of biological and ecological systems should ideally be conducted according to the iterative process of observation, experimentation, modelling, etc. Now is the time to go forward with the next cycle of the experiment-model-observation loop. The research conducted within the EURO-BASIN project will help to

achieve that goal. Once we have been through that process we will be better placed to decide on the optimal balance of model complexity and fidelity. Until that time, we must remain aware that ultimately models are only as good as the behaviour (performance) of the weakest submodel, and that zooplankton models are currently anything but as well founded as models are of the phytoplankton, or indeed of fish.

Acknowledgements

AC is funded by the Ministry of Science and Innovation of Spain through project CTM2009-08783. AM was part funded by NERC UK project NE/K001345/1. KJF was funded by NERC UK through projects NE/H01750X/1 and NE/F003455/1. Thanks to Angus Atkinson, Mike Blackett, Per Juel Hansen, and Diane Stoecker for their comments and help in the compilation of Table 2. This review was supported in part by project EURO-BASIN (Ref. 264933, 7FP, European Union), and by a Leverhulme International Network “Placing marine mixotrophs in context: modelling mixotrophy in a changing world”.

References

- Acheampong, E., Nielsen, M.H., Mitra, A., St. John, M.A., 2012. Towards an adaptive model for simulating growth of marine mesozooplankton: a macromolecular perspective. *Ecological Modelling* 225, 1–18.
- Adrian, R., Deneke, R., 1996. Possible impact of mild winters on zooplankton succession in eutrophic lakes of the Atlantic European area. *Freshwater Biology* 36, 757–770.
- Afik, D., Karasov, W.H., 1995. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* 76, 2247–2257.
- Agersted, M.D., Nielsen, T.G., Munk, P., Vismann, B., Arendt, K.E., 2011. The functional biology and trophic role of krill (*Thysanoessa raschii*) in a Greenlandic fjord. *Marine Biology* 158, 1387–1402.
- Agutter, P.S., Tuszynski, J.A., 2011. Analytic theories of allometric scaling. *Journal of Experimental Biology* 214, 1055–1062.
- Allan, J.D., 1976. Life history patterns in zooplankton. *American Naturalist* 110, 165–180.
- Allen, J.L., Polimene, L., 2011. Linking physiology to ecology: towards a new generation of plankton models. *Journal of Plankton Research* 33, 989–997.
- Anderson, T.R., Hessen, D.O., Elser, J.J., Urabe, J., 2005. Metabolic stoichiometry and the fate of excess carbon and nutrients in consumers. *American Naturalist* 165, 1–15.
- Anderson, T.R., Gentleman, W.C., Sinha, B., 2010. Influence of grazing formulations on the emergent properties of a complex ecosystem model in a global ocean general circulation model. *Progress in Oceanography* 87, 201–213.
- Anderson, T.R., Hessen, D.O., Mitra, A., Mayor, D.J., Yool, A., 2013. Sensitivity of secondary production and export flux to choice of trophic transfer formulation in marine ecosystem models. *Journal of Marine Systems* 125, 41–53.
- Arendt, K.E., Jónasdóttir, S.H., Hansen, P.J., Gärtner, S., 2005. Effects of dietary fatty acids on the reproductive success of the Calanoid copepod *Temora longicornis*. *Marine Biology* 146, 513–530.
- Artoli, Y., Blackford, J.C., Butenschön, M., Holt, J.T., Wakelin, S.L., Thomas, H., Borges, A.V., Allen, J.L., 2012. The carbonate system in the North Sea: sensitivity and model validation. *Journal of Marine Systems* 102–104, 1–13.
- Atkinson, D., Hirst, A.G., 2007. Life history and body size. In: Hildrew, A.G., Raffaelli, D.G., Edmonds-Brow, R. (Eds.), *Body Size: The Structure and Function of Aquatic Ecosystems*. Ecological Reviews. Cambridge Univ. Press, pp. 33–48.
- Atrill, M.J., Wright, J., Edwards, M., 2007. Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography* 52, 480–485.
- Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, F., 1983. The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* 10, 257–263.
- Bagøien, E., Kaartvedt, S., Aksnes, D.L., Eiane, K., 2001. Vertical distribution and mortality of overwintering *Calanus*. *Limnology and Oceanography* 46 (6), 1494–1510.
- Båmstedt, U., Karlson, K., 1998. Euphausiid predation on copepods in coastal waters of the Northeast Atlantic. *Marine Ecology Progress Series* 172, 149–168.
- Banavar, J.R., Moses, M.E., Brown, J.H., Damuth, J., Rinaldo, A., Sibly, R.M., Maritan, A., 2010. A general basis for quarter-power scaling in animals. *Proceedings of the National Academy of Sciences USA* 107, 15816–15820.
- Bargu, S., Marinovic, B., Mansergh, S., Silver, M.W., 2003. Feeding responses of krill to toxin-producing diatom *Pseudo-nitzschia*. *Journal of Experimental Marine Biology and Ecology* 284, 87–104.
- Bartholme, S., Samchyshyna, L., Santer, B., Lampert, W., 2005. Subitaneous eggs of freshwater copepods pass through fish guts: survival, hatchability, and potential ecological implications. *Limnology and Oceanography* 50, 923–929.

- Baumgartner, M.F., Cole, T.V.N., Campbell, R.G., Teegarden, G.J., Durbin, E.G., 2003. Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. *Marine Ecology Progress Series* 264, 155–166.
- Bé, A.W.H., Gilmer, R.W., 1977. A zoogeographic and taxonomic review of euthecosomatous pteropoda. In: Ramsey, A.T.S. (Ed.), *Oceanic Micropaleontology*, vol. 1. Academic Press, London, pp. 733–808.
- Beklemishev, C.W., 1957. Superfluous feeding of the zooplankton and the problem of sources of food for bottom animals. *Trudy vses. gidrobiol. Obsch.* 8, 354–358.
- Berggreen, U., Hansen, B., Kjørboe, T., 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. *Marine Biology* 99, 341–352.
- Besiktepe, S., Dam, H.G., 2002. Coupling of ingestion and defecation as a function of diet in the calanoid copepod *Acartia tonsa*. *Marine Ecology Progress Series* 229, 151–164.
- Bi, H., Rose, K.A., Benfield, M.C., 2011. Estimating copepod stage-specific mortality rates in open ocean waters: a case study from the northern Gulf of Mexico, USA. *Marine Ecology Progress Series* 427, 145–159.
- Bissinger, J.E., Montagnes, D.J.S., Sharples, J., Atkinson, D., 2008. Predicting marine phytoplankton maximum growth rates from temperature: improving on the Eppley curve using quantile regression. *Limnology and Oceanography* 53, 487–493.
- Blackford, J.C., Allen, J.I., Gilbert, F.J., 2004. Ecosystem dynamics at six contrasting sites: a generic modelling study. *Journal of Marine Systems* 52, 191–215.
- Bode, A., Barquero, S., González, N., Alvarez-Ossorio, M.T., Varela, M., 2004. Contribution of heterotrophic plankton to nitrogen regeneration in the upwelling ecosystem of A Coruña (NW Spain). *Journal of Plankton Research* 26, 1–18.
- Boero, F., Bouillon, J., Gravili, C., Miglietta, M.P., Parsons, T., Piraino, S., 2008. Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series* 356, 299–310.
- Bokma, F., 2004. Evidence against universal metabolic allometry. *Functional Ecology* 18, 184–187.
- Bonnet, D., Lindeque, P., Harris, R.P., 2010. *Sagitta setosa* predation on *Calanus helgolandicus* in the English Channel. *Journal of Plankton Research* 32, 725–737.
- Brett, J.R., 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of the Fisheries Research Board of Canada* 21, 1183–1226.
- Broglio, E., Jónasdóttir, S.H., Calbet, A., Jakobsen, H.H., Saiz, E., 2003. Effect of heterotrophic versus autotrophic food on feeding and reproduction of the calanoid copepod *Acartia tonsa*: relationship with prey fatty acid composition. *Aquatic Microbial Ecology* 31, 267–278.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Towards a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Butler, E.I., Corner, E.D.S., Marshall, S.M., 1970. On the nutrition and metabolism of zooplankton. VIII. Seasonal survey of nitrogen and phosphorus excretion by *Calanus* in the Clyde Sea area. *Journal of the Marine Biological Association of the United Kingdom* 50, 525–560.
- Calbet, A., 2008. The trophic roles of microzooplankton in marine systems. *ICES Journal of Marine Science* 65 (3), 325–331.
- Calbet, A., Landry, M.R., 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnology and Oceanography* 49, 51–57.
- Calbet, A., Saiz, E., 2005. The ciliate-copepod link in marine ecosystems. *Aquatic Microbial Ecology* 38, 157–167.
- Calbet, A., Garrido, S., Saiz, E., Alcaraz, M., Duarte, C.M., 2001. Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. *Journal of Plankton Research* 23, 319–331.
- Calbet, A., Vaqué, D., Felipe, J., Vila, M., Sala, M.M., Alcaraz, M., Estrada, M., 2003. Relative grazing impact of microzooplankton and mesozooplankton on a bloom of the toxic dinoflagellate *Alexandrium minutum*. *Marine Ecology Progress Series* 259, 303–309.
- Campbell, R.G., Wagner, M.M., Teegarden, G.J., Boudreau, C.A., Durbin, E.G., 2001. Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Marine Ecology Progress Series* 221, 161–183.
- Caparroy, P., Carlotti, F., 1996. A model for *Acartia tonsa*: effect of turbulence and consequences for the related physiological processes. *Journal of Plankton Research* 18 (2139), 2177.
- Capriulo, G.M., Degnan, C., 1991. Effect of food concentration on digestion and vacuole passage time in the heterotrichous marine ciliate *Fibrea salina*. *Marine Biology* 11, 199–202.
- Carlotti, F., Hirche, H.-J., 1997. Growth and egg production of female *Calanus finmarchicus*: an individual-based physiological model and experimental validation. *Marine Ecology Progress Series* 149, 91–104.
- Carlotti, F., Poggiale, J.C., 2010. Towards methodological approaches to implement the zooplankton component in “end to end” food web models. *Progress in Oceanography* 84, 20–38.
- Carlotti, F., Wolf, K.-U., 1998. A Lagrangian ensemble model of *Calanus finmarchicus* coupled with a 1D ecosystem model. *Fisheries Oceanography* 7, 191–204.
- Carlotti, F., Giske, J., Werner, F., 2000. Modeling zooplankton dynamics. In: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), *Zooplankton Methodology Manual*. Academic Press, San Diego, CA, pp. 571–643.
- Castellani, C., Altunbaş, Y., 2014. Seasonal change in acclimatised respiration rate of *Temora longicornis*. *Marine Ecology Progress Series* 500, 83–101.
- Castellani, C., Altunbaş, Y., 2006. Factors controlling the temporal dynamics of egg production in the copepod *Temora longicornis*. *Marine Ecology: Progress Series* 308, 143–153.
- Castellani, C., Irigoien, X., Harris, R.P., Lampitt, R.S., 2005a. Feeding and egg production of *Oithona similis* in the North Atlantic. *Marine Ecology Progress Series* 288, 173–182.
- Castellani, C., Robinson, C., Smith, T., Lampitt, R.S., 2005b. Temperature affects respiration rate of *Oithona similis*. *Marine Ecology Progress Series* 285, 129–135.
- Chang, K.H., Hanazato, T., 2005. Impact of selective predation by *Mesocyclops pehpeiensis* on a zooplankton community: experimental analysis using mesocosms. *Ecological Research* 20, 726–732.
- Christaki, U., Dolan, J.R., Pelegri, S., Rassoulzadegan, F., 1998. Consumption of picoplankton-size particles by marine ciliates: effects of physiological state of the ciliate and particle quality. *Limnology and Oceanography* 43, 458–464.
- Clarke, A., 1993. Seasonal acclimatization and latitudinal compensation in metabolism: do they exist? *Functional Ecology* 7, 139–149.
- Clarke, A., Fraser, K.P.P., 2004. Why does metabolism scale with temperature? *Functional Ecology* 18, 243–251.
- Cohen, J.H., Forward Jr., R.B., 2009. Zooplankton diel vertical migration – a review of proximate control. *Oceanography and Marine Biology: An Annual Review* 47, 77–110.
- Colin, S.P., Dam, H.G., 2002. Latitudinal differentiation in the effects of the toxic dinoflagellate *Alexandrium* spp. on the feeding and reproduction of populations of the copepod *Acartia hudsonica*. *Harmful Algae* 1, 113–125.
- Colin, S.P., Dam, H.G., 2003. Effects of the toxic dinoflagellate *Alexandrium fundyense* on the copepod *Acartia hudsonica*: a test of the mechanisms that reduce ingestion rates. *Marine Ecology Progress Series* 248, 55–65.
- Conover, R.J., Corner, E.D.S., 1968. Respiration and nitrogen excretion by some zooplankton in relation to their life cycles. *Journal of the Marine Biological Association of the United Kingdom* 48, 49–75.
- Conover, R.J., Huntley, M., 1991. Copepods in ice-covered seas – distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *Journal of Marine Systems* 2, 1–41.
- Corner, E.D.S., Head, R.N., Kilvington, C.C., 1972. On the nutrition and metabolism of zooplankton VIII. The grazing of *Biddulphia* cells by *Calanus helgolandicus*. *Journal of the Marine Biological Association of the United Kingdom* 52, 847–861.
- Cossins, A.R., Bowler, K., 1987. *Temperature Biology of Animals*. Chapman and Hall.
- Coull, B.C., Grant, J., 1981. Encystment discovered in a marine copepod. *Science* 212 (342), 344.
- Cripps, G., Lindeque, P., Flynn, K.J., 2014. Have we been underestimating the effects of ocean acidification in zooplankton? *Global Change Biology*. <http://dx.doi.org/10.1111/gcb.12582>.
- Cushing, D.H., 1975. *Marine Ecology and Fisheries*. Cambridge Univ. Press, Cambridge, UK.
- Cushing, D.H., 1995. *Population Production and Regulation in the Sea: A Fisheries Perspective*. Cambridge Univ. Press, Cambridge, UK.
- Cushing, D.H., Vučetić, T., 1963. Studies on a *Calanus* patch. III. The quantity of food eaten by *Calanus finmarchicus*. *Journal of the Marine Biological Association of the United Kingdom* 43, 349–371.
- Daan, R., Gonzalez, S.R., Klein Breteler, W.C.M., 1988. Cannibalism in omnivorous calanoid copepods. *Marine Ecology Progress Series* 47, 45–54.
- Dagg, M.J., Walser, W.E., 1987. Ingestion, gut passage, and egestion by the copepod *Neocalanus plumchrus* in the laboratory and in the subarctic Pacific Ocean. *Limnology and Oceanography* 32, 178–188.
- Dam, H.G., Peterson, W.T., 1988. The effect of temperature on the gut clearance constant of planktonic copepods. *Journal of Experimental Marine Biology and Ecology* 123, 1–14.
- Darchambeau, F., Faerøvig, P.J., Hessen, D.O., 2003. How *Daphnia* copes with excess carbon in its food. *Oecologia* 136, 336–346.
- Davies, K.T.A., Ross, T., Taggart, C.T., 2013. Tidal and subtidal currents affect deep aggregations of right whale prey, *Calanus* spp., along a shelf-basin margin. *Marine Ecology Progress Series* 479, 263–282.
- Deevey, G.B., 1960. Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. *Bulletin of the Bingham Oceanographic Collection* 17, 54–85.
- Ducklow, H.W., Purdie, D.A., Williams, P.J.leB., Davies, J.M., 1986. Bacterioplankton: a sink for carbon in a coastal marine plankton community. *Science* 232, 865–867.
- Ducklow, H.W., Kirchman, D.L., Anderson, T.R., 2002. The magnitude of spring bacterial production in the North Atlantic Ocean. *Limnology and Oceanography* 47, 1684–1693.
- Dutz, J., Koski, M., Jónasdóttir, S.H., 2008. Copepod reproduction is unaffected by diatom aldehydes or lipid composition. *Limnology and Oceanography* 53, 225–235.
- Edwards, A.M., Yool, A., 2000. The role of higher predation in plankton population models. *Journal of Plankton Research* 22, 1085–1112.
- Eiane, K., Ohman, M.D., 2004. Stage-specific mortality of *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Oithona similis* on Fladen Ground, North Sea, during a spring bloom. *Marine Ecology Progress Series* 268, 183–193.
- Elliott, D.T., Tang, W.W., 2011. Influence of carcass abundance on estimates of mortality and assessment of population dynamics in *Acartia tonsa*. *Marine Ecology Progress Series* 427, 1–12.
- Engel, M., Hirche, H.-J., 2004. Seasonal variability and inter-specific differences in hatching of calanoid copepod resting eggs from sediments of the German Bight (North Sea). *Journal of Plankton Research* 26 (9), 1083–1093.

- Eppley, R.W., 1972. Temperature and phytoplankton growth in the sea. *Fishery Bulletin* 70, 1063–1085.
- Evans, G.T., 1989. The encounter speed of moving predator and prey. *Journal of Plankton Research* 11, 415–417.
- Fasham, M.J.R., 1993. Modelling the marine biota. In: Heimann, M. (Ed.), *The Global Cycle*, NATO ASI Series, vol. I 15. Springer-Verlag, Berlin, pp. 457–504.
- Fasham, M.J.R., 1995. Variations in the seasonal cycle of biological production in subarctic oceans: a model sensitivity analysis. *Deep-Sea Research* 42, 1111–1149.
- Fasham, M.J.R., Ducklow, H.W., McKelvie, S.M., 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *Journal of Marine Research* 48, 591–639.
- Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J., Millero, F.J., 2004. Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science* 305, 362–366.
- Feinberg, L.R., Dam, H.G., 1998. Effects of diet on dimensions, density and sinking rates of fecal pellets of the copepod *Acartia tonsa*. *Marine Ecology Progress Series* 175, 87–96.
- Fenchel, T., 1982. Ecology of heterotrophic microflagellates II. Bioenergetics and growth. *Marine Ecology Progress Series* 8, 211–223.
- Fenchel, T., 2005. Respiration in aquatic protists. In: Del Giorgio, P.A., Williams, P.J.leB. (Eds.), *Respiration in Aquatic Ecosystems*. Oxford Univ. Press, Oxford, pp. 47–56.
- Fenchel, T., Finlay, B.J., 1983. Respiration rates in heterotrophic, free-living protozoa. *Microbial Ecology* 9, 99–122.
- Fiksen, Ø., Carlotti, F., 1998. A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. *Sarsia* 83, 129–147.
- Fiksen, Ø., Giske, F., 1995. Vertical distribution and population dynamics of copepods by dynamic optimization. *ICES Journal of Marine Science* 52, 483–503.
- Flynn, K.J., 1998. Estimation of kinetic parameters for the transport of nitrate and ammonium into marine phytoplankton. *Marine Ecology Progress Series* 169 (13), 28.
- Flynn, K.J., 2009. Food-density-dependent inefficiency in animals with a gut as a stabilizing mechanism in trophic dynamics. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 276, 1147–1152.
- Flynn, K.J., Davidson, K., 1993. Predator-prey interactions between *Isochrysis galbana* and *Oxyrrhis marina*. II. Release of non-protein amines and faeces during predation of *Isochrysis*. *Journal of Plankton Research* 15, 893–905.
- Flynn, K.J., Irigoien, X., 2009. Aldehyde-induced insidious effects cannot be considered as a diatom defence mechanism against copepods. *Marine Ecology Progress Series* 377, 79–89.
- Flynn, K.J., Davidson, K., Cunningham, A., 1996. Prey selection and rejection by a microflagellate; implications for the study and operation of microbial food webs. *Journal of Experimental Marine Biology and Ecology* 196, 357–372.
- Flynn, K.J., Blackford, J.C., Baird, M.E., Raven, J.A., Clark, D.R., Beardall, J., Brownlee, C., Fabian, H., Wheeler, G.L., 2012. Changes in pH at the exterior surface of plankton with ocean acidification. *Nature Climate Change*. <http://dx.doi.org/10.1038/NCLIMATE1489>.
- Flynn, K.J., Stoecker, D.K., Mitra, A., Raven, J.A., Glibert, P.M., Hansen, P.J., Granéli, E., Burkholder, J.A., 2013. Misuse of the phytoplankton-zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. *Journal of Plankton Research* 35, 3–11.
- Follows, M.J., Dutkiewicz, S., Grant, S., Chisholm, S.W., 2007. Emergent biogeography of microbial communities in a model ocean. *Science* 315, 1843–1846.
- Franks, P.J.S., 2002. NPZ models of plankton dynamics: their construction, coupling to physics, and application. *Journal of Oceanography* 58, 379–387.
- Frost, B.W., 1987. Grazing control of phytoplankton stock in the open subarctic Pacific Ocean: a model assessing the role of mesozooplankton, particularly the large calanoid copepods *Neocalanus* spp. *Marine Ecology Progress Series* 39, 49–68.
- Fulton, E.A., Smith, A.D.M., Johnson, C.R., 2003. Mortality and predation and ecosystem models: is it important how these are expressed? *Ecological Modelling* 169 (157), 178.
- Fulton, E.A., Parslow, J.S., Smith, A.D.M., Johnson, C.R., 2004. Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance. *Ecological Modelling* 173, 371–406.
- Fulton, E.A., 2010. Approaches to end-to-end ecosystem models. *Journal of Marine Systems* 81, 171–183.
- Gaudy, R., Thibault-Botha, D., 2007. Metabolism of *Centropages* species in the Mediterranean Sea and the North Atlantic Ocean. *Progress in Oceanography* 72, 151–163.
- Gemmell, B.J., Jiang, H., Strickler, J.R., Buskey, E.J., 2012. Plankton reach new heights in effort to avoid predators. *Proceedings of the Royal Society of London, Series B: Biological Sciences*. <http://dx.doi.org/10.1098/rspb.2012.0163>.
- Gentleman, W.C., Neuheimer, A.B., 2008. Functional responses and ecosystem dynamics: how clearance rates explain the influence of satiation, food-limitation and acclimation. *Journal of Plankton Research* 30, 1215–1231.
- Gentleman, W.C., Neuheimer, A.B., Campbell, R.G., 2008. Modelling copepod development: current limitations and a new realistic approach. *ICES Journal of Marine Science* 65, 399–413.
- Gentleman, W., Leising, A., Frost, B., Strom, S., Murray, J., 2003. Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. *Deep Sea Research II* 50, 2847–2875.
- Gentleman, W.C., Pepin, P., Doucette, S., 2012. Estimating mortality: clarifying assumptions and sources of uncertainty in vertical methods. *Journal of Marine Systems* 105–108, 1–19.
- Gerritsen, J., Strickler, J.R., 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *Journal of the Fisheries Research Board of Canada* 34, 73–82.
- Gifford, D.J., 1991. The protozoan-metazoan trophic link in pelagic ecosystems. *Journal of Protozoology* 38, 81–86.
- Gill, C.W., 1986. Suspected mechano- and chemo-sensory structures of *Temora longicornis* Müller (Copepoda: Calanoida). *Marine Biology* 93, 449–457.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of size and temperature on metabolic rate. *Science* 293, 2248–2251.
- Gislason, A., Eiane, K., Reynisson, P., 2007. Vertical distribution and mortality of *Calanus finmarchicus* during overwintering in oceanic waters southwest of Iceland. *Marine Biology* 150, 1253–1263.
- Gismervik, I., 2006. Top-down impact by copepods on ciliate numbers and persistence depends on copepod and ciliate species composition. *Journal of Plankton Research* 28, 499–507.
- Glazier, D.S., 2005. Beyond the ‘3/4-power law’: variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews* 80, 611–662.
- Glazier, D.S., 2006. The 3/4-Power law is not universal: evolution of isometric, ontogenetic metabolic scaling in pelagic animals. *BioScience* 56, 325–332.
- Glazier, D.S., 2009. Metabolic level and size scaling of rates of respiration and growth in unicellular organisms. *Functional Ecology* 23, 963–968.
- Glazier, D.S., 2010. A unifying explanation for diverse metabolic scaling in animals and plants. *Biological Reviews* 85, 111–138.
- Goldman, J.C., Dennett, M.R., 1992. Phagotrophy and NH₄⁺ regeneration in a three-member microbial food loop. *Journal of Plankton Research* 14, 649–663.
- Gorsky, G., Chrétiennot-Dinet, M.J., Blanchot, J., Palazzoli, I., 1999. Picoplankton and nanoplankton aggregation by appendicularians- fecal pellet contents of *Megalocercus huxleyi* in the equatorial Pacific. *Journal of Geophysical Research* 104, 3381–3390.
- Granéli, E., Johansson, N., Panosso, R., 1998. Cellular toxin contents in relation to nutrient conditions for different groups of phycotoxins. In: Reguera, B., Blanco, J., Fernández, M.L., Wyatt, T. (Eds.), *Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO, Grafisant, Santiago de Compostela, Spain*, pp. 321–324.
- Grice, G.D., Marcus, N.H., 1981. Dormant eggs of marine copepods. *Oceanography and Marine Biology: An Annual Review* 19, 125–140.
- Hada, A., Uye, S., 1991. Cannibalistic feeding behavior of the brackish-water copepod *Sinocalanus tenellus*. *Journal of Plankton Research* 13, 155–166.
- Haddock, S.H.D., 2007. Comparative feeding behaviour of planktonic ctenophores. *Integrative and Comparative Biology* 47, 847–853.
- Haefner, J.W., 1996. *Modeling Biological Systems*. Chapman and Hall, New York, USA.
- Hallberg, E., Hirche, H.J., 1980. Differentiation of mid-gut in adults and overwintering copepodites of *Calanus finmarchicus* (Gunnerus) and *C. helgolandicus* (Claus). *Journal of Experimental Marine Biology and Ecology* 48, 283–295.
- Halsband, C., Hirche, H.-J., 2001. The reproductive cycles of dominant calanoid copepods in the North Sea. *Marine Ecology Progress Series* 209, 219–229.
- Halsband-Lenk, C., Pierson, J.J., Leising, A.W., 2005. Reproduction of *Pseudocalanus newmani* (Copepoda: Calanoida) is deleteriously affected by diatom blooms – a field study. *Progress in Oceanography* 67, 332–348.
- Halsband-Lenk, C., Carlotti, F., Greve, W., 2004. Life-history strategies of calanoid congeners under two different climate regimes: a comparison. *ICES Journal of Marine Science* SI 61, 709–720.
- Halsband-Lenk, C., Hirche, H.-J., Carlotti, F., 2002. Temperature effects on reproduction and development of congener copepod populations in the North Sea and the Mediterranean. *Journal of Experimental Marine Biology and Ecology* 271, 121–153.
- Hamner, W.M., Hamner, P.P., Strand, S.W., Gilmer, R.W., 1983. Behavior of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling, and molting. *Science* 220, 433–435.
- Hansen, P.J., 1992. Prey size selection, feeding rates and growth dynamics of heterotrophic dinoflagellates with special emphasis on *Gyrodinium aureolum*. *Marine Biology* 114, 327–334.
- Hansen, P.J., Calado, A.J., 1999. Phagotrophic mechanisms and prey selection in free-living dinoflagellates. *Journal of Eukaryotic Microbiology* 46, 382–389.
- Hansen, P.J., Lundholm, N., Rost, B., 2007. Growth limitation in marine red-tide dinoflagellates: effects of pH versus inorganic carbon availability. *Marine Ecology Progress Series* 334, 63–71.
- Harms, I.H., Heath, M.R., Bryant, A.D., Backhaus, J.O., Hainbucher, D.A., 2000. Modelling the Northeast Atlantic circulation: implications for the spring invasion of shelf regions by *Calanus finmarchicus*. *ICES Journal of Marine Science* 57, 1694–1707.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S., Samuel, M.D., 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296, 2158–2162.
- Hasegawa, T., Koike, I., Mukai, H., 2001. Fate of food nitrogen in marine copepods. *Marine Ecology Progress Series* 210, 167–174.
- Havskum, H., 2003. Effects of small-scale turbulence on interactions between the heterotrophic dinoflagellate *Oxyrrhis marina* and its prey, *Isochrysis* sp. *Ophelia* 57, 125–135.

- Havskum, H., Hansen, P.J., Berdalet, E., 2005. Effect of turbulence on sedimentation and net population growth of the dinoflagellate *Ceratium tripos* and interactions with its predator, *Fragilidium subglobosum*. *Limnology and Oceanography* 50, 1543–1551.
- Hays, G.C., 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503, 163–170.
- Head, E.J.H., 1992. Comparison of the chemical composition of particulate material and faecal pellets at stations off the coast of Labrador and in the Gulf of St. Lawrence. *Marine Biology* 112, 593–600.
- Heath, M.R., Jónasdóttir, S.H., 1999. Distribution and abundance of overwintering *Calanus finmarchicus* in the Faroe-Shetland Channel. *Fisheries Oceanography* 8 (Suppl. 1), 40–60.
- Hemmingsen, A.M., 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. Reports of the Steno Memorial Hospital and the Nordisk Insulin Laboratorium 9, 1–110.
- Hernández-León, S., Ikeda, T., 2005. Zooplankton respiration. In: del Giorgio, P., Williams, P.J.leb. (Eds.), *Respiration in aquatic ecosystems*. Oxford Univ. Press, Oxford, UK.
- Hirche, H.-J., 1983. Overwintering of *Calanus finmarchicus* and *Calanus helgolandicus*. *Marine Ecology Progress Series* 11, 281–290.
- Hirche, H.-J., 1997. Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. *Marine Biology* 128, 607–618.
- Hirst, A.G., Kiørboe, T., 2002. Mortality of marine planktonic copepods: global rates and patterns. *Marine Ecology Progress Series* 230, 195–209.
- Hirst, A.G., Lampitt, R.S., 1998. Towards a global model of in situ weight-specific growth in marine planktonic copepods. *Marine Biology* 132, 247–257.
- Hirst, A.G., Bonnet, D., Conway, D.V.P., Kiørboe, T.K., 2010. Does predation control adult sex ratios and longevity in marine pelagic copepods? *Limnology and Oceanography* 55, 2193–2206.
- Hirst, A.G., Peterson, W.T., Rothery, P., 2005. Errors in juvenile copepod growth rate estimates are widespread: problems with the Moulting Rate method. *Marine Ecology Progress Series* 296, 263–279.
- Holste, L., St. John, M.A., Peck, M.A., 2008. The effects of temperature and salinity on reproductive success of *Temora longicornis* in the Baltic Sea: a copepod coping with a tough situation. *Marine Biology* 156, 527–540.
- Horn, M.H., Messer, K.S., 1992. Fish guts as chemical reactors: a model of the alimentary canals of marine herbivorous fishes. *Marine Biology* 113, 527–535.
- ICES WKMR Report, 2010. Report of the Workshop on Understanding and Quantifying Mortality in Fish Early-Life Stages: Experiments, Observations, and Models. Aberdeen, UK. CM 2010/SSGEF:13, 30 pp.
- Ikeda, T., 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. *Marine Biology* 85, 1–11.
- Ikeda, T., Kanno, Y., Ozaki, Y., Shinada, A., 2001. Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Marine Biology* 139, 587–596.
- Ince, L.S., Hebert, D., Wolff, N., Oakey, N., Dye, D., 2001. Changes in copepod distributions associated with increased turbulence from wind stress. *Marine Ecology Progress Series* 213, 229–240.
- Ingvarsdóttir, A., Houlihan, D.F., Heath, M.R., Hay, S.J., 1999. Seasonal changes in respiration rates of copepodite stage V of *Calanus finmarchicus* (Gunnerus). *Fisheries Oceanography* 8 (Suppl 1), 73–83.
- IPCC, 2007. Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 996 pp.
- Irigoin, X., 1998. Gut clearance rate constant, temperature and initial gut contents: a review. *Journal of Plankton Research* 20, 997–1003.
- Irigoin, X., Harris, R.P., Verheye, H.M., Joly, P., Runge, J., Starr, M., Pond, D., Campbell, R., Shreeve, R., Ward, P., Smith, A.N., Dam, H.G., Peterson, W., Tirelli, V., Koski, M., Smith, T., Harbord, D., Davidson, R., 2002. Copepod hatching success in marine ecosystems with high diatom concentrations. *Nature* 419, 387–389.
- Isaac, N.J., Carbone, C., 2010. Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecology Letters* 13, 728–735.
- Jacobson, D.M., Anderson, D.M., 1986. Thecate heterotrophic dinoflagellates: feeding behaviour and mechanisms. *Journal of Phycology* 22, 249–258.
- Jakobsen, H.H., Everett, L.M., Strom, S.L., 2006. Hydromechanical signaling between the ciliate *Mesodinium pulex* and motile protist prey. *Aquatic Microbial Ecology* 44, 197–206.
- Jeong, H.J., Latz, M.I., 1994. Growth and grazing rates of the heterotrophic dinoflagellates *Prorocentrum* spp. on red tide dinoflagellates. *Marine Ecology Progress Series* 106, 173–185.
- Jeong, H.J., Yoo, Y.D., Kim, J.S., Seong, K.A., Kang, N.S., Kim, T.H., 2010. Growth, feeding and ecological roles of the mixotrophic and heterotrophic dinoflagellates in marine planktonic food webs. *Ocean Science Journal* 45, 65–91.
- Jónasdóttir, S.H., Trung, N.H., Hansen, F., 2005. Egg production and hatching success of the Calanoid copepods *Calanus helgolandicus* and *Calanus finmarchicus* in the North Sea from March to September 2001. *Journal of Plankton Research* 27, 1239–1259.
- Jónasdóttir, S.H., Visser, A.W., Jespersen, C., 2009. Assessing food quality in the production and hatching of *Temora longicornis* eggs. *Marine Ecology Progress Series* 382, 139–150.
- Jones, R.H., Flynn, K.J., 2005. Nutritional status and diet composition affect the value of diatoms as copepod prey. *Science* 307, 1457–1459.
- Kaartvedt, S., 1996. Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus*. *Ophelia* 44, 145–156.
- Kimmerer, W.J., McKinnon, A.D., 1987. Growth, mortality, and secondary production of the copepod *Acartia tranteri* in Westernport Bay, Australia. *Limnology and Oceanography* 32, 14–28.
- Kjørboe, T., Saiz, E., 1995. Planktivorous feeding in calm and turbulent environments with emphasis on copepods. *Marine Ecology Progress Series* 120, 285–298.
- Kjørboe, T., Sabatini, M., 1994. Reproductive and life cycle strategies in egg-carrying cyclopoid and free-spawning calanoid copepods. *Journal of Plankton Research* 16, 1353–1366.
- Kjørboe, T., Møhlenberg, F., Hamburger, K., 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. *Marine Ecology Progress Series* 26, 85–97.
- Kjellerup, S., Dünweber, M., Swalethorpe, R., Nielsen, T.G., Möller, E.F., Markager, S., Hansen, B.W., 2012. Effects of a future warmer ocean on the coexisting copepods *Calanus finmarchicus* and *C. glacialis* in Disko Bay, western Greenland. *Marine Ecology Progress Series* 447, 87–108.
- Kleiber, M., 1932. Body size and metabolism. *Hilgardia* 6, 315–353.
- Klein Breteler, W.C.M., Schogt, N., Baas, M., Schouten, S., Kraay, G.W., 1999. Trophic upgrading of food quality by protozoans enhancing copepod growth: role of essential lipids. *Marine Biology* 135, 191–198.
- Knutsen, J.A., 1992. Feeding behaviour of North Sea turbot (*Scophthalmus maximus*) and Dover sole (*Solea solea*) larvae elicited by chemical stimuli. *Marine Biology* 113, 543–548.
- Kolokotronis, T., Savage, V., Deeds, E.J., Fontana, W., 2010. Curvature in metabolic scaling. *Nature* 464, 753–756.
- Koski, M., Klein Breteler, W., Schogt, N., Gonzalez, S., Jakobsen, H.H., 1998. Life-stage-specific differences in exploitation of food mixtures: diet mixing enhances copepod egg production but not juvenile development. *Journal of Plankton Research* 28, 919–936.
- Kruskopf, M., Flynn, K.J., 2006. Chlorophyll content and fluorescence responses cannot be used to gauge reliably phytoplankton biomass, nutrient status or growth rate. *New Phytologist* 169, 525–536.
- Kurihara, H., Ishimatsu, A., 2008. Effects of elevated CO₂ on the life cycle of copepod *Acartia tsuensis*. *Marine Pollution Bulletin* 56, 1086–1090.
- Landry, M.R., 1993. Predicting excretion rates of microzooplankton from carbon metabolism and elemental ratios. *Limnology and Oceanography* 38, 468–472.
- Landry, M.R., Lehnert-Fournier, J.M., Sundstrom, J.A., Fagerness, V.L., Selph, K.E., 1991. Discrimination between living and heat-killed prey by a marine zooflagellate, *Paraphysomonas vestita* (Stokes). *Journal of Experimental Marine Biology and Ecology* 146, 139–151.
- Lass, S., Tarling, G.A., Virtue, P., Matthews, J.B.L., Mayzaud, P., Buchholz, F., 2001. On the food of northern krill *Meganyctiphanes norvegica* in relation to its vertical distribution. *Marine Ecology Progress Series* 214, 177–200.
- Lee, R.F., Hagen, W., Kattner, G., 2006. Lipid storage in marine zooplankton. *Marine Ecology Progress Series* 307, 273–306.
- Lehman, J.T.L., 1976. The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. *Limnology and Oceanography* 21, 501–516.
- Leising, A.W., 2001. Copepod foraging in patchy habitats and thin layers using a 2-D individual-based model. *Marine Ecology Progress Series* 216, 167–179.
- Leising, A.W., Franks, P.J.S., 2000. Copepod vertical distribution within a spatially variable food source: a simple foraging-strategy model. *Journal of Plankton Research* 22, 999–1024.
- Leising, A.W., Pierson, J.J., Halsband-Lenk, C., Horner, R.A., Postel, J., 2005a. Copepod grazing during spring blooms: Does *Calanus pacificus* avoid harmful diatoms? *Progress in Oceanography* 67, 384–405.
- Leising, A.W., Pierson, J.J., Halsband-Lenk, C., Horner, R.A., Postel, J., 2005b. Copepod grazing during spring blooms: Can *Pseudocalanus newmani* induce trophic cascades? *Progress in Oceanography* 67, 406–421.
- Leising, A.W., Pierson, J.J., Cary, S., Frost, B.W., 2005c. Copepod foraging and predation risk within the surface layer during night-time feeding forays. *Journal of Plankton Research* 27, 987–1001.
- Lochte, K., Ducklow, H.W., Fasham, M.J.R., Stienen, C., 1993. Plankton succession and carbon cycling at 47°N 20°W during the JGOFS North Atlantic Bloom Experiment. *Deep Sea Research II* 40, 91–114.
- Lombard, F., Selander, E., Kiørboe, T., 2011. Active prey rejection in the filter-feeding appendicularian *Oikopleura dioica*. *Limnology and Oceanography* 56, 1504–1512.
- Lynch, D.R., Gentleman, W.C., McGillicuddy Jr., D.J., Davis, C.S., 1998. Biological/physical simulations of *Calanus finmarchicus* population dynamics in the Gulf of Maine. *Marine Ecology Progress Series* 169, 189–210.
- Maar, M., Nielsen, T.G., Stips, A., Visser, A.W., 2003. Microscale distribution of zooplankton in relation to turbulent diffusion. *Limnology and Oceanography* 48, 1312–1325.
- Maas, A.E., Wishner, K.F., Seibel, B.A., 2012. The metabolic response of pteropods to acidification reflects natural CO₂-exposure in oxygen minimum zones. *Biogeosciences* 9, 747–757.
- Mackie, G.O., Pugh, P.R., Purcell, J.E., 1987. Siphonophore biology. *Advances in Marine Biology* 24, 97–262.
- Martel, C.M., 2006. Prey location, recognition and ingestion by the phagotrophic marine dinoflagellate *Oxyrrhis marina*. *Journal of Experimental Marine Biology and Ecology* 335, 210–220.
- Mauchline, J., 1998. *The Biology of Calanoid Copepods*. Academic Press, San Diego, USA.

- Mayor, D., Matthews, C., Cook, K., Zuur, A., Hay, S., 2007. CO₂-induced acidification affects hatching success in *Calanus finmarchicus*. *Marine Ecology Progress Series* 350, 91–97.
- Mayzaud, P., Tirelli, V., Bernard, J.M., Roche-Mayzaud, O., 1998. The influence of food quality on the nutritional acclimation of the copepod *Acartia clausi*. *Journal of Marine Systems* 14 (483), 493.
- McLaren, I., 1965. Some relationships between temperature and egg size, body size, development rate, and fecundity, of the copepod *Pseudocalanus*. *Limnology and Oceanography* 10, 528–538.
- Menden-Deuer, S., Grünbaum, D., 2006. Individual foraging behaviors and population distributions of a planktonic predator aggregating to phytoplankton thin layers. *Limnology and Oceanography* 59, 109–116.
- Metcalfe, A.M., Pedley, T.J., Thingstad, T.F., 2004. Incorporating turbulence into a plankton foodweb model. *Journal of Marine Systems* 49, 105–122.
- Miller, C.B., Cowles, T.J., Wiebe, P.H., Copley, N.J., Grigg, H., 1991. Phenology in *Calanus finmarchicus*; hypotheses about control mechanisms. *Marine Ecology Progress Series* 72, 79–91.
- Miller, C.B., Crain, J.A., Morgan, C.A., 2000. Oil storage variability in *Calanus finmarchicus*. *ICES Journal of Marine Science* 57, 1786–1799.
- Miralto, A., Barone, G., Romano, G., Poulet, S.A., Ianora, A., Russo, G.L., Buttino, I., Mazzarella, G., Laabir, M., Cabrini, M., Giacobbe, M.G., 1999. The insidious effect of diatoms on copepod reproduction. *Nature* 402, 173–176.
- Mitra, A., 2006. A multi-nutrient model for the description of stoichiometric modulation of predation (SMP) in micro- and mesozooplankton. *Journal of Plankton Research* 28, 597–611.
- Mitra, A., 2009. Are closure terms appropriate or necessary descriptors of zooplankton loss in nitrogen-phytoplankton-zooplankton models? *Ecological Modelling* 220, 611–620.
- Mitra, A., Davis, C., 2010. Defining the “to” in end-to-end models. *Progress in Oceanography* 84, 39–42.
- Mitra, A., Flynn, K.J., 2005. Predator-prey interactions: is “ecological stoichiometry” sufficient when good food goes bad? *Journal of Plankton Research* 27, 393–399.
- Mitra, A., Flynn, K.J., 2006a. Promotion of harmful algal blooms by zooplankton predatory activity. *Biology Letters* 2, 194–197.
- Mitra, A., Flynn, K.J., 2006b. Accounting for variation in prey selectivity by zooplankton. *Ecological Modelling* 199, 82–92.
- Mitra, A., Flynn, K.J., 2007. Effects of food quality and quantity on consumer gut passage time; impacts on predation kinetics and trophic dynamics. *American Naturalist* 169, 632–646.
- Mitra, A., Flynn, K.J., 2010. Modelling mixotrophy in Harmful Algal Blooms; more or less the sum of the parts? *Journal of Marine Systems* 83, 158–169.
- Mitra, A., Flynn, K.J., Fasham, M.J.R., 2007. Accounting correctly for grazing dynamics in Nutrient-Phytoplankton-Zooplankton models. *Limnology and Oceanography* 52, 649–661.
- Mitra, A., Flynn, K.J., Burkholder, J.M., Berge, T., Calbet, A., Raven, J.A., Granéli, E., Gilbert, P.M., Hansen, P.J., Stoecker, D.K., Thingstad, F., Tillmann, U., Våge, S., Wilken, S., Zubkov, M.V., 2014. The role of mixotrophic protists in the biological carbon pump. *Biogeosciences* 11, 995–1005.
- Møller, E.F., 2005. Sloppy feeding in marine copepods: prey-size-dependent production of dissolved organic carbon. *Journal of Plankton Research* 27, 341–356.
- Møller, E.F., 2007. Production of dissolved organic carbon by sloppy feeding in the copepods *Acartia tonsa*, *Centropages typicus* and *Temora longicornis*. *Limnology and Oceanography* 52, 79–84.
- Møller, E.F., Thor, P., Nielsen, T.G., 2003. Production of DOC by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* through sloppy feeding and leakage from fecal pellets. *Marine Ecology Progress Series* 262, 185–191.
- Møller, E.F., Maar, M., Jónasdóttir, S.H., Nielsen, T.G., Tönnesson, K., 2012. The effect of changes in temperature and food on the development of *Calanus finmarchicus* and *Calanus helgolandicus* populations. *Limnology and Oceanography* 57, 211–220.
- Moloney, C.L., Gibbons, M.J., 1996. Sampling and analysis of gut contents in relation to environmental variability and diel vertical migration by herbivorous zooplankton. *Journal of Plankton Research* 18, 1535–1556.
- Morozov, A., Arashkevich, E., Nikishina, A., Solovyev, K., 2011. Nutrient-rich plankton communities stabilized via predator-prey interactions: revisiting the role of vertical heterogeneity. *Mathematical Medicine and Biology* 28, 185–215.
- Myers, R.A., Runge, J.A., 1983. Predictions of seasonal natural mortality rates in a copepod population using life-history theory. *Marine Ecology Progress Series* 11, 189–194.
- Nakamura, Y., Suzuki, S.Y., Hiromi, J., 1995. Growth and grazing of a naked heterotrophic dinoflagellate, *Gyrodinium dominans*. *Aquatic Microbial Ecology* 9, 157–164.
- Neubert, M.G., Klanjscek, T., Caswell, H., 2004. Reactivity and transient dynamics of predator-prey and food web models. *Ecological Modelling* 179, 29–38.
- Neuheimer, A.B., Gentleman, W.C., Galloway, C.L., 2009. Modeling larval *Calanus finmarchicus* on Georges Bank: time-varying mortality rates and a cannibalism hypothesis. *Fisheries Oceanography* 18, 147–160.
- Neuheimer, A.B., Gentleman, W.C., Pepin, P., Head, E.J.H., 2010a. How to build and use individual-based models (IBMs) as hypothesis testing tools. *Journal of Marine Systems* 81, 122–133.
- Neuheimer, A.B., Gentleman, W.C., Pepin, P., Head, E.J.H., 2010b. Explaining regional variability in copepod recruitment: Implications for a changing climate. *Progress in Oceanography* 87, 94–105.
- Ohman, M.D., 1986. Predator-limited population growth of the copepod *Pseudocalanus* sp. *Journal of Plankton Research* 8, 673–713.
- Ohman, M.D., 1984. Omnivory by *Euphausia superba*: the role of copepod prey. *Marine Ecology Progress Series* 19, 125–131.
- Ohman, M.D., Aksnes, D.L., Runge, J.A., 1996. The interrelationship of copepod fecundity and mortality. *Limnology and Oceanography* 41, 1470–1477.
- Ohman, M.D., Durbin, E.G., Runge, J.A., Sullivan, B.K., Field, D.B., 2008. Relationship of predation potential to mortality of *Calanus finmarchicus* on Georges Bank, northwest Atlantic. *Limnology and Oceanography* 53, 1643–1655.
- Ohman, M.D., Hirche, H.J., 2001. Density-dependent mortality in an oceanic copepod population. *Nature* 412, 638–641.
- Ohman, M.D., Wood, S.N., 1995. The inevitability of mortality. *ICES Journal of Marine Science* 52, 517–522.
- Onsrud, M.S.R., Kaartvedt, S., 1998. Diel vertical migration of the krill *Meganyctiphanes norvegica* in relation to physical environment, food and predators. *Marine Ecology Progress Series* 171, 209–219.
- Öpik, H., Flynn, K.J., 1989. The digestive process of the dinoflagellate *Oxyrrhis marina* Dujardin, feeding on the chlorophyte, *Dunaliella primolecta* Butcher: a combined study of ultrastructure and free amino acids. *New Phytologist* 113, 143–151.
- Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R.M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R.G., Plattner, G.-K., Rodgers, K.B., Sabine, C.L., Sarmiento, J.L., Schlitzer, R., Slater, R.D., Totterdell, I.J., Weirig, M.-F., Yamanaka, Y., Yool, A., 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437, 681–686.
- Osgood, K.E., Frost, B.W., 1994. Ontogenetic diel vertical migration behaviors of the marine planktonic copepods *Calanus pacificus* and *Metridia lucens*. *Marine Ecology Progress Series* 104, 13–24.
- Paffenhöfer, G.A., Van Sant, K.B., 1985. The feeding response of a marine planktonic copepod to quantity and quality of particles. *Marine Ecology Progress Series* 27, 55–65.
- Pagès, F., Madin, L., 2010. Siphonophores eat fish larger than their stomachs. *Deep-Sea Research II* 57, 2248–2250.
- Park, Y.C., Carpenter, E.J., Falkowski, P.G., 1986. Ammonium excretion and glutamate dehydrogenase activity of zooplankton in Great South Bay, New York. *Journal of Plankton Research* 8, 489–503.
- Parry, G.D., 1983. The influence of the cost of growth on ectotherm metabolism. *Journal of Theoretical Biology* 101, 453–477.
- Pedersen, M.F., Hansen, P.J., 2003a. Effects of high pH on a natural marine planktonic community. *Marine Ecology Progress Series* 260, 33–41.
- Pedersen, M.F., Hansen, P.J., 2003b. Effects of high pH on the growth and survival of six marine heterotrophic protists. *Marine Ecology Progress Series* 260, 19–31.
- Peters, R.H., 1983. *The Ecological Implications of Body Size*. Cambridge University Press, New York.
- Peterson, W.T., 1999. Life cycle strategies of copepods in coastal upwelling zones. *Journal of Marine Systems* 15, 313–326.
- Peterson, W.T., 2001. Patterns in stage duration and development among marine and freshwater calanoid and cyclopoid copepods: a review of rules, physiological constraints, and evolutionary significance. *Hydrobiologia* 453 (454), 91–105.
- Peterson, C.G., Jones, T.L., 2003. Diatoms viability in insect fecal material: comparison between two species, *Achnanthes lanceolatum* and *Synedra ulna*. *Hydrobiologia* 501, 93–99.
- Pierson, J.J., Leising, A.W., Halsband-Lenk, C., Ferm, N., 2005. Vertical distribution and abundance of *Calanus pacificus* and *Pseudocalanus newmani* in relation to chlorophyll a concentrations in Dabob Bay, Washington. *Progress in Oceanography* 67, 349–365.
- Plagányi, E.E., 2007. *Models for an Ecosystem Approach to Fisheries*. FAO (Food and Agriculture Organization of the United Nations) Fisheries Technical Paper 477.
- Plath, K., Boersma, M., 2001. Mineral limitation of zooplankton: stoichiometric constraints and optimal foraging. *Ecology* 82, 1260–1269.
- Plourde, S., Maps, F., Joly, P., 2009. Mortality and survival in early stages controls recruitment in *Calanus finmarchicus*. *Journal of Plankton Research* 31, 371–388.
- Pomeroy, L.R., 1974. The ocean's food web, a changing paradigm. *BioScience* 9, 499–504.
- Pond, D.W., Tarling, G.A., 2011. Phase transitions of wax esters adjust buoyancy in diapausing, *Calanoides acutus*. *Limnology and Oceanography* 56, 1310–1318.
- Pond, D.W., 2012. The physical properties of lipids and their role in controlling the distribution of zooplankton in the oceans. *Journal of Plankton Research* 34 (6), 443–453.
- Poulet, S.A., Ouellet, G., 1982. The role of amino acids in the chemosensory swarming and feeding of marine copepods. *Journal of Plankton Research* 4, 341–361.
- Poulsen, L.K., Moldrup, M., Berge, T., Hansen, P.J., 2011. Feeding on copepod fecal pellets: a new trophic role of dinoflagellates as detritivores. *Marine Ecology Progress Series* 441, 65–78.
- Purcell, J.E., Arai, M.N., 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* 451, 27–44.
- Ribaut, F., Wichard, T., Pohnert, G., Ianora, A., Miralto, A., Casotti, R., 2007. Age and nutrient limitation enhance polyunsaturated aldehyde production in marine diatoms. *Phytochemistry* 68, 2059–2067.
- Richardson, A.J., Gibbons, M.J., 2008. Are jellyfish increasing in response to ocean acidification? *Limnology and Oceanography* 53, 2040–2045.
- Richardson, K., Jónasdóttir, S.H., Hay, S.J., Christoffersen, A., 1999. *Calanus finmarchicus* egg production and food availability in the Faroe-Shetland

- Channel and northern North Sea: October – March. Fisheries Oceanography 8 (Suppl. 1), 153–162.
- Roberts, E.C., Wootton, E.C., Davidson, K., Jeong, H.J., Lowe, C.D., Montagnes, D.J.S., 2011. Feeding in the dinoflagellate *Oxyrrhis marina*: linking behaviour with mechanisms. Journal of Plankton Research 33, 603–614.
- Rose, K.A., Werner, F.E., Megrey, B.A., Aita, M.N., Yamanakae, Y., Hayf, D.E., Schweigert, J.F., Foster, M.B., 2007. Simulated herring growth responses in the Northeastern Pacific to historic temperature and zooplankton conditions generated by the 3-dimensional NEMURO nutrient–phytoplankton–zooplankton model. Ecological Modelling 202, 184–195.
- Rose, K.A., Allen, J.I., Artioli, Y., Barange, M., Blackford, J., Carlotti, F., Cropp, R., Daewel, U., Edwards, K., Flynn, K.J., Hill, S.L., Hille Ris Lambers, R., Huse, G., Mackinson, S., Megrey, B., Moll, A., Rivkin, R., Salihoglu, B., Schrum, C., Shannon, L., Shin, Y.-J., Smith, S.L., Smith, C., Solidoro, C., St. John, M., Zhou, M., 2010. End-To-End models for the analysis of marine ecosystems: challenges, issues, and next steps. Marine and Coastal Fisheries and Dynamic Management Ecosystem Science 2, 115–130.
- Rothschild, B.J., Osborn, T.R., 1988. Small-scale turbulence and plankton contact rates. Journal of Plankton Research 10, 465–474.
- Royal Society of London, 2005. Ocean Acidification due to Increased Atmospheric Carbon Dioxide. Policy Document 12/05. The Royal Society of London.
- Rubino, F., Belmonte, G., Miglietta, A.M., Geraci, S., Boero, F., 2000. Resting stages of plankton in recent North Adriatic sediments. Marine Ecology PSZNI 21, 263–284.
- Saborowski, R., Bröhl, S., Tarling, G.A., Buchholz, F., 2002. Metabolic properties of Northern krill, *Meganyctiphanes norvegica*, from different climatic zones. I. Respiration and excretion. Marine Biology 140, 547–556.
- Saito, H., Ota, T., Suzuki, K., Nishioka, J., Tsuda, A., 2006. Role of heterotrophic dinoflagellate *Gyrodinium* sp. in the fate of an iron induced diatom bloom. Geophysical Research Letters 33, L09602. <http://dx.doi.org/10.1029/2005GL025366>.
- Saiz, E., Calbet, A., 2007. Scaling of feeding in marine calanoid copepods. Limnology and Oceanography 52, 668–675.
- Saiz, E., Kiørboe, T., 1995. Predatory and suspension feeding of the copepod *Acartia tonsa* in turbulent environments. Marine Ecology Progress Series 122, 147–158.
- Saiz, E., Alcaraz, M., Paffenhöfer, G.A., 1992. Effects of small-scale turbulence on feeding rate and gross-growth efficiency of three *Acartia* species (Copepoda: Calanoida). Journal of Plankton Research 14, 1085–1097.
- Saiz, E., Calbet, A., Broglie, E., 2003. Effects of small-scale turbulence on copepods: The case of *Oithona davisae*. Limnology and Oceanography 48, 1304–1311.
- Sanders, R.W., Porter, K.G., 1987. Transfer efficiencies of microbial carbon to higher trophic levels: The heterotrophic flagellate–crustacean link. Eos 68, 1705.
- Schnack-Schiel, S.B., 2001. Aspects of the study of the life cycles of Antarctic copepods. Hydrobiologia 453–454, 9–24.
- Secor, S.M., 2009. Specific dynamic action: a review of the postprandial metabolic response. Journal of Comparative Physiology B 179, 1–56.
- Sell, A.F., Van Keuren, D., Madin, L.P., 2001. Predation by omnivorous copepods on early developmental stages of *Calanus finmarchicus* and *Pseudocalanus* spp. Limnology and Oceanography 46, 953–959.
- Sherr, E.B., Sherr, B.F., 1994. Bacterivory and herbivory – key roles of phagotrophic protists in pelagic food webs. Microbial Ecology 28, 223–235.
- Skarðhamar, J., Reigstad, M., Caroll, J., Eiane, K., Riser, C.W., Slagstad, D., 2011. Effects of mortality changes on biomass and production in *Calanus* spp. populations. Aquatic Biology 12, 129–145.
- Speirs, D.C., Gurney, W.S.C., Heath, M.R., Horbelt, W., Wood, S.N., de Cuevas, B.A., 2006. Ocean-scale modelling of the distribution, abundance and seasonal dynamics of the copepod *Calanus finmarchicus*. Marine Ecology Progress Series 313, 173–192.
- Stalder, L.C., Marcus, N.H., 1997. Zooplankton responses to hypoxia: behavioral patterns and survival of three species of calanoid copepods. Marine Biology 127, 599–607.
- Steele, J.H., 1974. The Structure of Marine Ecosystems. Harvard Univ. Press, Cambridge, UK.
- Steele, J.H., Henderson, E.W., 1981. A simple plankton model. American Naturalist 117, 676–691.
- Steele, J.H., Henderson, E.W., 1992. The role of predation in plankton models. Journal of Plankton Research 14, 157–172.
- Steele, J.H., Henderson, E.W., 1995. Predation control of plankton demography. ICES Journal of Marine Science 52, 565–573.
- Steele, J.H., Mullin, M.M., 1977. Zooplankton dynamics. In: Goldberg, E.D. (Ed.), The Sea, Ideas and Observations on Progress in the Study of the Seas. Wiley and Sons, New York, pp. 857–890.
- Sterner, R.W., Elser, J.J., 2002. Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. Princeton Univ. Press, Princeton, New Jersey.
- Stoecker, D.K., Long, A., Suttles, S.E., Sanford, L.P., 2006. Effect of small-scale shear on grazing and growth of the dinoflagellate *Pfiesteria piscicida*. Harmful Algae 5, 407–418.
- Stoecker, D.K., Johnson, M.D., de Vargas, C., Not, F., 2009. Acquired phototrophy in aquatic protists. Aquatic Microbial Ecology 57, 279–310.
- Suttle, C.A., Chan, A.M., Taylor, W.D., Harrison, P.J., 1986. Grazing of planktonic diatoms by microflagellates. Journal of Plankton Research 8, 393–398.
- Tande, K.S., 1982. Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: generation cycles and variations in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus* (Gunnerus). Journal of Experimental Marine Biology and Ecology 62, 129–142.
- Thébault, J.M., 1985. Experimental study of nutrition of common copepods (*Temora stylifera* Dana) – effects of temperature and concentration of nutrition. Journal of Experimental Marine Biology and Ecology 93, 223–234.
- Thor, P., Wendt, I., 2010. Functional response of carbon absorption efficiency in the pelagic calanoid copepod *Acartia tonsa* Dana. Limnology and Oceanography 55, 1779–1789.
- Tirelli, V., Mayzaud, P., 2005. Relationship between functional response and gut transit time in the calanoid copepod *Acartia clausi*: role of food quantity and quality. Journal of Plankton Research 27, 557–568.
- Tiselius, P., Borg, C.M.A., Hansen, B.W., Hansen, P.J., Nielsen, T.G., Vismann, B., 2008. High reproduction, but low biomass: mortality estimates of the copepod *Acartia tonsa* in a hyper-eutrophic estuary. Aquatic Biology 2, 93–103.
- Titelman, J., Kiørboe, T., 2003. Motility of copepod nauplii and implications for food encounter. Marine Ecology Progress Series 247, 123–135.
- Tong, S., 1997. Heterotrophic flagellates and other protists from Southampton water, U.K. Ophelia 47, 71–131.
- Tönnesson, K., Tiselius, P., 2005. Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. Marine Ecology Progress Series 289, 177–190.
- Travers, M., Shin, Y.-J., Jennings, S., Cury, P., 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. Progress in Oceanography 75, 751–770.
- Trumble, S.J., Castellini, M.A., 2005. Diet mixing in an aquatic carnivore, the harbour seal. Canadian Journal of Zoology 83, 851–859.
- Tsuda, A., 1994. Starvation tolerance of a planktonic marine copepod *Pseudocalanus newmani* Frost. Journal of Experimental Marine Biology and Ecology 181, 81–89.
- Turner, J.T., Tester, P.A., 1997. Toxic marine phytoplankton, zooplankton grazers, and pelagic food webs. Limnology and Oceanography 42, 1203–1214.
- Twombly, S., 1994. Comparative demography and population dynamics of two coexisting copepods in a Venezuelan floodplain lake. Limnology and Oceanography 39, 234–247.
- Van Donk, E., Lüring, M., Hessen, D.O., Lokhorst, G.M., 1997. Altered cell wall morphology in nutrient-deficient phytoplankton and its impact on grazers. Limnology and Oceanography 42, 357–364.
- Varpe, O., Jørgensen, C., Tarling, G.A., Fiksen, O., 2007. Early is better: Seasonal egg fitness and timing of reproduction in a zooplankton life-history model. Oikos 116, 1331–1342.
- Verity, P.G., Paffenhöfer, G.A., 1996. On assessment of prey ingestion by copepods. Journal of Plankton Research 18, 1767–1779.
- Verity, P.G., Smetacek, V., 1996. Organism life cycles, predation, and the structure of marine pelagic ecosystems. Marine Ecology Progress Series 130, 277–293.
- Visser, A.W., 2007. Motility of zooplankton: fitness, foraging and predation. Journal of Plankton Research 29, 447–461.
- Visser, A.W., Saito, H., Saiz, E., Kiørboe, T., 2001. Observations of copepod feeding and vertical distribution under natural turbulent conditions in the North Sea. Marine Biology 138, 1011–1019.
- Ward, J.E., Targett, N.M., 1989. Influence of marine microalgal metabolites on the feeding behavior of the blue mussel *Mytilus edulis*. Marine Biology 101, 313–321.
- West, G.B., Brown, J.H., Enquist, B.J., 1997. A general model for the origin of allometric scaling laws in biology. Science 276, 122–126.
- West, G.B., Brown, J.H., 2005. The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. Journal of Experimental Biology 208, 1575–1592.
- White, C.R., Cassey, P., Blackburn, T.M., 2007. Allometric exponents do not support a universal metabolic allometry. Ecology 88, 315–323.
- White, C.R., Phillips, N.F., Seymour, R.S., 2006. The scaling and temperature dependence of vertebrate metabolism. Biology Letters 2, 125–127.
- Williams, P.J.leb., 1981. Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. Kieler Meeresforsch. (Sonderh.) 5, 1–28.
- Zakardjian, B.A., Sheng, J., Runge, J.A., McLaren, I., Plourde, S., Thompson, K.R., Gratton, Y., 2003. Effects of temperature and circulation on the population dynamics of *Calanus finmarchicus* in the Gulf of St. Lawrence and Scotian Shelf: Study with a coupled, three-dimensional hydrodynamic, stage-based life history model. Journal of Geophysical Research 108 (C11), 8016.
- Zhang, D., Li, S., Wang, G., Guo, D., 2011. Impacts of CO₂-driven seawater acidification on survival, egg production rate and hatching success of four marine copepods. Acta Oceanologica Sinica 30, 86–94.