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ADAPTIVE FEEDING BEHAVIOR AND FUNCTIONAL RESPONSES IN ZOOPLANKTON

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For Review Only

10 *Abstract*

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

27

28 *Introduction*

29 The functional response in feeding rate to prey concentration is the primary quantification of
30 predator-prey interactions and it has direct implications for population dynamics and stability of
31 both prey and predators (Holling 1965; Murdoch 1977). A type II functional response is typically
32 described by some saturating function of prey concentration in which the parameters (maximum
33 ingestion and prey search rates) are assumed constant. However, the assumption of constant search
34 rate may not be true, and at both low and high prey densities it may be advantageous for the
35 predator or grazer to reduce its food searching effort to minimize its exposure to predators and
36 energetic costs of food acquisition (Abrams 1982, 1990; Werner and Anholt 1993; Visser 2007). At
37 low prey densities, the costs are simply not warranted by the gains and the grazer may reduce or
38 stop searching for prey, which may lead to a sigmoid type III functional response. At high prey
39 densities, feeding rate is limited by digestion rather than by encounter rate and the grazer may
40 therefore reduce its foraging effort. The presence of predators may induce a further reduction in
41 foraging effort, particularly at high prey densities. Reduced feeding efforts at high prey densities,
42 whether due to predation risk or energy saving, will not necessarily change the type of the
43 functional response (i.e., a type II may remain a type II, Abrams 1990), but predator-induced
44 changes in behaviors may cause behavioral cascading effects that are very important in shaping
45 food webs and organism abundances, as has been demonstrated in both terrestrial (Suraci et al.
46 2016) and freshwater environments (Peacor and Werner 2001; Romare and Hansson 2003; Biro et
47 al. 2005).

48 Zooplankton, the main consumers of oceanic primary production, may also modify their foraging
49 effort in response to prey concentration and presence of predators with important implications to
50 their function in pelagic food webs. The significance of behavioral adaptations to fundamental

51 properties of pelagic food webs, such as primary production and material fluxes (Anderson et al.
52 2010), diversity of the phytoplankton prey (Prowse et al. 2012), and the seasonal successions in
53 plankton communities (Visser 2007; Mariani et al. 2013; Visser and Fiksen 2013) has been
54 demonstrated in multiple modelling studies. Yet, actual demonstrations of the behavioral
55 adaptations to prey and predators assumed in these models are rare, particularly in marine
56 zooplankton (Price and Paffenhöfer 1986; Saiz et al. 1993; Saiz 1994; Duren and Videler 1995; Van
57 Duren and Videler 1996). Early zooplankton-specific models of optimal foraging (Lam and Frost
58 1976; Lehman 1976) were consistent with more general models (Abrams 1982, 1990; Werner and
59 Anholt 1993) in typically predicting reduced feeding effort at low prey concentration, but were
60 based on fundamentally wrong assumptions about the feeding behavior and considered, similar to
61 the more recent model of Pahlow and Prowse (2010), only the energetic costs of feeding, not
62 predation. Finally, experimental studies of functional responses in zooplankton are abundant but are
63 inconsistent in their findings, reporting both type II and type III responses (Online Appendix 1), and
64 without the mechanistic underpinning that is important in assessing the food web effects predicted
65 by models.

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

75

76 ***Material and methods***77 **Fitness optimization model**

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

79
$$F = F_{max} \frac{\beta R}{\beta R + F_{max}} \quad (1)$$

80 where F is the ingestion rate and F_{max} the maximum ingestion rate (biomass per time), R is the prey
 81 concentration (biomass per volume), and β is the ‘instantaneous rate of prey discovery’ or
 82 maximum clearance rate (volume per time). Assume that the zooplankter feeds only a fraction of
 83 the time, p (non-dimensional foraging effort), and that p vary in response to food availability and
 84 predation risk in order to optimize the zooplankter’s fitness. The foraging effort, p , modulates the
 85 effective clearance rate ($p\beta$) and the resulting functional response becomes (Werner and Anholt
 86 1993):

87
$$F(p) = F_{max} \frac{p\beta R}{p\beta R + F_{max}} \quad (2)$$

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

92
$$F(p) = F_{max} p \frac{\beta R}{\beta R + F_{max}} \quad (3)$$

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

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

$$99 \quad \text{Metabolism } M(p) = m_0 + pm_f \quad (4)$$

$$100 \quad \text{Mortality } \mu(p) = \mu_0 + p\mu_f \quad (5)$$

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

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

$$119 \quad \frac{F(p) - M(p)}{\mu(p)} \quad \text{for } F - M \geq 0$$

$$120 \quad (6)$$

$$121 \quad F(p) - M(p) \quad \text{for } F - M < 0 \quad (7)$$

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

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

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

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

$$131 \quad R_c = \frac{F_{\max}(m_0 + m_f)}{F_{\max} - m_0 - m_f} \frac{1}{\beta}. \quad (9)$$

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

$$135 \quad R_0 \approx \frac{m_f}{\beta}. \quad (10)$$

136 Note that this result is general, i.e., it does not rely on the cost of feeding effort being linear in p
 137 (eq. 4) since m_f is the feeding cost of feeding at the maximal rate. Using these fitness measures and

138 depending on the magnitude of the tradeoffs, the model predicts that feeding effort (p) is highest at
139 intermediate prey concentrations, and declines at both lower and higher concentrations (Fig. 1A),
140 which results in a type III functional response (Fig 1C). It also predicts that the feeding effort is
141 further reduced in the presence of predators (compare black and grey lines). Specifically, for an
142 ambush feeder, since $\mu_f = m_f = 0$ we would not expect a feeding threshold but predict that $p = 1$
143 and independent prey concentration and, hence, a type II functional response (dashed lines in Fig.
144 1).

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

150 *Parameter estimates:* Based on observations in Kiørboe et al. (1985) we provide rough estimates of
151 F_{max} ($0.65 \mu\text{g C } (\mu\text{g dry body weight})^{-1}\text{d}^{-1}$), β ($1.65 \text{ mL } (\mu\text{g dry body weight})^{-1}\text{d}^{-1}$), m_0 ($0.015 \mu\text{g C}$
152 $(\mu\text{g dry body weight})^{-1}\text{d}^{-1}$), and m_f ($0.1 \mu\text{g C } (\mu\text{g dry body weight})^{-1}\text{d}^{-1}$) for one of the study species,
153 *Acartia tonsa*, feeding on one of the prey, *Rhodomonas baltica*. The two metabolic rate estimates
154 were taken as starvation metabolism (m_0) and maximum metabolism (m_f) of feeding individuals,
155 respectively. The latter includes also the cost of processing and metabolizing the food and we added
156 also losses to defecation, which are not strictly ‘costs of feeding’. We have no estimates of mortality
157 rates for the study species but assume $\mu_0 = \mu_f = 0.05 \text{ d}^{-1}$. This implies a mortality rate of $\sim 0.1 \text{ d}^{-1}$
158 for a small, feeding copepod in the ocean, a magnitude typical for mm-sized feeding-current feeding
159 copepods (Hirst and Kiørboe 2002).

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

162

163 **Experimental organisms**

164 We quantified feeding behavior and feeding rate as a function of prey concentration in the adult
165 females of 4 species of copepods: an ambush feeder, *Oithona davisae* (cephalothorax length 0.3
166 mm), a copepod that can switch between ambush and active feeding, *Acartia tonsa* (0.8 mm), and
167 two species that are obligate active feeders, *Temora longicornis* (0.8 mm) and *Centropages*
168 *hamatus* (1.0 mm). *A. tonsa* generates a feeding current when offered small prey, and acts as an
169 ambush feeder when offered large, motile prey (Jonsson and Tiselius 1990). All copepods were
170 taken from our continuous cultures; the two first species were from our long-term cultures (> 10
171 years), the latter two had been in culture for < ½ year. We used three different types of prey, the
172 flagellate *Rhodomonas baltica* (6.5 µm equivalent spherical diameter) and the dinoflagellates
173 *Oxyrrhis marina* (16.5 µm) and *Akashiwo sanguinea* (42 µm), all in exponential growth. We did not
174 do all possible predator-prey combinations, and some data were taken from our earlier work (Table
175 1).

176

177 **Measures of foraging effort**

178 The active feeders beat their cephalic appendages to generate a feeding current and/or to propel
179 themselves through the water during shorter or longer ‘feeding bouts’ (Tiselius and Jonsson 1990)
180 and we used the fraction of time that the organism beats the appendages as the main measure of
181 foraging effort, but note that some minimum beat-activity may be necessary to keep the copepod
182 suspended, irrespective of feeding. Additional, but secondary measures of foraging effort are
183 appendage beat frequency and swimming speed. The interpretation of swimming speed is not
184 straightforward, because with a given beat frequency (~ force), a hovering copepod feeds more
185 efficiently than one that cruises through the water, but it also produces a stronger fluid signal and

186 becomes more detectable to rheotactic predators (Kiørboe and Jiang 2013). The ambush feeding *O.*
187 *davisae* only moves the cephalic appendages in connection with prey capture, but relocates
188 occasionally in short, rapid jumps using the swimming legs (Kiørboe et al. 2009); in this species
189 there is no foraging effort and, hence, no measure of foraging effort, but we recorded jump
190 frequency as a measure of activity.

191

192 **Feeding behavior**

193 Adult females were isolated from the cultures and starved overnight. 50 individuals were then
194 added to each observation aquaria (250 mL NUNC bottles) containing fresh food suspension and
195 acclimated for 2 h before filming commenced. We used seven different food concentrations for
196 each prey, including no food (Table 1), selected to yield similar prey biovolume ranges for each
197 prey ($\sim 0\text{-}5 \text{ mm}^3 \text{ L}^{-1}$). Prey concentration was adjusted just prior to filming. We used a high-speed
198 (200 fps), high resolution (1280 x 800 pixels) Phantom v210 camera equipped with optics to yield
199 fields of view ranging between ca. 20x32 and 52x78 mm depending on the size of the copepods.
200 Collimated infrared light was shined through the aquarium toward the camera. Three 27 s sequences
201 were filmed during a 15 min period for each treatment. The water in the aquaria was then replaced
202 with water containing fish smell (see below) and the appropriate prey concentration, and after 5 min
203 the animals were filmed again during the subsequent ca. 15 min.

204 Swimming trajectories were extracted from the movies using the tracking software LabTrack
205 (DiMedia). The movies were analyzed both at 20 Hz to construct time budgets (fraction of time
206 feeding) and estimate event durations (feeding bouts) and speeds (swimming speed), and at 33 or 67
207 Hz to estimate jump frequencies. Between 20 and 150 tracks were analyzed per treatment; in a few
208 cases we retrieved only 10 tracks. The output from the tracking analyses were run through an R-
209 script that distinguished between jump, sinking, and swimming events based on species-specific

210 thresholds that were selected to match what a manual frame-by-frame analysis would yield, but the
211 patterns observed were very robust to choice of thresholds. We finally also estimated appendage
212 beat-frequencies in 1-s long sequences by frame-by-frame analyses of 20 random, active animals
213 per treatment.

214 **Exposure to predation risk**

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

223

224 **Functional response**

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

234 and in most cases also in the microscope. At low prey concentrations electronic counts were always
235 verified by microscopic counts.

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

$$238 \quad F = \alpha\beta e^{1-\alpha/R} \quad , \quad (11)$$

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

245

246 **Literature survey**

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

258 that both metabolism and clearance scale approximately in proportion with body mass in
259 zooplankton (Kiørboe and Hirst 2014), and that the metabolic cost of feeding is likely to be
260 proportional to the clearance rate.

261

262 **Results**

263 **Feeding behavior and functional response**

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

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

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

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

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

312 **Comparison between modelled and observed responses**

313 For actively foraging *A. tonsa* the modelled pattern in foraging effort describes both qualitatively
314 and quantitatively very well the observations, but only when predator presence is assumed (Fig.
315 2C). This resemblance to observations is robust to at least a ± 50 % variation in the magnitude of
316 the default parameters. However, in the absence of a foraging induced predation risk the predicted
317 foraging effort remains 100% at concentrations exceeding the feeding threshold. A decline in
318 foraging effort with increasing prey concentration and in the absence of predators is only predicted
319 to occur at very high prey concentrations, $> 6 \text{ mm}^3\text{L}^{-1}$, far beyond what is examined here and
320 typically found in the ocean, and a pattern in foraging effort that resembles the observed pattern is
321 never achieved with any combination of parameters (Fig. 2C).

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

326 **Feeding and maintenance thresholds**

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

337

338 ***Discussion***

339 **Mechanistic underpinning of the functional response**

340 Overall, there is consistency between the observed feeding behaviors and the measured functional
341 responses for all predator-prey combinations examined here, and the former thus provides a
342 mechanistic underpinning of the latter. We found both type II and type III functional responses
343 among the copepods studied, partly in agreement with the predictions from the optimization model.
344 Type III responses may arise in several ways, including through prey switching in mixed diet
345 environments (Murdoch and Oaten 1975; Elliott 2004; Leeuwen et al. 2007), but here we show that
346 the type III is due to a change in foraging effort with prey concentration. We are unaware of
347 previous reports that provide a direct behavioral underpinning of the observed functional response
348 in copepod or other zooplankton although there are a few studies that have examined how relevant
349 components of feeding behavior vary with prey density. For example, the copepod *Eucalanus*

350 *elongates* spends the highest fraction of time feeding at intermediate prey concentrations, (Price and
351 Paffenhöfer 1986) and a previous study of *A. tonsa* showed that, similarly to clearance rates, the
352 time spent in long feeding bouts peaked at intermediate concentrations of a small diatom (Saiz
353 1994), consistently with our finding. There are also reports that the copepod *Temora longicornis*
354 modifies its swimming speed (Duren and Videler 1995; Van Duren and Videler 1996; Moison et al.
355 2013) or appendage beat frequency (Gill and Poulet 1988) in response to concentration of food or
356 presence of dissolved amino acids or predators. We are unaware of studies in other zooplankton
357 groups. The scarcity of such evidence hampers a complete understanding of the role of zooplankton
358 in pelagic food webs.

359 **Functional response**

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

374 active feeders, contrary to our expectations, have a high resource-independent level of foraging
375 activity and a type II functional response.

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

383 **Induced responses and phenotypic plasticity**

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

394 The lack of a response to predator cues is surprising in light of the commonly documented effect of
395 predator kairomones in freshwater zooplankton, including induction of reduced feeding efforts in
396 freshwater copepods (see reviews by Lass and Spaak 2003; Heuschele and Selander 2014). Our

397 protocol to produce chemical fish cues appear not to deviate from what is typically used in
398 freshwater studies. One may argue that the overnight starvation of the copepods and the only 2 h
399 acclimation to prey concentration prior to behavioral observations may lead to a more bold behavior
400 of the copepod, where the need for food dominates over predator avoidance behavior. Indeed,
401 starvation may result in significantly increased feeding in *Acartia* spp, but the effect is reduced or
402 has disappeared within 100 min of feeding (Tiselius 1998), consistent with gut turnover times at
403 the experimental temperature of just 20-25 min (Kjørboe and Tiselius 1987; Dam and Peterson
404 1988) allowing the animals to fill their guts 5-6 times during the acclimation period. Also, predator
405 avoidance behavior is in fact observed in *A. tonsa* at the high prey concentrations. The lack of
406 response to cues in our experiments is, however, consistent with the almost entirely lack of reports
407 on behavioral effects of kairomones in marine zooplankton and copepods. Thus, Buskey et al.
408 (2012) in a review failed to find evidence of predator-induced responses for marine zooplankton,
409 and only three studies were identified in the review by Heuschele and Selander (2014) in addition to
410 Bjærke et al. (2014), of which only two report effects on feeding-related behavioral changes
411 (reduced swimming speed or reduced gut fullness with predator cues (Van Duren and Videler 1996;
412 Cieri and Stearns 1999). There is also one report that diurnal vertical behavior can be induced by
413 the presence of fish, but the cue that elicited the response was not identified, except that it was not
414 of chemical nature (Bollens and Frost 1989). The literature may be biased towards negative results
415 not being reported, and therefore the scarcity of evidence may thus reflect rarity of responses at
416 ecological time scales. Freshwater systems, in particular smaller lakes and ponds, may vary with
417 respect to the presence of fish predators, while marine systems are all large and interconnected and,
418 hence, always contain planktivorous fish. Thus, adaptations to predator avoidance is commonly
419 found among marine zooplankton, including vertical migration (Ringelberg 2010; Ohman and
420 Romagnan 2016) and reduced feeding during daytime to reduce susceptibility to visual predators

421 (review by Torgersen 2003), but they are typically elicited by light intensity (Stearns 1986; Buskey
422 et al. 1989) or some other proximate cue, not by the actual presence of predators. The apparent lack
423 of phenotypic plasticity may simply reflect the constant need for a behavior that reduces predation
424 risk.

425 **Ecological implications**

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

441 Secondly, the behavior that generates the functional response may have implications beyond prey
442 mortality and grazer growth rates. Specifically, behavioral adaptations to the presence of predators
443 (or their cues) may lead to a behavioral cascade and a ‘landscape of fear’ (Suraci et al. 2016), where
444 grazing and growth rates are determined as much by the presence of predators as by the availability

445 of food, as demonstrated in freshwater zooplankton (Gliwicz and Maszczyk 2007) and many other
446 organisms. The scarcity of predator-induced behavioral responses in copepods and other marine
447 zooplankton suggests that ‘behavioral cascades’ are less important in controlling marine planktonic
448 systems than what has been demonstrated for higher trophic levels in freshwater systems (Romare
449 and Hansson 2003; Biro et al. 2005) and assumed in models (e.g., Visser 2007).

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

463

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468

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639 **FIGURE LEGENDS**

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

645 **Fig. 2.** *Acartia tonsa* feeding on *Rhodomonas baltica* as a function of cell density in the presence
 646 and absence of fish cues. A. Foraging effort (% time swimming); D. Feeding bout duration; C.
 647 Modelled foraging effort at various values of predator induced mortality risk and metabolic costs of
 648 feeding. The black line is for the default parameters estimated from (Kiørboe et al. 1985); E.
 649 Swimming speed; C and F. Observed clearance and ingestion rates, from Kiørboe et al. (1985); The
 650 curves are fits of a type III functional response model to the data with $\alpha = 0.58 \pm 0.04$, $\beta = 12.4 \pm 0.6$,
 651 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
 652 coefficients with standard error). Experimental values are given as averages \pm 95 % Confidence
 653 limits.

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

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

662 $F_{\max} = 11.6 \pm 2.4$, $\beta = 46.6 \pm 32.7$, and $R^2 = 0.28$ (panel F). Values of behavioral parameters are given
663 as averages $\pm 95\%$ Confidence limits; clearance and ingestion rates are individual values (grey) and
664 averages (black).

665 **Fig. 5.** Feeding thresholds (R_0) and maintenance threshold (R_c) estimated for pelagic copepods with
666 a 'active' (black symbols) and 'passive' (grey symbols) feeding strategies. Maximum clearance (β)
667 and ingestion (F_{\max}) rates were estimated from literature data on functional responses (see Online
668 Appendix 1), and we assumed body mass specific metabolic cost of feeding of ($m_f = 0.1 \mu\text{g C (mg}$
669 $\text{dry body weight)}^{-1}\text{d}^{-1}$) $\sim 0.01 \mu\text{g C (mg body C)}^{-1}\text{h}^{-1}$) identical to that estimated for *A. tonsa*. A:
670 Frequency distribution of feeding thresholds threshold for active feeders; B: Frequency distribution
671 of maintenance thresholds for active and passive feeders; C: Feeding threshold as a function of the
672 prey:predator carbon-mass ratio for active feeders; the regression line is $\log(R_0) = -1.1 - 0.22 \text{ Log}$
673 $(\text{prey:predator mass ratio})$; $R^2 = 0.35$, $n = 182$; D: Maintenance thresholds as a function of the
674 prey:predator carbon-mass ratio for active and passive feeders; the regression line is $\log(R_0) = -1.0$
675 $- 0.18 \text{ Log}(\text{prey:predator mass ratio})$; $R^2 = 0.19$, $n = 209$.

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

679

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

680

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682

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

683

684 Table 2. Summary statistics of behaviors for copepod-prey (± Fish) combinations where behavior is

685 (near) independent on prey concentration and prey type. Values given are averages ± 95 %

686 Confidence limits. All the data have been plotted in Online Appendix 2.

687

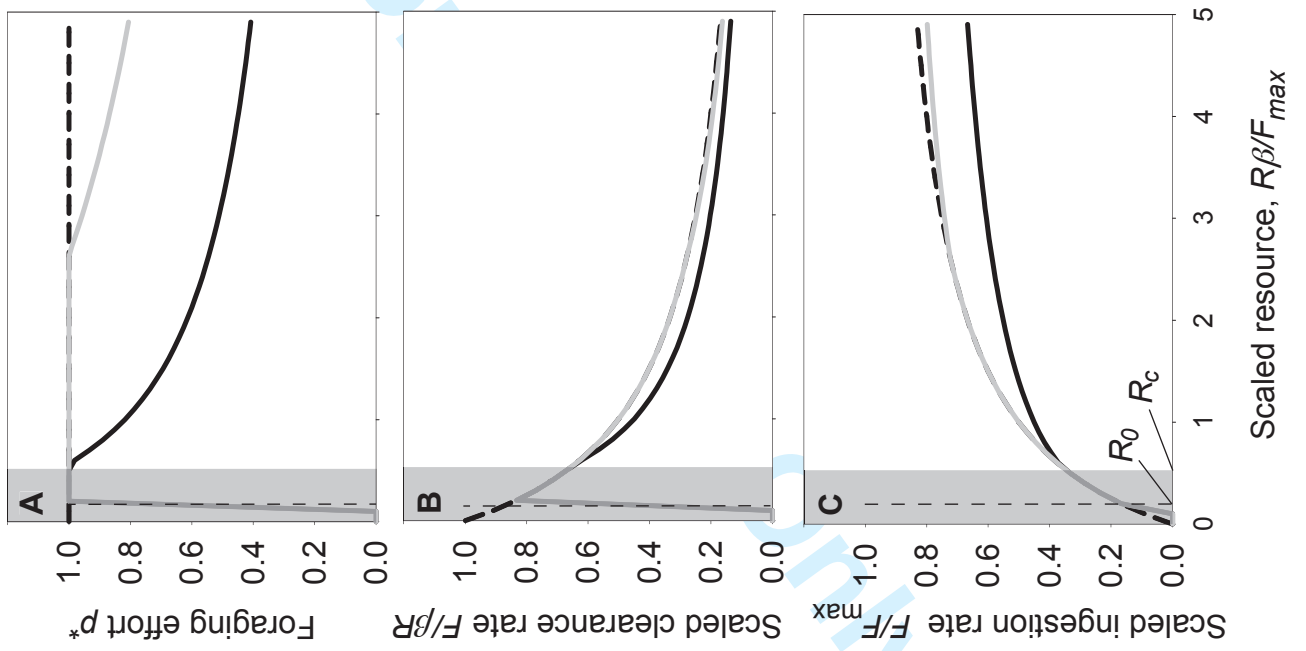


Fig. 1

Fig 2

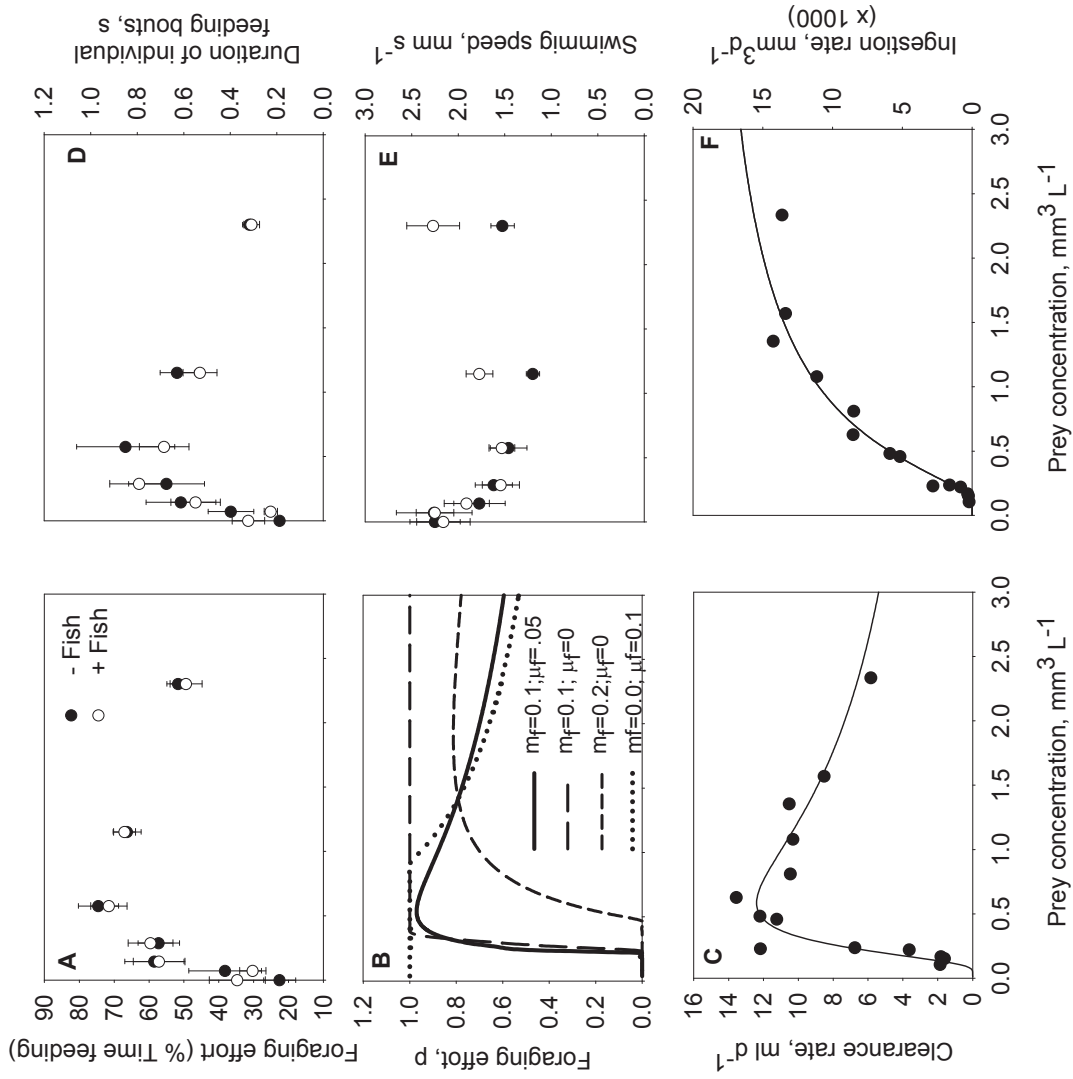


Fig. 3

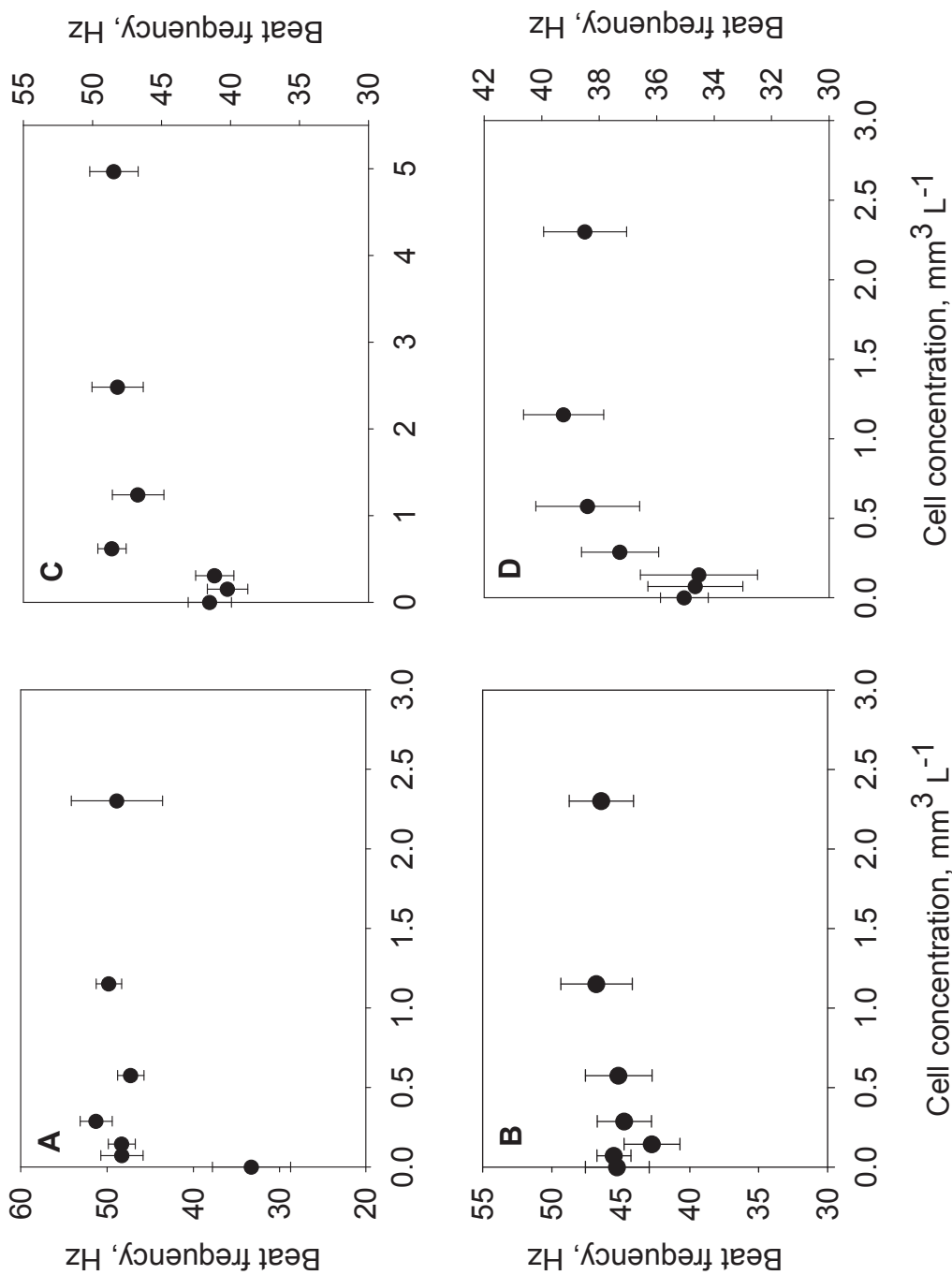


Fig. 4

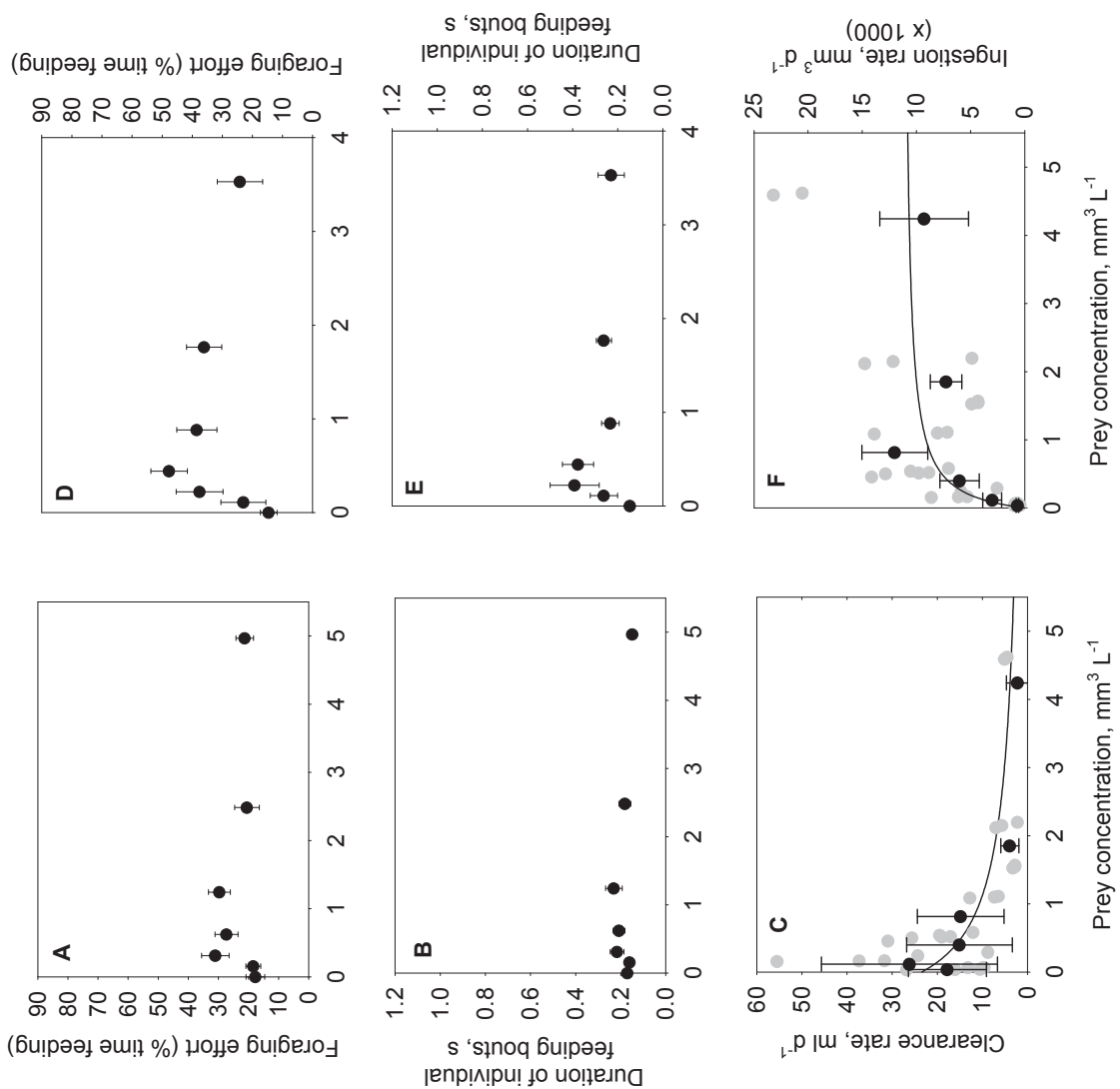
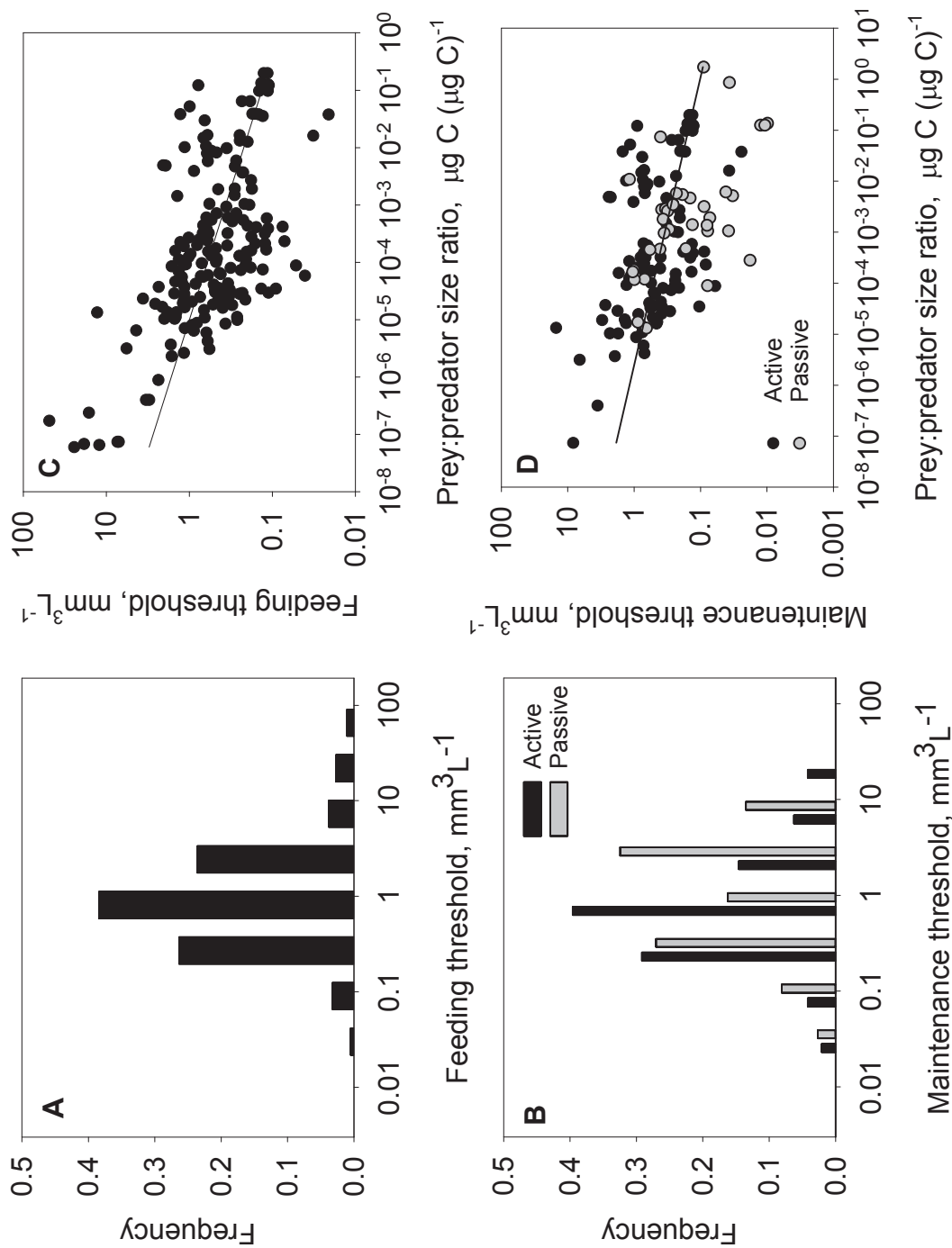


Fig. 5



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	$\mu\text{g C h}^{-1}$	ml h^{-1}	$\mu\text{gC}(\mu\text{gC})^{-1}$	$\text{mm}^3 \text{L}^{-1}$	$\text{mm}^3 \text{L}^{-1}$	
<i>Acartia grani</i> naupl	<i>Heterocapsa</i> sp	Ambush	II	20	0.040	0.00137	0.0094	0.0047		0.143	(Henriksen et al. 2007)
<i>Acartia grani</i> naupl	<i>Thalassiosira weisflogii</i>	Ambush	II	20	0.040	0.00108	0.0072	0.0055		0.185	(Henriksen et al. 2007)
<i>Acartia tonsa</i>	<i>Strombidium sulcatum</i>	Ambush	II	18	3.000	0.10638	5.6141	0.00028		0.018	(Saiz and Kiørboe 1995)
<i>Corycaeus angelicus</i>	<i>Acartia clausi</i> male	Ambush	II	11	2.400		0.2412	0.9375			(Landry et al. 1985)
<i>Oithona davisae</i>	<i>Isochrysis galbana</i>	Ambush	II	18	0.390	0.00106	0.0150	0.00002		0.871	(Saiz et al. 2014)
<i>Oithona davisae</i>	<i>Tetraselmis chunii</i>	Ambush	II	18	0.384	0.00557	0.0130	0.00012		0.987	(Saiz et al. 2014)
<i>Oithona davisae</i>	<i>Heterocapsa</i> sp.	Ambush	II	18	0.368	0.01813	0.0303	0.00047		0.405	(Saiz et al. 2014)
<i>Oithona davisae</i>	<i>Prorocentrum minimum</i>	Ambush	II	18	0.375	0.01417	0.0218	0.00046		0.575	(Saiz et al. 2014)
<i>Oithona davisae</i>	<i>Oxyrrhis marina</i>	Ambush	II	18	0.336	0.01928	0.1416	0.00138		0.079	(Saiz et al. 2014)
<i>Oithona davisae</i>	<i>Scrippsiella trochoidea</i>	Ambush	II	18	0.389		0.0452	0.00192			(Saiz et al. 2014)
<i>Oithona davisae</i>	<i>Prorocentrum micans</i>	Ambush	II	18	0.383		0.0653	0.00338			(Saiz et al. 2014)

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

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

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

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

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

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

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

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

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

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

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

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

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

<i>Tortanus</i> spp male	<i>Oithona davisae</i> CV-VI	Active	(II)	25	3.40	0.04616	1.4688	0.06471	0.231489	0.268	(Uye and Kayano 1994b)
<i>Tortanus</i> spp male	<i>Oithona davisae</i> 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 °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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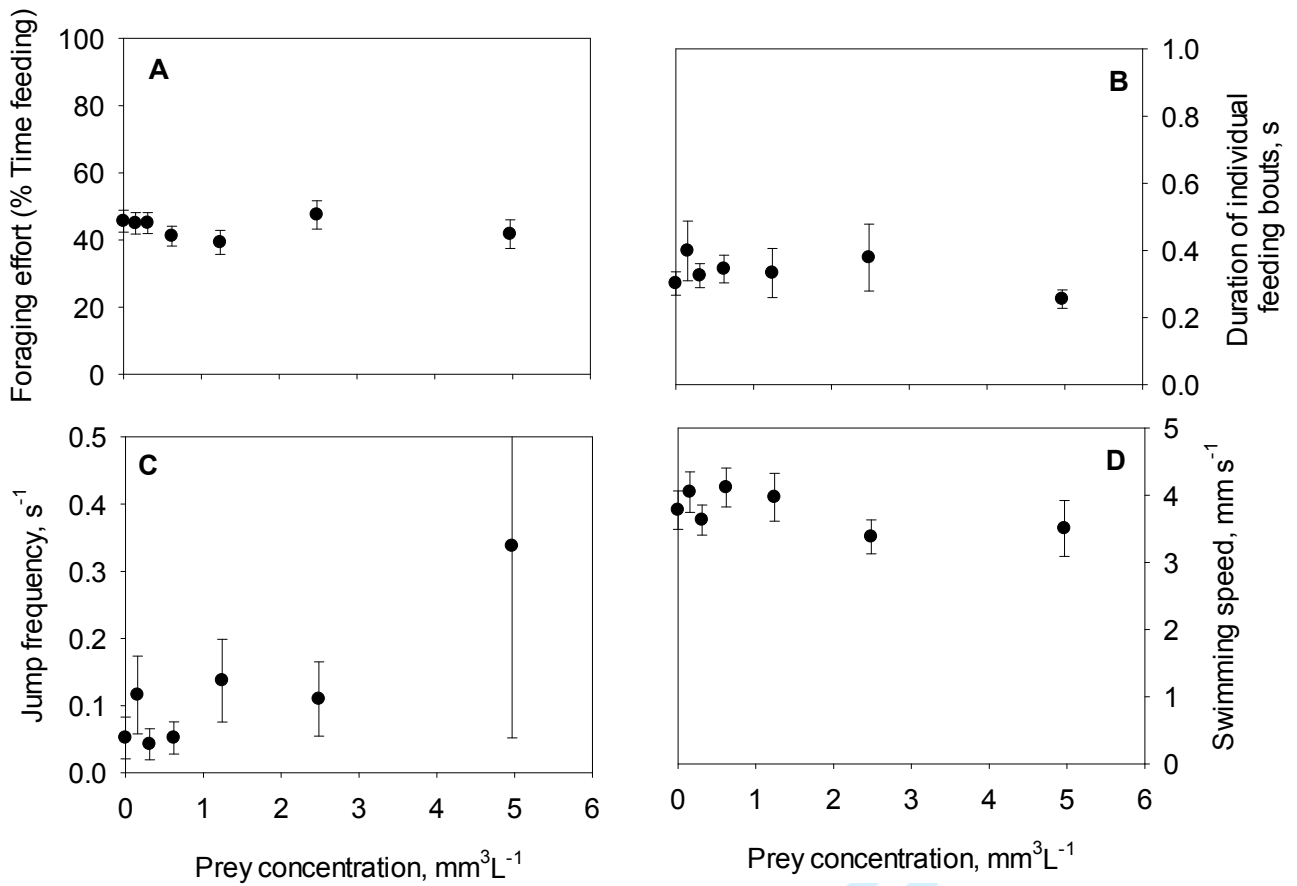
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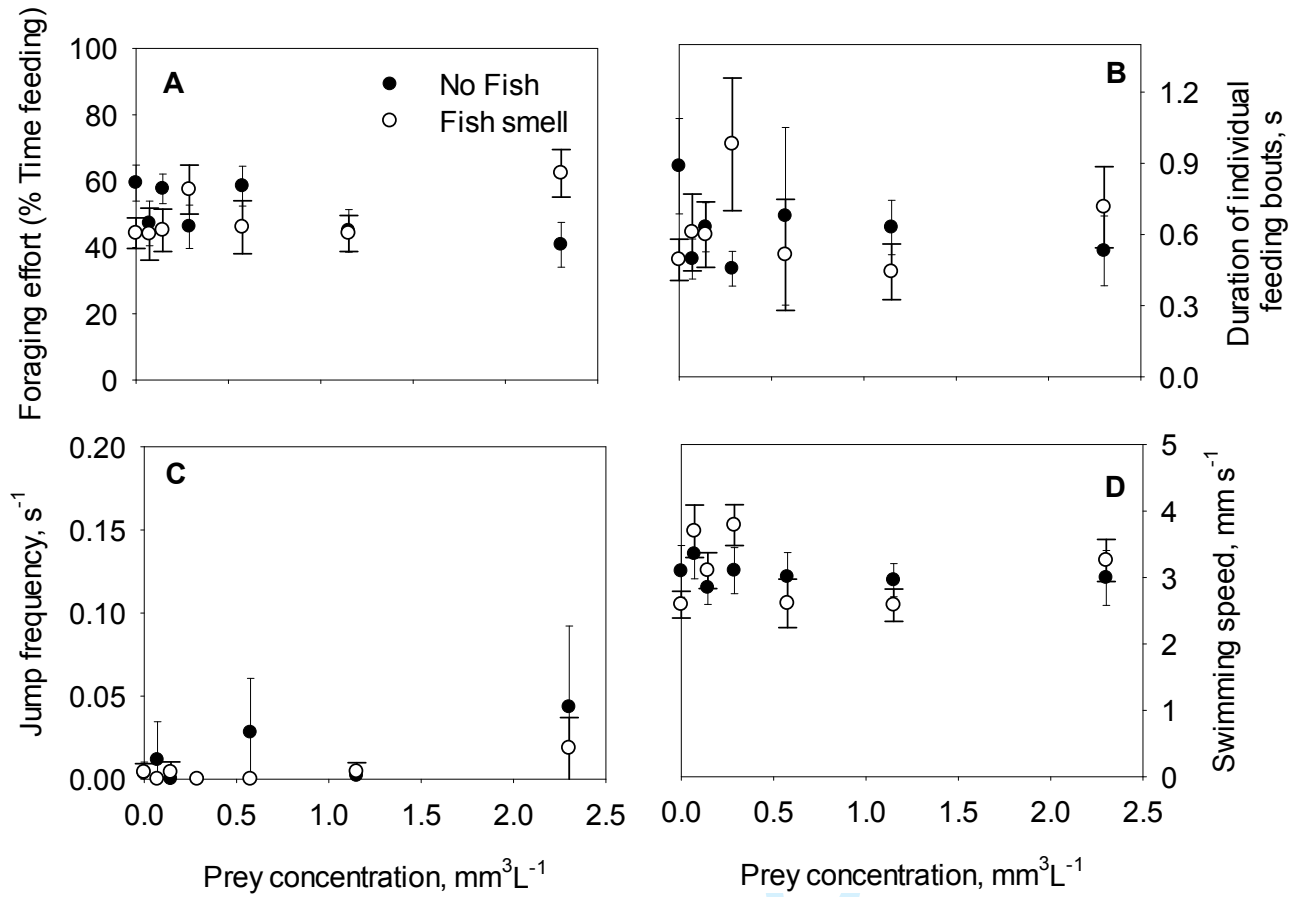
Online Appendix II

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

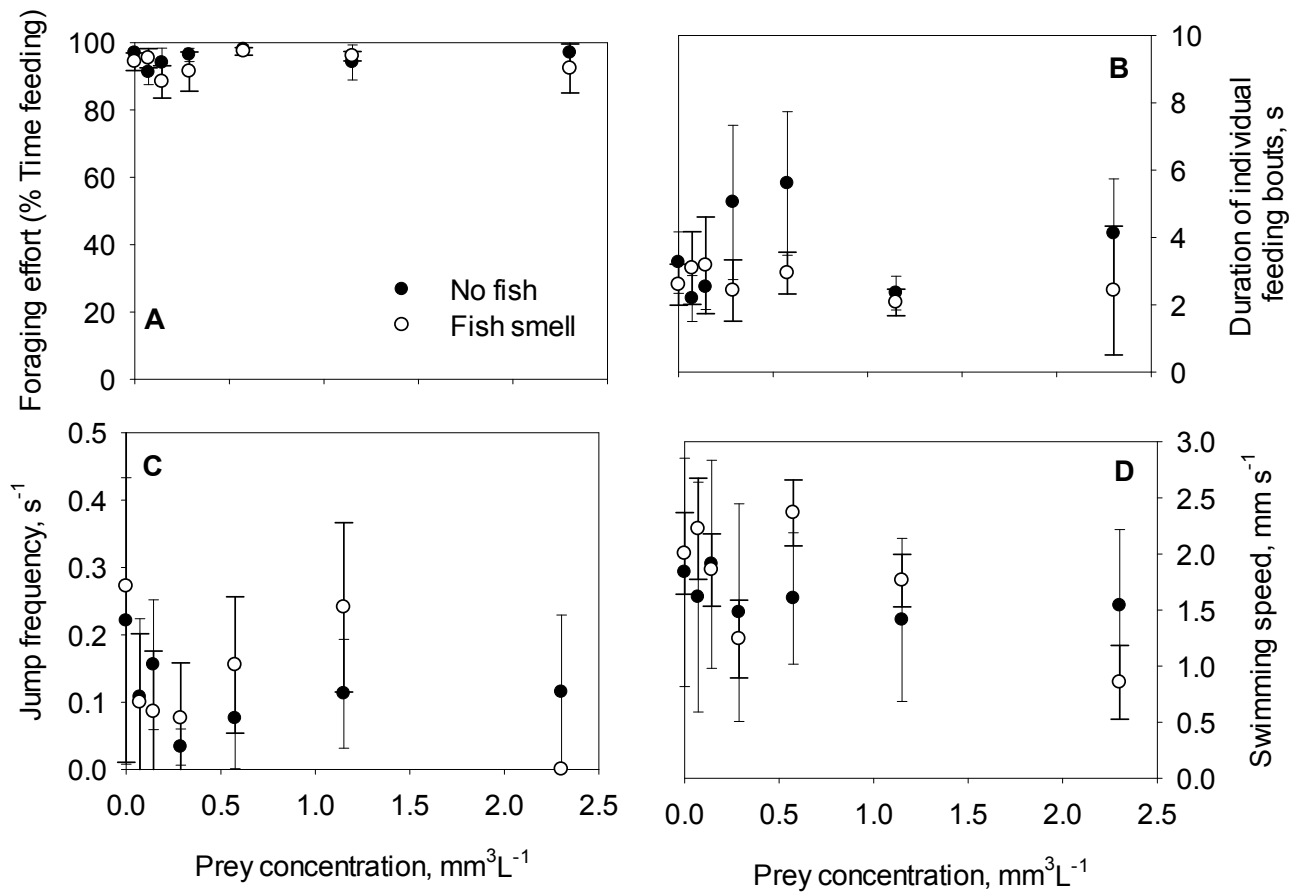
Appendix Fig. 1. *Centropages hamatus* feeding on *Akashiwo sanguinea*. All values are averages \pm 95 % confidence limits.



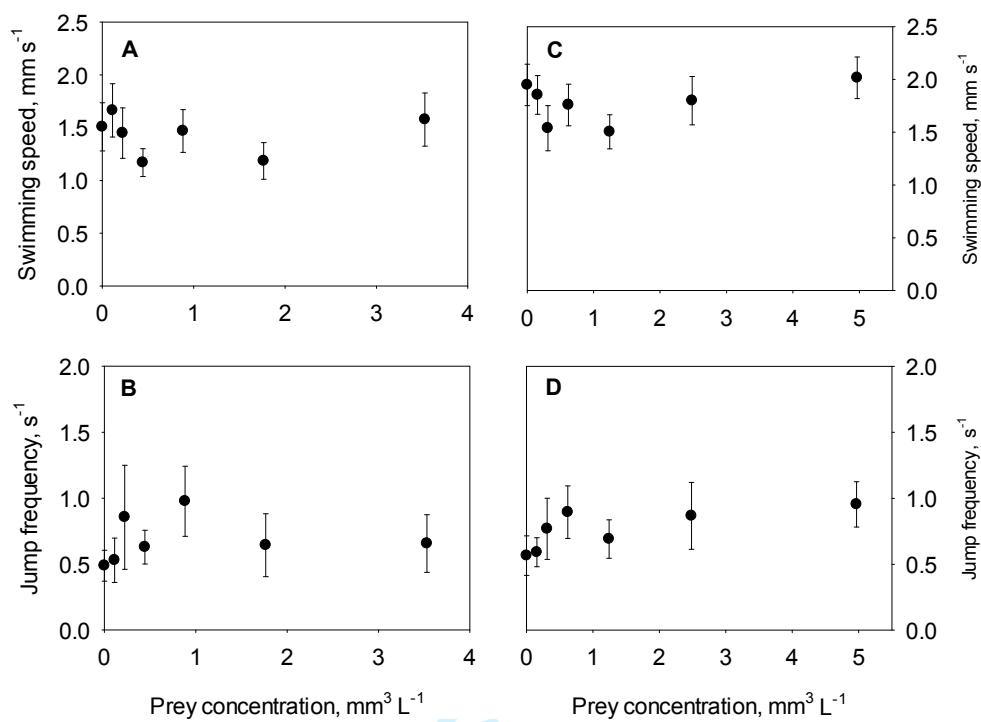
Appendix Fig. 2. *Centropages hamatus* feeding on *Rhodomonas baltica*. All values are averages \pm 95 % confidence limits.



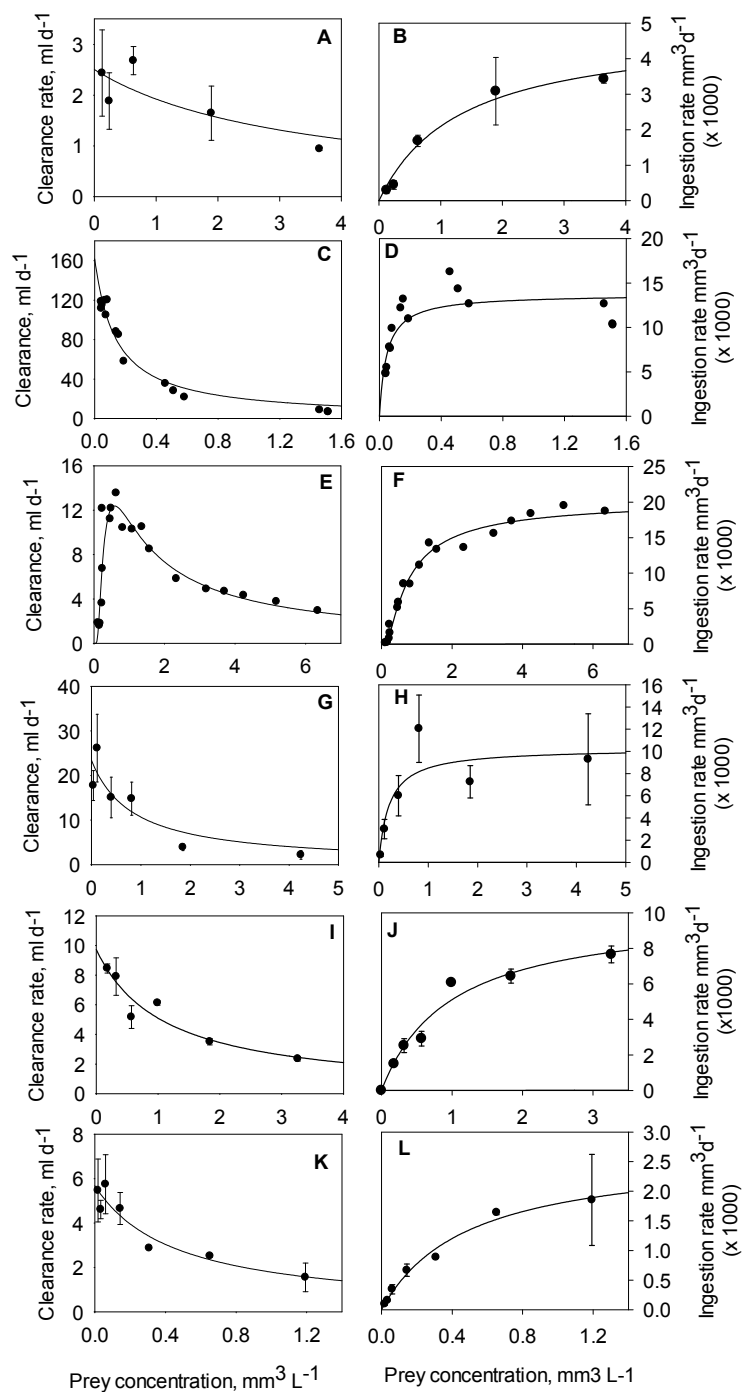
Appendix Fig. 3. *Temora longicornis* feeding on *Rhodomonas baltica*. All values are averages \pm 95 % confidence limits.



Appendix Fig. 4. *Acartia tonsa* feeding on *Oxyrrhis marina* (A,B) and *Akashiwo sanguinea* (C, D). All values are averages \pm 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 Grève, 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
<i>Centropages hamatus</i>	<i>Rhodomonas baltica</i>	$F_{\max} = 8.3 \pm 4.9$ $\beta = 2.5 \pm 0.4$ $R^2 = 0.68$	$F_{\max} = 4.9 \pm 0.65$ $\beta = 3.7 \pm 0.8$ $R^2 = 0.97$
<i>Centropages hamatus</i>	<i>Akashiwo sanguinea</i>	$F_{\max} = 22.2 \pm 3.1$ $\beta = 162 \pm 13$ $R^2 = 0.96$	$F_{\max} = 13.7 \pm 1.0$ $\beta = 290 \pm 79$ $R^2 = 0.67$
<i>Acartia tonsa</i>	<i>Rhodomonas baltica</i>	$\alpha = 0.58 \pm 0.04$ $\beta = 12.4 \pm 0.62$ $R^2 = 0.83$	$\alpha = 0.61 \pm 0.04$ $\beta = 12.1 \pm 0.60$ $R^2 = 0.98$
<i>Acartia tonsa</i>	<i>Akashiwo sanguinea</i>	$F_{\max} = 10.7 \pm 2.7$ $\beta = 9.7 \pm 1.1$ $R^2 = 0.90$	$F_{\max} = 10.1 \pm 1.1$ $\beta = 10.3 \pm 1.9$ $R^2 = 0.97$
<i>Temora longicornis</i>	<i>Rhodomonas baltica</i>	$F_{\max} = 2.6 \pm 0.6$ $\beta = 5.7 \pm 0.4$ $R^2 = 0.91$	$F_{\max} = 2.7 \pm 0.3$ $\beta = 5.5 \pm 0.7$ $R^2 = 0.99$
<i>Oithona davisae</i>	<i>Oxyrrhis marina</i>	$F_{\max} = 19.6 \pm 10.0$ $\beta = 23.4 \pm 3.9$ $R^2 = 0.81$	$F_{\max} = 19.6 \pm 10.0$ $\beta = 23.4 \pm 3.9$ $R^2 = 0.81$