To eat and not be eaten: optimal foraging behaviour in suspension feeding copepods

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Zooplankton feed on microscopic prey that they either entrain in a feeding current or encounter as they cruise through the water. They generate fluid disturbances as they feed and move, thus elevating their risk of being detected and encountered by predators. Different feeding modes generate different hydrodynamic signals to predators and different predator encounter speeds but may also differ in their efficiency; the optimal behaviour is that which maximizes the net energy gain over the predation risk. Here, we show by means of flow visualization and simple hydrodynamic and optimization models that copepods with a diversity of feeding behaviours converge on optimal, size-independent specific clearance rates that are consistent with observed clearance rates of zooplankton, irrespective of feeding mode, species and size. We also predict magnitudes and size-scaling of swimming speeds that are consistent with observations. The rationalization of the magnitude and scaling of the clearance rates of zooplankton makes it more suitable for development of models of marine ecosystems, and is particularly relevant in predicting the size structure and biomass of pelagic communities.

1. Introduction

Marine zooplankton are the principal consumers of the oceans’ primary production. They feed in a viscous and nutritionally dilute environment and they must daily clear an enormous volume of water of prey to cover their needs. The maximum clearance rate of zooplankton varies substantially between species, but it scales with body mass when considered over the entire size, taxonomic and feeding type range of zooplankton, from heterotrophic flagellates a few micrometres long to centimetre-sized krill, and the specific clearance rates scatter around a value corresponding to approximately 10^6 times their own body volume per day [1,2]. However, feeding not only leads to acquisition of food but also involves an elevated mortality risk because feeding and swimming generate hydrodynamic disturbances that may be perceived by rheotactic predators [3], and motility increases encounter velocities [4]. Different feeding modes imply different risks but may also differ in efficiency in terms of volume of water cleared. For example, passive ambush feeding creates minimal fluid signals and predator encounter velocities but is inherently less efficient than the more active but ‘noisy’ feeding strategies of generating a feeding current or cruising through the water to hunt for prey [5,6]. The optimal foraging strategy is that which maximizes the clearance rate or energy gain over the mortality risk. Thus, the trade-offs associated with the three principal feeding behaviours of zooplankton—ambush feeding, feeding-current feeding (hovering) and cruise feeding—determine the optimal feeding strategy and the magnitude and scaling of the clearance rate [2,7–9]. The magnitude of the clearance rate of zooplankton cannot be explained by its sufficiency to maintain a population, because natural selection operates at the level of the individual. The question of what governs the magnitude of the clearance rate may be addressed, however, by quantifying the trade-offs and determining the behaviour that optimizes these trade-offs.
Illustration of the three simple models used to describe (a,d) a hovering zooplankter (stokeslet), (b,e) a cruising zooplankter that is neutrally buoyant (stresselet), and (c,f) a cruising zooplankter that is negatively buoyant (stokeslet + stresselet). (a–c) Forces acting on the water (as vectors) and (d–f) velocity contour lines superimposed on flow velocity vectors for the three models. The forces acting on the water owing to a hovering and a cruising zooplankter are described in the text. The negatively buoyant cruising zooplankter acts with three forces on the water (c), one downward force to counter gravity (the stokeslet component), and two forces corresponding to the propulsion and drag forces (the stresselet component). The flow velocity at any point in space in the combined model is simply the sum of velocity contributions from the stokeslet and the stresselet components. The cruising zooplankter swims at velocity \( \mathbf{U} \); the stokeslet is of the point-force magnitude \( W_{\text{excess}} \) (the zooplankter’s excess weight) and the stresselet of intensity \( 6\pi \mu a U \times 2\pi r \). The calculation example uses parameters for the *Centropages typicus* shown in figure 2b.

Here, we attempt to quantify the trade-offs and determine the optimal foraging strategies and resulting clearance rates for zooplankton. We consider only the two active feeding modes, because ambush feeding is restricted to a few groups of zooplankton [2]. The clearance rate is determined by the flow of water past the animal and by its ability to remotely detect and capture prey. The feeding-dependent mortality risk is governed by the fluid disturbances that the animal produces that make it detectable by rheotactic predators, and by the velocity at which it translates through the water that influences the encounter rate with predators irrespective of their sensory modes (rheotactic, visual or tactic).

Hydrodynamics of swimming and feeding in zooplankters are rather well understood, both through observations and flow visualization [10–13] and by means of fluid dynamical models [10,14–17]. The simplest analytical models to describe zooplankton feeding consider either a hovering zooplankter that generates a feeding current, or a neutrally buoyant one that cruises through the water. Far-field flow fields generated by these behaviours are traditionally approximated by, respectively, a stokeslet, i.e. a stationary downwards-directed force that works in a point in the water and exactly balances the gravitational force acting on the animal; or a stresselet, two oppositely directed forces of equal magnitude corresponding to the propulsion force that drives the animal through the water and counterbalances the oppositely directed drag force (figure 1; [15]). One conclusion from such simple models is that not only do the imposed flow fields differ significantly, making the hovering feeding mode the more efficient of the two [14]: the hovering zooplankter also generates a fluid signal that extends much further in the water than that generated by the cruising one, thus exposing it to a greater predation risk. This conclusion is generally supported by observations of copepods [10,12] and micro-organisms [18,19]. Real zooplankters, however, are neither exactly neutrally buoyant nor apply a force that exactly balances gravity. Rather, most are negatively buoyant; so part of the force generated by the vibrating appendages or cilia goes into countering gravity and generating a feeding current and part into translating the zooplankter through the water. The resulting far-field flow may be described by the sum of a stokeslet and a stresselet (16; figure 1). This idealized model describes the entire range of active feeding behaviours, from pure hovering to pure cruising and, importantly, it quantifies the associated trade-offs, i.e. the clearance rate from which the animal gains food, and the translation velocity and fluid disturbance that together govern the risk of feeding.

Here, we use flow visualization of feeding zooplankters and simple stokeslet–stresselet and optimization models. We show that optimal foraging is consistent with the entire range of feeding behaviours reported for zooplankton and that it predicts specific clearance within the range observed. As study object, we use planktonic copepods, the absolutely dominating mesozooplankton group in the ocean [20].

2. Material and methods

2.1. Experiments

Late copepods and adults of two species of copepods, *Temora longicornis* (prosome length: 0.5–1.0 mm) and *Centropages typicus*
(0.9–1.3 mm), were collected from a pier in Woods Hole, MA, USA, at approximately 5°C and acclimated overnight at room temperature (approx. 20°C). Observations were made in small aquaria (65–200 ml) containing five to 10 copepods, flagellates and diatoms (to stimulate feeding) and 5 μm neutrally buoyant beads to visualize the flow. The flow generated by feeding copepods was visualized using particle image velocimetry (PIV). A red, vertically oriented laser sheet (1 W, 1 mm thick) was directed into the aquarium to illuminate the beads occurring in a well-defined plane. We filmed through a dissecting microscope oriented perpendicular to the laser sheet using a high-resolution (1024 x 1024 pixels) Photron Fastcam 1024 PCI camera with a field of view of 8.24 x 8.24 mm². Recordings were made at 500 Hz, and sequences of feeding copepods swimming in the illuminated plane were analysed at 250 Hz, with standard PIV software (DaVis 8, LaVision) to yield flow fields.

We analysed 12 sequences for T. longicornis and 11 for C. typicus (all different individuals). Sequences varied in duration between 500 and 3000 ms. The animal itself was excluded from the PIV analysis by masking it. The areas (excl. the animal) within which the imposed fluid velocity exceeded threshold values, $U^*$, were measured using ImageJ software for set values of $U^*$ between 0.1 and 3.0 mm s⁻¹. For $U^*$ exceeding the translation velocity of the copepod, the cross-sectional area of influence, $S^*$, in the illuminated plane were analysed at 250 Hz, with standard PIV software (DaVis 8, LaVision) to yield flow fields.

We recorded the fluid flow generated by two free-swimming copepods, T. longicornis and C. typicus. Temora longicornis (0.5–1.0 mm prosome length) vibrates its feeding appendages more or less continuously at a frequency of 28 ± 4 Hz, generating a rather constant feeding current that extends a few body lengths away from the animal (figure 2). The animal also translates slowly through the water at a speed,...
Foraging behaviour and the fitness contribution of the activity (swimming–sinking) of the animal, but the response is not immediate: the area of influence increases for some time after the onset of the vibration of the feeding appendages; similarly, after cessation of appendage movements, the area of influence attenuates over some time. For example, it takes about 300 ms for $S$ ($U^* = 0.6$ mm s$^{-1}$) to stabilize. This timescale may be compared with the viscous timescale ($S$/viscosity), which is of the order of 1 s for $S \sim 1$ mm$^2$. For smaller values of $U^*$, the area of influence increases, and the temporal variation in the extension of the flow field declines. Hence, at further distances, the signal perceived by a predator becomes more temporally uniform. The extension and dependency of $U^*$ of the stabilized area of influence are again well approximated by the combined stokeslet–stresslet model (figure 3d–f).

4. Discussion

The simple stokeslet–stresslet model captures essential features of the observed flow fields generated by two copepod species with rather different behaviours, i.e. one near hovering and with a rather well-developed feeding current ($T. longicornis$), and one that cruises relatively fast through the water and has a less well-developed feeding current ($C. typicus$). The spatial extension of the flow field is of the same magnitude as that predicted (figures 2 and 3). The observed scaling of the area of influence ($S$) with the threshold velocity ($U^*$) appears to deviate slightly but systematically from that predicted, having a slightly steeper slope. The main reason for the slower-than-anticipated spatial attenuation of the flow is likely to be the unavoidable background convection in the observation aquaria. However, the overall fair correspondence warrants using this idealized model to evaluate the trade-offs associated with the hovering, cruising, and intermediate behaviours. The trade-offs are in the magnitude of the clearance rate ($D$), the area of influence ($S$) and the swimming velocity ($u$) that together determine the fitness-contribution of the behaviour, as defined by the foraging index, $\chi$.

Feeding behaviour and the fitness contribution of the feeding behaviour so defined are solely functions of the magnitude of the force that the zooplankter generates and of its excess density ($\Delta \rho$). Both are under partial control of the animal on an evolutionary timescale, and we can therefore construct landscapes of the foraging index within this
parameter space (figure 4). The diagonal in these plots corresponds to the force exactly balancing gravity: the zooplankter is hovering. Below this line, the animal produces a feeding current and translates through the water, the faster the further away from the diagonal. At $\Delta \rho = 0$, the zooplankter is a ‘pure’ cruiser with no feeding current.

In the presence of visual or tactile predators only (figure 4a–c), the global optimum of the foraging index landscape suggests that the zooplankter should be hovering and be very heavy and generate a correspondingly large force. However, there is a limit to how much muscle force a zooplankter can produce and how heavy it can be, and the optimal strategy depends on whether the zooplankter is limited by its density or by the force it can produce (figure 4a–f). The maximum mass-specific net force output of muscle motors is strikingly constant across all animal taxa, including both vertebrates and invertebrates, it is limited by material fatigue rather than power production, and it averages a temperature-independent value of 57 N kg$^{-1}$ muscle [23,24]. Assuming that 20 per cent of the copepod volume is muscle [29], this corresponds to about 10$^3$ N m$^{-3}$. Mass-specific force output of ciliary motors may be higher [23]. If force rather than excess density is the limiting factor, hovering should always be the preferred strategy independent of organism size if visual and tactile predators dominate (figure 4a–c).

The limit to how dense a zooplankter can be, however, typically defines a more narrow constraint. Excess densities of most zooplankters, evaluated from direct measurements or from sinking speeds, are less than 30 kg m$^{-3}$—from ciliates to copepods and including even larvae of echinoderms with calcified skeletons [26–28]. Only shelled forms, such as bivalve larvae and pteropods (wing snails), have much higher densities, approximately 100 kg m$^{-3}$ [29,30]. There are obvious disadvantages to a high excess density; there are costs of maintaining ion pumps and depositing ballast [9], and a high density hampers rapid escape jumps, essential for predator avoidance in many zooplankters, from flagellates and ciliates to copepods [31,32]. With density as the limiting factor, there is a clear optimum in the foraging index landscape that depends on the excess density that the zooplankter can achieve (figure 4a–c). The optimum force production and the resulting specific clearance rate are both largely invariant with density, and the optimum specific clearance is approximately 10$^3$ d$^{-1}$. The optimum swimming velocity depends on the excess density (the denser and slower the better) but the predicted magnitudes are comparable with those observed for zooplankters of this size (figure 5) and realized by the experimental organisms examined here.

In the presence of only rheotactic predators, or for zooplankters too small to be detected by vision and where

**Figure 4.** Landscapes of the foraging index for three sizes of zooplankters in the presence of (a–c) visual/tactile predators or (d–f) rheotactic predators, and (g–i) optimum swimming velocities ($u_{optimal}$) as a function of excess density ($\Delta \rho$) of the zooplankter. The landscapes are contoured in the parameter space of the excess density of the zooplankter and the body-volume specific force that it produces ($f^*$). (a–f) Black lines are contour lines for body-volume specific clearance rates ($\times 10^3$ d$^{-1}$); purple and blue lines describe the optimum foraging behaviour when, respectively, force production or excess density limits the performance of the zooplankter. (g–i) Red line, visual; blue line, rheotactic. We used $V = 0.059 L^3$ to convert between body length ($L$) and body volume ($V$).
hydrodynamic perception are more important, there is a global optimum in the foraging index landscape within the likely constraints set by density and force production, at least for intermediately sized zooplankters (figure 4d–f).

The predicted specific clearance rate at the optimum is similar to that predicted above, i.e. of order $10^6$ d$^{-1}$. Again, the predicted strategy changes if the optimum excess density or force is unachievable and depends on whether one or the other is limiting. If force is the limiting factor, the optimum strategy is either hovering at low forces, or slow swimming with higher forces, and the optimum density is less than $100$ kg m$^{-3}$, consistent with observations. The predicted swimming velocities are of the same order as for tactile and visual predation (figure 5).

Zooplankters may overcome limitations caused by low excess density in various ways: they may attach to solid surfaces such as those provided by marine snow and used by some flagellates [33]; they may increase their drag by attaching to particles as reported for some free-living flagellates [19] or by producing mucus strings such as done by some bivalve larvae [34]; or they can otherwise be equipped with 'drift anchors', such as some copepods that have long, plumose appendages [2]. These are common strategies that can be readily understood in the foraging optimization framework.

While the predicted optimum strategy is sensitive to the choice of parameters and underlying assumptions, the magnitude of the optimum specific clearance rate is not; even order-of-magnitude variation in input parameters leads to rather small changes in predicted specific clearance rate that remains of order $10^6$–$10^7$ d$^{-1}$ and within the range observed (table 1). Even if we make the extreme assumption that there are no metabolic costs and no background mortality (i.e. $V^0 = 0$ and $E_0 = 0$) then for realistic excess densities (say, $5$ kg m$^{-3}$), the predicted clearance rates are within a factor of 5 of those predicted for default parameters, and well within the range observed (figure 5).

Our model considers the feeding behaviours that are hardwired in the genes of the zooplankter and, hence, the potential clearance rates that are adapted to the general environment. This is the clearance rate that one can measure at non-saturating concentrations in an experimental bottle, and these are the rates taken from the literature and to which we compare our predictions (figure 5) [1,2]. Obviously, zooplankton may in addition adapt behaviourally on short timescales to their immediate environment, and realized clearance rates may therefore be lower as a result of food saturation or presence of predators [8].

While we have used copepods as model organisms in this study, our results may apply more generally to marine
zooplankton, because the present categorization of feeding behaviours applies to other zooplankters as well [2]. However, the model is invalid for some very small zooplankters that operate at low Péclet numbers, where diffusion rather than advection governs prey encounter [35], and for the largest zooplankters (krill, jellyfish), where the assumption of low Reynolds number is violated.

Sensitivity of the predicted feeding behaviour to changes in parameter values and in particular to variation in the excess density that a zooplankter can achieve may account for the huge diversity in feeding behaviours that one can observe in nature. Copepod feeding behaviours, for example, range from very nearly hovering to very fast cruising with swimming velocities of greater than 10 body lengths s$^{-1}$, and cruising and hovering may even be found within the same species [10,36]. The same range of behaviours is found among different species of copepods and zooplankton may be adapted to different environments and possess defence and sensory capabilities as indicated above, which together may account for the substantial scatter in clearance rates observed between species.

The magnitude of the zooplankton clearance rate has interest on its own as it governs the growth, reproduction and entire bioenergetics of the individuals. However, it also has implications for properties of the ecosystem: the biomass—not the productivity—of planktonic ecosystems is inversely related to the magnitude of the clearance rate of the zooplankton. This result follows both from ecosystem size spectra theory [38] and from simple predator–prey models, such as Lotka–Volterra: the biomass of both predators and prey are inversely related to the magnitude of the clearance rate of the zooplankton. This result follows both from ecosystem size spectra theory [38] and from simple predator–prey models, such as Lotka–Volterra: the biomass of both predators and prey are inversely related to the magnitude of the predator’s clearance rate [39]. Thus, the biomass of planktonic ecosystems is a property that partly emerges from interactions between individuals that, in turn, are governed by natural selection.

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Table 1. Sensitivity analyses. Predicted body-volume-specific clearance rates ($\times 10^6$ d$^{-1}$) for a $L = 1$ mm zooplankter using default input parameters (see the electronic supplementary material, appendix S1) and input parameters varying by one or two orders of magnitude relative to the default. Predictions are reported for scenarios with only rheotactic or only visual/tactic predators and assuming excess densities ($\Delta \rho$) of 5 or 99 kg m$^{-3}$ for the latter scenarios.

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