



*J. Plankton Res.* (2013) 35(3): 473–484. First published online March 26, 2013 doi:10.1093/plankt/fbt019

## HORIZONS

# Trait-based approaches to zooplankton communities

ELENA LITCHMAN<sup>1,2,\*</sup>, MARK D. OHMAN<sup>3</sup> AND THOMAS KIØRBOE<sup>2</sup>

<sup>1</sup>KELLOGG BIOLOGICAL STATION, MICHIGAN STATE UNIVERSITY, HICKORY CORNERS, MI, USA, <sup>2</sup>CENTRE FOR OCEAN LIFE, NATIONAL INSTITUTE FOR AQUATIC RESOURCES, TECHNICAL UNIVERSITY OF DENMARK, KVAALERGÅRDEN 6, CHARLOTTENLUND 2920, DENMARK AND <sup>3</sup>INTEGRATIVE OCEANOGRAPHY DIVISION, SCRIPPS INSTITUTION OF OCEANOGRAPHY, UNIVERSITY OF CALIFORNIA, SAN DIEGO, CA 92093-0218, USA

\*CORRESPONDING AUTHOR: litchman@msu.edu

Received August 31, 2012; accepted February 19, 2013

Corresponding editor: Roger Harris

Zooplankton are major primary consumers and predators in most aquatic ecosystems. They exhibit tremendous diversity of traits, ecological strategies and, consequently, impacts on other trophic levels and the cycling of materials and energy. An adequate representation of this diversity in community and ecosystem models is necessary to generate realistic predictions on the functioning of aquatic ecosystems but remains extremely challenging. We propose that the use of trait-based approaches is a promising way to reduce complexity while retaining realism in developing novel descriptions of zooplankton in ecosystem models. Characterizing zooplankton traits and trade-offs will also be helpful in understanding the selection pressures and diversity patterns that emerge in different ecosystems along major environmental gradients. Zooplankton traits can be characterized according to their function and type. Some traits, such as body size and motility, transcend several functions and are major determinants of zooplankton ecological strategies. Future developments of trait-based approaches to zooplankton should assemble a comprehensive matrix of key traits for diverse groups and explore it for general patterns; develop novel predictive models that explicitly incorporate traits and associated trade-offs; and utilize these traits to explain and predict zooplankton

community structure and dynamics under different environmental conditions, including global change scenarios.

**KEYWORDS:** functional trait; fitness; trade-off; zooplankton

## INTRODUCTION

Understanding and predicting the structure and function of plankton communities under different environmental conditions, including a changing climate, is an important challenge for aquatic ecologists, oceanographers and limnologists. Zooplankton are among the most abundant aquatic organisms and they occupy key trophic positions in most marine and freshwater environments (Kjørboe, 2008a). Knowledge of the structure and functioning of zooplankton communities is, therefore, a key component of our general understanding of aquatic ecosystems. Zooplankton in marine and freshwater environments exhibit significant diversity of ecological strategies, dominance patterns and effects on ecosystems. Adequately representing this diversity in conceptual and mathematical models is challenging and only just beginning.

Parallel challenges of representing ecological diversity exist for phytoplankton. The most common approach is to explicitly model key functional groups and their impacts on ecosystems. Such models, however, can lead to a large number of equations representing functional groups, rapidly increasing the complexity of the models (Litchman and Klausmeier, 2008; Follows and Dutkiewicz, 2011). Another shortcoming of this approach is that setting up functional groups *a priori* limits model flexibility and precludes the possible rise of new functional groups under novel conditions. A more promising approach that is gaining interest is to focus on key traits rather than functional groups and to consider a continuum of traits inter-related through trade-offs (Bruggeman and Kooijman, 2007; Follows *et al.*, 2007; Litchman and Klausmeier, 2008; Merico *et al.*, 2009). This approach permits the reduction of model complexity while maintaining an adequate representation of diversity and, moreover, it allows the emergence of species and groups with novel combinations of traits that may arise under changing environmental conditions.

Here we propose that such a trait-based approach can also be useful for describing and modeling zooplankton communities and pelagic ecosystems. We discuss possible zooplankton traits that can be included, propose a general trait classification framework and outline future research directions and main challenges to this approach. Parts of zooplankton ecology are mature fields

with a wealth of studies on different aspects of zooplankton behavior, physiology and biogeography. Using existing studies for a trait-based synthesis is a productive way to gain new insights and to increase our mechanistic understanding of the structure and functioning of zooplankton communities and aquatic ecosystems in general (Barnett *et al.*, 2007).

## TRAITS AND TRADE-OFFS

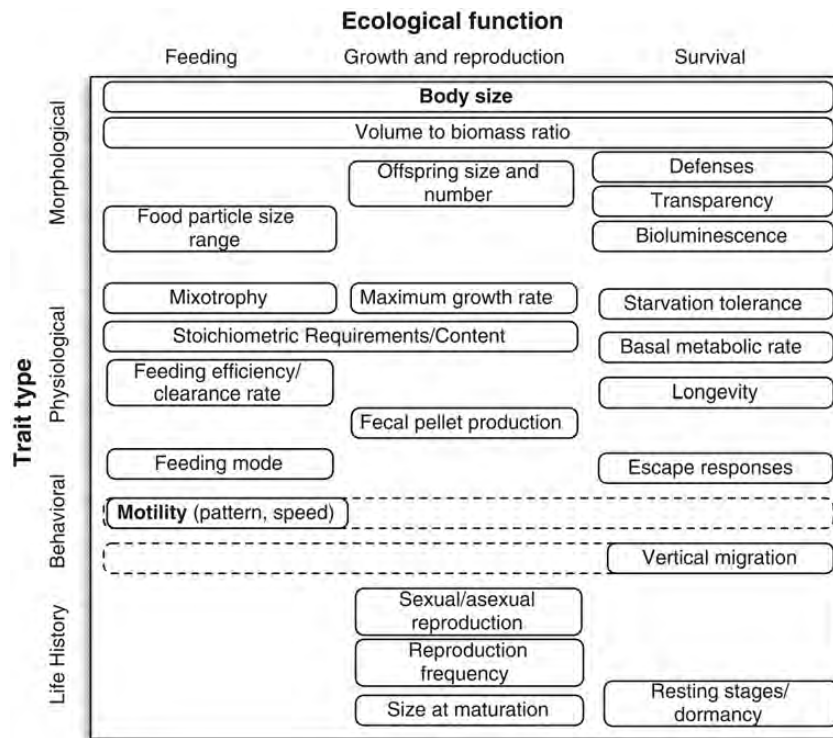
The key traits of an organism are those few traits that best characterize its fitness. There are various measures of fitness that are applicable to zooplankton, such as the summation of the reproductive rate discounted by the mortality rate. If integrated over the lifetime, this is the net reproductive rate,  $R_0$ :

$$R_0 = \int_0^{\infty} l_x m_x dx \quad (1)$$

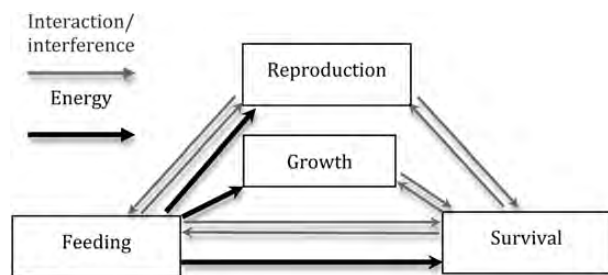
where  $l_x$  is the probability of surviving to age  $x$  and  $m_x$  is the number of progeny per female produced at age  $x$ . Other formulations include the reproductive rate minus the mortality rate, the Malthusian parameter ( $r = \ln R_0 / T$ , where  $T$  is the average generation time), or Gilliam's rule: the minimization of mortality rate relative to energy gain (Gilliam and Fraser, 1987).

In all cases, fitness is a function of the feeding, growth, survival and the reproductive rates of the organism. These three fundamental activities, in turn, depend on the details of the biology of an organism, and may be expressed differently for different life forms. A combination of morphological, physiological, behavioral and life history traits is involved in these functions. Consequently, we propose classifying traits according to their type and the function in which they are involved (Fig. 1), similar to a recent trait classification for phytoplankton (Litchman and Klausmeier, 2008). Obviously, this classification scheme is not the only possible or an exhaustive one, but we hope that it stimulates a search for general patterns and further trait categorizations.

Natural selection tends to maximize individual fitness by optimizing the net result of feeding, survival, growth



**Fig. 1.** Zooplankton trait classification according to function and type. Key traits that transcend several functions and influence many other traits are indicated in bold. Dotted lines indicate traits that may have a secondary importance for other functions.



**Fig. 2.** The fundamental Darwinian missions of an organism are to feed, survive and reproduce. These activities may interfere with one another, and the energy obtained from feeding may be allocated to different competing functions: growth, reproduction and longevity/survival (investment in maintenance, storage and repair). The optimum behavior and energy allocation pattern is that which maximizes the fitness of the individual in a particular environment.

and reproduction. However, there are potential conflicts—trade-offs—between these activities, and all cannot be maximized simultaneously (Fig. 2). For example, a non-motile ambush feeder will never encounter a mate unless it swims and, hence, sacrifices feeding (Kjørboe, 2008b); searching for a mate or for food increases encounter rates with predators and generates fluid disturbances that may be perceived by rheotactic predators, and thus reduces survival (Tiselius *et al.*, 1997; Kjørboe *et al.*, 2010; Lasley-Rasher and Yen, 2012) and

migrating to deep water during daytime to avoid visual predators (Aksnes and Giske, 1990; Fiksen, 1997) or during nighttime to avoid non-visual predators (Ohman, 1990) implies lost feeding opportunities. Thus, an organism cannot maximize performance with respect to all fundamental activities simultaneously. Energy from food must similarly be allocated to different competing functions, i.e. maintenance, growth and reproductive products (Fig. 2). Investment in maintenance, storage and repair enhances longevity but leaves less energy for growth and reproduction. Investment in growth allows the organism to achieve a large size and a high-reproductive potential in the future, while investment in gonads contributes directly to current reproduction.

Quantifying the risks and trade-offs associated with key traits may allow us to predict the behavior, physiology and morphology that optimize the fitness of an organism in any particular environment (Gilliam and Fraser, 1987) and to predict the distribution of traits along environmental gradients. We, therefore, argue that zooplankton traits and the associated trade-offs should be considered in light of their effects on fitness, as the same fitness can be achieved through optimizing different components, e.g. traits affecting feeding, survival, growth and reproduction. An explicit consideration of the trait relationships to fitness will help not only to systematize traits and

determine relationships between them but would allow ecological and evolutionary perspectives to be connected in a trait-based framework.

Below we briefly describe traits of different types within each of the three fundamental functions (Fig. 1) and provide some examples of associated trade-offs.

### Feeding traits

Feeding includes a diverse range of behavioral, morphological, physiological and life history traits (Fig. 1). Behavioral feeding modes include (Kjørboe, 2011): (i) ambush feeding, where prey encounter depends on the motility of the prey; prey encounter may be passive and by direct interception (most protozoans), or it may depend on remote detection of prey and active prey capture (dinoflagellates, most copepods); (ii) feeding current feeding, where the feeding current is either a scanning current from which remotely detected prey are captured (copepods), or the current is passed through a filter that screens prey particles (tunicates, choanoflagellates) or over other structures that intercept the prey (many cnidarians, ctenophores) without the possibility for remote prey detection; (iii) cruise feeding, where prey are encountered via remote detection (not direct interception) and captured. The feeding mode has implications for prey selection: ambush feeders target only motile prey; feeding current feeders may be less efficient towards those motile prey that can perceive and escape feeding currents (which applies to many protists, e.g. Jakobsen, 2001); feeding current feeders with a scanning current may select prey based on their chemical characteristics (e.g. avoidance of toxic algae, selection of nutritious species), whereas prey retained on a filter are generally selected only by their size and shape. Each feeding mode has associated costs and benefits. For example, ambush feeding allows low-energy expenditure and a low predator encounter rate but results in relatively low feeding efficiency and a low mate encounter rate (Kjørboe *et al.*, 2010). Employing mixotrophy as a mode of nutrition results in a trade-off between feeding efficiency and, consequently, the maximum growth rate and ability to survive low-food conditions. Some trade-offs extend beyond pairwise relationships and need to be considered in higher dimensions.

The food size spectrum consumed by the organism is another important feeding trait. The average size ratio between prey and predator in zooplankton has sometimes been assumed to be around 1:10, but there is substantial variation between taxa, with the gelatinous salps and appendicularians generally feeding on relatively small prey, while flagellates may feed on relatively large prey (Hansen *et al.*, 1994; Lombard *et al.*, 2011).

Dinoflagellates, for example, can ingest prey that are several times their cell length (Calbet, 2008; Jeong *et al.*, 2010). Different groups may differ in their trophic niche breadth, at least in the size range of prey consumed: salps may consume a wide range of prey (Vargas and Madin, 2004). These differences in prey size ranges and types of food have profound effects on the structure of the food webs and energy and material cycling in ecosystems.

The absolute size of zooplankton prey may be equally important because there are significant trade-offs related to absolute prey size, namely prey availability and prey selection. The biomass of small picophytoplankton fluctuates much less than the biomass of micro-phytoplankton, both seasonally and spatially (Chisholm, 1992; Kjørboe, 2008b). Large diatoms typically bloom in spring (in temperate waters) and during periods of upwelling and at spatio-temporal discontinuities in the water column (e.g. Taylor *et al.*, 2011). The biomass of picophytoplankton is constantly low, but they are the dominant phytoplankton in oligotrophic regions, i.e. in most of the ocean.

Small phytoplankton produce chemical and hydromechanical signals that are too small to allow remote detection because the signals attenuate almost instantaneously due to diffusion or viscosity. Hence, pico-sized prey cells must be collected by some automatic process by their grazers (filter feeding, diffusional deposition), which has mainly been developed by the large gelatinous forms (appendicularians, salps, doliolids) and by small flagellates. Signals from larger prey cells (nano- and microplankton) are strong enough to allow remote detection. This leads to other feeding strategies (scanning current, ambush feeding, cruise feeding) and allows for active prey selection.

### Stoichiometric and nutritional requirements

Zooplankton in general have more constant nutrient ratios, such as C:N:P (carbon:nitrogen:phosphorus) than phytoplankton (Sterner and Elser, 2002). A much smaller variability in elemental ratios occurs because zooplankton generally do not store or deplete such large percentages of elements in their bodies as phototrophs (Sterner and Elser, 2002). Zooplankton may also have a higher content of certain essential fatty acids than their phytoplankton prey, despite their inability to synthesize them. Such trophic upgrading may be achieved by selective feeding (see above). Dinoflagellates and copepods can select prey cells based on their nutrient content (e.g. Cowles *et al.*, 1988; Meunier *et al.*, 2012). Different groups and species of zooplankton differ significantly in their average nutrient ratios and requirements (Andersen and Hessen, 1991). Among freshwater zooplankton, for example, the cladoceran *Daphnia* has high P requirements compared with other cladocerans (e.g. *Bosmina*) and, hence, low C:P and N:P

ratios (Andersen and Hessen, 1991). When fed on low P phytoplankton, *Daphnia* have slower growth and reproduction rates, demonstrating that not only food quantity but also food quality affects zooplankton growth (Main *et al.*, 1997). According to the growth rate hypothesis, fast growing organisms contain high concentration of P-rich ribosomes and, therefore, have high P content and low C:P and N:P ratios (Sterner and Elser, 2002). Freshwater zooplankton may often be P-limited (Sterner *et al.*, 1993), while marine zooplankton may more often be limited by N or Fe (Checkley, 1980; Jones *et al.*, 2002; Chen *et al.*, 2011).

Despite being more homeostatic than in phytoplankton, zooplankton stoichiometric ratios do exhibit seasonal, latitudinal and developmental variability (Sterner and Elser, 2002). Potential trade-offs may include lower nutrient (e.g. phosphorus) requirements allowing survival in low-nutrient environments but leading to lower maximum growth rates according to the growth rate hypothesis (Sterner and Elser, 2002).

### Survival traits

Zooplankton may enhance their longevity by reducing predation risk and by adapting to periods of food shortage (e.g. over winter). Traits to minimize predation risk can occur at several successive steps in a prey–predator interaction. They include prey morphological (e.g. transparency) and behavioral traits that reduce initial encounter rates with predators, behaviors that promote successful escape once encounter has occurred, or morphological and chemical defenses that reduce the probability of successful ingestion once captured (Ohman, 1988). Reduction of encounter rates with predators can be accomplished via diel vertical migration (Aksnes and Giske, 1990, Ohman, 1990), the use of other temporal or spatial refugia, or hydrodynamically cryptic swimming behavior that minimizes detectability by predators (Ohman, 1988). Tissue transparency (e.g. cnidarians, chaetognaths, ctenophores, pelagic tunicates) also reduces encounter rates with visual predators. Body pigmentation in small zooplankton taxa is positively correlated with diel vertical migration (Hays *et al.*, 1994). Sensory detection of predators (Jakobsen, 2001) followed by prey escape responses (Lenz and Hartline, 1999) permits motile zooplankton to evade capture. Bioluminescence may also function as a predator evasion strategy though the “burglar alarm” mechanism, i.e. by attracting the predators of the predator (Burkenroad, 1943; Abrahams and Townsend, 1993). Although many zooplankton taxa have morphologically fixed spines and other structures that help defend against ingestion by predators, inducible mechanical defenses are probably best documented for freshwater cladocerans that

develop spiny helmets in predator-rich environments (Tollrian and Dodson, 1999). Dinoflagellates may be chemically defended against predators (e.g. Sykes and Huntley, 1987). There are obvious trade-offs associated with all these traits in terms of investment in structures, sensory apparatus, escape muscles and lost feeding opportunities, but it remains challenging to quantify these costs and, hence, to predict optimal behaviors through fitness optimization.

Strategies to survive harsh periods, typically winters (or between upwelling events in the upwelling systems), include starvation tolerance, dormancy and the production of resting stages. The trade-off is survival during harsh periods vs. reduced and/or delayed reproduction. Starvation tolerance has been studied in a range of zooplankton groups, including protozoans (Menden-Deuer *et al.*, 2005), copepods (Borchers and Hutchings, 1986), jellyfish (Costello, 1998) and pteropods (Böer *et al.*, 2007). In copepods, starvation tolerance is typically studied in the context of winter dormancy. Preparation for dormancy in copepods is characterized by the accumulation of lipid reserves (typically wax esters) and reduced metabolism (Ohman *et al.*, 1998) that allow survival at depth during long winters. Wax ester accumulation may be considered a proxy for “dormancy potential” and shows a characteristic latitudinal pattern in copepods, with increasing accumulation at high latitudes (Kattner and Hagen, 2009).

The formation of resting stages is an alternative to dormancy: many protozoans form resting cysts (Corliss and Esser, 1974), and some copepods (some species from the genera *Acartia*, *Eurytemora* and *Centropages*) and many cladocerans (genera *Alona*, *Daphnia*, *Ceriodaphnia* and many others) produce resting eggs (Marcus, 1996; Vandekerhove *et al.*, 2005). In addition to the different physiology of resting stages, this strategy also differs from the dormancy strategy in that every individual typically produces many survival vehicles (eggs) and each egg can survive in the sediment for many years (in the extreme, up to 300 years or more for copepods, Hairston *et al.*, 1999). One would expect the formation of resting eggs to be restricted to the forms living in lakes and shallow areas of the ocean because an egg sedimented several kilometers to the deep ocean floor has a minute chance of returning to the upper ocean. Currently, little is known how these traits are related to each other and what the relevant trade-offs may be.

### Reproductive traits

Zooplankton display a considerable diversity in their reproduction modes and associated traits, from asexual reproduction during at least part of the life history (some

protozoans, cladocerans, tunicates and jellyfish), hermaphroditism (chaetognaths, all gelatinous forms) to sex change (some decapods and copepods) and fixed dioecious reproduction, and from internal to external fertilization. The key issue is encounter rates between either gametes or sexes, as this occurs in a 3D world where the distance to the nearest mate may be substantial. The behavior and ecology of zooplankton must to a very large extent be dictated by this ultimate Darwinian mission, but its significance is underappreciated.

Asexual reproduction and hermaphroditism with self-fertilization solve the encounter issue, but result in lower genetic diversity that potentially can impede adaptation to changing environmental conditions. For zooplankton with sexual reproduction one important distinction is whether gametes (eggs and sperm) are spawned freely into the water where fertilization takes place externally (broadcast spawning), or whether adult males and females have to meet and mate. Broadcast spawning requires the production of many gametes, mainly of sperm, and hence may limit the initial minimum size of the animals. The gelatinous plankton (cnidarians, ctenophores, tunicates) are generally broadcast spawners, while all other taxa with sexual reproduction appear to have mating. Mate finding may be facilitated by the utilization of hydrodynamic and pheromone signaling, and is rather well understood for zooplankton with mating encounters, but even broadcast spawners may need behavioral adaptations to enhance gamete encounter rates. Spawning aggregations (e.g. some appendicularians, Alldredge, 1982), colony formation (salps), spawning synchronization (some ctenophores, Purcell and Madin, 1991), self-fertilization (ctenophores, Martindale, 1987) may all help ensure sufficient gamete encounter rates. Sexual reproduction is wasteful (superfluous gamete production) or involves investment in sensory equipment to enhance mate encounter rates, and mate finding as well as mating itself implies elevated predation risks but allows for a higher genetic diversity, deletion of bad mutations and the promotion of good genes through sexual selection. These trade-offs are difficult to quantify.

### Energy allocation and life history strategies

The energy gained from feeding must be allocated among growth, reproduction and maintenance and defines important aspects of the life history of an organism. Maintenance here includes the inescapable minimum metabolic cost to maintain body tissues, feed and locomote, but also energy invested in predator evasion and in tissue repair. The latter is rarely considered in zooplankton studies, but has implications for the rate of senescence and

longevity of an organism and may vary widely among species (e.g. Ceballos and Kiørboe, 2011; Sichelau and Kiørboe, 2011). Some life histories appear to be fixed (and hence a real trait), but strategies may also be malleable in response to local conditions (known mainly for cladocerans and rotifers in freshwater). As an example, the investment in reproduction vs. growth determines the age and size at maturity. The trade-offs are relatively clear: investment in reproduction now is at the cost of reduced growth—and, hence, potential for future reproduction and reduced maintenance (and, hence, survival). Fitness optimization predicts relatively low investment in maintenance (and, hence, longevity) and early maturation at a small size when mortality is high. Copepods appear to have rather fixed life history strategies, with age and size at maturation depending solely on temperature and availability of food (Checkley, 1980; Huntley and Lopez, 1992). Perhaps predation risk and simple optimization models predict development times in copepods well (Kiørboe and Hirst, 2008). Life histories in rotifers, in contrast, are plastic, and these organisms allocate more energy to reproduction and less to maintenance in the presence of predator cues, as predicted (Garcia *et al.*, 2007).

The maximum growth rate of zooplankton is also a result of energy allocation. While specific growth rates typically scale with the body mass to a power of about  $-1/4$  within zooplankton groups (e.g. Hansen *et al.*, 1997), the magnitude of the maximum growth rate may vary significantly between groups (Hirst *et al.*, 2003), suggesting different energy allocation optima. For example, pelagic tunicates typically grow much faster than, for example, copepods of comparable body mass (carbon) and at similar temperatures (by a factor of  $\sim 5$ ; see Hirst *et al.*, 2003). It may be hypothesized that copepods allocate more energy into predator avoidance and defense, in the form of a very well-developed sensory apparatus and powerful musculature that allows for rapid escape jumps, with a consequent lower growth rate and mortality rate than tunicates. Such relations are poorly examined but may represent fertile future research avenues.

Finally, the trade-off in the ‘progeny size’, where a large number of progeny is associated with a decreased size of individual offspring and, as a result, a decreased individual survival, determines contrasting reproductive strategies. The trade-off between high- or low-reproductive investment in individual progeny also extends to trade-offs in embryonic care. For taxa that carry their eggs, in contrast to broadcast spawners, embryonic size may be greater and the number of offspring lower, which can be compensated by the higher survivorship of protected eggs relative to those that drift freely in the plankton (Hirst and Kiørboe, 2002). Hatching time of protected eggs is also

greater (>3-fold) than of unprotected eggs (Hirst and Lopez-Urrutia, 2006).

### Traits transcending functions

The relative importance of individual traits varies. Some traits have a disproportionate influence on the overall ecology and physiology of a zooplankter, transcending multiple functions (Fig. 1). Adult body size and carbon density are among such traits. Maximum body sizes relates to energy allocation and size at maturity (see above). A large number of properties and vital rates scale with size, e.g. feeding rate, prey size, growth rate, metabolism, mortality and vital rates, typically increase with body mass to a power of <1 within taxonomic groups. The maximum size and size at age may therefore be used as a proxy for many traits. Another trait related to size and life form is the biomass to body volume ratio. Zooplankton separate into two main life forms related to their body carbon density: the “typical” zooplankters with carbon densities on order  $10^2 \text{ mg C cm}^{-3}$  body volume, and those that have inflated volumes and body carbon densities  $\sim 2$  orders of magnitude lower. The latter group includes the taxonomically diverse group of gelatinous zooplankton (tunicates, ctenophores, cnidarians, chaetognaths) but also some protists, such as *Noctiluca*. An immediate advantage of an inflated body volume is the increase in prey capture area and potential feeding rate, which applies across the very different feeding modes of the gelatinous taxa (Alldredge and Madin, 1982; Acuna *et al.*, 2011; Kiørboe, 2011), but mortality rates may also be smaller for an inflated organism, because size *per se* can lead to lower predation mortality, the nutritional quality of a watery zooplankter is low, and high water content is often associated with tissue transparency and lower visibility to predators. This pattern is contrary to the typical trade-offs associated with feeding behaviors, where a higher feeding rate typically implies elevated predation risk, cf. above. The inflated size strategy is also found among planktonic osmotrophs and was termed the “Winnie-the-Pooh” strategy by Thingstad *et al.* (Thingstad *et al.*, 2005) exactly for this reason (because Winnie, when asked whether he wanted honey or milk, answered “both”). There must be costs associated with an inflated body volume, otherwise this life form would dominate the zooplankton, but it remains a challenge to identify and quantify them. However, quantifying the trade-offs of the gelatinous vs. non-gelatinous life forms may allow us to predict the environmental conditions that select for one or the other and may be especially relevant, given the purported rise in

the dominance of gelatinous forms (but see Condon *et al.*, 2012).

Motility and body shape are composite traits that affect not only feeding strategy but also influence survival (predator avoidance) and reproduction (mate encounter) and are, therefore, under complex selection pressures (Visser, 2007). Both speed and patterns (e.g. pathways) vary considerably across and within species. Moving from small to large organisms, Reynolds number ( $Re$ ) increases and so does the optimal shape for locomotion (from near spherical at low  $Re$  to more streamlined with increasing  $Re$ ; see, e.g. Dusenberry, 2009); this transition is seen from nearly spherical flagellates and copepod nauplii to streamlined copepodites, etc. Among the non-gelatinous zooplankton, the dominant shape is that of fusiform copepods; even non-copepods tend to have a hydrodynamically shaped muscular body, adapted for high-escape velocities (Verity and Smetacek, 1996). While most non-gelatinous plankton are propelled by appendages, flagella or cilia, the gelatinous plankton have different propulsion mechanisms: jet propulsion (salps and some jellyfish) or rowing (some medusae). A major trade-off associated with motility is that it increases encounters with both prey and predators (Gerritsen and Strickler, 1977; Visser, 2007).

### TRAIT ASSOCIATIONS AND CORRESPONDING ECOLOGICAL STRATEGIES: EMERGING PATTERNS

Most traits in zooplankton are not independent of one another but are correlated. These trait correlations may represent fundamental physiological constraints resulting in trade-offs that can lead to different ecological strategies that transcend taxonomic groups. Identifying such trade-offs will help define trait associations and reduce the number of traits needed to adequately describe zooplankton communities. For example, one general pattern that may emerge, and serve as a working hypothesis, is that of the two main life history types among zooplankton that feed mainly on pico- vs. microplankton:

(i) Grazers on picoplankton often have high volume-specific clearance rates. They collect prey by automatic processes (filter feeding, diffusional deposition) and have no capability to select prey on the basis of their nutritional value. They have high potential population growth rates, often accomplished through asexual reproduction (at least during the part of the life cycle), minimum investment in defense mechanisms and

sensory systems, and minimum investment in overwintering strategies. Their food source is relatively stable in time and space, partly due to the controlling role of the grazers themselves, since the grazers and the prey have growth rates of similar order allowing for rapid numerical responses. The relative constancy of the food source permits minimum investment in survival during meager times. The group includes some protozooplankton (mainly heterotrophic nanoflagellates), the tunicates (at least appendicularians, salps and doliolids) and some cladocerans. The two first groups are often the main grazers of phytoplankton in the ocean and those of which we know the least.

(ii) Grazers on nano- and microplankton typically have relatively lower clearance rates, but they may be able to select prey on the basis of their nutritional content. They are generally organisms with lower potential growth rates and have mandatory sexual reproduction, high investment in defense (behaviorally or morphological) and well-developed sensory systems that allow efficient mate finding, prey selection and predator perception. They can afford low clearance and potential growth rates due to higher investment in escape behavior or defenses and, consequently, lower mortality rates. Due to the low growth rate and lagged numerical response they cannot control their prey populations, which consequently are very variable in time and space. This necessitates investment in mechanisms to survive periods of food shortage in the form of dormancy or production of resting stages (cysts, eggs). The group includes copepods, euphausiids and some protozoans, most notably the heterotrophic dinoflagellates; these groups are the dominant mesozooplankton groups in the ocean that were claimed to account only for a relatively small fraction of phytoplankton grazing in the ocean (Calbet and Landry, 2004), but this view has important exceptions (Landry *et al.*, 2009).

There are exceptions to these patterns. For example, freshwater cladocerans invest in resting stages as an adaptation to ephemeral freshwater systems, as well as in morphological defenses, and some heterotrophic nanoflagellates have been reported to be able to select prey based on their chemical content (e.g. Landry *et al.*, 1991; Jurgens and DeMott, 1995), although this evidence for active prey selection has later been questioned (Boenigk *et al.*, 2001; Langlois *et al.*, 2009).

While the relative significance of zooplankters with these two alternative trait combinations to a large extent will be governed by the size structure of the phytoplankton, it is much less clear what determines whether the zooplankton communities will be dominated by heterotrophic nanoflagellates or by pelagic tunicates, for example, or, similarly, by copepods or heterotrophic

dinoflagellates. Chance may of course play a role, since any enrichment mechanisms, including upwelling events, will stimulate production of whatever is there and what is seeded from deeper waters (resting stages, cysts), but differences in life history traits and associated trade-offs are likely to play a role in so far unknown ways.

Carnivorous zooplankton (e.g. ctenophores, cnidarians, predatory copepods and amphipods, chaetognaths, heteropods, fish larvae) are diverse in terms of phylogeny, morphology and behavior. For these taxa as well, trait-based organization may prove a useful means of simplifying this diversity. A first-order division among these predatory taxa is between those that search for prey visually (fish larvae and heteropods) and those that use non-visual means to locate prey (most others, e.g. Eiane *et al.*, 1999).

Given the eco-physiological and evolutionary constraints, certain traits or values of quantitative traits can only occur with a limited range of correlated traits: for example, a small-bodied zooplankter is unlikely to employ rapid swimming as an escape strategy from highly motile predators. Consequently, there are contrasting trait value associations that define different ecological strategies. Major taxonomic groups of zooplankton differ in their ecological strategies and trait associations. There is a good correspondence of taxonomic affiliation and certain trait combinations and, thus, ecological strategies, but it is not a perfect agreement and likely depends on the level of taxonomic aggregation. It may be a worthy exercise to map ecological strategies in the multi-trait space and, thus, quantitatively determine how similar or different major zooplankton groups may be.

It is well known that different zooplankton taxonomic groups are strongly associated with certain hydrographic and other physical and chemical conditions, as well as with phytoplankton composition (Calbet, 2008). This likely translates into certain traits or values of quantitative traits more or less robustly associated with specific physico-chemical conditions and phytoplankton composition. Trait-based models using fitness maximization approaches may be able to predict what strategies are selected for under given environmental conditions.

## TRAITS CHARACTERIZING INTERACTIONS ACROSS TROPHIC LEVELS

A particular challenge to trait-based approaches is to define traits that describe food web interactions, the relationships between different trophic levels in particular. How might the complexity of all possible pairwise interactions (e.g. between a phytoplankton cell and a



zooplankton) be reduced into a meaningful trait or a small number of traits? Some of such traits are likely to be related to cell or body size. For example, characterizing the size spectra of food particles (feeding kernels) for different size zooplankton as a function-value trait (i.e. not a single value but a function), the frequency distribution of food particles ingested, could help describe and compare diets and the effects of different groups of zooplankton on phytoplankton. Models that include frequency distributions of particle sizes ingested by different groups of grazers are starting to be implemented and provide a more realistic description of food web interactions (Armstrong, 1999; Banas, 2011). Explicitly including stoichiometric requirements and content of different trophic levels (e.g. consumers and their prey) may also help to represent adequately the interactions between different trophic levels (Sterner and Elser, 2002; Grover, 2003).

## CANDIDATE TRAITS FOR ECOSYSTEM MODELS

The selection of traits to consider will inevitably depend on the questions asked. For many ecosystem models that focus on nutrient cycling, there are a few zooplankton traits that will likely be particularly useful for characterizing zooplankton-related processes. Such traits could be the maximum growth rates, stoichiometric requirements, grazing rates and trophic niche breadths (size distributions of food particles). To reduce the complexity of the representation of these traits, scaling relationships may be introduced (Armstrong, 1999; Poulin and Franks, 2010), as many of these traits scale allometrically with body size (Vidal and Whitley, 1982; Hirst and Lampitt, 1998; Saiz and Calbet, 2007). The scaling relationships may be obtained empirically by compiling relevant data or derived theoretically based on scaling rules. Using these and other traits often requires a proper conversion of units (e.g. from individual-based to mass-based units). Models built to investigate the role of climate change and rising temperatures in particular will need to include the temperature dependence of many traits (Forster *et al.*, 2011). Compiling diverse traits from empirical studies into accessible databases will allow better parameterizations of marine ecosystem models.

## FUTURE DIRECTIONS

A promising approach to increasing the mechanistic understanding of the structure and function of zooplankton communities is to look systematically at zooplankton

trait distributions along various environmental gradients, such as latitudinal gradients (associated with temperature and other physical parameters), primary productivity or nutrient concentrations. There are already such studies (Roman *et al.*, 2002) and they can offer insights into latitudinal trait distributions. The associations of certain trait values or suites of traits and corresponding strategies with particular environmental parameters, such as hydrographic conditions, should help understand how environmental factors structure zooplankton communities and affect their functioning. This knowledge can then be used to predict potential zooplankton community reorganizations under changing environmental conditions. For example, looking at latitudinal gradients in body size or reproductive strategies can provide insights into how changing climate may affect zooplankton communities, e.g. how warming temperatures might alter the dominant body size or reproductive strategies and, consequently, lead to changes in community structure and ecosystem functioning.

There is a significant body of literature reporting various traits of different species and groups of zooplankton in marine and freshwater environments. Assembling a comprehensive zooplankton trait matrix and synthesizing the trait value distributions can be a high-payoff undertaking that will also be helpful for parameterizing zooplankton in various ecosystem models. Several such meta-analytical studies have been published and they provide excellent syntheses on the distribution and scaling of such traits as growth rates, reproduction, feeding and mortality, mostly in marine copepods (Hirst *et al.*, 2003; Bunker and Hirst, 2004) but also in freshwater crustacean zooplankton (Barnett *et al.*, 2007).

Comparing zooplankton trait distributions between marine and freshwater environments will likely provide valuable insights into the mechanisms that structure zooplankton communities in each environment. An intriguing difference in taxonomic diversity of zooplankton between the marine and freshwater realm is that marine zooplankton are much more taxonomically diverse, covering a wide range of taxa that are absent in freshwater zooplankton (salps, appendicularians, cephalopods, pteropods, etc.). This difference begs the question whether the zooplankton grazing and ecosystem effects are qualitatively and quantitatively different between the two environments. Another unanswered question is a comparison of the importance of microzooplankton in freshwater vs. marine environments. Numerous studies in marine ecosystems demonstrated that microzooplankton often are the dominant grazers, especially in oligotrophic systems (Calbet, 2008). The estimates of the importance of microzooplankton in lakes are much more scarce but it is likely that the

freshwater microzooplankton contribution to total grazing can be substantial as well, even in eutrophic systems (Hambright *et al.*, 2007). It would be of interest to compare the types of marine and freshwater ecosystems that have a greater importance of micrograzers.

Allometric approaches are powerful ways to generalize the relationships among various traits. However, sometimes these relationships differ across major taxonomic groups: allometric exponents can be taxon specific. A simultaneous consideration of allometric and taxonomic constraints may improve the trait-based description of food webs (Rall *et al.*, 2011).

Trait-based approaches to zooplankton may in the future be integrated into a general trait-based framework for modeling not only planktonic communities (bacterioplankton, phytoplankton and zooplankton) but the whole aquatic ecosystem as well, including end-to-end models encompassing multiple trophic levels and organismal groups, from bacteria, to plankton to fish and to mammals and birds.

## ACKNOWLEDGMENTS

We thank Maurizio Ribera d'Alcalá, Daniele Iudicone and other staff of the Stazione Zoologica Anton Dohrn Napoli for organizing and hosting a EUROCEANS workshop on “Constraining, understanding and modeling biocomplexity in plankton communities” in Naples, Italy in 2008, where the ideas of this paper were first synthesized. We thank anonymous reviewers for helpful comments and suggestions.

## FUNDING

EL acknowledges funding from the US National Science Foundation (DEB-0845932, OCE-0928819 and DEB-1136710) and MDO from NSF (OCE-1026607) via the California Current Ecosystem LTER site.

## REFERENCES

- Abrahams, M. V. and Townsend, L. D. (1993) Bioluminescence in dinoflagellates: a test of the burglar alarm hypothesis. *Ecology*, **74**, 258–260.
- Acuna, J. L., Lopez-Urrutia, A. and Colin, S. (2011) Faking giants: the evolution of high prey clearance rates in jellyfishes. *Science*, **333**, 1627–1629.
- Aksnes, D. L. and Giske, J. (1990) Habitat profitability in pelagic environments. *Mar. Ecol. Prog. Ser.*, **64**, 209–215.
- Allredge, A. L. (1982) Aggregation of spawning appendicularians in surface windrows. *Bull. Mar. Sci.*, **32**, 250–254.
- Allredge, A. L. and Madin, L. P. (1982) Pelagic tunicates—unique herbivores in the marine plankton. *Bioscience*, **32**, 655–663.
- Andersen, T. and Hessen, D. O. (1991) Carbon, nitrogen and phosphorus content of freshwater zooplankton. *Limnol. Oceanogr.*, **36**, 807–814.
- Armstrong, R. A. (1999) Stable model structures for representing biogeochemical diversity and size spectra in plankton communities. *J. Plankton Res.*, **21**, 445–464.
- Banas, N. S. (2011) Adding complex trophic interactions to a size-spectral plankton model: emergent diversity patterns and limits on predictability. *Ecol. Model.*, **222**, 2663–2675.
- Barnett, A. J., Finlay, K. and Beisner, B. E. (2007) Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshw. Biol.*, **52**, 796–813.
- Boenigk, J., Matz, C., Jurgens, K. *et al.* (2001) Confusing selective feeding with differential digestion in bacterivorous nanoflagellates. *J. Eukaryot. Microbiol.*, **48**, 425–432.
- Borchers, P. and Hutchings, L. (1986) Starvation tolerance, development time and egg production of *Calanoides carinatus* in the southern benguela. *J. Plankton Res.*, **8**, 855–874.
- Bruggeman, J. and Kooijman, S. (2007) A biodiversity-inspired approach to aquatic ecosystem modeling. *Limnol. Oceanogr.*, **52**, 1533–1544.
- Bunker, A. J. and Hirst, A. G. (2004) Fecundity of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature and body weight. *Mar. Ecol. Prog. Series*, **279**, 161–181.
- Burkenroad, M. D. (1943) A possible function of bioluminescence. *J. Mar. Res.*, **5**, 161–164.
- Calbet, A. (2008) The trophic roles of microzooplankton in marine systems. *ICES J. Mar. Sci.*, **65**, 325–331.
- Calbet, A. and Landry, M. R. (2004) Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnol. Oceanogr.*, **49**, 51–57.
- Ceballos, S. and Kiørboe, T. (2011) Senescence and sexual selection in a pelagic copepod. *Plos One*, **6**, e18870
- Checkley, D. M. (1980) Food limitation of egg production by a marine, planktonic copepod in the sea off southern California. *Limnol. Oceanogr.*, **25**, 991–998.
- Chen, X., Baines, S. B. and Fisher, N. S. (2011) Can copepods be limited by the iron content of their food? *Limnol. Oceanogr.*, **56**, 451–460.
- Chisholm, S. W. (1992) Phytoplankton size. In Falkowski, P. G. and Woodhead, A. D. (eds), *Primary Productivity and Biogeochemical Cycles in the Sea*. Plenum Press, New York, pp. 213–237.
- Condon, R. H., Graham, W. M., Duarte, C. M. *et al.* (2012) Questioning the rise of gelatinous zooplankton in the world's oceans. *Bioscience*, **62**, 160–169.
- Corliss, J. O. and Esser, S. C. (1974) Comments on the role of the cyst in the life cycle and survival of free-living protozoa. *Trans. Am. Microscopical. Soc.*, **93**, 578–593.
- Costello, J. (1998) Physiological response of the hydromedusa *Cladonema californicum* Hyman (Anthomedusa: Cladonemidae) to starvation and renewed feeding. *J. Exp. Mar. Biol. Ecol.*, **225**, 13–28.
- Cowles, T. J., Olson, R. J. and Chisholm, S. W. (1988) Food selection by copepods—discrimination on the basis of food quality. *Mar. Biol.*, **100**, 41–49.
- Dusenberry, D. B. (2009) *Living at Micro Scale: The Unexpected Physics of Being Small*. Harvard University Press, Cambridge, MA.

- Eiane, K., Aksnes, D. L., Bagoien, E. *et al.* (1999) Fish or jellies—a question of visibility? *Limnol. Oceanogr.*, **44**, 1352–1357.
- Fiksen, Ø. (1997) Allocation patterns and diel vertical migration: modeling the optimal *Daphnia*. *Ecology*, **78**, 1446–1456.
- Follows, M. J. and Dutkiewicz, S. (2011) Modeling diverse communities of marine microbes. *Ann. Rev. Mar. Sci.*, **3**, 427–451.
- Follows, M. J., Dutkiewicz, S., Grant, S. *et al.* (2007) Emergent biogeography of microbial communities in a model ocean. *Science*, **315**, 1843–1846.
- Forster, J., Hirst, A. G. and Woodward, G. (2011) Growth and development rates have different thermal responses. *Am. Nat.*, **178**, 668–678.
- Garcia, C. E., Chaparro-Herrera, D. D., Nandini, S. *et al.* (2007) Life-history strategies of *Brachionus havanaensis* subject to kairomones of vertebrate and invertebrate predators. *Chem. Ecol.*, **23**, 303–313.
- Gerritsen, J. and Strickler, J. R. (1977) Encounter probabilities and community structure in a zooplankton—mathematical-model. *J. Fisheries Res. Board Canada*, **34**, 73–82.
- Gilliam, J. F. and Fraser, D. F. (1987) Habitat selection under predation hazard—test of a model with foraging minnows. *Ecology*, **68**, 1856–1862.
- Grover, J. P. (2003) The impact of variable stoichiometry on predator-prey interactions: a multinutrient approach. *Am. Nat.*, **162**, 29–43.
- Hairston, N. G., Lampert, W., Caceres, C. E. *et al.* (1999) Lake ecosystems—rapid evolution revealed by dormant eggs. *Nature*, **401**, 446.
- Hambright, K. D., Zohary, T. and Güde, H. (2007) Microzooplankton dominate carbon flow and nutrient cycling in a warm subtropical freshwater lake. *Limnol. Oceanogr.*, **52**, 1018–1025.
- Hansen, B., Bjørnsen, P. K. and Hansen, P. J. (1994) The size ratio between planktonic predators and their prey. *Limnol. Oceanogr.*, **39**, 395–403.
- Hansen, P. J., Bjørnsen, P. K. and Hansen, B. W. (1997) Zooplankton grazing and growth: scaling within the 2–2,000 µm body size range. *Limnol. Oceanogr.*, **42**, 687–704.
- Hays, G. C., Proctor, C. A., John, A. W. G. *et al.* (1994) Interspecific differences in the diel vertical migration of marine copepods—the implications of size, color, and morphology. *Limnol. Oceanogr.*, **39**, 1621–1629.
- Hirst, A. and Lopez-Urrutia, A. (2006) Effects of evolution on egg development time. *Mar. Ecol. Prog. Ser.*, **326**, 29–35.
- Hirst, A. G. and Kiørboe, T. (2002) Mortality of marine planktonic copepods: global rates and patterns. *Mar. Ecol. Prog. Ser.*, **230**, 195–209.
- Hirst, A. G. and Lampitt, R. S. (1998) Towards a global model of in situ weight-specific growth in marine planktonic copepods. *Mar. Biol.*, **132**, 247–257.
- Hirst, A. G., Roff, J. C. and Lampitt, R. S. (2003) A synthesis of growth rates in marine epipelagic invertebrate zooplankton. *Adv. Mar. Biol.*, **44**, 1–142.
- Huntley, M. E. and Lopez, M. D. G. (1992) Temperature-dependent production of marine copepods—a global synthesis. *Am. Nat.*, **140**, 201–242.
- Jakobsen, H. H. (2001) Escape response of planktonic protists to fluid mechanical signals. *Mar. Ecol. Prog. Ser.*, **214**, 67–78.
- Jeong, H. J., Yoo, Y. D., Kang, N. S. *et al.* (2010) Ecology of *Gymnodinium aureolum*. I. Feeding in western Korean waters. *Aquat. Microb. Ecol.*, **59**, 239–255.
- Jones, R. H., Flynn, K. J. and Anderson, T. R. (2002) Effect of food quality on carbon and nitrogen growth efficiency in the copepod *Acartia tonsa*. *Mar. Ecol. Prog. Ser.*, **235**, 147–156.
- Jurgens, K. and Demott, W. R. (1995) Behavioral flexibility in prey selection by bacterivorous nanoflagellates. *Limnol. Oceanogr.*, **40**, 1503–1507.
- Kattner, G. and Hagen, W. (2009) Lipids in marine copepods: latitudinal characteristics and perspective to global warming. In Arts, M. T., Brett, M. and Kainz, M. (eds), *Lipids in Aquatic Environments*. Springer, New York, pp. 257–280.
- Kjørboe, T. (2008a) *A Mechanistic Approach to Plankton Ecology*. Princeton University Press, Princeton, NJ.
- Kjørboe, T. (2008b) Optimal swimming strategies in mate-searching pelagic copepods. *Oecologia*, **155**, 179–192.
- Kjørboe, T. (2011) How zooplankton feed: mechanisms, traits and trade-offs. *Biol. Rev.*, **86**, 311–339.
- Kjørboe, T. and Hirst, A. G. (2008) Optimal development time in pelagic copepods. *Mar. Ecol. Prog. Ser.*, **367**, 15–22.
- Kjørboe, T., Jiang, H. S. and Colin, S. P. (2010) Danger of zooplankton feeding: the fluid signal generated by ambush-feeding copepods. *Proc. R. Soc. B Biol. Sci.*, **277**, 3229–3237.
- Landry, M., Lehner-Fournier, J., Sundstrom, J. *et al.* (1991) Discrimination between living and heat-killed prey by a marine zooflagellate, *Paraphysomonas vestita* (Stokes). *J. Exp. Mar. Biol. Ecol.*, **146**, 139–151.
- Landry, M. R., Ohman, M. D., Goericke, R. *et al.* (2009) Lagrangian studies of phytoplankton growth and grazing relationships in a coastal upwelling ecosystem off southern California. *Prog. Oceanogr.*, **83**, 208–216.
- Langlois, V. J., Andersen, A., Bohr, T. *et al.* (2009) Significance of swimming and feeding currents for nutrient uptake in osmotrophic and interception-feeding flagellates. *Aquat. Microb. Ecol.*, **54**, 35–44.
- Lasley-Rasher, R. S. and Yen, J. (2012) Predation risk suppresses mating success and offspring production in the coastal marine copepod, *Eurytemora herdmani*. *Limnol. Oceanogr.*, **57**, 433–440.
- Lenz, P. H. and Hartline, D. K. (1999) Reaction times and force production during escape behavior of a calanoid copepod, *Undinula vulgaris*. *Mar. Biol.*, **133**, 249–258.
- Litchman, E. and Klausmeier, C. A. (2008) Trait-based community ecology of phytoplankton. *Ann. Rev. Ecol. Evol. Syst.*, **39**, 615–639.
- Lombard, F., Selander, E. and Kiørboe, T. (2011) Active prey rejection in the filter-feeding appendicularian *Oikopleura dioica*. *Limnol. Oceanogr.*, **56**, 1504–1512.
- Main, T. M., Dobberfuhl, D. R. and Elser, J. J. (1997) N:P stoichiometry and ontogeny of crustacean zooplankton: a test of the growth rate hypothesis. *Limnol. Oceanogr.*, **42**, 1474–1478.
- Marcus, N. (1996) Ecological and evolutionary significance of resting eggs in marine copepods: past, present, and future studies. *Hydrobiologia*, **320**, 141–152.
- Martindale, M. Q. (1987) Larval reproduction in the ctenophore *Mnemiopsis murrayi* (order lobata). *Mar. Biol.*, **94**, 409–414.
- Menden-Deuer, S., Lessard, E. J., Satterberg, J. *et al.* (2005) Growth rates and starvation survival of three species of the pallium-feeding, thecate dinoflagellate genus *Protoperidinium*. *Aquat. Microb. Ecol.*, **41**, 145–152.
- Merico, A., Bruggeman, J. and Wirtz, K. (2009) A trait-based approach for downscaling complexity in plankton ecosystem models. *Ecol. Model.*, **220**, 3001–3010.

- Meunier, C. L., Hantzsche, F. M., C.-Dupont, A. Ö. *et al.* (2012) Intraspecific selectivity, compensatory feeding, and flexible homeostasis in the phagotrophic flagellate *Oxyrrhis marina*: three ways to handle food quality fluctuations. *Hydrobiologia*, **68**, 53–62.
- Ohman, M. D. (1988) Behavioral responses of zooplankton to predation. *Bull. Mar. Sci.*, **43**, 530–550.
- Ohman, M. D. (1990) The demographic benefits of diel vertical migration by zooplankton. *Ecol. Monogr.*, **60**, 257–281.
- Ohman, M. D., Drits, A. V., Clarke, M. E. *et al.* (1998) Differential dormancy of co-occurring copepods. *Deep-Sea Res. Pt. II Topical Stud. Oceanogr.*, **45**, 1709–1740.
- Poulin, F. J. and Franks, P. J. S. (2010) Size-structured planktonic ecosystems: constraints, controls and assembly instructions. *J. Plankton Res.*, **32**, 1121–1130.
- Purcell, J. E. and Madin, L. P. (1991) Diel patterns of migration, feeding, and spawning by salps in the sub-arctic pacific. *Mar. Ecol. Prog. Ser.*, **73**, 211–217.
- Rall, B. C., Kalinkat, G., Ott, D. *et al.* (2011) Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos*, **120**, 483–492.
- Roman, M. R., Dam, H. G., Le Borgne, R. *et al.* (2002) Latitudinal comparisons of equatorial pacific zooplankton. *Deep-Sea Res. Pt. II Topical Stud. Oceanogr.*, **49**, 2695–2711.
- Saiz, E. and Calbet, A. (2007) Scaling of feeding in marine calanoid copepods. *Limnol. Oceanogr.*, **52**, 668–675.
- Sichlau, M. H. and Kiørboe, T. (2011) Age- and size-dependent mating performance and fertility in a pelagic copepod, *Temora longicornis*. *Mar. Ecol. Prog. Ser.*, **442**, 123–132.
- Sterner, R. W. and Elser, J. J. (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton.
- Sterner, R. W., Hagemeier, D. D. and Smith, W. L. (1993) Phytoplankton nutrient limitation and food quality for *Daphnia*. *Limnol. Oceanogr.*, **38**, 857–871.
- Sykes, P. F. and Huntley, M. E. (1987) Acute physiological reactions of *Calanus pacificus* to selected dinoflagellates—direct observations. *Mar. Biol.*, **94**, 19–24.
- Taylor, B. B., Torrecilla, E., Bernhardt, A. *et al.* (2011) Bio-optical provinces in the eastern Atlantic ocean and their biogeographical relevance. *Biogeosciences*, **8**, 3609–3629.
- Thingstad, T. F., Ovreas, L., Egge, J. K. *et al.* (2005) Use of non-limiting substrates to increase size; a generic strategy to simultaneously optimize uptake and minimize predation in pelagic osmotrophs? *Ecol. Lett.*, **8**, 675–682.
- Tiselius, P., Jonsson, P. R., Kaartvedt, S. *et al.* (1997) Effects of copepod foraging behavior on predation risk: an experimental study of the predatory copepod *Pareuchaeta norvegica* feeding on *Acartia clausi* and *A. tonsa* (copepoda). *Limnol. Oceanogr.*, **42**, 164–170.
- Tollrian, R. and Dodson, S. I. (1999) Inducible defenses in cladocera. In Tollrian, R. and Harvell, C. D. (eds), *The Ecology and Evolution of Inducible Defenses*. Princeton University Press, Princeton, pp. 177–202.
- Vandekerckhove, J., Declerck, S., Brendonck, L. *et al.* (2005) Hatching of cladoceran resting eggs: temperature and photoperiod. *Freshw. Biol.*, **50**, 96–104.
- Vargas, C. A. and Madin, L. P. (2004) Zooplankton feeding ecology: clearance and ingestion rates of the salps *Thalia democratica*, *Cyclosalpa affinis* and *Salpa cylindrica* on naturally occurring particles in the mid-Atlantic bight. *J. Plankton Res.*, **26**, 827–833.
- Verity, P. G. and Smetacek, V. (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol. Prog. Ser.*, **130**, 277–293.
- Vidal, J. and Whitley, T. E. (1982) Rates of metabolism of planktonic crustaceans as related to body weight and temperature of habitat. *J. Plankton Res.*, **4**, 77–84.
- Visser, A. W. (2007) Motility of zooplankton: fitness, foraging and predation. *J. Plankton Res.*, **29**, 447–461.