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# Organismal trade-offs and the pace of planktonic life

Thomas Kiørboe\* *Centre for Ocean Life, DTU Aqua, Technical University of Denmark, 2800 Kgs. Kemitorvet, Kgs. Lyngby, Denmark*

## ABSTRACT

No one is perfect, and organisms that perform well in some habitat or with respect to some tasks, do so at the cost of performance in others: there are inescapable trade-offs. Organismal trade-offs govern the structure and function of ecosystems and attempts to demonstrate and quantify trade-offs have therefore been an important goal for ecologists. In addition, trade-offs are a key component in trait-based ecosystem models. Here, I synthesise evidence of trade-offs in plankton organisms, from bacteria to zooplankton, and show how a slow–fast gradient in life histories emerges. I focus on trade-offs related to the main components of an organism’s Darwinian fitness, that is resource acquisition, survival, and propagation. All consumers need to balance the need to eat without being eaten, and diurnal vertical migration, where zooplankton hide at depth during the day to avoid visual predators but at the cost of missed feeding opportunities in the productive surface layer, is probably the best documented result of this trade-off. However, there are many other more subtle but equally important behaviours that similarly are the result of an optimisation of these trade-offs. Most plankton groups have also developed more explicit defence mechanisms, such as toxin production or evasive behaviours that are harnessed in the presence of their predators; the costs of these have often proved difficult to quantify or even demonstrate, partly because they only materialise under natural conditions. Finally, all multicellular organisms must allocate time and resources among growth, reproduction, and maintenance (e.g. protein turnover and DNA repair), and mate finding may compromise both survival and feeding. The combined effects of all these trade-offs is the emergence of a slow–fast gradient in the pace-of-life, likely the most fundamental principle for the organisation of organismal life histories. This crystallisation of trade-offs may offer a path to further simplification of trait-based models of marine ecosystems.

*Key words:* life histories, stealth *vs* bold behaviour, defence, growth *vs* reproduction, resource acquisition.

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## I. INTRODUCTION

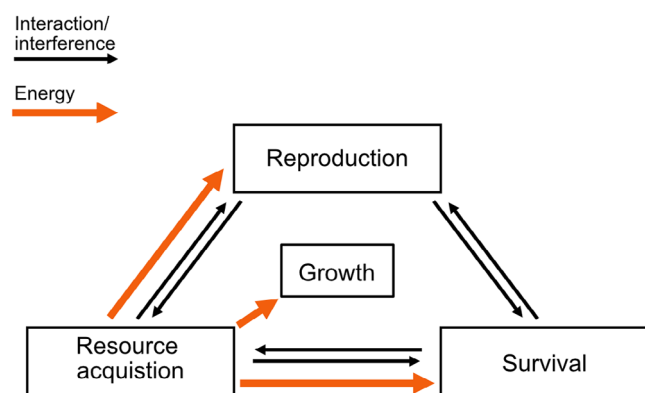
The fitness of an organism depends on its ability to acquire resources, to survive, and to reproduce. These life functions

materialise differently for different life forms, but natural selection has, through evolution, shaped all organisms towards optimising these fundamental activities, whether a bacterium or an elephant. However, no organism can

\* Author for correspondence (Tel.: +45 4011 1884; E-mail: [tk@aqu.dtu.dk](mailto:tk@aqu.dtu.dk)).

optimise all fitness components at the same time; there are always trade-offs (Fig. 1). A hypothesised “Darwinian Demon” that performs optimally with respect to all aspects of its fitness would outcompete all other organisms and, thus, reduce organismal diversity to a minimum. Such an organism does not exist. Trade-offs create species diversity, and organismal trade-offs together with environmental constraints govern the structure and function of ecosystems (Tilman, 1990; Thingstad, 2022). Therefore, a major task for ecologists is to identify and quantify organismal trade-offs (Metcalf, 2016). In this review I explore organismal trade-offs among plankton organisms with the goal of understanding and modelling plankton ecosystems better.

An essential ingredient in the trait-based models of pelagic ecosystems that many researchers are currently developing is quantitative trade-off relations for the key traits that relate to resource acquisition, survival, and reproduction (Kjørboe, Visser & Andersen, 2018). Trait-based models, rather than considering species, focus on individuals characterised by a few key traits that are interrelated through trade-offs. If such trade-offs, and their environmental dependencies, can be quantified for the main life forms, then in a trait-based model the structure of the ecosystem emerges – rather than being prescribed – as a result of interactions between individuals and the environment. Trade-offs can either be postulated or hypothesised (Smith *et al.*, 2016), they can be heuristic, that is supported by observed environmental dependencies and negative correlations between traits (Follows & Dutkiewicz, 2011; Edwards, Klausmeier & Litchman, 2011; Litchman, Edwards & Klausmeier, 2015), or they can be rationalised – ideally from first principles – by an understanding of the underlying mechanisms, for example obtained through experiments, observations, or theory (Kjørboe, 2008). The latter is preferable since the resulting models may be more robust as



**Fig. 1.** Conflicts – trade-offs – exist between the main components of an organism’s Darwinian fitness: growth/reproduction, survival, and resource acquisition. Acquired resources must be allocated between growth, reproduction, and survival (red arrows). Time must be allocated between foraging, hiding (defence), and mate finding; and foraging and mate-finding activities may compromise survival (black arrows). Modified from Litchman *et al.* (2013).

they can be extrapolated outside their calibration envelope and beyond the (few) species for which trade-off relations have been observed.

In this review I synthesise information on organismal trade-offs between the three main fitness components in plankton organisms – from bacteria to zooplankton. I consider how an organism allocates its time or resources between different activities, for example to feed or hide, to grow or reproduce, or to harness defence in the face of anticipated risks at the cost of reduced growth, etc. It is the optimisation of such trade-offs to diverse environmental conditions that shapes the life histories of organisms, the emergent slow–fast gradient in the “pace-of-life”, and the structure and function of pelagic communities.

Trade-offs may be difficult to demonstrate in nature because there is heterogeneity in resource availability among individuals, which may lead to positive rather than negative correlations between trait values (van Noordwijk & de Jong, 1986). For example, a trade-off in energy allocation between growth and reproduction leads to an expected negative correlation between the two among individuals. However, when comparing individuals in nature, some individuals will encounter more resources than others and, hence, can afford both a higher growth and a higher reproductive rate than those encountering fewer resources, thus leading to a positive correlation. Such trade-offs may be better explored in the laboratory. Conversely, other trade-offs only materialise in nature, for example the benefits (reduced predation risk) and costs (reduced foraging opportunities) of diurnal vertical migration found in many zooplankton and fish.

The most fundamental trade-offs are those between resource acquisition, defence (survival) and reproduction (Fig. 1). Resource acquisition and consequent growth may require substantial investment costs in machinery (e.g. chloroplasts) or may expose the organism to elevated predation risks during prey search, while defence may reduce foraging efficiency and take energy or time away from other activities and, eventually, lead to reduced growth. It is such trade-offs that are the focus of this review. Other resource acquisition trade-offs exist, for example between different trophic strategies, that is whether a heterotrophic, mixotrophic, or autotrophic strategy is the most favourable for a protist. This depends mainly on organism size as well as on environmental conditions (Andersen *et al.*, 2016; Chakraborty, Nielsen & Andersen, 2017), but does not generally trade off against survival and thus is not considered here. Unicellular organisms reproduce mainly by cell division and there is no real conflict between growth and reproduction. Reproduction trade-offs relate mainly to metazoans that may spend time searching for mates (at the cost of an elevated predation risk and reduced time for searching for food) and allocate energy to reproductive products, both at the cost of resource acquisition, growth, and/or survival. In the following I first consider foraging and defence trade-offs in both unicellular organisms and metazoan zooplankton. I then explore reproduction trade-offs in zooplankton and show how the trade-offs relate

to foraging behaviour. And finally, I argue that these trade-offs lead to a slow–fast gradient in the “pace-of-life”, which is arguably the most fundamental principle for the organisation of animal and plant life histories (Salguero-Gómez *et al.*, 2016; Healy *et al.*, 2019).

## II. TO EAT AND NOT BE EATEN

Zooplankton are squeezed between two trophic layers: they are predators of lower trophic-level organisms while also prey for higher trophic levels. Because foraging often implies elevated exposure to predators, there is a fundamental dilemma between eating and not being eaten, and many aspects of zooplankton behaviour can be considered adaptations to optimise this trade-off.

Many zooplankton perform diel vertical migration (DVM): they forage in the food-rich surface layer during the night and hide from visual predators at depth during the day (Klevjer *et al.*, 2016; Bandara *et al.*, 2021). Hiding at depth has the clear advantage of reducing mortality, and an equally clear cost in terms of reduced feeding opportunities – thus represents a trade-off (Loose & Dawidowicz, 1994). This is likely the most widespread strategy to optimise the fundamental trade-off between eating and being eaten among zooplankton. DVM has in several species been shown to be a plastic behaviour that is induced by the presence of predators (Bollens & Frost, 1989, 1991; Loose & Dawidowicz, 1994; Möller *et al.*, 2020). The response in vertical positioning of the predators of zooplankton to the vertical behaviour of zooplankton and the consequent optimisation game between multiple “players” may lead to a range of DVM patterns, including reverse migration and size-dependent diurnal migration, all consistent with fitness optimisation (Ohman, Frost & Cohen, 1983; Ohman & Romagnan, 2016; Pinti *et al.*, 2019).

However, there are other more subtle but equally important behaviours that may similarly be interpreted as an optimisation of this trade-off. Zooplankton feed on a dilute suspension of food and thus must search large volumes of water for food to satisfy their needs. Not all foraging strategies are equally efficient. We may differentiate between “active” and “passive” foragers, a classification that transcends taxonomy (Greene, 1986; Kiørboe, 2011). Active foragers cruise through the water and/or generate a feeding current to encounter prey, while passive foragers are sit-and-wait ambush foragers that depend on prey motility for prey encounter. Theory and experiments with copepods both demonstrate that active foragers are more efficient than passive foragers, particularly because non-motile prey are essentially unavailable to the latter (Kiørboe, 2011; Almeda, van Someren Gréve & Kiørboe, 2018). However, the active foraging strategy comes at the cost of a higher predation risk: an actively foraging zooplankton is likely to have a higher predation risk than a passive forager, both due to an increased predator encounter velocity and by generating fluid disturbances that

may increase its “visibility” to flow-sensing predators. The lower predation risk of passive ambush feeders with stealth behaviour relative to “active” cruise-feeding or feeding-current feeders with more “bold” behaviours is supported by theory, has been documented in laboratory experiments with copepods (Almeda, van Someren Gréve & Kiørboe, 2017; van Someren Gréve, Almeda & Kiørboe, 2017) and is also evident from reported order-of-magnitude differences in mortality rates experienced by co-existing copepod populations in nature (Eiane & Ohman, 2004). Again there is a clear foraging trade-off. This trade-off may be modified by food availability; at very low or very high, saturating food concentrations, some copepods may reduce their foraging effort (swimming speed, fraction of time active) and, consequently, their predation risk (Van Duren & Videler, 1996; Kiørboe *et al.*, 2017; Van Someren Gréve, Kiørboe & Almeda, 2019). I am unaware of zooplankton that modify their foraging effort in response to predator cues, as found in other aquatic organisms (Ferrari, Wisenden & Chivers, 2010).

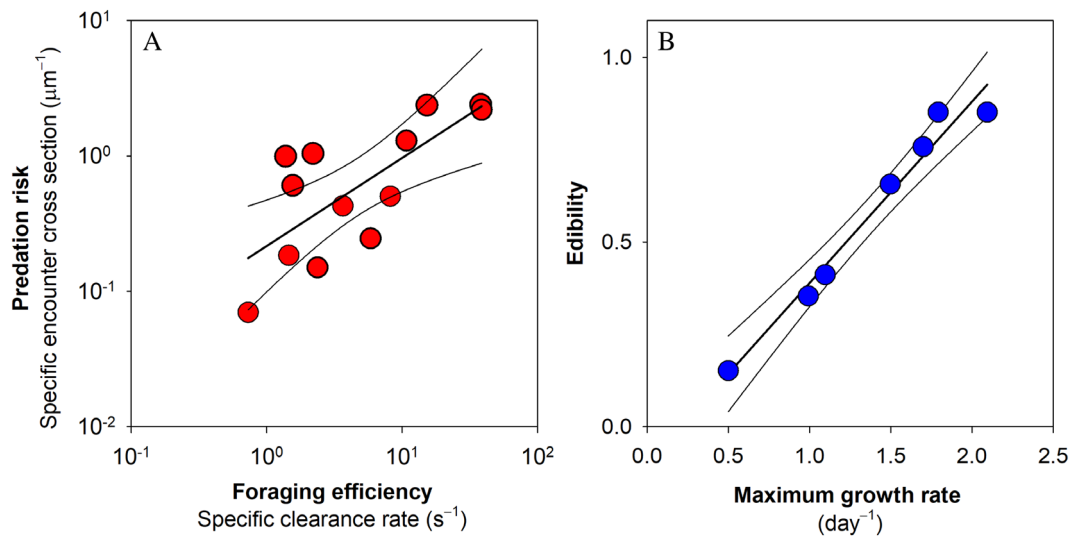
The gradient in stealth–bold foraging behaviours exemplified by copepods is found more generally among zooplankton, ranging from flagellates and ciliates to rotifers, cladocerans, and copepods, and predictions suggest an order-of-magnitude difference in predation risk along this gradient (Kiørboe *et al.*, 2014). The implied foraging–mortality risk trade-off has been explicitly demonstrated in flagellates, where a positive relation exists between foraging efficiency (measured as clearance rate) and predation risk (Fig. 2A) (Nielsen & Kiørboe, 2021).

This pattern is not different from what is found among organisms in any other environment. All prey organisms operate in a landscape of fear and adjust their behaviour accordingly leading to a gradient in bold–stealth behaviour (Werner & Peacor, 2003; Preisser, Bolnick & Benard, 2005; Palmer *et al.*, 2022), but the resulting behaviour of course materialises somewhat differently for (small) aquatic organisms than for terrestrial organisms.

## III. DEFENCE MECHANISMS AND TRADE-OFFS

While stealth behaviour in some sense can be considered a defence strategy in zooplankton, there are many more explicit defence mechanisms that plankton organisms may harness in the presence of their predators. These will all have associated costs, although these costs in many cases have not been quantified or even identified and demonstrated. There are several reviews of such defences and the associated trade-offs (Lass & Spaak, 2003; Pančić & Kiørboe, 2018; Lürling, 2021) and, hence, they are summarised only briefly here.

Many (freshwater) zooplankton organisms change shape in response to the presence of predators or predator cues: well-known examples include cladocerans that form a helmet, spines, or neck “teeth”, and rotifers that form long spines, the direct costs of which have been difficult to establish



**Fig. 2.** Example of foraging–predation risk trade-off in heterotrophic protists (A) and growth–edibility trade-off in phytoplankton (B). Each dot represents a species. In A, predation risk was estimated from the fluid disturbance generated by a feeding/swimming protist, while foraging efficiency was estimated as maximum clearance rate normalised by cell volume [see Nielsen & Kiørboe (2021) for details]. In B, edibility is zooplankton grazing rate on the focal phytoplankton species, divided by grazing rate on the maximally grazed species [see Sommer (1988) and Wirtz & Eckhardt (1996) for details]. Data from Nielsen & Kiørboe (2021) (A) and Wirtz & Eckhardt (1996) (B).

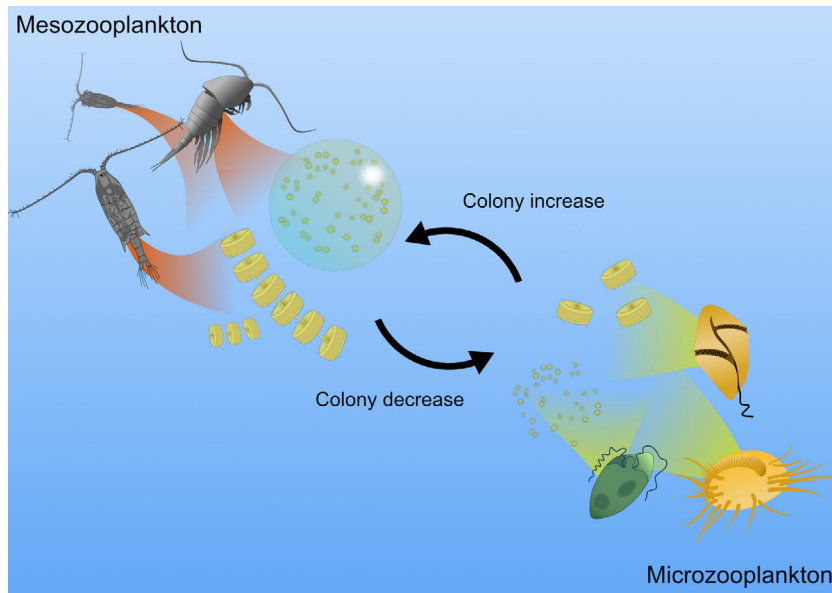
(Lass & Spaak, 2003). Interestingly, similar defensive morphological changes appear not to be found among marine mesozooplankton. Shape changes in response to predator cues have been established in protozoans (Fyda & Wiqckowski, 1998) and in phytoplankton in terms of forming or splitting up colonies (Jakobsen & Tang, 2002; Long *et al.*, 2007; Wang & Tang, 2022) making the cells less susceptible to predation by micro- and mesozooplankton, respectively (Bjærke *et al.*, 2015; Ryderheim, Hansen & Kiørboe, 2022b) (Fig. 3). While the direct costs of splitting up or forming colonies are uncertain, the trade-off may be realised only in nature as elevated predation risk from either micro- or mesozooplankton. In chain-forming dinoflagellates an additional cost of splitting up chains in response to copepod cues is that single cells swim more slowly than chains, preventing the dinoflagellates from performing DVM to harvest nutrients at depth during the night, and light at the surface during the day (Selander *et al.*, 2011).

Upon approach of a predator, many plankters, including flagellates, ciliates, and copepods, can perform powerful escape jumps (Jakobsen, 2001; Fenchel & Hansen, 2006; Jakobsen, Everett & Strom, 2006; Kiørboe *et al.*, 2010). While the energy consumption of an individual escape jump is minute, and is also small when summed over many jumps (Wadhwa, Andersen & Kiørboe, 2014), the real cost is rather the investment in the ability to produce these jumps. This is most obvious in copepods, where most of the muscle mass is dedicated to these powerful escape movements (Boxshall, 1985).

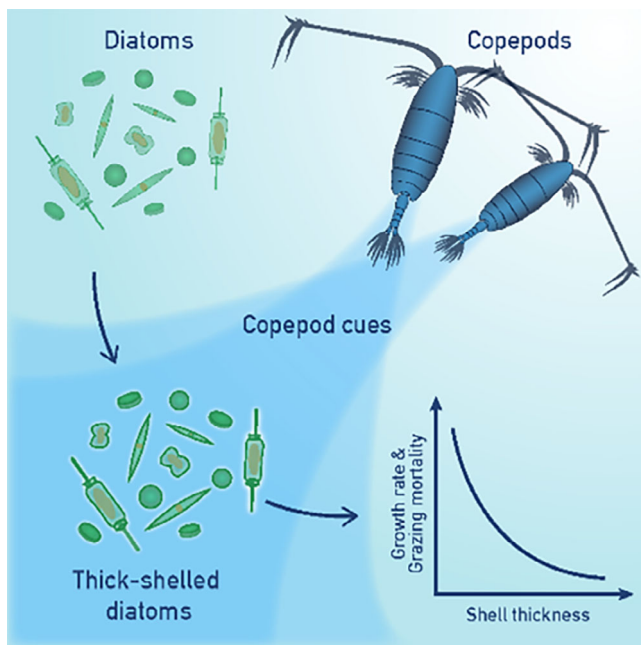
Many phytoplankton produce grazer-deterrent toxins and may increase toxin production when exposed to grazers

(Teegarden, 1999; Selander *et al.*, 2006). Again, the costs have been difficult to demonstrate as reduced growth in laboratory experiments (Selander *et al.*, 2006; John *et al.*, 2015; Ryderheim, Selander & Kiørboe, 2021), except in a few cases (Brown & Kubanek, 2020; Olesen *et al.*, 2022; Park *et al.*, 2023), and may lead to subtle changes in cell size that have implications for mortality only under natural conditions. Other defences in phytoplankton include thickening of the silica shell, which leads to reduced predation mortality at the cost of reduced cell division rate (Pondaven *et al.*, 2007; Pančić *et al.*, 2019; Grønning & Kiørboe, 2020; Ryderheim, Grønning & Kiørboe, 2022a) (Fig. 4), or expensive bioluminescent flashing to evade capture by a copepod (Prevett *et al.*, 2019). Finally, Wirtz & Eckhardt (1996) demonstrated a very strong trade-off between maximum growth rate and “edibility” in freshwater phytoplankton across a spectrum of taxa: the species with the highest cell division are also those most likely to be consumed by freshwater zooplankton (cladocerans) (Fig. 2B).

Bacteria have similarly evolved defences against protist grazing, by changing shape, forming colonies, or by increasing the production of defensive metabolites when exposed to grazer (protist) cues (Salcher *et al.*, 2005; Corno & Jürgens, 2006; Justice *et al.*, 2008; Blom *et al.*, 2010; Klapper *et al.*, 2018; Tophøj *et al.*, 2018). The costs of these defences are largely unknown. Viral attack is an important source of mortality in suspended bacteria, and bacteria may evolve resistance against specific viruses at the cost of cell division rates. The broader the resistance the lower the growth rate, and a clear trade-off between resistance and growth rate emerges (Winter *et al.*, 2010; Thingstad *et al.*, 2014; Våge *et al.*, 2018).



**Fig. 3.** Phytoplankton may split up or form colonies in response to chemical cues from meso- and microzooplankton, respectively.



**Fig. 4.** Diatoms thicken their shell in response to grazer cues, which reduces their risk of being consumed by a copepod but at the cost of a reduced cell division rate.

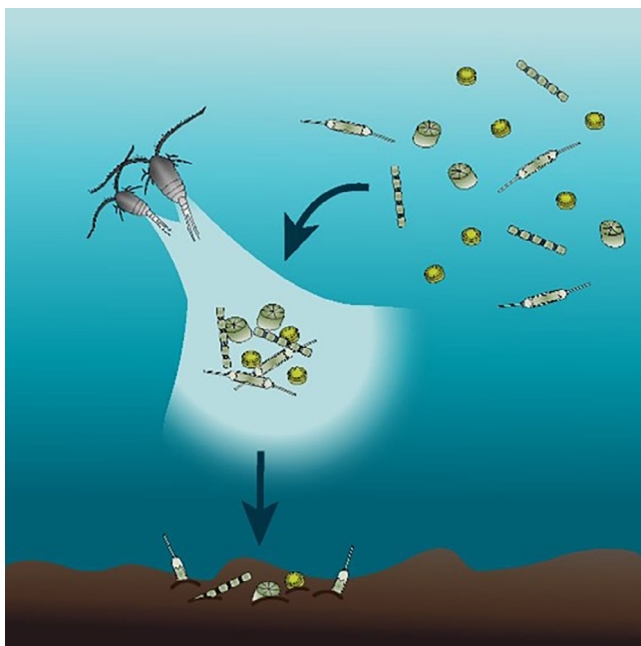
Many organisms – including protists and mesozooplankton – may form spores or resting stages (eggs) in response to adverse conditions, in some cases also as an explicit, inducible defence mechanism. Thus, resting cysts of dinoflagellates may delay excystment in the presence of zooplankton (Rengefors, Karlsson & Hansson, 1998). Diatoms may form rapidly sinking aggregates in response to grazer cues, surviving in a low-predation environment on the seafloor until conditions in

the pelagic zone improve (Fig. 5) (Grønning & Kiørboe, 2022). Resting stages of both metazoans (cladocerans, copepods) and protists typically have spines, a morphological feature that is predicted to reduce predation risk (Belmonte *et al.*, 1997). The obvious cost of formation of resting stages is lost growth opportunities.

#### IV. REPRODUCTION TRADE-OFFS

Unicellular organisms mainly reproduce by cell division, and typically cells divide once they have doubled in size. Thus, growth and reproduction are part of the same process. By contrast, multicellular organisms – zooplankton – mainly reproduce sexually and thus have life histories with ontogenetic development from egg to adult. This implies a trade-off between allocation of resources to growth and reproduction. It may also mean that males and females need to spend energy and time finding one another, and mate searching as well as mating itself may imply an elevated predation risk. The life histories of zooplankton are governed by such trade-offs and predation risk is thus an important life-history determinant.

The optimal allocation of energy between growth and reproduction is partly governed by environmental conditions and seasonality (Visser *et al.*, 2020), similarly to the formation of resting stages, but also by mortality rates and, hence, predation risk. The trade-off is between late maturation at a large size that allows a greater offspring production rate but has the cost of a smaller chance of survival to reproductive age *versus* early maturation at a smaller size with an implied lower capacity to produce offspring but a higher chance of survival to reproduction. Life-history theory



**Fig. 5.** Some diatoms become “sticky” and form rapidly sinking aggregates in the presence of cues from grazing copepods. The aggregates may survive for years in the sediment where grazing mortality is much lower than in the pelagic zone (Hansen & Josefson, 2001, 2004). Aggregation and sedimentation become favourable when grazing mortality exceeds growth rate in the ocean surface layers, as such conditions will lead to the largest seeding population surviving in the sediment.

predicts that high (juvenile) mortality favours early maturation at a small size (Stearns, 1989; Taylor & Gabriel, 1992). Applying life-history theory and assuming typical juvenile mortality rates for copepods in the ocean of the order of  $0.1 \text{ day}^{-1}$  (Hirst & Kiørboe, 2002) leads to predicted development times from egg to adult that are similar to average values observed in natural populations (Kiørboe & Hirst, 2008). However, variation in predation pressure may lead to variation in the optimal time for maturation; it is well documented that freshwater cladocerans reproduce at an earlier age in the presence than in the absence of predation risk (Taylor & Gabriel, 1992; Diel *et al.*, 2020). A similar response has recently been demonstrated for a marine copepod, *Calanus finmarchicus* (Kvile *et al.*, 2021).

Reproduction in zooplankton implies sex and, thus, that males and females must meet. Depending on the foraging strategy this may imply trade-offs between foraging, mate searching, and predator avoidance. Mate-searching behaviour has mainly been examined in copepods, where chemical or hydrodynamic signals are used to increase mate encounter rates (Griffiths & Frost, 1976; Doall *et al.*, 1998; Tsuda & Miller, 1998). In species that use hydrodynamic signals, for example *Acartia* spp., mate searching is symmetric between the sexes: fluid signals produced during foraging are perceived by the other sex, and pre-mating synchronised jumps help to identify the signaller as a relevant sexual partner

(Bagoien & Kiørboe, 2005). As mate-finding takes place during foraging, there may be no significant trade-offs in these species. In cruise-feeding and feeding-current-feeding copepods, the female produces pheromones that leave a chemical trail in her wake or form an odour plume around her as she searches for food. The optimal search strategy for such a chemical plume or trail is simply to swim in a straight line, and males accordingly have a high degree of directional persistence in their (ballistic) swimming pattern. This, however, also increases the risk of encountering a predator, and therefore involves a clear trade-off. Females, by contrast, swim in a much more convoluted (diffusive) way, which does not compromise foraging efficiency but reduces the predator-encounter risk. Males of some species in this group simply cease foraging upon maturation and dedicate all their efforts to finding females (Kiørboe & Bagoien, 2005). The resulting higher male mortality from predation or starvation results in a female-biased sex ratio in wild populations (Kiørboe, 2006). This becomes even more pronounced in ambush-feeding copepods, like *Oithona* spp. (Kiørboe, 2007): a sit-and-wait foraging strategy means that males and females will be unable to meet while both are foraging. In *Oithona davisae* the males cease feeding for about one third of their time to search for females, leaving less time for foraging. During mate searching, the males swim very fast; in fact, mate-searching males have the highest sustained swimming speeds among copepods, at about 50 body lengths  $\text{s}^{-1}$ , likely leading to a highly elevated predator encounter rate. This double price paid by males leads to male mortality about 10 times larger than that of females, with a highly female-biased sex-ratio in field populations as a result. Clearly, trade-offs related to mate-finding can be severe, mainly for males, and depend strongly on foraging behaviour.

An additional cost is that of mating itself, which may also be a risky activity, since the male attaches to the female for up to several minutes while the female tries to remove him through rapid, abrupt swimming leading to elevated visibility to predators.

## V. TRADE-OFF BETWEEN MAINTENANCE, GROWTH, AND REPRODUCTION

The survival of an organism is not solely a question of not being eaten or otherwise killed; all organisms also senesce and will eventually die from old age if not killed before this. Proteins are constantly being turned over, mutations need to be repaired, and these and other maintenance processes require energy (Ryazanov & Nefsky, 2002). Investment in maintenance thus detracts from potential investment into growth or reproduction. When extrinsic mortality is high and age dependent, and if the population is under density-dependent regulation, then fitness optimisation predicts low investment in maintenance, compared to a situation with low extrinsic mortality (Ricklefs, 2008; Baudisch & Vaupel, 2010).

Why invest in a long life if the chance of achieving it is minimal? Thus, the performance of risky foraging and mate-finding behaviours implies low investment in maintenance, a high reproductive output, and a short lifespan in the absence of external mortality. These predictions have been confirmed for pelagic copepods (Kiørboe, Ceballos & Thygesen, 2015) (Fig. 6).

## VI. OTHER ALLOCATION TRADE-OFFS

In addition to trade-offs between the fitness components considered above – resource acquisition, survival, growth and reproduction – additional allocation trade-offs may exist *within* these components, for example between different resource allocation strategies.

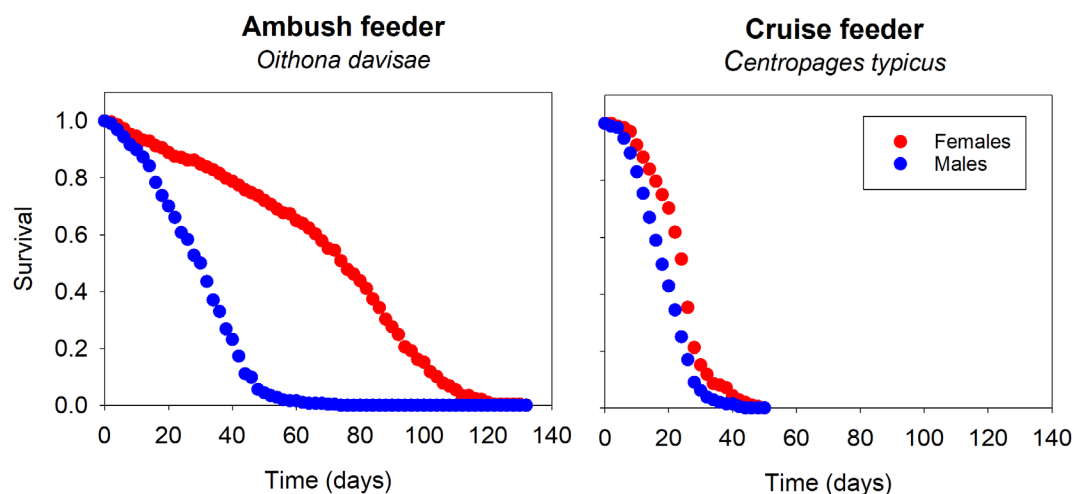
Most or many pelagic flagellates are mixotrophic, that is they are both phototrophic and phagotrophic, implying that they invest in two different resource acquisition systems or acquire plastids necessary for phototrophy through consumed prey (Stoecker *et al.*, 2017). The advantage of mixotrophy is high flexibility in resource choices in a fluctuating environment, but mixotrophic generalists also have a lower performance than pure autotrophs in the absence of prey, and a lower clearance rate of prey than pure heterotrophs (Edwards *et al.*, 2023a; Edwards, Li & Steward, 2023b).

Another hypothesised trade-off is between a high capacity to harvest resources when these are scarce – that is a high maximum clearance rate or affinity – and an ability to utilise resources maximally when they are plentiful – that is a high maximum ingestion or uptake rate (Smith *et al.*, 2014; Kiørboe & Thomas, 2020). Organisms living in nutrient-poor habitats would benefit from a capacity to scan large volumes of water for prey, that is high clearance rates, while

organisms living in nutrient-rich habitats would rather be selected for their capacity to consume and process food at high rates, that is high maximum consumption rates. The rationale is that investment in efficient systems to harvest resources, for example in the form of efficient feeding appendages and sensory systems, would compete with investment in systems to process resources at high rates, for example in the form of a long gut or high enzyme-production rates. Therefore, allocation of limited resources leads to a predicted negative relation between maximum clearance rate and maximum ingestion rate in pelagic suspension feeders. Similar arguments can be made for osmotrophs (phytoplankton and bacteria that take up dissolved minerals and organic nutrients) having a negative relation between affinity (equivalent to maximum clearance rate) and maximum uptake rate (Brandenburg *et al.*, 2018; Fernandez, Yawata & Stocker, 2019). Pahlow (2005) and Smith *et al.* (2009) developed a model of phytoplankton nutrient uptake kinetics in which nitrogen is allocated between uptake sites (affinity) and enzymes to assimilate the nutrients (maximum uptake), suggesting a mechanistic basis for such a trade-off. However, in neither phagotrophs nor osmotrophs has such a trade-off emerged when considered over a broad range of species (Fig. 7). In fact, rather than the expected negative relation there is a positive slope for both phagotrophs and osmotrophs.

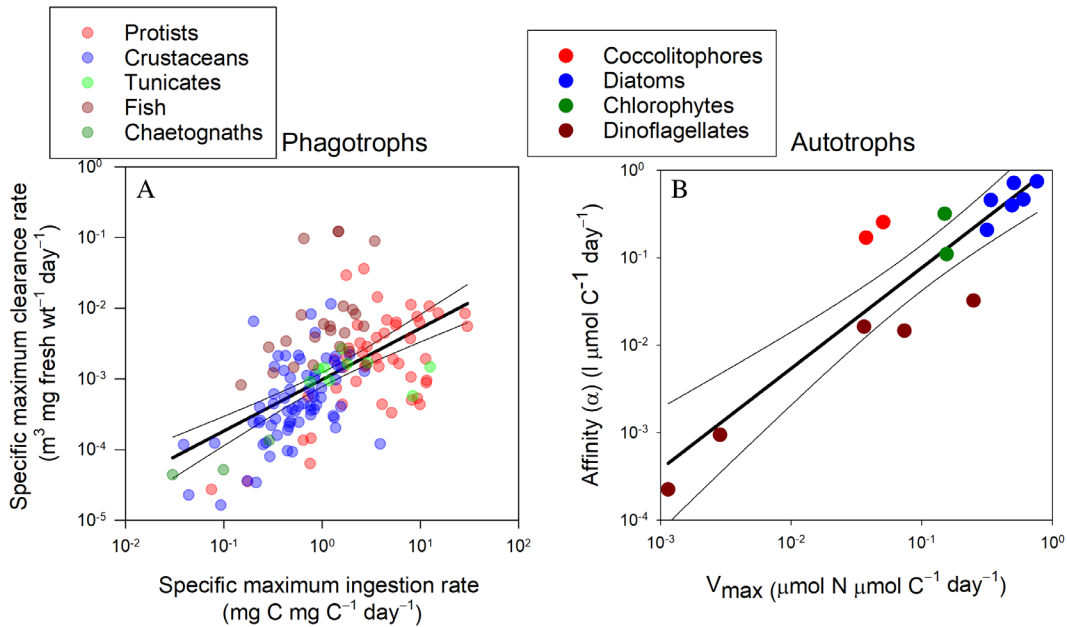
## VII. THE SLOW-FAST GRADIENT IN PACE-OF-LIFE AND ECOSYSTEM MODELLING

The pattern that consistently emerges from the trade-offs considered above, and has been demonstrated quantitatively in a few examples (Figs 2 and 7), is a slow-fast gradient in the pace-of-life. The ultimate currency of trade-offs related to



**Fig. 6.** Survivorship curves of adult copepods in a predator-free, high-food laboratory environment. The ambush feeder (*Oithona davisae*, left panel) has a low-risk foraging behaviour, although males perform high-risk mate-searching behaviour. Males consequently have a shorter lifespan (senesce faster) than females, but both genders have longer lifespans than the active high-risk cruise feeder (*Centropages typicus*, right panel). Data from Kiørboe *et al.* (2015).





**Fig. 7.** Maximum clearance rate ( $\beta$ ) versus maximum ingestion rate ( $I_{\max}$ ) for planktonic phagotrophs (A) and affinity ( $\alpha$ ) versus maximum uptake rate ( $V_{\max}$ ) of nitrate for osmotrophic phytoplankton (B). All properties have been normalised by cell or body size. Data from Kjørboe & Hirst (2014) (A) and Litchman *et al.* (2007) (B). In B, affinity was computed as the ratio of  $V_{\max}$  to the half-saturation constant, the two parameters reported by Litchman *et al.* (2007). The regression lines are  $\log_{10} \alpha = -0.3 + 0.73 \log_{10} I_{\max}$ ,  $R^2 = 0.31$ ,  $P < 0.001$  (A) and  $\log_{10} \alpha = 0.04 + 1.15 \log_{10} V_{\max}$ ,  $R^2 = 0.82$ ,  $P < 0.001$  (B).

growth, resource acquisition, and survival are growth (reproduction) and mortality rates (e.g. Wirtz & Pahlow, 2010), and their difference or ratio can be taken a measure of organismal fitness: allocation of resources to defence reduces resources available for growth/reproduction, but also reduces mortality risk; efficient foraging increases growth/reproduction but typically also increases mortality risk; efficient mate finding increases reproduction rate but typically at the risk of higher mortality, etc. Thus, through various mechanisms, organisms with a high growth rate typically have a high mortality risk (and *vice versa*), and this is the pace-of-life gradient. Thus, the pace-of-life gradient is an inescapable emergent property of the organismal trade-offs demonstrated herein. The existence of other (additional) trade-offs, independent of the resource acquisition, survival and reproduction “triangle” (Fig. 1), will not change this.

The slow–fast pace-of-life syndrome is the result of a fundamental trade-off between current *versus* future growth and reproduction (Wright *et al.*, 2019). This trade-off is expressed in different ways for different life forms and is the result of the more specific trade-offs in each case. That is, the allocation between hiding and feeding, between defence and growth, between mate finding and survival, or between maintenance and growth/reproduction, etc., all lead to gradients in stealth *versus* bold behaviours and slow *versus* fast lifestyles. The positive rather than negative correlations between maximum clearance rate and maximum consumption rate for phagotrophs (Fig. 7A), or between affinity and maximum uptake rate for osmotrophs (Fig. 7B), are

manifestations of this syndrome; the hypothesised trade-off must be overridden by the more fundamental trade-off between current and future reproduction and applies to eukaryotic heterotrophs in general, whether aquatic or terrestrial (Kjørboe & Thomas, 2020).

### VIII. TRAIT-BASED MODELLING OF PELAGIC FOOD WEB

Fast and slow lifestyles have implications for how fast matter and energy are channelled through food webs as well as for the structure of pelagic food webs. One can speculate about the food-web implications of the fast–slow pace-of-life syndrome, but this may be too complex to cover in a verbal model. In fact, an environment that selects for high growth or high reproductive rates for certain life forms may not necessarily imply high population growth rates due to higher mortality. In a simple steady-state situation, a high-food/low-risk environment would favour a fast lifestyle, a high-food/high-risk environment would favour a slow lifestyle, whereas the two other combinations (low-food/low-risk and low-food/high-risk) would favour intermediate lifestyles distributed between the two extremes on the slow–fast gradient. However, the situation becomes more complex when considering the temporal aspects. For example, fast, bold, and risky lifestyles may be most successful in fluctuating resource-rich environments that favour organisms that reproduce rapidly,

allowing them to utilise ephemeral resources (e.g. diatoms during spring blooms in temperate waters). Some predators (e.g. copepods) may not be able to respond numerically to such increasing consumer populations in the short term because of their longer generation times, thus making the penalty for risky behaviour in their prey small. Other predators (e.g. microzooplankton) breed more rapidly, or predators that integrate environmental variation over longer timescales may benefit from increased abundance of susceptible prey, making the penalty for risky behaviour by prey larger but potentially affordable over a range of conditions. On a longer timescale, predators with a slow numerical response (e.g. copepods) may become abundant, increasing the predation pressure and, hence favouring a slower, defensive lifestyle (e.g. diatoms thickening their shell or aggregating to sink and hide in the sediment).

What is obvious from the above discussion is that environmental fluctuations are experienced differently by organisms with different lifespans, and their effects also depend on whether the organisms are producers, primary consumers, or higher order consumers (Visser *et al.*, 2020). The implications of these can be explored further through modelling, and the concept of the slow–fast pace-of-life gradient is particularly well suited for a trait-based modelling approach. Rather than modelling how the many species in the ocean interact with the environment and with one another, the trait-based approach focuses on how individuals characterised by a few traits interrelated by trade-offs interact. The pace-of-life trait is a summation of the many specific trade-offs considered here, too many to be considered explicitly in a model, but all important for the dynamics of the system. Trait-based models allow the description of complex systems in a relatively simple manner and use of the compound pace-of-life trait, like the examples in Figs 2 and 7, can allow further simplification to describe large-scale global patterns in ecosystem structure and functioning. I am unaware of models that have achieved this level of simplicity, but several models of pelagic microbial systems incorporating generic defence–growth (competition) trade-offs, and an implicit slow–fast gradient, are approaching this (Thingstad *et al.*, 2014; Våge *et al.*, 2014, 2018; Cadier *et al.*, 2019).

## IX. CONCLUSIONS

(1) The “paradox of the plankton” poses the question of how so many species of phytoplankton can co-exist on a few limiting resources – light and a few mineral nutrients (Hutchinson, 1961). The competitive exclusion principle allows only one species per limiting resource at steady state. Organismal trade-offs offer one (of several) solution to this paradox, both because it allows coexistence of competition and defence specialists in a stable environment (Winter *et al.*, 2010), but also because it implies the adaptation of different species to different environmental niches in a fluctuating environment. In this review, I have, for plankton

organisms ranging from bacteria to mesozooplankton, documented clear trade-offs of fundamental traits that are the main determinants of an organism’s Darwinian fitness. In some cases, particularly for defence traits, it has been difficult or impossible to identify explicitly the costs of a particular trait in laboratory experiments, likely because these costs only manifest in natural environments or under resource-limited conditions. Yet, such costs must exist. Many details in our mechanistic understanding of these processes remain to be revealed.

(2) The general and robust pattern that emerges from the optimisation of the many trade-offs related to resource acquisition, growth, and survival in planktonic organisms is a slow–fast gradient in the pace-of-life. There is a gradient between a bold “live-fast-die-young” strategy with a high reproductive rate and high mortality risk at one extreme, and a safer and slower lifestyle with a low reproductive rate at the other. This gradient transcends taxonomy and life form and is found among organisms ranging from bacteria to zooplankton.

(3) The same pace-of-life gradient has been found for organisms in other environments, across species, and for both animals and plants. The pace-of-life syndrome was first applied to compare life histories among populations, then to examine variation within populations (Mathot & Frankenhuis, 2018), and here I have applied the concept in a comparison across species. For a trait-based approach the level of comparison makes no difference, and I suggest that it offers a way to simplify further trait-based models of complex pelagic systems. This promising avenue has yet to be fully explored.

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