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ADAPTIVE FEEDING BEHAVIOR AND FUNCTIONAL RESPONSES IN ZOOPLANKTON

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Abstract

Zooplankton may modify their feeding behavior in response to prey availability and presence of predators with implications to populations of both predators and prey. Optimal foraging theory predicts that such responses result in a type II functional response for passive foragers and a type III response for active foragers, with the latter response having a stabilizing effect on prey populations. Here, we test the theoretical predictions and the underlying mechanisms in pelagic copepods that are actively feeding (feeding-current feeders), passively feeding (ambushers), or that can switch between the two feeding modes. In all cases individual behaviors are consistent with the resulting functional response. Passive ambushing copepods have invariant foraging behavior and a type II functional response, as predicted. When foraging actively, the species with switching capability change its functional response from type II to III and modify its foraging effort in response to prey density and predation risk, also as predicted by theory. The obligate active feeders, however, follow a type II response inconsistent with the theoretical prediction. A survey of the literature similarly finds consistent type II response in ambush feeding copepods, but variable (II or III) responses in active feeders. We examine reasons for why observed behaviors at times deviate from predictions, and discuss the population dynamics and food web implications of the two types of functional responses and their underlying mechanisms.

Introduction

The functional response in feeding rate to prey concentration is the primary quantification of predator-prey interactions and it has direct implications for population dynamics and stability of both prey and predators (Holling 1965; Murdoch 1977). A type II functional response is typically described by some saturating function of prey concentration in which the parameters (maximum ingestion and prey search rates) are assumed constant. However, the assumption of constant search rate may not be true, and at both low and high prey densities it may be advantageous for the predator or grazer to reduce its food searching effort to minimize its exposure to predators and energetic costs of food acquisition (Abrams 1982, 1990; Werner and Anholt 1993; Visser 2007). At low prey densities, the costs are simply not warranted by the gains and the grazer may reduce or stop searching for prey, which may lead to a sigmoid type III functional response. At high prey densities, feeding rate is limited by digestion rather than by encounter rate and the grazer may therefore reduce its foraging effort. The presence of predators may induce a further reduction in foraging effort, particularly at high prey densities. Reduced feeding efforts at high prey densities, whether due to predation risk or energy saving, will not necessarily change the type of the functional response (i.e., a type II may remain a type II, Abrams 1990), but predator-induced changes in behaviors may cause behavioral cascading effects that are very important in shaping food webs and organism abundances, as has been demonstrated in both terrestrial (Suraci et al. 2016) and freshwater environments (Peacor and Werner 2001; Romare and Hansson 2003; Biro et al. 2005).

Zooplankton, the main consumers of oceanic primary production, may also modify their foraging effort in response to prey concentration and presence of predators with important implications to their function in pelagic food webs. The significance of behavioral adaptations to fundamental properties of pelagic food webs, such as primary production and material fluxes (Anderson et al. 2010), diversity of the phytoplankton prey (Prowe et al. 2012), and the seasonal successions in plankton communities (Visser 2007; Mariani et al. 2013; Visser and Fiksen 2013) has been demonstrated in multiple modelling studies. Yet, actual demonstrations of the behavioral adaptations to prey and predators assumed in these models are rare, particularly in marine zooplankton (Price and Paffenhöfer 1986; Saiz et al. 1993; Saiz 1994; Duren and Videler 1995; Van Duren and Videler 1996). Early zooplankton-specific models of optimal foraging (Lam and Frost 1976; Lehman 1976) were consistent with more general models (Abrams 1982, 1990; Werner and Anholt 1993) in typically predicting reduced feeding effort at low prey concentration, but were based on fundamentally wrong assumptions about the feeding behavior and considered, similar to the more recent model of Pahlow and Prowe (2010), only the energetic costs of feeding, not predation. Finally, experimental studies of functional responses in zooplankton are abundant but are inconsistent in their findings, reporting both type II and type III responses (Online Appendix 1), and without the mechanistic underpinning that is important in assessing the food web effects predicted by models.

Here, we test the predictions of a simple fitness optimization model through direct observations of the behavioral basis of the functional response in pelagic copepods, the dominating group of metazoan zooplankton in the oceans. We consider two contrasting foraging modes: ambush feeding, in which the copepod waits for prey to arrive, and active feeding, in which the copepod generates a feeding current or swims to encounter prey. The active foraging modes are more efficient in terms of prey encounter than the passive mode (Kiørboe 2011). We demonstrate that ambush feeders consistently have invariant foraging behavior and type II responses, while active feeders may modify their foraging effort in response to prey concentration and predation risk and have a type III response, but that the predation response is “hard-wired” and not plastic.

Material and methods

Fitness optimization model

We take a Holling type II functional response as a starting point:

$$F = F_{max} \frac{\beta R}{\beta R + F_{max}} \tag{1}$$

where F is the ingestion rate and F_{max} the maximum ingestion rate (biomass per time), R is the prey concentration (biomass per volume), and β is the 'instantaneous rate of prey discovery' or maximum clearance rate (volume per time). Assume that the zooplankter feeds only a fraction of the time, p (non-dimensional foraging effort), and that p vary in response to food availability and predation risk in order to optimize the zooplankter's fitness. The foraging effort, p, modulates the effective clearance rate ($p\beta$) and the resulting functional response becomes (Werner and Anholt 1993):

$$F(p) = F_{max} \frac{p\beta R}{p\beta R + F_{max}} \tag{2}$$

Note that if feeding rate is ultimately limited by handling of the prey during the capture process (with $1/F_{max}$ being the "handling time"), as is typically assumed (Abrams 1982; Abrams 1990; Pahlow and Prowe 2010) the resulting functional response then becomes proportional to foraging effort:

$$F(p) = F_{max} p \frac{\beta R}{\beta R + F_{max}} \tag{3}$$

However, in suspension feeding zooplankton and many other organisms, the handling of prey is rarely, if ever, the limiting factor (Tiselius et al. 2013). Rather, ingestion is limited by the capacity of the gut to process food, and the appropriate equation in our case is therefore (2) and not (3).

We now examine what foraging effort (p) optimizes the fitness of the zooplankter when considering the energetic cost as well as the predation risk of feeding. To estimate energetic (metabolic) expenses and mortality risk, we assume

$$\text{Metabolism } M(p) = m_0 + pm_f \tag{4}$$

$$\text{Mortality } \mu(p) = \mu_0 + p\mu_f \tag{5}$$

where m_0 and μ_0 are background metabolism (mass per time) and mortality (per time), and m_f and μ_f are metabolic costs and mortality risk of feeding, respectively. There is both theoretical and experimental evidence that mortality risk increases with foraging activity in zooplankton (Tiselius et al. 1997, Kiørboe et al. 2014; Almeda et al. 2016). The interpretation of p as the fraction of time spent feeding makes it natural to assume a linear dependence of foraging metabolism and predation mortality risk on p.

The optimal behavior is the one that optimizes life-time reproductive output. To avoid a full life-time calculation, two different fitness proxies are frequently used: either to optimize the difference between birth ($\propto$ net energy gain, $F(p) - M(p)$) and mortality rates (e.g. Abrams 1982, 1990), or the ratio between the two (behavioral optimization; e.g. Werner and Anholt 1993; Visser 2007; Gillam's rule: Gilliam and Fraser 1987). If the environment is constant, it has been demonstrated that Gillam's rule optimizes life-time reproductive output (Sainmont et al. 2015). We therefore use Gillam's rule as a fitness proxy. However, a special case occurs when the resource levels are insufficient to ensure a positive net energy gain, where $F - M < 0$. In that case survival is limited and life-time reproductive output would be less than zero. We argue that under such adverse prey conditions the organism will adjust its behavior to maximize the time it can survive by minimizing energy losses. Thus, under low resource concentration the fitness proxy is to minimize the net energy loss. The two fitness proxies are now:

$$\frac{F(p)-M(p)}{\mu(p)} \quad \text{for} \quad F-M \geq 0$$

(6)

$$F(p)-M(p) \text{ for } F-M<0 \qquad (7)$$

The optimal value of p is the one that maximizes the relevant fitness criterion. For the specific choices of functional response (2) and linear costs of metabolism (4) and mortality (5), the optimal foraging effort is:

$$p^* = \frac{1}{\rho}\frac{f_c(m-\mu)-\sqrt{\rho\mu - f_c(\rho-\mu)(\mu-m)}}{f_c(\mu-m)-\mu} \quad \text{for } F-M \geq 0, \qquad (8)$$

where $\rho = R\beta/F_{\max}$ is the scaled resource concentration, $f_c = m_0/F_{\max}$ is scaled standard metabolism and $m = m_f/m_0$ and $\mu = \mu_f/\mu_0$ are scaled costs of feeding. This expression shows that foraging effort generally declines with resource concentration (the $1/\rho$ term). Feeding is, however, limited by the condition that p^* should be ≤ 1 (Fig 1A).

The critical resource concentration R_c, where gains equal losses even while feeding all the time ($p=1$), is found by equating gains from eq. (2) with metabolic losses from eq. (4), $F(1)=M(1)$:

$$R_c = \frac{F_{max}(m_0+m_f)}{F_{max}-m_0-m_f}\frac{1}{\beta}\,. \qquad (9)$$

Below this concentration the functional response is approximately linear, $F \approx p\beta R$ and, hence, the optimization problem (7) is linear. The organism will then feed continuously ($p=1$) as long as the net energy loss is less the loss while not feeding, i.e., $F(1)-M(1) > -M(0) = -m_0$:

$$R_0 \approx \frac{m_f}{\beta}. \qquad (10)$$

Note that this result is general, i.e., it does not rely on the cost of feeding effort being linear in p (eq. 4) since m_f is the feeding cost of feeding at the maximal rate. Using these fitness measures and depending on the magnitude of the tradeoffs, the model predicts that feeding effort (*p*) is highest at intermediate prey concentrations, and declines at both lower and higher concentrations (Fig. 1A), which results in a type III functional response (Fig 1C). It also predicts that the feeding effort is further reduced in the presence of predators (compare black and grey lines). Specifically, for an ambush feeder, since $\mu_f = m_f = 0$ we would not expect a feeding threshold but predict that $p = 1$ and independent prey concentration and, hence, a type II functional response (dashed lines in Fig. 1).

Note the difference between the realized clearance rate ($\neq \beta$), which is $F(p)/R$, and the foraging effort, *p* (Fig. 1B). Both may vary with resource concentration: At low resource concentrations, they show similar dependencies on the resource (the clearance rate = $F(p)/R \approx p$); at high resource concentration, the clearance rate varies with $1/R$, independent of the variation in *p*. This follows directly from the optimization and equation (2).

Parameter estimates: Based on observations in Kiørboe et al. (1985) we provide rough estimates of F_{max} (0.65 µg C (µg dry body weight)$^{-1}$d^{-1}), β (1.65 mL (µg dry body weight)$^{-1}$d^{-1}), m_0 (0.015 µg C (µg dry body weight)$^{-1}$d^{-1}), and m_f (0.1 µg C (µg dry body weight)$^{-1}$d^{-1}) for one of the study species, *Acartia tonsa,* feeding on one of the prey, *Rhodomonas baltica*. The two metabolic rate estimates were taken as starvation metabolism (m_0) and maximum metabolism (m_f) of feeding individuals, respectively. The latter includes also the cost of processing and metabolizing the food and we added also losses to defecation, which are not strictly 'costs of feeding'. We have no estimates of mortality rates for the study species but assume $\mu_0 = \mu_f = 0.05$ d^{-1}. This implies a mortality rate of ~ 0.1 d^{-1} for a small, feeding copepod in the ocean, a magnitude typical for mm-sized feeding-current feeding copepods (Hirst and Kiørboe 2002).

The predictions of this model of optimal foraging, as illustrated in Fig. 1, are the hypotheses that we test experimentally here.

Experimental organisms

We quantified feeding behavior and feeding rate as a function of prey concentration in the adult females of 4 species of copepods: an ambush feeder, *Oithona davisae* (cephalothorax length 0.3 mm), a copepod that can switch between ambush and active feeding, *Acartia tonsa* (0.8 mm), and two species that are obligate active feeders, *Temora longicornis* (0.8 mm) and *Centropages hamatus* (1.0 mm). *A. tonsa* generates a feeding current when offered small prey, and acts as an ambush feeder when offered large, motile prey (Jonsson and Tiselius 1990). All copepods were taken from our continuous cultures; the two first species were from our long-term cultures (> 10 years), the latter two had been in culture for < ½ year. We used three different types of prey, the flagellate *Rhodomonas baltica* (6.5 µm equivalent spherical diameter) and the dinoflagellates *Oxyrrhis marina* (16.5 µm) and *Akashiwo sanguinea* (42 µm), all in exponential growth. We did not do all possible predator-prey combinations, and some data were taken from our earlier work (Table 1).

Measures of foraging effort

The active feeders beat their cephalic appendages to generate a feeding current and/or to propel themselves through the water during shorter or longer ‘feeding bouts’ (Tiselius and Jonsson 1990) and we used the fraction of time that the organism beats the appendages as the main measure of foraging effort, but note that some minimum beat-activity may be necessary to keep the copepod suspended, irrespective of feeding. Additional, but secondary measures of foraging effort are appendage beat frequency and swimming speed. The interpretation of swimming speed is not straightforward, because with a given beat frequency (~ force), a hovering copepod feeds more efficiently than one that cruises through the water, but it also produces a stronger fluid signal and becomes more detectable to rheotactic predators (Kiørboe and Jiang 2013). The ambush feeding O. *davisae* only moves the cephalic appendages in connection with prey capture, but relocates occasionally in short, rapid jumps using the swimming legs (Kiørboe et al. 2009); in this species there is no foraging effort and, hence, no measure of foraging effort, but we recorded jump frequency as a measure of activity.

Feeding behavior

Adult females were isolated from the cultures and starved overnight. 50 individuals were then added to each observation aquaria (250 mL NUNC bottles) containing fresh food suspension and acclimated for 2 h before filming commenced. We used seven different food concentrations for each prey, including no food (Table 1), selected to yield similar prey biovolume ranges for each prey (~ 0-5 mm^3 L^{-1}). Prey concentration was adjusted just prior to filming. We used a high-speed (200 fps), high resolution (1280 x 800 pixels) Phantom v210 camera equipped with optics to yield fields of view ranging between ca. 20x32 and 52x78 mm depending on the size of the copepods. Collimated infrared light was shined through the aquarium toward the camera. Three 27 s sequences were filmed during a 15 min period for each treatment. The water in the aquaria was then replaced with water containing fish smell (see below) and the appropriate prey concentration, and after 5 min the animals were filmed again during the subsequent ca. 15 min.

Swimming trajectories were extracted from the movies using the tracking software LabTrack (DiMedia). The movies were analyzed both at 20 Hz to construct time budgets (fraction of time feeding) and estimate event durations (feeding bouts) and speeds (swimming speed), and at 33 or 67 Hz to estimate jump frequencies. Between 20 and 150 tracks were analyzed per treatment; in a few cases we retrieved only 10 tracks. The output from the tracking analyses were run through an R-script that distinguished between jump, sinking, and swimming events based on species-specific thresholds that were selected to match what a manual frame-by-frame analysis would yield, but the patterns observed were very robust to choice of thresholds. We finally also estimated appendage beat-frequencies in 1-s long sequences by frame-by-frame analyses of 20 random, active animals per treatment.

Exposure to predation risk

Predation risk was mimicked by the addition of fish smell to the observational aquaria. Fish smell was produced by a mixture of small, coastal planktivorous fish: juveniles of corkwing (*Symphosus melops*), sea stickleback (*Spinacia spinachia*), and black goby (*Gobius niger*) that had all been feeding on copepods. 13 g wet weight of this costal fish assemblage were incubated in 2-L of filtered seawater for > 2 h. This water was then filtered through a GF/C filter and diluted to 50 % by adding an algal suspension of twice the nominal concentration, thus having a fish smell solution with the nominal phytoplankton concentration. Effect of fish smell was only tested with *R. baltica* as prey.

Functional response

All functional responses were measured in our laboratories, either for the purpose of this study or earlier (Table 1), and followed the same protocol: Adult females were incubated in 325-650 mL bottles at 5-6 different prey concentrations with 3 bottles with copepods and 3 controls at each concentration. The bottles were mounted on a slowly rotating wheel for ca. 24 h at ~17ºC. *O. davisae* were incubated at 21ºC and we had only two 72-mL bottles with copepods and two control at each concentration. We added enough copepods to get a reduction in phytoplankton concentration of ~25 % during the incubation period. Cell concentrations were measured both at start and termination of the experiments, and clearance and ingestion rates were computed as in Kiørboe et al. (1982). Cell concentrations were either measured electronically on a Coulter Counter and in most cases also in the microscope. At low prey concentrations electronic counts were always verified by microscopic counts.

We fitted functional response functions to the observed ingestion rates, either the disc equation (eq. 1) or a descriptive sigmoid equation (Kiørboe et al 1982):

$$F = \alpha\beta e^{1-\alpha/R} \quad , \qquad (11)$$

where α is the prey concentration where the clearance rate is the highest and equals β, and the maximum ingestion rate $F_{\max} = \alpha\beta e^{1}$. We also fitted the same functional response functions expressed as clearance rates (F/R) to the estimated clearance rates. We decided on the most appropriate description of the functional response (type II or III) based on (i) whether or not observed clearance rates decline at low prey concentrations, and (ii) which formulation yielded the best description (highest R^2).

Literature survey

Expanding on the data base of Kiørboe and Hirst (2014) we compiled from the literature experimental observations of functional responses in marine suspension feeding copepods offered a variety of prey sizes (Online Appendix 1). We used the measured clearance rates to decide on the shape of the functional response type, cf. above. We also computed maximum clearance rates (β) and maximum ingestion rate (F_{max}) for each data set, either by using the functional response fits in the original paper or by our own fits to the data after correcting for differences in temperature, all as described in Kiørboe and (Hirst 2014). In some cases only maximum clearance rates were reported. We finally computed the feeding and maintenance thresholds, R_0 (only species with active foraging behavior) and R_c for each dataset using equation 9 and 10 and the computed maximum clearance and ingestion rates and assuming the above default values for the mass-specific metabolism (m_0) and mass-specific metabolic cost of feeding (m_f). We find the latter assumptions justified by the fact that both metabolism and clearance scale approximately in proportion with body mass in zooplankton (Kiørboe and Hirst 2014), and that the metabolic cost of feeding is likely to be proportional to the clearance rate.

Results

Feeding behavior and functional response

The behavioral responses to prey concentration varied significantly between copepod species and was also dependent on the prey type (Figs. 2-4, Table 2). The most diverse behavioral repertoire is shown by *A. tonsa*. This copepod beats its feeding appendages to generate a feeding current during feeding bouts each lasting between ca. 0.2-0.8 s on average (Fig. 2D); between feeding bouts it is inactive and sinks slowly. When offered the small flagellate (*R. baltica*) its foraging effort varied with prey concentration pretty much as predicted by the optimization model (with predation): the highest feeding effort (~80 %) is at an intermediate prey concentration and it declines at both higher and lower concentrations (Fig. 2A, 2B). There is no distinct feeding threshold and even in filtered seawater the animals are active for ~25 % of the time, probably simply to remain suspended. This is accomplished by frequent, but short-lasting feeding bouts, whereas the longer feeding bouts at intermediate concentration mainly serve the purpose of feeding (Fig. 2D). Swimming speed shows an inverse pattern with the slowest speeds at intermediate concentrations (Fig. 2E), while appendage beat frequency was independent of prey concentration and only reduced in the absence of food (Fig. 3A). The patterns in these two secondary foraging effort measures thus also suggest the most efficient and potentially most risky feeding behavior at intermediate concentrations and declining at both higher and lower concentrations. There is no significant effect on the behavior of adding fish smell (Fig. 2A, D, E).

The measured functional response in clearance rate of *A. tonsa* to the concentration of *R. baltica* showed peak clearance at an intermediate prey concentration and lower clearance at both lower and higher resource concentrations (Fig. 2C). This translates directly to a type III sigmoid functional response in ingestion rate to prey concentration (Fig. 2F), and the observed functional response is thus consistent with the observed variation in foraging effort.

When *A. tonsa* is offered large motile prey (*Ox. marina* and *Ak. sanguinea*) it changes its behavior and functional response compared to when offered the small *R. baltica* prey in a way that is consistent with a change in foraging mode from feeding-current feeding to ambush feeding (Fig. 4). This is most evident with the largest prey (*Ak. sanguinea*): The feeding bouts are short and the foraging effort remains low, independent of prey concentration, and not different from a situation with no prey (Fig. 4B); the 'feeding bouts' thus mainly serve to keep the animal suspended while waiting for prey to pass within its sensory reach. With the intermediately sized prey (*Ox. marina*), the behavioral changes with prey concentration are intermediate between that observed with the smaller and the larger prey (Fig. 4D,E), suggesting partial active and partial passive feeding. The functional response in clearance and ingestion rates when offered the largest prey (*Ak. sanguinea*) is of type II (Fig. 4 C, F), and thus consistent with the observed behavior.

None of the 3 other copepod species showed consistent behavioral changes with prey concentration, prey type, or presence of fish cues except that appendage beat frequencies were slightly reduced at the lowest prey concentrations (Fig. 3) and that *C. hamatus* jumps more frequently when offered the large prey as compared to the small prey (Table 2). In a few cases small differences in the other parameters are statistically significant, but the patterns are inconsistent (Table 2; all data are plotted in Online Appendix 2). Consistent with the concentration-independent behavior, all predator-prey combinations for the 3 species showed a type II functional response (Online Appendix 2). This was unexpected, since type II responses were *a priori* only predicted for the ambush feeding *O. davisae*.

The behavior and foraging effort of the 4 studied species are, however, very different (Table 2). *T. longicornis* is actively beating its feeding appendages almost constantly while cruising or hovering, whereas *C. hamatus* has a feeding behavior that resembles that of *A. tonsa*, i.e., alternating between short upwards-directed feeding bouts (~ about 50 % of the time) and sinking with occasionally longer swimming events, although in this species the pattern is invariant with prey concentration. Finally, the ambush feeding *O. davisae* never beats the feeding appendages but just performs relocation jumps every 2-3 s (Table 2).

Comparison between modelled and observed responses

For actively foraging *A. tonsa* the modelled pattern in foraging effort describes both qualitatively and quantitatively very well the observations, but only when predator presence is assumed (Fig. 2C). This resemblance to observations is robust to at least a ± 50 % variation in the magnitude of the default parameters. However, in the absence of a foraging induced predation risk the predicted foraging effort remains 100% at concentrations exceeding the feeding threshold. A decline in foraging effort with increasing prey concentration and in the absence of predators is only predicted to occur at very high prey concentrations, > 6 mm^3L^{-1}, far beyond what is examined here and typically found in the ocean, and a pattern in foraging effort that resembles the observed pattern is never achieved with any combination of parameters (Fig. 2C).

For passively feeding *A. tonsa* (i.e. when fed *Ak. sanguinea*) and *O. davisae* the prey concentration-invariant foraging behavior and type II responses are consistent with model predictions (Fig. 4 and Table 2), while the invariant foraging behavior of actively feeding *T. longicornis* and *C. hamatus* (Table 2) deviated from the expected (i.e. adaptive foraging effort and type III response).

Feeding and maintenance thresholds

The predicted concentration threshold, R_c, where the net energy gain is zero, is a minimum measure of the lowest prey concentration at which the copepod is able to survive in the long run, whether or not it stops feeding at the lower concentration R_0. For ambush feeders there is no feeding threshold ($R_0 = 0$), and for active feeders the two thresholds are related and rather similar (using default parameters, $R_c = 1.4 \times R_0$). Both thresholds were computed to be able to utilize a larger number of observations. The feeding and maintenance thresholds vary over several orders of magnitude and scatter around a phytoplankton concentration of ~ 1 $mm^3 L^{-1}$, corresponding to ~100 µg C L^{-1}, and not very different between active and passive feeders (Fig. 5A, B). The thresholds are dependent on the size of the prey relative to the size of the copepod: with small relative prey sizes the feeding and maintenance threshold are high, and *vice versa* (Fig. 5 C, D)

Discussion

Mechanistic underpinning of the functional response

Overall, there is consistency between the observed feeding behaviors and the measured functional responses for all predator-prey combinations examined here, and the former thus provides a mechanistic underpinning of the latter. We found both type II and type III functional responses among the copepods studied, partly in agreement with the predictions from the optimization model. Type III responses may arise in several ways, including through prey switching in mixed diet environments (Murdoch and Oaten 1975; Elliott 2004; Leeuwen et al. 2007), but here we show that the type III is due to a change in foraging effort with prey concentration. We are unaware of previous reports that provide a direct behavioral underpinning of the observed functional response in copepod or other zooplankton although there are a few studies that have examined how relevant components of feeding behavior vary with prey density. For example, the copepod *Eucalanus* *elongates* spends the highest fraction of time feeding at intermediate prey concentrations, (Price and Paffenhöfer 1986) and a previous study of *A. tonsa* showed that, similarly to clearance rates, the time spent in long feeding bouts peaked at intermediate concentrations of a small diatom (Saiz 1994), consistently with our finding. There are also reports that the copepod *Temora longicornis* modifies its swimming speed (Duren and Videler 1995; Van Duren and Videler 1996; Moison et al. 2013) or appendage beat frequency (Gill and Poulet 1988) in response to concentration of food or presence of dissolved amino acids or predators. We are unaware of studies in other zooplankton groups. The scarcity of such evidence hampers a complete understanding of the role of zooplankton in pelagic food webs.

Functional response

Both type II and III functional responses have previously been reported for pelagic copepods, and a survey of ~ 120 functional response experiments reported in the literature (Online Appendix 1) reveals that ambush feeding copepods consistently show type II responses (43 experiments) as predicted, while active cruising or feeding-current feeding species either showed a type II (45 cases) or a type III response (30 cases). The latter result is consistent with the finding here of variable responses in the active feeders. For at least 21 out of the 45 reported type II responses in active feeders, prey concentrations lower than the predicted feeding threshold were not tested and consequently those experiments are inconclusive with respect to the actual type of functional response (see Online Appendix 1). Moreover, clearance measurements at low prey concentrations, where a type III response is best distinguished from a type response II, can be challenging, and some of the reports may not provide very strong evidence for the type of response. For this reason, in our experiments we intentionally examined behaviors also at very low prey concentrations, including the absence of prey, and still found high foraging effort at low and no prey in two species. We must therefore conclude that the observed differences among species are real and that some active feeders, contrary to our expectations, have a high resource-independent level of foraging activity and a type II functional response.

What causes the deviation from prediction in some species? Swimming in active feeders is accomplished by the beating of the feeding appendages and the need to swim to areas with more food or fewer predators may override other effects, a tradeoff that has not been considered here and that may vary between species. Kinetic motility responses to prey concentration has been reported in copepods (Tiselius 1992) and other zooplankters (Buskey and Stoecker 1988; Fenchel and Jonsson 1988; Menden-Deuer and Grünbaum 2006), thus potentially explaining why several active feeders appear to have no lower feeding threshold and type II functional responses.

Induced responses and phenotypic plasticity

None of the three examined species showed a response to the presence of a predator cue, and the reduced foraging effort at high prey concentrations demonstrated in one species (*A. tonsa*) occurred both in the absence and presence of predator cues. This suggests limited behavioral plasticity and that any adaptation to predation risk is wired into the genes of *A. tonsa* rather than being triggered in response to the actual presence of predators. One may argue that a copepods susceptibility to visual predators (fish) is less dependent on the feeding activity than its susceptibility to rheotactic predators, but it is well documented that feeding copepods are much more prone to visual predators than non-feeding individuals due to the elevated visual contrast that a full gut implies in an otherwise near transparent copepod (Tsuda et al. 1998; Torgersen 2003). Thus, a fish cue seems to be relevant.

The lack of a response to predator cues is surprising in light of the commonly documented effect of predator kairomones in freshwater zooplankton, including induction of reduced feeding efforts in freshwater copepods (see reviews by Lass and Spaak 2003; Heuschele and Selander 2014). Our protocol to produce chemical fish cues appear not to deviate from what is typically used in freshwater studies. One may argue that the overnight starvation of the copepods and the only 2 h acclimation to prey concentration prior to behavioral observations may lead to a more bold behavior of the copepod, where the need for food dominates over predator avoidance behavior. Indeed, starvation may result in significantly increased feeding in *Acartia* spp, but the effect is reduced or has disappeared within 100 min of feeding(Tiselius 1998), consistent with gut turnover times at the experimental temperature of just 20-25 min (Kiørboe and Tiselius 1987; Dam and Peterson 1988) allowing the animals to fill their guts 5-6 times during the acclimation period. Also, predator avoidance behavior is in fact observed in *A. tonsa* at the high prey concentrations. The lack of response to cues in our experiments is, however, consistent with the almost entirely lack of reports on behavioral effects of kairomones in marine zooplankton and copepods. Thus, Buskey et al. (2012) in a review failed to find evidence of predator-induced responses for marine zooplankton, and only three studies were identified in the review by Heuschele and Selander (2014) in addition to Bjærke et al. (2014), of which only two report effects on feeding-related behavioral changes (reduced swimming speed or reduced gut fullness with predator cues (Van Duren and Videler 1996; Cieri and Stearns 1999). There is also one report that diurnal vertical behavior can be induced by the presence of fish, but the cue that elicited the response was not identified, except that it was not of chemical nature (Bollens and Frost 1989). The literature may be biased towards negative results not being reported, and therefore the scarcity of evidence may thus reflect rarity of responses at ecological time scales. Freshwater systems, in particular smaller lakes and ponds, may vary with respect to the presence of fish predators, while marine systems are all large and interconnected and, hence, always contain planktivorous fish. Thus, adaptations to predator avoidance is commonly found among marine zooplankton, including vertical migration (Ringelberg 2010; Ohman and Romagnan 2016) and reduced feeding during daytime to reduce susceptibility to visual predators (review by Torgersen 2003), but they are typically elicited by light intensity (Stearns 1986; Buskey et al. 1989) or some other proximate cue, not by the actual presence of predators. The apparent lack of phenotypic plasticity may simply reflect the constant need for a behavior that reduces predation risk.

Ecological implications

The functional response in feeding rate to prey concentration provides the fundamental description of predator-prey interactions and thus is fundamental to the understanding of population dynamics and food web structure in several ways. First, a type III functional response may stabilize prey populations due to the density-dependent prey mortality that it implies, while a type II response may drive the prey population to (local) extinction (Holling 1965). The often significant impact of the choice of functional response type in models of both simple pelagic food chains and more complex food webs has been recognized by many authors (Anderson et al. 2010) and ‘‘inappropriate choices may incorrectly quantify biologically mediated fluxes and predict spurious dynamics” (Gentleman et al. 2003). This realization warrants the search for a fundamental understanding of the mechanisms that are generating one functional response or another to allow the ‘correct’ choice. The attempt in this study to find such ‘rules’ for a very important group of phytoplankton consumers has been partly successful and has demonstrated the utility of optimal foraging theory in this endeavor. However, it has also pointed to gaps in our understanding and identified possible additional mechanisms, particularly kinetic motility responses, which may lead to more robust predictions of the functional response in copepods and other zooplankton.

Secondly, the behavior that generates the functional response may have implications beyond prey mortality and grazer growth rates. Specifically, behavioral adaptations to the presence of predators (or their cues) may lead to a behavioral cascade and a ‘landscape of fear’ (Suraci et al. 2016), where grazing and growth rates are determined as much by the presence of predators as by the availability of food, as demonstrated in freshwater zooplankton (Gliwicz and Maszczyk 2007) and many other organisms. The scarcity of predator-induced behavioral responses in copepods and other marine zooplankton suggests that ‘behavioral cascades’ are less important in controlling marine planktonic systems than what has been demonstrated for higher trophic levels in freshwater systems (Romare and Hansson 2003; Biro et al. 2005) and assumed in models (e.g., Visser 2007).

Finally, the dependency of the maintenance resource concentration on the prey:predator size ratio, which is a function of the copepod prey size spectra (Kiørboe 2016), suggests that environmental food conditions may put predictable constraints on the size distribution and biogeography of copepods. Thus, the smaller the relative size of the prey, the higher the required prey concentration, and therefore large copepods are constrained to regions with high concentration of large (phytoplankton) prey. This prediction accords well with observed body-size biogeographies of copepods, where the larger species occur in polar and temperate regions characterized by seasonal high concentrations of large diatoms; and smaller species dominate in tropical and subtropical regions, characterized by lower biomasses of small phytoplankton (Brun et al. 2016). Because maximum clearance rates and metabolic rates scale approximately in proportion to body mass when considered over the entire range of pelagic organisms in the ocean (Makarieva et al. 2008; Kiørboe and Hirst 2014), and assuming that the cost of clearing water for food is proportional to the volume cleared, this prediction may be generalized to zooplankton in general, not just copepods.

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FIGURE LEGENDS

Fig 1. Foraging patterns as a function of scaled resource concentration. Three cases are shown: foraging constant with $p = 1$ (dashed); optimal foraging under no predation risk ($\mu_f = 0$, $\mu_0 = 0.05$ d^{-1}, grey); optimal foraging under a predation risk ($\mu_f = \mu_0 = 0.05$ d^{-1}, black full line). A) Foraging effort, p. B) Realized clearance rate normalized by maximum clearance rate. C) The functional response in ingestion rate normalized by the maximum ingestion rate ($F_{\max}$).

Fig. 2. *Acartia tonsa* feeding on *Rhodomonas baltica* as a function of cell density in the presence and absence of fish cues. A. Foraging effort (% time swimming); D. Feeding bout duration; C. Modelled foraging effort at various values of predator induced mortality risk and metabolic costs of feeding. The black line is for the default parameters estimated from (Kiørboe et al. 1985); E. Swimming speed; C and F. Observed clearance and ingestion rates, from Kiørboe et al. (1985); The curves are fits of a type III functional response model to the data with $\alpha = 0.58 \pm 0.04$, $\beta = 12.4 \pm 0.6$, and $R^2 = 0.83$ (panel B), and $\alpha = 0.561 \pm 0.04$, $\beta = 12.1 \pm 0.6$, and $R^2 = 0.98$ (Panel F) (estimates of coefficients with standard error). Experimental values are given as averages ± 95 % Confidence limits.

Fig. 3. Beating frequencies (average ± 95 % confidence limits) of feeding appendages as a function of prey concentration in 3 species of copepods. A. *A. tonsa* feeding on *R. baltica*. B. *C. hamatus* feeding on *R. baltica*; C. *C. hamatus* feeding on *Ak. sanguinea*. D. *T. longicornis* feeding on *R. baltica*. Averages ± 95 % confidence limits.

Fig. 4. *Acartia tonsa* feeding on and *Akashiwo sanguinea* (A-C, F) and *Oxyrrhis marina* (B, D) as a function of prey density. A and D: Foraging effort (% time swimming); B and E: Duration of individual feeding bouts; E and F: Observed clearance and ingestion rates and (curves) Hollings disk equation fitted to the data, with $F_{\max} = 22.3 \pm 12.8$, $\beta = 23.5 \pm 4.6$, and $R^2 = 0.30$ (panel C), and

$F_{\max}$ = 11.6 $\pm$ 2.4, β =46.6$\pm$32.7, and R^2 = 0.28 (panel F). Values of behavioral parameters are given as averages $\pm$ 95 % Confidence limits; clearance and ingestion rates are individual values (grey) and averages (black).

Fig. 5. Feeding thresholds (R_0) and maintenance threshold (R_c) estimated for pelagic copepods with a 'active' (black symbols) and 'passive' (grey symbols) feeding strategies. Maximum clearance (β) and ingestion (F_{max}) rates were estimated from literature data on functional responses (see Online Appendix 1), and we assumed body mass specific metabolic cost of feeding of (m_f = 0.1 µg C (mg dry body weight)$^{-1}$d^{-1}) ~ 0.01 µg C (mg body C)$^{-1}$ h^{-1}) identical to that estimated for *A. tonsa*. A: Frequency distribution of feeding thresholds threshold for active feeders; B: Frequency distribution of maintenance thresholds for active and passive feeders; C: Feeding threshold as a function of the prey:predator carbon-mass ratio for active feeders; the regression line is log (R_0) = -1.1 – 0.22 Log (prey:predator mass ratio); R^2 = 0.35, n = 182; D: Maintenance thresholds as a function of the prey:predator carbon-mass ratio for active and passive feeders; the regression line is log (R_0) = -1.0 – 0.18 Log (prey:predator mass ratio); R^2 = 0.19, n = 209.

Species of grazer\prey	*Rhodomonas baltica*	*Oxyrrhis marina*	*Akashiwo sanguinea*
Prey size, Equivalent spherical diameter, µm	6.5	16.5	42
Acartia tonsa	Behavior: this study Functional response: Kiørboe et al. (1985)	Behavior: this study	Behavior: this study Functional response: This study
Temora longicornis	Behavior: this study Functional response: Gonçalves et al. (2014)		
Centropages hamatus	Behavior: this study Functional response: Sommeren-Greve et al. unpublished		Behavior: this study Functional response: Sommeren-Greve et al. unpublished
Oithona davisae		Behavior: this study Functional response: Saiz et al. (2003)	

Table 1: Predator-prey combinations examined for feeding behavior and functional responses.

Predator-Prey	# tracks	Total time, s	% Active	Swim speed, mm s^{-1}	Bout duration, s	Jump frequency, s^{-1}
Acartia-Oxyrrhis	292	3052	Fig. 3	1.4 ± 0.1	Fig. 3	0.68 ± 0.09
Acartia-Akashiwo			Fig. 3	1.7 ± 0.1	Fig. 3	0.75 ± 0.07
Temora-Rhodomonas	163	1235	96 ± 1.7	1.7 ± 0.1	3.3± 0.5	0.12 ± 0.05
Temora-Rhodomonas +Fish	206	1116	94 ± 1.2	1.9 ± 0.2	2.6 ± 0.3	0.16 ± 0.06
Centropages-Rhodomonas	442	2263	50 ± 2.5	3.0 ± 0.1	0.6 ± 0.1	0.01 ± 0.01
Centropages-Rhodomonas + Fish	482	2235	48 ± 2.5	3.1 ± 0.1	0.6± 0.1	0.00 ± 0.00
Centropages-Akashiwo	809	4654	43 ± 1.3	3.8 ± 0.1	0.3 ± 0.02	0.11± 0.03
Oithona davisae	163	2101	0	-	-	0.39 ± 0.07

Table 2. Summary statistics of behaviors for copepod-prey (± Fish) combinations where behavior is (near) independent on prey concentration and prey type. Values given are averages ± 95 % Confidence limits. All the data have been plotted in Online Appendix 2.

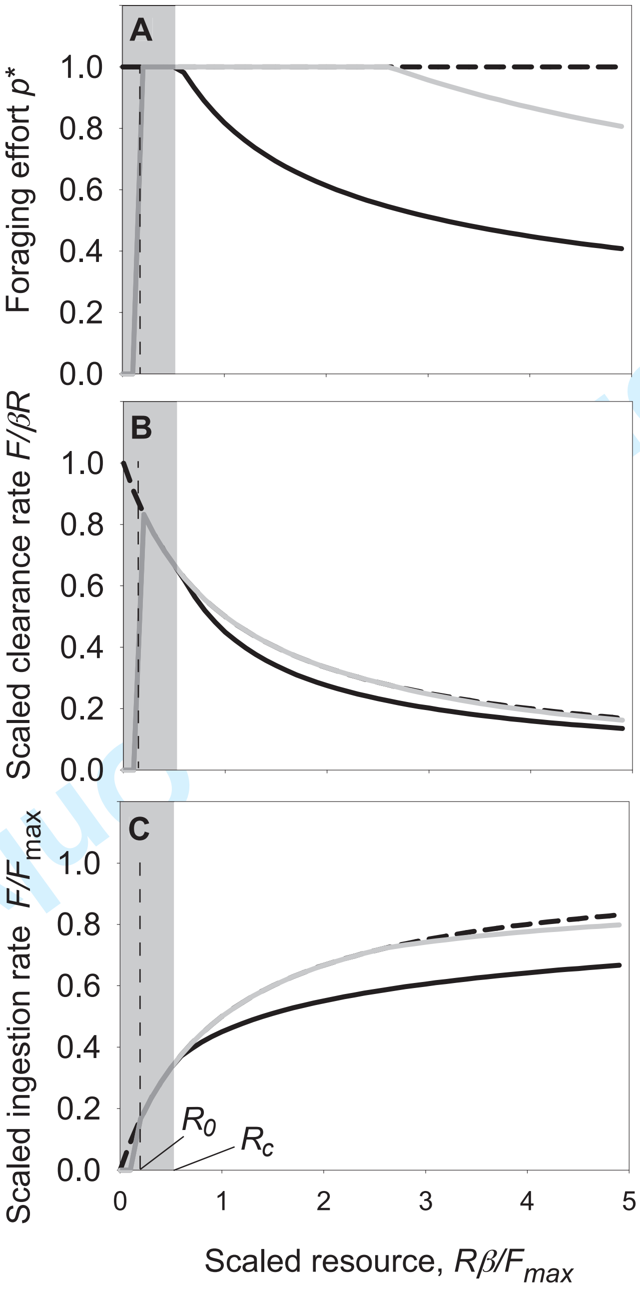

A
Foraging effort p^*
1.0
0.8
0.6
0.4
0.2
0.0
B
Scaled clearance rate $F/\beta R$
1.0
0.8
0.6
0.4
0.2
0.0
C
Scaled ingestion rate F/F_{max}
1.0
0.8
0.6
0.4
0.2
0.0
R_0
R_c
0
1
2
3
4
5
Scaled resource, $R\beta/F_{max}$

Fig. 1

Fig 2

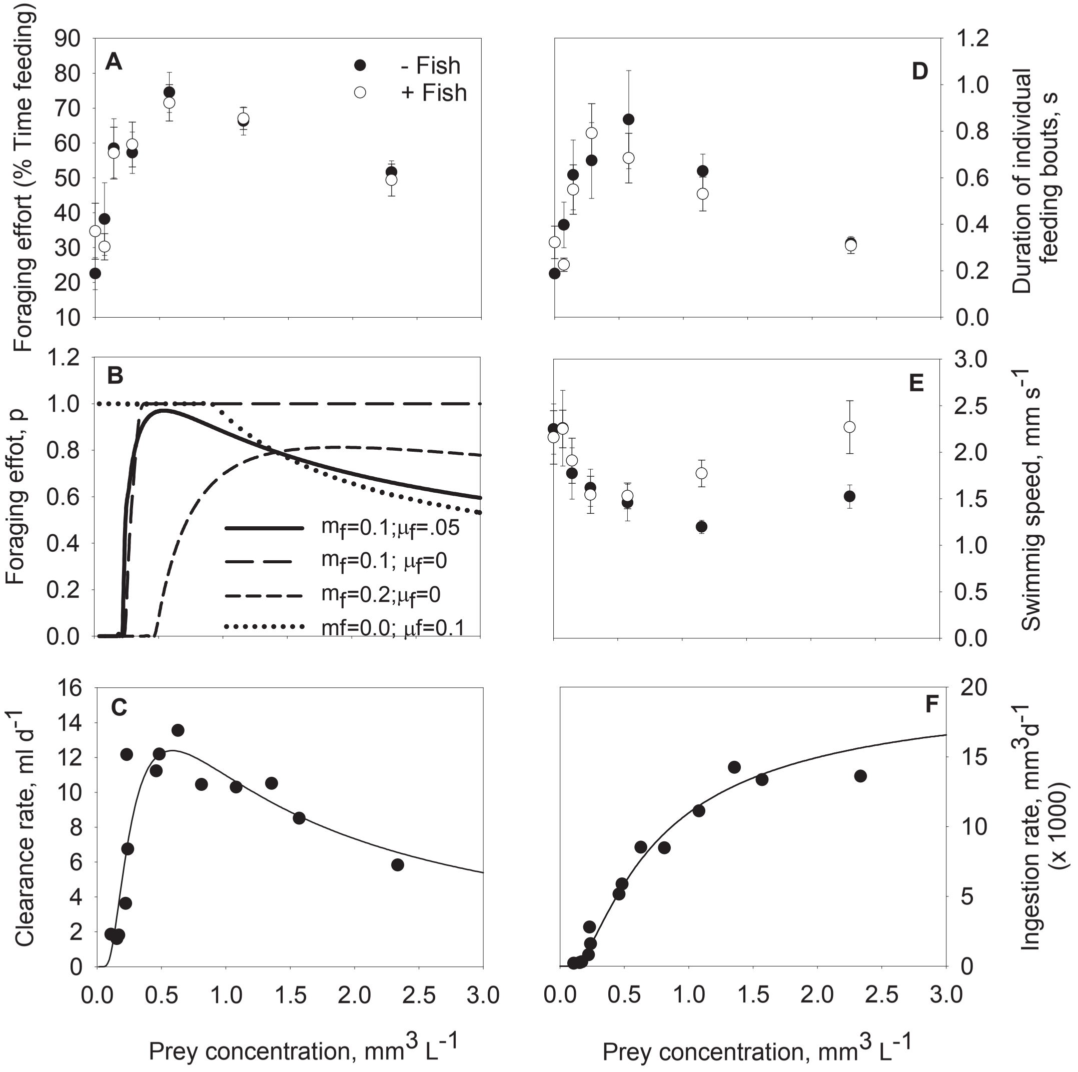

A
- Fish
+ Fish
Foraging effort (% Time feeding)
90
80
70
60
50
40
30
20
10
B
Foraging effot, p
1.2
1.0
0.8
0.6
0.4
0.2
0.0
m_f=0.1;μ_f=.05
m_f=0.1; μ_f=0
m_f=0.2;μ_f=0
mf=0.0; μf=0.1
C
Clearance rate, ml d^{-1}
16
14
12
10
8
6
4
2
0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Prey concentration, mm^3 L^{-1}
D
Duration of individual feeding bouts, s
1.2
1.0
0.8
0.6
0.4
0.2
0.0
E
Swimmig speed, mm s^{-1}
3.0
2.5
2.0
1.5
1.0
0.5
0.0
F
Ingestion rate, mm^3d^{-1} (x 1000)
20
15
10
5
0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Prey concentration, mm^3 L^{-1}

Fig. 3

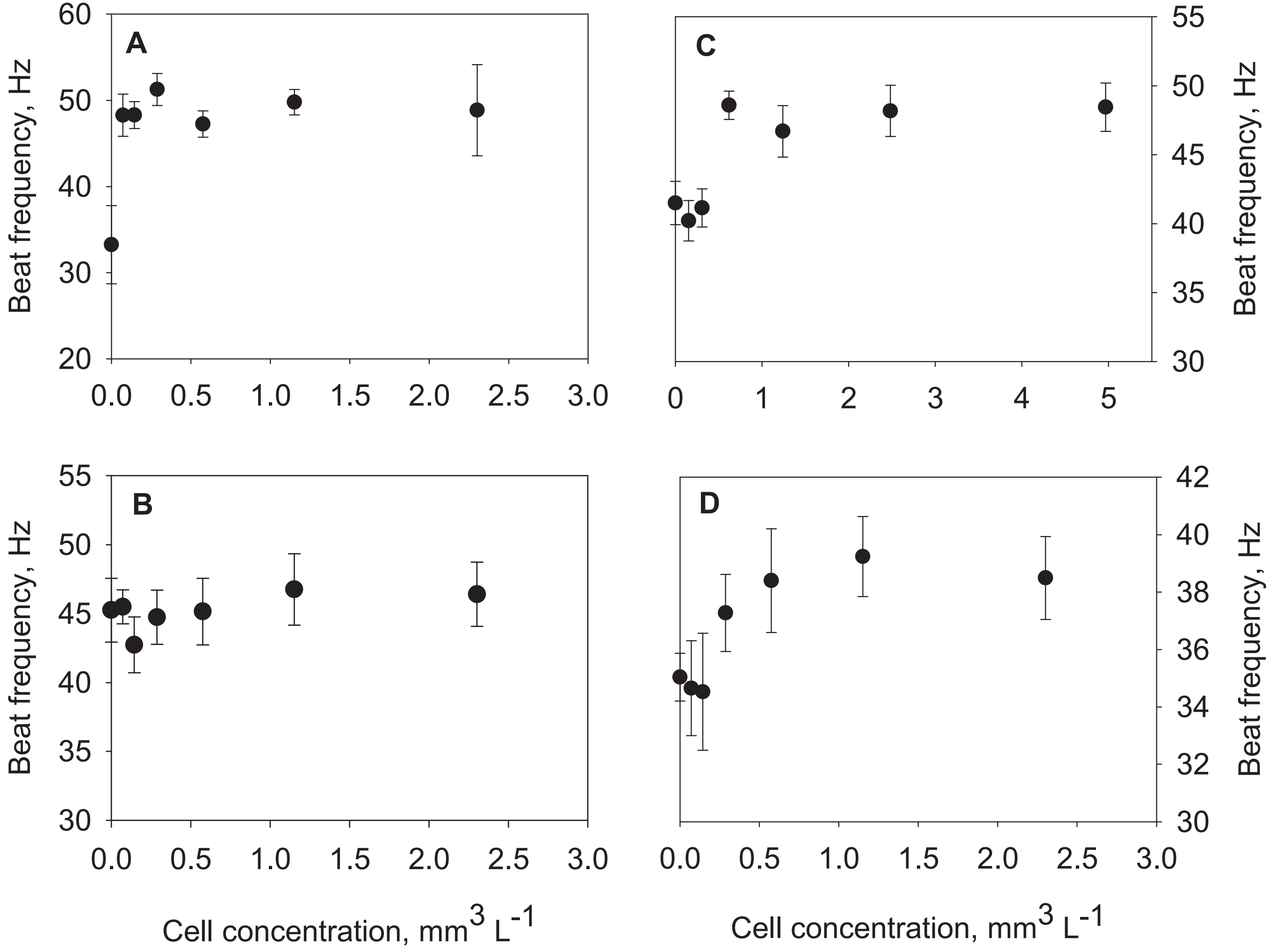

A
B
C
D
Beat frequency, Hz
Cell concentration, mm^3 L^{-1}
60
50
40
30
20
55
45
35
42
40
38
36
34
32
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
1
2
3
4
5

Fig. 4

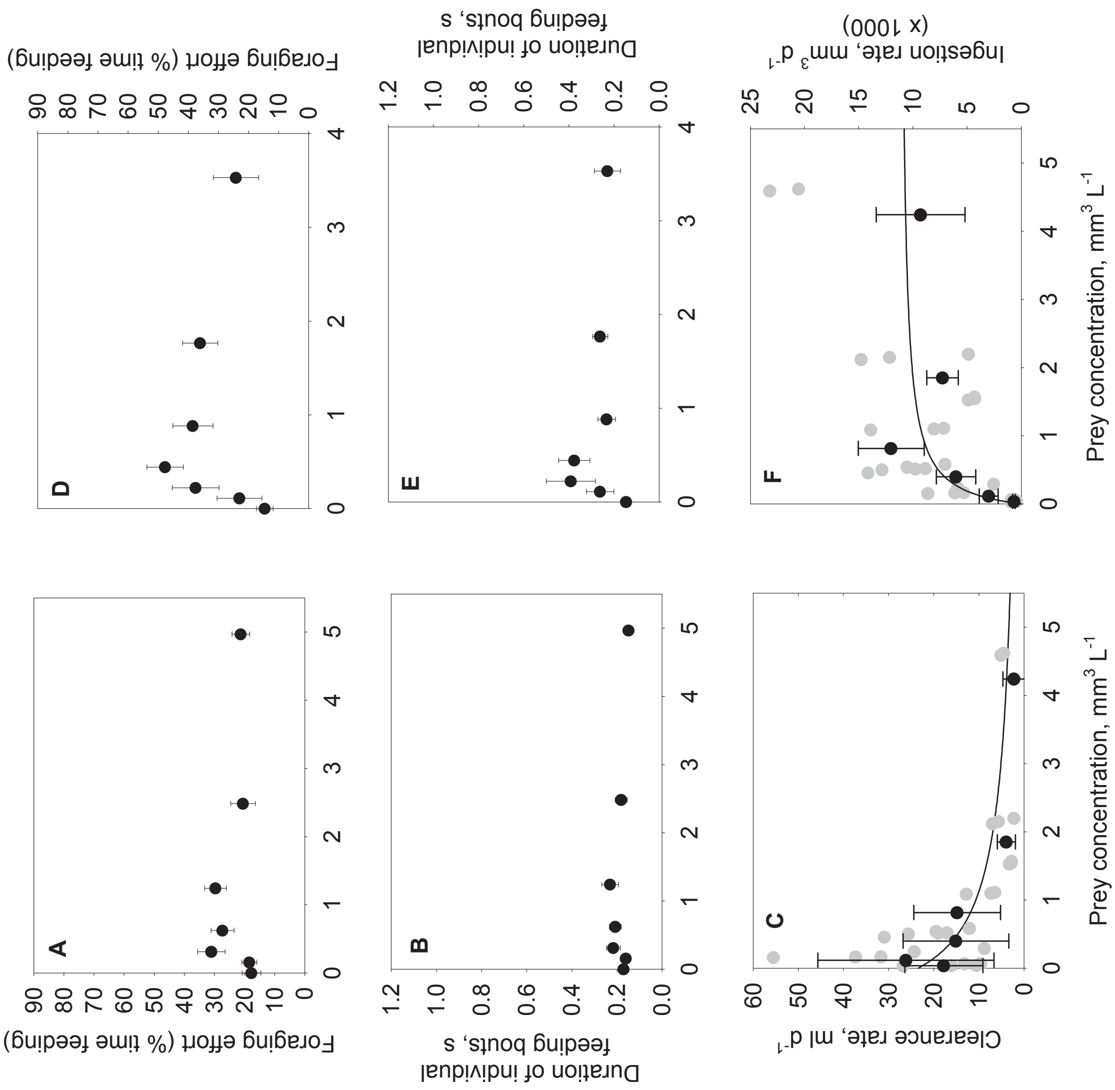
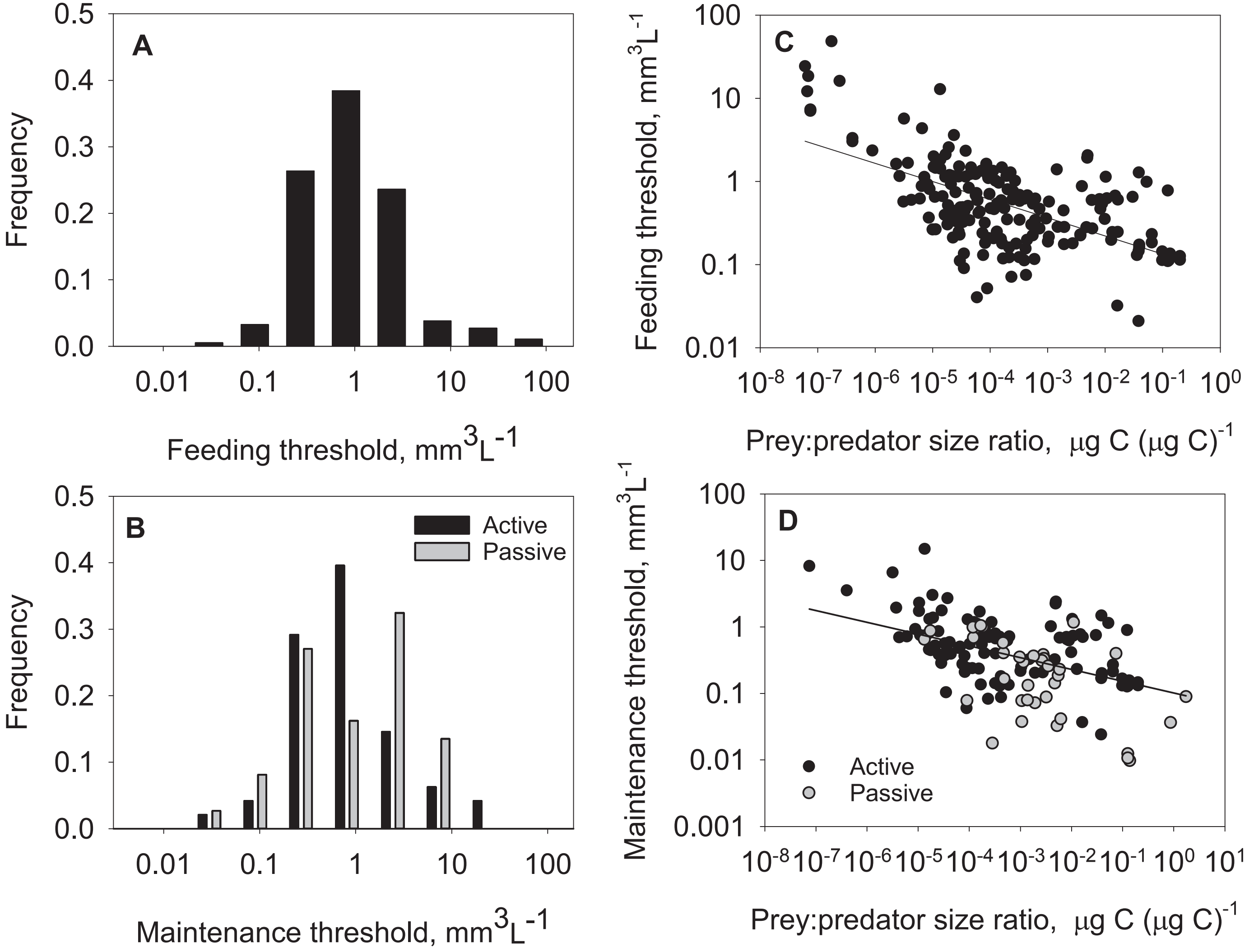

A
B
C
D
E
F
Foraging effort (% time feeding)
Duration of individual feeding bouts, s
Clearance rate, ml d-1
Ingestion rate, mm3 d-1 (x 1000)
Prey concentration, mm3 L-1
0
10
20
30
40
50
60
70
80
90
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0
5
10
15
20
25
0
1
2
3
4
5

Fig. 5


A
Frequency
0.5
0.4
0.3
0.2
0.1
0.0
0.01
0.1
1
10
100
Feeding threshold, mm^{3}L^{-1}
B
Active
Passive
Frequency
0.5
0.4
0.3
0.2
0.1
0.0
0.01
0.1
1
10
100
Maintenance threshold, mm^{3}L^{-1}
C
Feeding threshold, mm^{3}L^{-1}
100
10
1
0.1
0.01
10^{-8} 10^{-7} 10^{-6} 10^{-5} 10^{-4} 10^{-3} 10^{-2} 10^{-1} 10^{0}
Prey:predator size ratio, μg C (μg C)$^{-1}$
D
Maintenance threshold, mm^{3}L^{-1}
100
10
1
0.1
0.01
0.001
Active
Passive
10^{-8} 10^{-7} 10^{-6} 10^{-5} 10^{-4} 10^{-3} 10^{-2} 10^{-1} 10^{0} 10^{1}
Prey:predator size ratio, μg C (μg C)$^{-1}$

Online Appendix I

Species	Prey type	Feeding mode	FR	Temp	Body mass	F_{max}	β	prey mass/cop mass	R_0	R_c	Source
				C	μgC	μg C h^{-1}	ml h^{-1}	μgC(μgC)$^{-1}$	mm^3 L^{-1}	mm^3 L^{-1}	
Acartia grani naupl	*Heterocapsa* sp	Ambush	II	20	0.040	0.00137	0.0094	0.0047		0.143	(Henriksen et al. 2007)
Acartia grani naupl	*Thalassiosira weisflogii*	Ambush	II	20	0.040	0.00108	0.0072	0.0055		0.185	(Henriksen et al. 2007)
Acartia tonsa	*Strombidium sulcatum*	Ambush	II	18	3.000	0.10638	5.6141	0.00028		0.018	(Saiz and Kiørboe 1995)
Corycaeus angelicus	*Acartia clausi male*	Ambush	II	11	2.400		0.2412	0.9375			(Landry et al. 1985)
Oithona davisae	*Isochrysis galbana*	Ambush	II	18	0.390	0.00106	0.0150	0.00002		0.871	(Saiz et al. 2014)
Oithona davisae	*Tetraselmis chuii*	Ambush	II	18	0.384	0.00557	0.0130	0.00012		0.987	(Saiz et al. 2014)
Oithona davisae	*Heterocapsa* sp.	Ambush	II	18	0.368	0.01813	0.0303	0.00047		0.405	(Saiz et al. 2014)
Oithona davisae	*Prorocentrum minimum*	Ambush	II	18	0.375	0.01417	0.0218	0.00046		0.575	(Saiz et al. 2014)
Oithona davisae	*Oxyrrhis marina*	Ambush	II	18	0.336	0.01928	0.1416	0.00138		0.079	(Saiz et al. 2014)
Oithona davisae	*Scrippsiella trochoidea*	Ambush	II	18	0.389		0.0452	0.00192			(Saiz et al. 2014)
Oithona davisae	*Prorocentrum micans*	Ambush	II	18	0.383		0.0653	0.00338			(Saiz et al. 2014)

Oithona davisae	*Strombidium sulcatum*	Ambush	II	18	0.351	0.02597	0.3593	0.00522		0.033	(Saiz et al. 2014)
Oithona davisae	*Strombidium sulcatum*	Ambush	II	18	0.390		0.2940	0.0052			(Saiz et al. 2014)
Oithona davisae	*Akashiwo sanguinea*	Ambush	II	18	0.393	0.01268	0.0112	0.01097		1.166	(Saiz et al. 2014)
Oithona davisae	*Paracartia grani nauplii*	Ambush	II	18	0.369	0.00241	0.0310	0.07429		0.397	(Saiz et al. 2014)
Oithona davisae	*Thalassiosira weissflogii*	Ambush	II	18	0.348		0.0278	0.00029			(Saiz et al. 2014)
Oithona davisae	*Oxhyrris marina*	Ambush	II	21	0.250	0.00494	0.1078	0.00106		0.077	(Saiz et al. 2003)
Oithona davisae male	*Oxhyrris marina*	Ambush	II	22	0.188	0.00253	0.0477	0.00142		0.131	(Kiørboe 2008)
Oithona davisae naupl	*Heterocapsa sp*	Ambush	II	20	0.032	0.00060	0.0047	0.00585		0.229	(Henriksen et al. 2007)
Oithona davisae naupl	*Isochrysis galbana*	Ambush	II	18	0.051	0.00020	0.0016	0.00017		1.042	(Saiz et al. 2014)
Oithona davisae naupl	*Tetraselmis chuii*	Ambush	II	18	0.056	0.00090	0.0053	0.00097		0.351	(Saiz et al. 2014)
Oithona davisae naupl	*Heterocapsa* sp.	Ambush	II	18	0.055	0.00137	0.0071	0.00349		0.256	(Saiz et al. 2014)
Oithona davisae naupl	*Oxyrrhis marina*	Ambush	II	18	0.059	0.00221	0.0477	0.00615		0.041	(Saiz et al. 2014)
Oithona davisae naupl	*Thalassiosira weissflogii*	Ambush	II	18	0.058		0.0045	0.00173			(Saiz et al. 2014)
Oithona davisae, CII-III	*Oxyrrhis marina*	Ambush	II	20.5	0.233	0.00325	0.0263	0.00114		0.296	(Almeda et al. 2010)
Oithona davisae	*Oxyrrhis marina*	Ambush	II	18	0.250	0.00600	0.2233	0.00106		0.037	(Zamora-Terol and Saiz 2013)

Oithona davisae, NI-II	*Oxyrrhis marina*	Ambush	II	20.5	0.089	0.00074	0.0090	0.00298		0.332	(Almeda et al. 2010)
Oithona davisae, NI-II	*Oxyrrhis marina*	Ambush	II	20.5	0.092	0.00088	0.0092	0.00288		0.334	(Almeda et al. 2010)
Oithona davisae, NII-III	*Oxyrrhis marina*	Ambush	II	20.5	0.101	0.00099	0.0109	0.00263		0.310	(Almeda et al. 2010)
Oithona davisae, NV-VI	*Oxyrrhis marina*	Ambush	II	20.5	0.147	0.00186	0.0135	0.00181		0.364	(Almeda et al. 2010)
Oithona nana	*Acartia nauplii*	Ambush	II	10	0.230	0.00192	0.6226	0.12609		0.012	(Lampitt 1978)
Oithona nana	*Isochysis galbana*	Ambush	II	10	0.230	0.00064	0.0119	0.00001		0.650	(Lampitt and Gamble 1982)
Oithona nana male	*Acartia nauplii*	Ambush	II	10	0.210	0.00673	0.7197	0.13810		0.010	(Lampitt 1978)
Oithona nana male	*Dunaliella euchlora*	Ambush	II	10	0.230	0.00293	0.0112	0.00012		0.688	(Lampitt and Gamble 1982)
Oithona nana male	*Chricosphaera elongata*	Ambush	II	10	0.230	0.00359	0.0467	0.00048		0.164	(Lampitt and Gamble 1982)
Oithona nana male	*Thalassiosira weisflogii*	Ambush	II	10	0.230	0.00146	0.0077	0.00018		1.002	(Lampitt and Gamble 1982)
Oithona nana male	*Prorocentrum micans*	Ambush	II	10	0.230	0.00128	0.0202	0.00282		0.380	(Lampitt and Gamble 1982)
Oithona nana male	*Acartia clausi* NI	Ambush	II	10	0.230	0.00603	0.7195	0.12609		0.011	(Lampitt and

											Gamble 1982)
Oithona nana male	*Calanus finmarchicus* NI	Ambush	II	10	0.230	0.00530	0.2106	0.86957		0.036	(Lampitt and Gamble 1982)
Oithona nana male	*Calanus finmarchicus* NII	Ambush	II	10	0.230	0.00006	0.0906	1.73913		0.090	(Lampitt and Gamble 1982)
Oithona similis	*Prorocentrum micans*	Ambush	II	8.5	0.360	0.00931	0.1369	0.00321		0.088	Drits & Semenova 1984
Oithona similis	*Peridinium trochoideum*	Ambush	II	8.5	0.360	0.01051	0.1665	0.00193		0.072	Drits & Semenova 1984
Oithona similis	*Platymonas viridis*	Ambush	II	8.5	0.360	0.01250	0.1543	0.00009		0.078	Drits & Semenova 1984
Acartia clausi	*Rhodomonas baltica*	Active	(II)	15	5.000	0.23000	0.3335	0.00001	1.499251	1.728	(Dutz 1998)
Acartia clausi	*Alexandrium lusitanicum*	Active	(II)	15	5.000	0.27000	0.6244	0.00020	0.800818	0.923	(Dutz 1998)
Acartia Erythraea	*Chattonella antiqua*	Active	II	20	4.580	0.14462	0.7889	0.00033	0.580591	0.670	Uye 1986
Acartia hudsonica	*Thalassiosira constricta*	Active	III	4.5	6.790	0.38937	2.7416	0.00003	0.247669	0.285	(Durbin and Durbin 1992)
Acartia hudsonica	*Thalassiosira constricta*	Active	III	8	5.940	0.18246	1.7887	0.00003	0.332091	0.383	(Durbin and Durbin 1992)
Acartia hudsonica	*Thalassiosira constricta*	Active	III	12	4.420	0.18159	1.3619	0.00003	0.324545	0.374	(Durbin and Durbin 1992)

Acartia hudsonica	*Thalassiosira constricta*	Active	III	16	3.880	0.15750	0.8751	0.00004	0.44338	0.511	(Durbin and Durbin 1992)
Acartia tonsa	*Thalassiosira weisflogii*	Active	III	20	3.710		3.3586	0.00003	0.110463		(Durbinl and Durbinl 1990)
Acartia tonsa	*Thalassiosira weisflogii*	Active	(II)	18	3.000	0.09545	5.8007	0.00009	0.051718	0.060	(Saiz and Kiørboe 1995)
Acartia tonsa	*Isochrysis galbana*	Active	III	18	2.484	0.40385	0.1247	0.00001	1.99254	2.293	(Støttrup and Jensen 1990)
Acartia tonsa	*Dunaliella tertiolecta*	Active	III	18	2.484	0.14685	0.4004	0.00001	0.620434	0.715	(Støttrup and Jensen 1990)
Acartia tonsa	*Rhodomonas baltica*	Active	III	18	2.484	0.19825	0.3750	0.00001	0.662394	0.763	(Støttrup and Jensen 1990)
Acartia tonsa	*Thalassiosira weifsflogii*	Active	III	18	2.484	0.17622	1.0415	0.00007	0.238507	0.275	(Støttrup and Jensen 1990)
Acartia tonsa	*Ditylum brightwellii*	Active	III	18	2.484	0.14685	0.7210	0.00033	0.344499	0.397	(Støttrup and Jensen 1990)
Acartia tonsa, copepodites	*Pavlova lutheri*	Active		17	0.898		0.0619	0.00001	1.451902		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Pavlova lutheri*	Active		17	1.239		0.1341	0.00001	0.923956		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Pavlova lutheri*	Active		17	0.555		0.1827	0.00002	0.303728		(Berggreen et al. 1988)

Acartia tonsa, copepodites	*Pavlova lutheri*	Active		17	0.448		0.2132	0.00002	0.210038		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Pavlova lutheri*	Active		17	0.898		0.3391	0.00001	0.26493		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Pavlova lutheri*	Active		17	1.174		0.3221	0.00001	0.364585		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Pavlova lutheri*	Active		17	3.248		0.5679	0.00000	0.571992		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Isochrysis galbana*	Active		17	0.555		0.0378	0.00005	1.466256		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Isochrysis galbana*	Active		17	0.448		0.0620	0.00006	0.722605		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Isochrysis galbana*	Active		17	1.535		0.0731	0.00002	2.100661		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Isochrysis galbana*	Active		17	1.174		0.1015	0.00002	1.156698		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Isochrysis galbana*	Active		17	1.239		0.1335	0.00002	0.927744		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Isochrysis galbana*	Active		17	0.852		0.1756	0.00003	0.48483		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Isochrysis galbana*	Active		17	1.901		0.1335	0.00001	1.423884		(Berggreen et al. 1988)

Acartia tonsa, copepodites	*Isochrysis galbana*	Active		17	3.615		0.3210	0.00001	1.126139		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Dunaliella tertiolecta*	Active		17	0.852		0.0748	0.00004	1.137956		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Rhodomonas baltica*	Active		17	0.420		0.0316	0.00011	1.331749		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Rhodomonas baltica*	Active		17	0.551		0.0339	0.00009	1.624873		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Rhodomonas baltica*	Active		17	0.850		0.0696	0.00006	1.220547		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Rhodomonas baltica*	Active		17	1.056		0.0864	0.00004	1.221581		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Rhodomonas baltica*	Active		17	1.114		0.1331	0.00004	0.837436		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Rhodomonas baltica*	Active		17	1.628		0.4208	0.00003	0.386952		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Rhodomonas baltica*	Active		17	3.477		0.1907	0.00001	1.823137		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Rhodomonas baltica*	Active		17	2.022		0.0561	0.00002	3.60392		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Amphidinium carterae*	Active		17	0.425		0.0561	0.00025	0.757912		(Berggreen et al. 1988)

Acartia tonsa, copepodites	*Amphidinium carterae*	Active		17	0.554		0.0477	0.00019	1.161111		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Amphidinium carterae*	Active		17	1.163		0.1016	0.00009	1.144427		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Amphidinium carterae*	Active		17	1.515		0.1132	0.00007	1.338614		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Amphidinium carterae*	Active		17	0.803		0.1482	0.00013	0.541509		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Amphidinium carterae*	Active		17	1.103		0.1565	0.00010	0.704854		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Amphidinium carterae*	Active		17	1.776		0.2990	0.00006	0.593945		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Amphidinium carterae*	Active		17	3.352		0.7090	0.00003	0.472724		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Thalassiosira weisflogii*	Active		17	0.439		0.1289	0.00061	0.340893		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Thalassiosira weisflogii*	Active		17	0.611		0.3083	0.00044	0.198051		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Thalassiosira weisflogii*	Active		17	0.947		0.5316	0.00028	0.17806		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Thalassiosira weisflogii*	Active		17	1.245		0.7786	0.00021	0.159932		(Berggreen et al. 1988)

Acartia tonsa, copepodites	*Thalassiosira weisflogii*	Active		17	1.245		1.0225	0.00021	0.121784		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Thalassiosira weisflogii*	Active		17	1.638		0.9169	0.00016	0.178639		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Thalassiosira weisflogii*	Active		17	2.040		0.8222	0.00013	0.248057		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Thalassiosira weisflogii*	Active		17	3.529		2.7270	0.00008	0.129401		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Scripsiella faroense*	Active		17	0.555		0.0399	0.00144	1.390723		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Scripsiella faroense*	Active		17	0.425		0.0949	0.00189	0.447189		(Berggreen et al. 1988)
Acartia tonsa, copepodites	*Scripsiella faroense*	Active		17	0.852		0.2385	0.00094	0.357122		(Berggreen et al. 1988)
Aetideus divergens	*Thallasiosira fluviatilis*	Active	II	12	21.2		0.4903	0.00001	4.332161		(Robertson and Frost 1977)
Aetideus divergens	*Coscinodiscus angstii*	Active	II	12	21.2		4.6032	0.00012	0.461414		(Robertson and Frost 1977)
Aetideus divergens	*Coscinodiscus angstii*	Active	(II)	12	21.2		9.4789	0.00055	0.224077		(Robertson and Frost 1977)
Aetideus divergens	*Artemaia nauplii*	Active	(II)	12	21.2		16.4053	0.03578	0.12947		(Robertson and Frost 1977)

Calanus finmarchicus CV + female	*Emiliania huxley*	Active		13	104.3		0.2156	0.00000	48.39151		(Nejstgaard et al. 1995)
Calanus finmarchicus CV + female	*Emiliania huxley*	Active		13	104.3		0.5658	0.00000	18.43486		(Nejstgaard et al. 1995)
Calanus finmarchicus CV + female	*Emiliania huxley*	Active		13	104.3		1.4280	0.00000	7.304379		(Nejstgaard et al. 1995)
Calanus finmarchicus CV + female	Prymnesium patelliferum	Active		13	104.3		0.6467	0.00000	16.1305		(Nejstgaard et al. 1995)
Calanus finmarchicus CV + female	*Thallasiosira nordenskioeldii*	Active		13	104.3		6.4127	0.00000	1.626605		(Nejstgaard et al. 1995)
Calanus finmarchicus CV + female	*Thallasiosira nordenskioeldii*	Active		13	104.3		9.0533	0.00000	1.152179		(Nejstgaard et al. 1995)
Calanus finmarchicus CV + female	*Chaetoceros calcitrans*	Active		13	104.3		0.8622	0.00000	12.09788		(Nejstgaard et al. 1995)
Calanus finmarchicus CV + female	*Pavlova lutheri*	Active		13	104.3		0.4311	0.00000	24.19576		(Nejstgaard et al. 1995)
Calanus finmarchicus CV + female	*Rhodomonas baltica*	Active		13	104.3		3.1525	0.00000	3.308821		(Nejstgaard et al. 1995)
Calanus finmarchicus CV + female	*Rhodomonas baltica*	Active	II	13	104.3	1.27473	3.4418	0.00000	3.030697	3.518	(Nejstgaard et al. 1995)
Calanus finmarchicus CV + female	*Emiliania huxley*	Active	III	13	104.3	0.92661	1.4826	0.00000	7.035695	8.197	(Nejstgaard et al. 1995)

Calanus pacificus C I	*Chlamydomonas* sp	Active	III	15	1.506	0.04001	0.1480	0.00012	1.01725	1.175	(Fernandez 1979)
Calanus pacificus C I	*Thallasiosira weisflogii*	Active	III	15	1.506	0.08810	0.3612	0.00006	0.416952	0.480	(Fernandez 1979)
Calanus pacificus C I	*Lauderia borealis*	Active	(II)	15	1.506	0.06943	1.2289	0.00032	0.122549	0.141	(Fernandez 1979)
Calanus pacificus C I	*Gymnodinium splendens*	Active	III	15	1.506	0.07824	0.5320	0.00150	0.28306	0.326	(Fernandez 1979)
Calanus pacificus	*Coscinodiscus angstii*	Active	III	12.5	76.5	1.59109	11.7792	0.00001	0.649451	0.751	(Frost 1972)
Calanus pacificus	*Coscinodiscus eccentricus*	Active	III	12.5	76.5	1.31944	17.0348	0.00002	0.44908	0.520	(Frost 1972)
Calanus pacificus	*Centric diatiom*	Active	II/III	12.5	76.5	1.50054	22.4979	0.00004	0.340031	0.393	(Frost 1972)
Calanus pacificus N V	*Isochrysis galbana*	Active	III	15	0.823	0.00460	0.0322	0.00002	2.558218	3.004	(Fernandez 1979)
Calanus pacificus N V	*Chlamydomonas* sp	Active	III	15	0.823		0.0645	0.00023	1.27531		(Fernandez 1979)
Calanus pacificus N V	Thallasiosira weisflogii	Active	III	15	0.823	0.03795	0.3985	0.00011	0.206537	0.238	(Fernandez 1979)
Calanus pacificus N V	Peridinium trochoideum	Active	(II)	15	0.823	0.04748	0.1329	0.00061	0.619123	0.713	(Fernandez 1979)
Calanus pacificus N V	Lauderia borealis	Active	III	15	0.823	0.04690	0.7083	0.00059	0.116201	0.134	(Fernandez 1979)
Calanus pacificus N V	Gymnodinium splendens	Active	III	15	0.823	0.04364	0.4582	0.00274	0.179601	0.207	(Fernandez 1979)
Calanus pacificus N V	Gonyaulax polyedra	Active	(II)	15	0.823	0.03708	0.3670	0.00373	0.224225	0.259	(Fernandez 1979)
Calanus pacificus N VI	Isochrysis galbana	Active	II	15	1.168	0.01823	0.0091	0.00001	12.80731	14.838	(Fernandez 1979)
Calanus pacificus N VI	*Chlamydomonas* sp	Active	(II)	15	1.168	0.04971	0.0795	0.00016	1.468064	1.693	(Fernandez 1979)

Calanus pacificus N VI	*Thallasiosira weisflogii*	Active	III	15	1.168	0.05757	0.3685	0.00008	0.316892	0.365	(Fernandez 1979)
Calanus pacificus N VI	*Lauderia borealis*	Active	III	15	1.168	0.07000	0.7490	0.00041	0.155879	0.180	(Fernandez 1979)
Calanus pacificus N VI	*Gymnodinium splendens*	Active	III	15	1.168	0.06206	0.6641	0.00193	0.175825	0.203	(Fernandez 1979)
Calanus pacificus NIII	*Thallasiosira weisflogii*	Active	III	15	0.384	0.02096	0.0629	0.00025	0.610736	0.704	(Fernandez 1979)
Calanus pacificus NIII	*Gymnodinium splendens*	Active	(II)	15	0.384	0.02478	0.0644	0.00587	0.596034	0.687	(Fernandez 1979)
Calanus pacificus NIII	*Gonyaulax polyedra*	Active	(II)	15	0.384	0.02096	0.0629	0.00799	0.610736	0.704	(Fernandez 1979)
Calanus pacificus NIV	*Chlamydomonas* sp	Active	III	15	0.479	0.01494	0.0777	0.00039	0.616672	0.712	(Fernandez 1979)
Calanus pacificus NIV	*Thallasiosira weisflogii*	Active	III	15	0.479	0.02374	0.1377	0.00020	0.347915	0.401	(Fernandez 1979)
Calanus pacificus NIV	*Peridinium trochoideum*	Active	(II)	15	0.479	0.01998	0.2218	0.00105	0.215946	0.249	(Fernandez 1979)
Calanus pacificus NIV	*Lauderia borealis*	Active	III	15	0.479	0.05403	0.2539	0.00101	0.188644	0.217	(Fernandez 1979)
Calanus pacificus NIV	*Gymnodinium splendens*	Active	III	15	0.479	0.03342	0.1704	0.00471	0.281062	0.324	(Fernandez 1979)
Calanus sinicus	*Alexandrium tamarense* ARC101	Active	II	18	30.2	0.68654	2.5333	0.00002	1.190136	1.376	(Liu and Wang 2002)
Calanus sinicus	*Alexandrium tamarense* CCMP1771	Active	II	18	30.2	0.50077	1.2966	0.00004	2.325241	2.693	(Liu and Wang 2002)
Calanus sinicus	*Thallasiosira weissflogii*	Active		18	30.2		1.2850	0.00000	2.346371		(Liu and Wang 2002)
Calanus sinicus	*Chattonella antiqua*	Active	II	20	51.8	0.75228	3.4303	0.00003	1.510069	1.750	(Uye 1986)

Centropages yamadaiu	*Chattonella antiqua*	Active	II	20	9.6	0.22960	1.6255	0.00016	0.590584	0.682	(Uye 1986)
Euchaete elongata	*Pseudocalanus* sp	Active	II	8	637	8.53215	117.8054	0.00890	0.540722	0.627	(Yen 1985)
Euchaete elongata	*Acartia clausii*	Active	II	8	637	6.80516	72.9859	0.00396	0.872771	1.015	(Yen 1985)
Euchaete norvegica	Larval cod	Active	II	7.5	1350	13.00897	224.0314	0.01667	0.602594	0.701	(Yen 1985)
Paracalanus crassirostris	*Alexandrium tamarense* ARC101	Active	II	18	4.19	0.08371	0.4338	0.00014	0.964658	1.116	(Liu and Wang 2002)
Paracalanus crassirostris	*Alexandrium tamarense* CCMP1771	Active	II	18	4.19	0.08077	0.4124	0.00027	1.014834	1.174	(Liu and Wang 2002)
Paracalanus crassirostris	*Thallasiosira weissflogii*	Active		18	4.19		0.4773	0.00001	0.876858		(Liu and Wang 2002)
Paracalanus parvus	*Chattonella antiqua*	Active	II	20	2.70	0.07225	0.5001	0.00056	0.53991	0.624	(Uye 1986)
Pseudocalanus marinus	*Chattonella antiqua*	Active	II	20	4.62	0.10231	0.6747	0.00032	0.684742	0.792	(Uye 1986)
Tortanus dextrilobatus	*Oithona davisae*	Active	II	14	24.4	0.15518	6.9186	0.00983	0.352963	0.413	(Hooff and Bollens 2004)
Tortanus dextrilobatus	*Oithona davisae*	Active	II	19	18.7	0.11979	2.9947	0.01070	0.6241	0.731	(Hooff and Bollens 2004
Tortanus dextrilobatus	*Acartia sp*	Active	II	14	24.4	1.94713	22.2983	0.12244	0.109515	0.126	(Hooff and Bollens 2004
Tortanus dextrilobatus	*Acartia sp*	Active	II	19	18.7	0.97222	16.7483	0.12734	0.111593	0.129	(Hooff and Bollens 2004

Tortanus discaudatus	*Calanus pacificus* NIII	Active	II	12.5	18.1	0.66554	56.5936	0.01626	0.031949	0.037	(Ambler and Frost 1974)
Tortanus discaudatus	*Calanus pacificus* NV	Active	II	12.5	18.1	0.92772	86.5515	0.03794	0.02089	0.024	(Ambler and Frost 1974)
Tortanus forcipatus	*Pseuodiaptomus nauplii*	Active	II	21	6.28	0.04241	3.1810	0.01273	0.197555	0.231	(Uye and Kayano 1994a)
Tortanus forcipatus	*Oithona davisae*	Active	II	21	6.28	0.08626	4.3132	0.03819	0.145697	0.169	(Uye and Kayano 1994a)
Tortanus forcipatus	*Artemia* nauplii	Active	II	21	6.16	0.34308	4.5468	0.13473	0.135488	0.156	(Uye and Kayano 1994a)
Tortanus spp CI-III	*Oithona davisae CV-VI*	Active	(II)	25	1.10	0.01637	0.9673	0.20000	0.113723	0.132	(Uye and Kayano 1994b)
Tortanus spp CI-III	*Oithona davisae CV-VI*	Active	(II)	20	1.10	0.02739	0.8715	0.20000	0.126216	0.146	(Uye and Kayano 1994b)
Tortanus spp CVIF	*Oithona davisae CV-VI*	Active	(II)	25	5.62	0.06515	3.2574	0.03915	0.172528	0.200	(Uye and Kayano 1994b)
Tortanus spp CVIF	*Oithona davisae CV-VI*	Active	(II)	20	5.62	0.07669	3.4861	0.03915	0.161212	0.187	(Uye and Kayano 1994b)
Tortanus spp IV-V	*Oithona davisae CV-VI*	Active	(II)	25	2.23	0.02848	1.5536	0.09865	0.14354	0.167	(Uye and Kayano 1994b)
Tortanus spp IV-V	*Oithona davisae CV-VI*	Active	(II)	20	2.23	0.03944	1.9721	0.09865	0.113076	0.131	(Uye and Kayano 1994b)

Tortanus spp male	*Oithona davisae CV-VI*	Active	(II)	25	3.40	0.04616	1.4688	0.06471	0.231489	0.268	(Uye and Kayano 1994b)
Tortanus spp male	*Oithona davisae CV-VI*	Active	(II)	20	3.40	0.05807	1.8476	0.06471	0.18402	0.213	(Uye and Kayano 1994b)

Appendix Table 1. Summary of functional response experiments reported in the literature, mainly compiled by Kiørboe and Hirst (2014). The copepods are adult females, unless otherwise noted (N = nauplii, C = copepodites). Feeding mode differentiates between ‘passive’ ambush feeders and ‘active’ cruise and feeding-current feeders. Maximum ingestion rates (F_{max}) and maximum clearance rates (β) were estimated from fitted functional response curves to observational data and temperature corrected to 15 ^{0}C as described in Kiørboe and Hirst (2014). FR refers to functional response type II or III evaluated from the observational data, preferentially plots of clearance rate versus prey concentration. Functional response (II) reported in parentheses are experiments where the lowest concentration used was larger than the threshold concentration and, thus, inconclusive with respect to functional response type. R_0 and R_c are the threshold concentrations for feeding and maintenance, respectively, computed from the data using equations 9 and 10, as explained in the main text.

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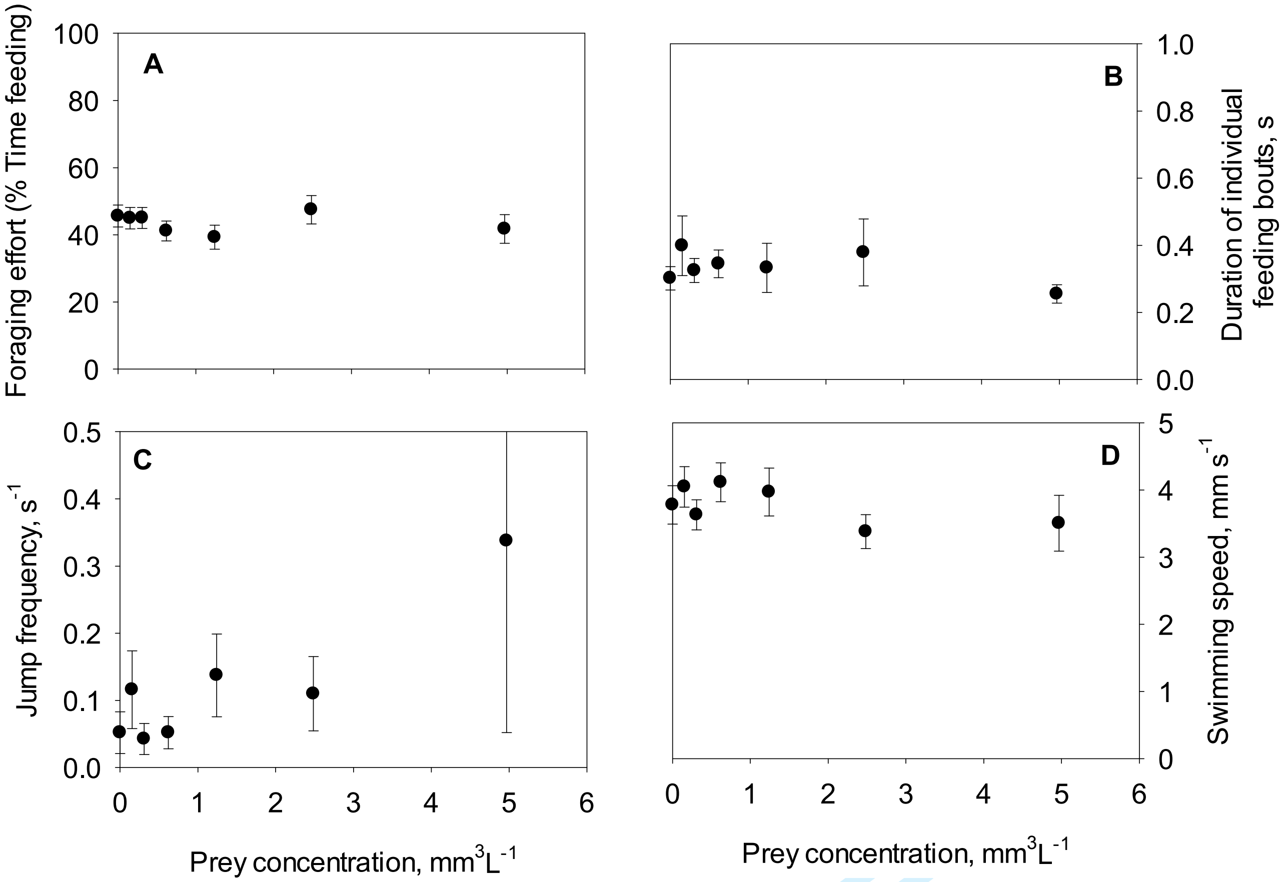
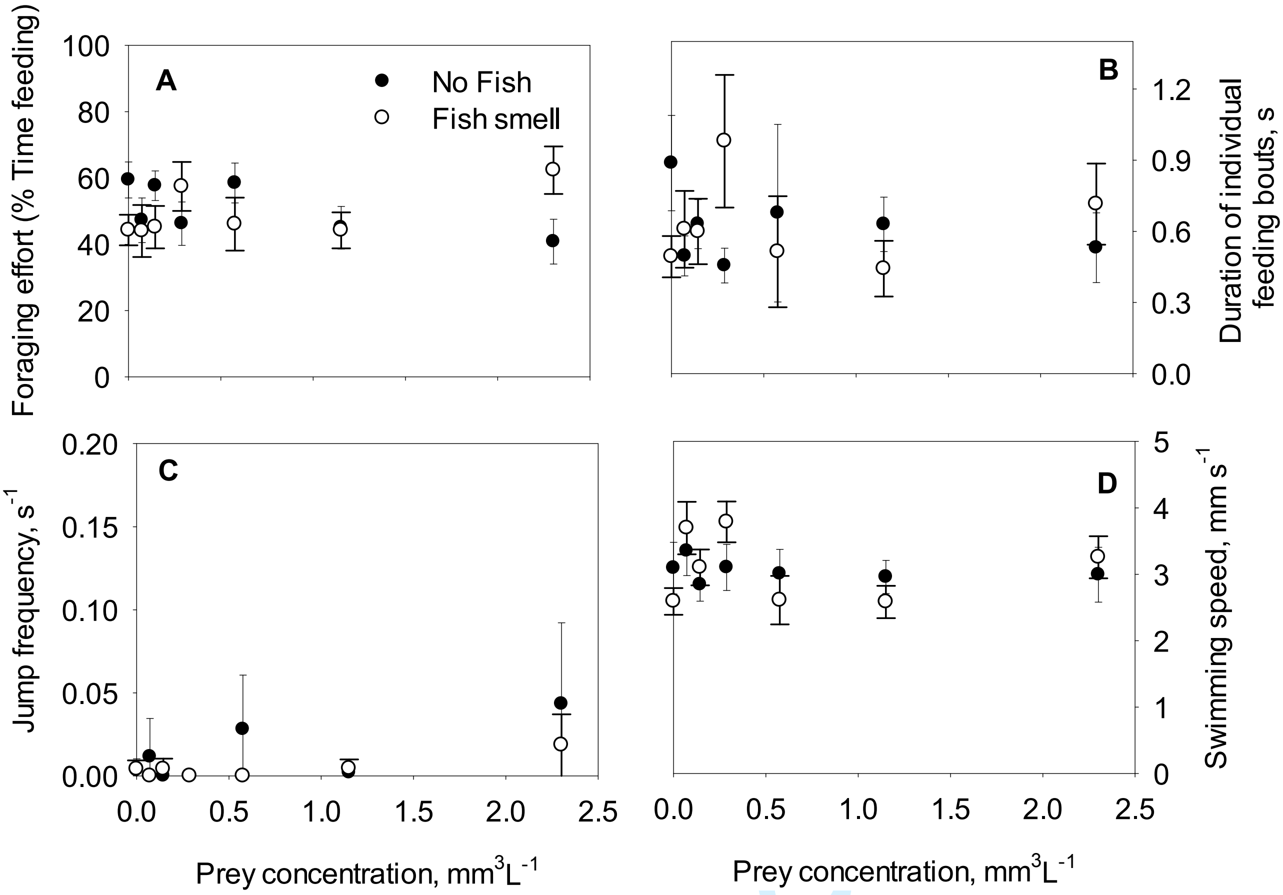
Online Appendix II

Here, all data reported as averages in Table 2 of the main paper are plotted

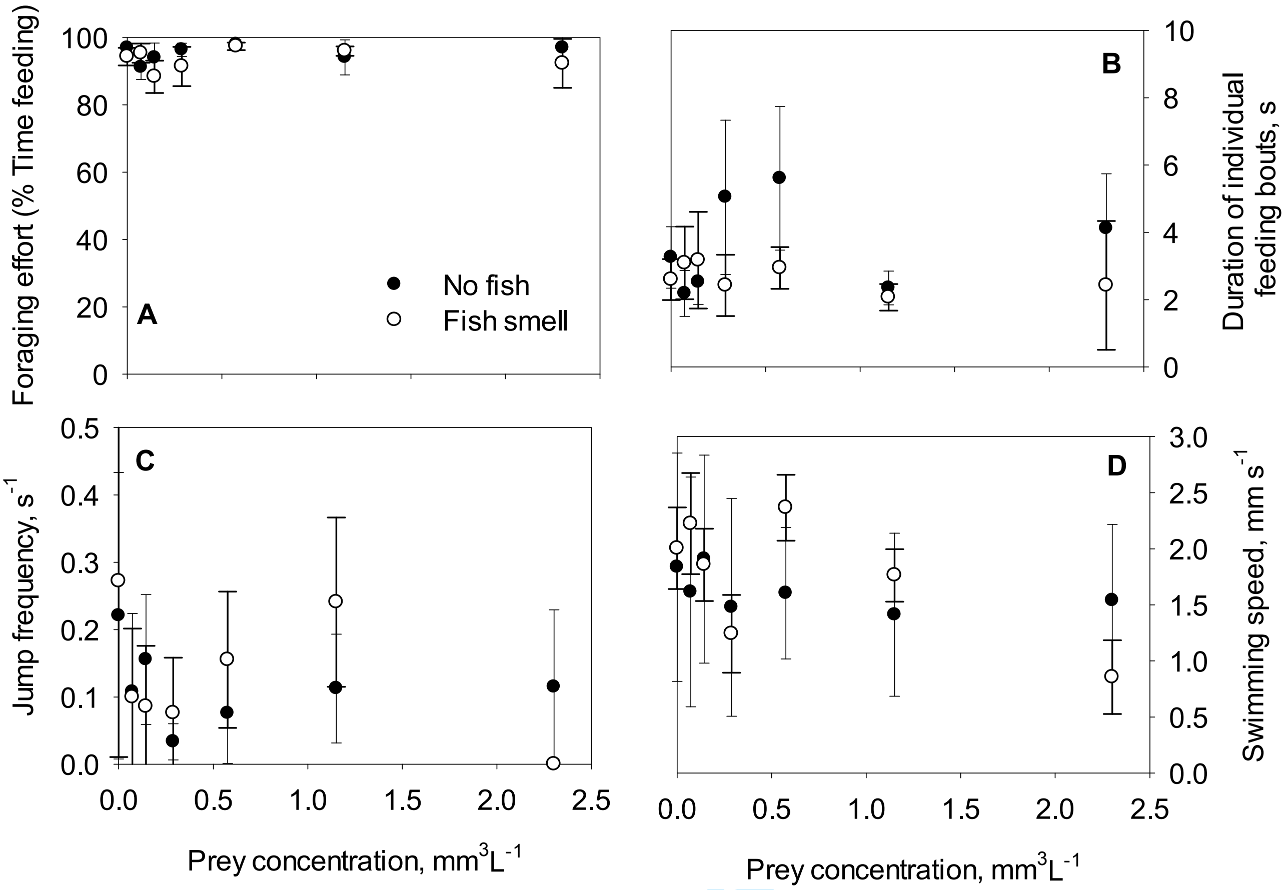
Appendix Fig. 1. *Centropages hamatus* feeding on *Akashiwo sanguinea*. All values are averages ± 95 % confidence limits.



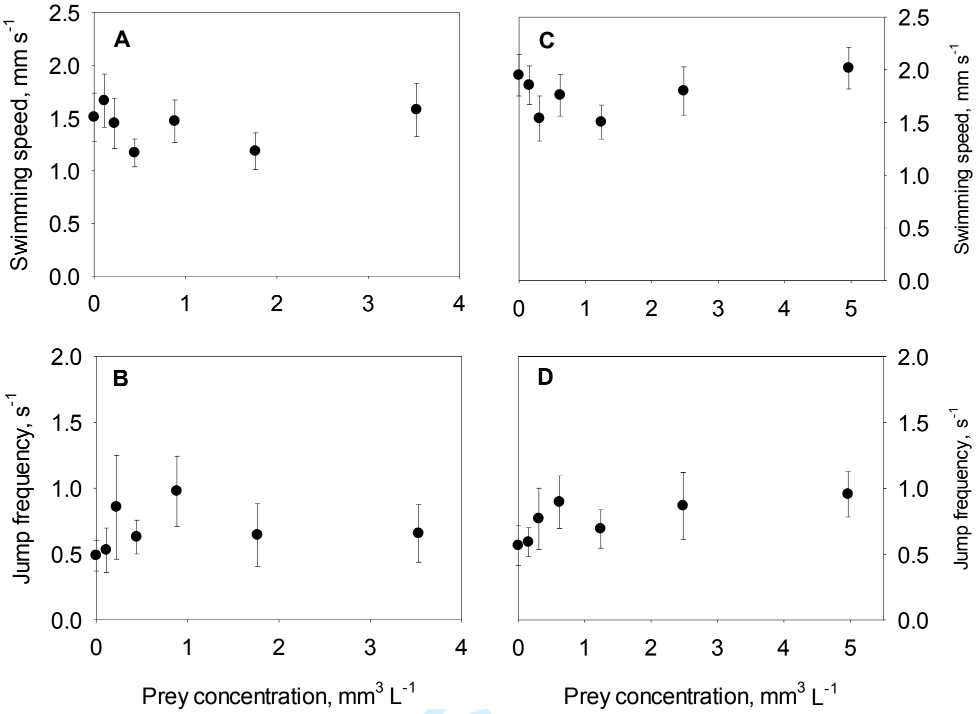
Appendix Fig. 2. *Centropages hamatus* feeding on *Rhodomonas baltica*. All values are averages ± 95 % confidence limits.



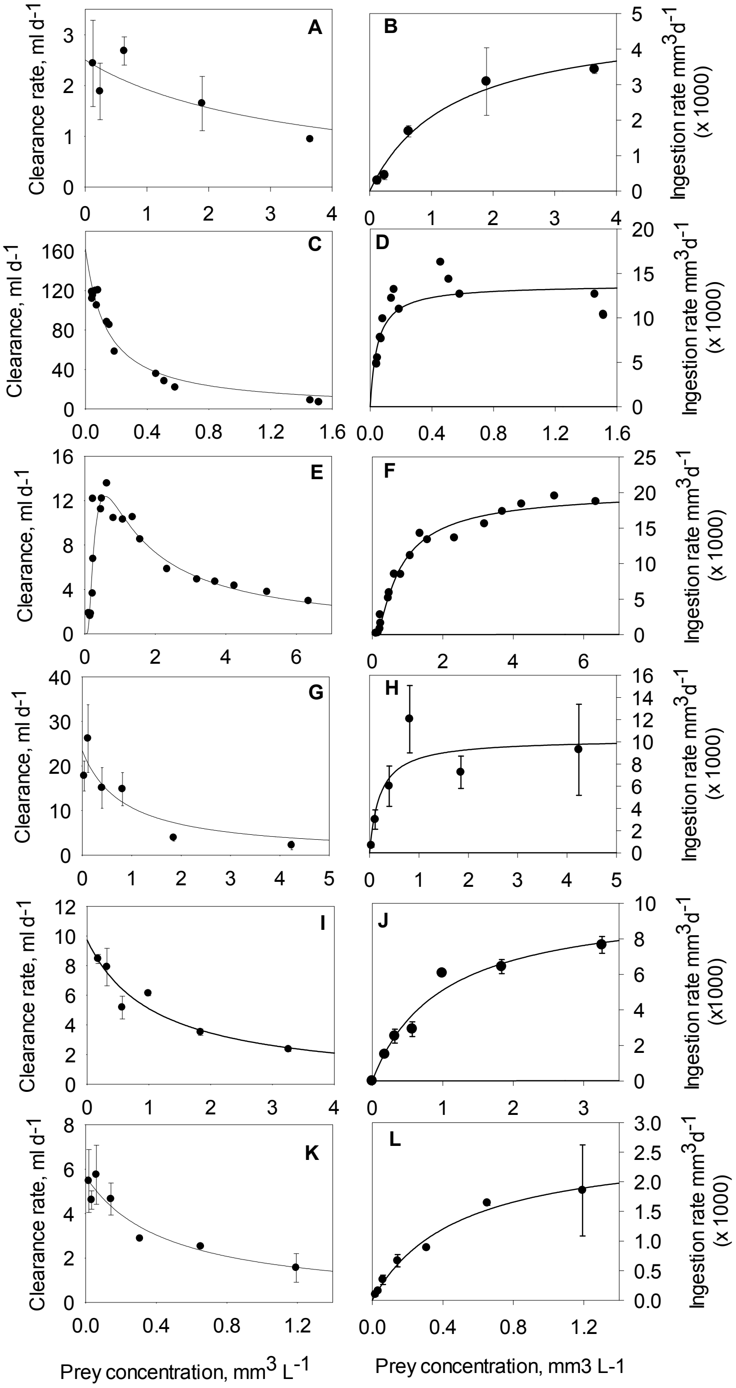
Appendix Fig. 3. *Temora longicornis* feeding on *Rhodomonas baltica*. All values are averages ± 95 % confidence limits.



Appendix Fig. 4. *Acartia tonsa* feeding on *Oxyrrhis marina* (A,B) and *Akashiwo sanguienea* (C, D). All values are averages ± 95 % confidence limits.



Appendix Figure 5. Functional response in clearance rate and ingestion rate for the copepod-prey combinations examined here. All observations are for adult females. Plots of clearance rates offer the best way to distinguish between a functional response type II and III. Most data are taken from our previous work: *C. hamatus* feeding on *R. baltica* (A,B) and *A. sanguinea* (C,D) (Sommeren Gréve, Almeda, Kiørboe *unpublished*); *A. tonsa* feeding on *R. baltica* (E, F) (Kiørboe et al. 1985). *A. tonsa* feeding on *A. sanguinea* is from the present work (G, H); *T. longicornis* feeding on *R. baltica* (I, J) (Gonçalves et al. 2014), *O. davisae* feeding on *O. marina* (K, L) (Saiz et al. 2003). The curves represent fits of type II or type III functional response models to the data, see appendix Table 1 for parameters.



Appendix Table 1. Parameter estimates for curve fits in Appendix figure 5

Copepod	Prey	Clearance	Ingestion
Centropages hamatus	*Rhodomonas baltica*	$F_{max} = 8.3 \pm 4.9$ $\beta = 2.5 \pm 0.4$ $R^2 = 0.68$	$F_{max} = 4.9 \pm 0.65$ $\beta = 3.7 \pm 0.8$ $R^2 = 0.97$
Centropages hamatus	*Akashiwo sanguinea*	$F_{max} = 22.2 \pm 3.1$ $\beta = 162 \pm 13$ $R^2 = 0.96$	$F_{max} = 13.7 \pm 1.0$ $\beta = 290 \pm 79$ $R^2 = 0.67$
Acartia tonsa	*Rhodomonas baltica*	$\alpha = 0.58 \pm 0.04$ $\beta = 12.4 \pm 0.62$ $R^2 = 0.83$	$\alpha = 0.61 \pm 0.04$ $\beta = 12.1 \pm 0.60$ $R^2 = 0.98$
Acartia tonsa	*Akashiwo sanguinea*	$F_{max} = 10.7 \pm 2.7$ $\beta = 9.7 \pm 1.1$ $R^2 = 0.90$	$F_{max} = 10.1 \pm 1.1$ $\beta = 10.3 \pm 1.9$ $R^2 = 0.97$
Temora longicornis	*Rhodomonas baltica*	$F_{max} = 2.6 \pm 0.6$ $\beta = 5.7 \pm 0.4$ $R^2 = 0.91$	$F_{max} = 2.7 \pm 0.3$ $\beta = 5.5 \pm 0.7$ $R^2 = 0.99$
Oithona davisae	*Oxyrrhis marina*	$F_{max} = 19.6 \pm 10.0$ $\beta = 23.4 \pm 3.9$ $R^2 = 0.81$	$F_{max} = 19.6 \pm 10.0$ $\beta = 23.4 \pm 3.9$ $R^2 = 0.81$