Prey perception mechanism determines maximum clearance rates of planktonic copepods

Behavior-dependent clearance rates in planktonic copepods

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3 Prey perception mechanism determines maximum clearance rates of planktonic copepods

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12 Running head: Behaviour-dependent clearance rates in planktonic copepods

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15 **Key words:** Zooplankton, Foraging strategies, Feeding behaviour, Maximum clearance rates, Trade-
16 offs.

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25 **Abstract**

26 The ecological consequences of “sit-and-wait” (ambushing) vs “searching” (active feeding)
27 foraging strategies are not well understood in marine plankton food webs. We determined the
28 maximum clearance rates of ambush and active feeders to evaluate the trade-off between foraging
29 gain and predation risk associated with the main foraging strategies in planktonic copepods. We
30 show that maximum clearance rates are similar among feeding behaviours for motile prey but one
31 order of magnitude lower for ambush than for active feeders towards non-motile prey. The prey size
32 spectrum is narrower and towards relatively larger prey in ambushers compared to active feeders.
33 Prey detection in ambushers relies on the hydrodynamic disturbances and is inefficient towards
34 non-motile prey but highly efficient for large motile prey. The effective prey perception mechanism
35 in ambushers compensates for the lower prey encounter velocity in ambush feeding copepods
36 compared to active feeding copepods. Therefore, ambushers are more restricted in target prey than
37 active feeders and prey perception mechanism determines the efficiency of planktonic copepod
38 foraging strategies. The lower clearance rates of ambush feeders on non-motile prey is compensated
39 for by a lower predation risk, which can partially explain the coexistence of both “high-gain &
40 high-risk” (active feeders) and “low-gain & low-risk” (ambush feeders) foraging strategies in
41 marine plankton food webs.

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47 **Introduction**

48 Zooplankton grazing is a pivotal biological process in the transfer of matter from lower to higher
49 trophic levels in the sea (Banse 1995). Knowledge of zooplankton predator-prey interactions is
50 therefore essential to understand the structure and dynamics of marine food webs. Traditionally,
51 models of pelagic food webs quantify interactions between taxonomic groups or functional types,
52 but attempts to embrace the inherent complexity of marine food webs make these models very
53 complex (Anderson 2005; Flynn 2005). An alternative approach in marine plankton ecology, the
54 trait-based approach, proposes to replace the many species with individuals that are characterized
55 by a few key traits that are interrelated through trade-offs (i.e., costs and benefits of a particular
56 trait) (Kiørboe 2011; Litchman et al. 2013). The key traits are those few properties that capture most
57 of the Darwinian fitness of an organism. Identifying the key traits and quantifying their associated
58 trade-offs in zooplankton will increase our ability to understand and predict the structure and
59 function of plankton food webs (Litchman et al. 2013; Benedetti et al. 2015; Hébert et al. 2016).
60 Foraging strategy is central to the success of copepods and must thus be considered a key trait
61 (Kiørboe 2011; Litchman et al. 2013).

62 Suspension-feeding zooplankton have three main ways of obtaining food: they can be (1)
63 “ambush feeders” that wait motionless for motile prey to pass within their sensory reach or capture
64 those prey that directly collide (Jiang and Paffenhöfer 2008; Kiørboe 2011, 2016), (2) “feeding-
65 current feeders” that hover while generating a feeding current and harvest prey that are entrained in
66 the current (Strickler 1982, 1985; Kiørboe 2011), or (3) “cruising feeders” that cruise through the
67 water and capture encountered prey (Tiselius and Jonsson 1990; Kiørboe 2011). These feeding
68 behaviours can be broadly classified into two main foraging strategies: “sit-and-wait” (ambushing)
69 vs. “searching” (active feeding). Some copepod species can switch between feeding behaviours
70 (“mixed feeding behaviour”) depending on prey type or/and food availability (Landry 1981;

71 Tiselius and Jonsson 1990; Kiørboe et al. 1996). This classification of feeding behaviours and
72 foraging strategies applies across taxonomic groups, from small flagellates to large gelatinous
73 zooplankton, and the different foraging modes are expected to have different benefits in terms of
74 ability of obtaining food (foraging gain) and different costs in terms of mortality (predation risk)
75 and metabolic expenses (Kiørboe et al. 2010, Abrams 2003). We have previously quantified the
76 different costs associated with the main foraging behaviours in zooplankton through theoretical
77 models and experimental testing, particularly mortality costs due to predation (Kiørboe et al. 2010;
78 Kiørboe et al. 2014; Almeda et al. 2017; van Someren Gréve et al. 2017a). Here we aim at
79 quantifying the benefits of the same foraging behaviours, specifically to quantify maximum
80 clearance rates, to achieve a fuller understanding of the trade-offs of zooplankton small-scale
81 foraging behaviours.

82 Zooplankton feeding has been extensively studied in both the laboratory and the field and
83 experimental studies have focused mainly on the effect of grazer and prey size and food
84 concentration (Harris and Paffenhöfer 1976; Ikeda 1977; Hansen et al. 1997; Saiz and Calbet 2007;
85 Almeda et al. 2010a; Gonçalves et al. 2014; Helenius and Saiz 2017), while none have compared
86 thoroughly the clearance efficiency of the different feeding behaviours/foraging strategies .
87 Differences in methods and environmental conditions among previous studies complicate direct
88 comparisons of maximum clearance rates in zooplankton feeding behaviours. Theoretical analyses
89 by Kiørboe (2011) suggest that feeding-current feeding (hovering) is the most efficient behaviour
90 and ambush feeding the least efficient in terms of volume of water cleared. Specifically, ambush
91 feeding is expected to be ~3–10 times less efficient than the active foraging behaviours, mainly
92 because the predator-prey encounter is higher when due to the predator velocity than to a smaller
93 prey velocity (Kiørboe 2011). In addition, ambush-feeding copepods depend on the fluid
94 disturbance generated by motile prey to perceive the prey (Kiørboe et al. 1999; Kiørboe and Visser

1999) and are therefore expected to be inefficient on non-motile prey and prey that does not create a sufficiently strong hydromechanical signal (Jiang and Paffenhöfer 2008; Kiørboe 2011; Henriksen et al. 2007; Saiz et al. 2014).

Here, we experimentally test the hypotheses that (i) ambush feeders are less efficient than the active feeders (feeding-current and cruising feeders) in acquiring resources, and (ii) that ambushers are particularly poor in collecting non-motile prey (Fig.1). We quantify the functional feeding responses, i.e., the changes in feeding rates as a function of food concentration (Holling 1959), of copepod nauplii and copepodites displaying the three main feeding strategies, to estimate maximum clearance rates of each strategy. We use prey of different size and motility to estimate the influence of these aspects on maximum clearance rates. Our results are relevant to quantify the gain over risk of the main zooplankton feeding strategies (Kiørboe 2011) and help to understand the spatiotemporal distribution and coexistence of the different zooplankton foraging strategies in marine environments (Barton et al. 2013; Brun et al. 2016).

Methods

Experimental organisms.

Nauplii and copepodites of *Oithona nana* (ambush feeders, Kiørboe 2011), *Temora longicornis* (feeding-current feeder, Kiørboe 2011), and *Centropages hamatus* (cruising feeder, Kiørboe 2011; Tiselius and Jonsson 1990) were used as model organisms for the three main feeding strategies in zooplankton (Table 1). *O. nana* is a strict ambush feeder during all its development. All *T. longicornis* life stages are feeding-current feeders. *C. hamatus* nauplii are strict cruising feeders without generating a feeding-current while the copepodites are considered cruising feeders that can also generate a feeding-current. The three experimental species were also selected because they are common and abundant in coastal waters (Razouls et al. 2005; Temperoni et al. 2010; Martynova et

119 al. 2011), play important ecological roles in food webs (Lampitt 1978; Casini et al. 2004), and can
 120 be reared in the laboratory. Description of the motile behaviours of the experimental stages can be
 121 found in van Gréve Someren et al. (2017a). We used four different prey in the experiments: the
 122 cryptophyte flagellate *Rhodomonas salina*, the diatom *Thalassiosira weissflogii*, the heterotrophic
 123 dinoflagellate *Oxyrrhis marina* and the mixotrophic dinoflagellate *Akashiwo sanguinea* (Table 1).
 124 *R. salina*, *T. weissflogii* and *A. sanguinea* cultures were kept in exponential growth in B1 culture
 125 medium (Hansen 1989) and maintained at 18°C and on a 12:12-h light/dark cycle in glass flasks. *O.*
 126 *marina* was fed on the *R. salina* and maintained at 18°C in 2-L glass bottles in dark.
 127 The copepods were grown in continuous laboratory cultures in 30- and 100-L plastic tanks at ~15–
 128 18°C in dark. Specimens of *O. nana*, *T. longicornis* and *C. hamatus* were originally isolated from
 129 the Port of Gijón (Cantabrian Sea, Spain), the Øresund strait (North Sea, Denmark) and the
 130 Skagerrak (North Sea, Sweden), respectively. *O. nana* cultures were fed on the heterotrophic
 131 dinoflagellate *O. marina ad libitum*. *T. longicornis* and *C. hamatus* cultures were fed with mixed
 132 cultured phytoplankton (*R. salina*, *T. weissflogii*, *Heterocapsa triquetra*, *Prorocentrum minimum*,
 133 *A. sanguinea* in a proportion of 1, 0.4, 0.2, 0.1 and 0.1, respectively), and in the case of *C. hamatus*,
 134 also with *O. marina*.
 135 To obtain cohorts of *O. nana*, *T. longicornis*, and *C. hamatus*, we separated adults from the stock
 136 culture with 125- or 200-µm-mesh sieves and placed them separately in a new tank. After 48 h,
 137 adults were removed with a 100- or 200-µm-mesh sieve, and eggs/hatched nauplii were transferred
 138 to a new tank with food *ad libitum*. We let nauplii grow until the desired stage/length was reached
 139 (Table 1).
 140 *Functional feeding response experiments*
 141 We determined feeding rates of nauplii and copepodites with different feeding behaviour using four
 142 different prey offered separately (Table 1). Functional response curves were obtained by

quantifying feeding rates at five different prey concentrations using bottle incubations (Frost 1972). Before starting the experiments, *T. weissflogii* stock culture was filtered through 12- μ m mesh to remove any cell aggregates. *O. marina* was not fed four days prior to the experiment to avoid the presence of *R. salina* in the experiment. We verified the absence of *R. salina* in the *O. marina* culture using a coulter counter and an inverted microscope before starting experiments. For each experiment, total body length of nauplii and prosome length in copepodites were measured in 30 individuals (Table 1). Length measurements were converted to carbon weight using the equations of Klein Breteler et al. (1982) for *T. longicornis* and *C. hamatus* and of Almeda et al. (2010b) for *O. nana* (Table 1). Prey size (equivalent spherical diameter, ESD, μ m) and prey concentrations (cells mL⁻¹) of the stock cultures were determined at the start of each experiment using a Beckman Multisizer III Coulter Counter. Cell volumes were converted to carbon content according to Pelegri et al. (1999) for *O. marina*, Henriksen et al. (2007) for *T. weissflogii*, Menden-Deuer and Lessard (2000) for *A. sanguinea* and Montagnes et al. (1994) for *R. salina*. Prey suspensions were prepared by successive dilution of the highest food concentration with 0.2 μ m filtered seawater and amended with growth medium (1 mL L⁻¹) to avoid differential phytoplankton growth between treatments due to nutrient excretion by copepods. For each prey concentration, bottles (35-68 mL) were filled with the corresponding prey suspension. For each concentration, 3 bottles were used to determine the initial prey concentration (“initials”), 3 bottles were used to determine prey growth rates during the incubation without copepods (“control bottles”) and 3 bottles with copepods served as experimental treatments (“experimental bottles”). Nauplii and copepodites were either picked individually under a stereomicroscope or, in most of the cases, concentrated using a 40 μ m mesh-sieve, counted and added as aliquots to the experimental bottles. The number of nauplii and copepodites added to the experimental bottles varied depending on copepod species, prey type and prey concentration (Table 1) and the grazer concentrations were

167 chosen to ensure a reduction of ~30 % in prey concentration during incubation according to
 168 previous studies (e.g., Almeda et al. 2010a; Saiz et al. 2014; Helenius and Saiz 2017). The
 169 experimental and control bottles were mounted on a rotating wheel (0.4 rpm) and incubated at 15°
 170 C for ~24 h in dark.

171 After incubation, the bottle contents were filtered through a 40-µm mesh and nauplii and
 172 copepodites were checked for mortality and fixed with 1% Lugol's solution. The mortality of
 173 nauplii and copepods was negligible and initial nominal grazer concentrations were considered for
 174 the calculations. Samples from initials, experimental, and control bottles were fixed with 1%
 175 Lugol's solution. Prey concentration in each sample was determined under an inverted microscopy
 176 using Sedgewick-Rafter counting chambers (1 mL) or Utermol settling chambers (5-100 mL)
 177 depending on cell densities to ensure that the entire samples (for low prey concentration) or at least
 178 200 cells were counted.

179 *Calculations*

180 Clearance rates, ingestion rates, and average prey concentration during the incubations were
 181 calculated according to Frost (1972). The functional feeding response of planktonic copepods
 182 commonly follows a type II or III model (Holling, 1959, Kiørboe et al. 2018). The type III
 183 functional response differs from type II in the presence of a 'feeding threshold', i.e., a prey
 184 concentration below which the copepod reduces its clearance rates (Kiørboe et al., 1985, 2018). The
 185 measured clearance rates (F , mL ind.⁻¹ d⁻¹) and ingestion rates (I , cells ind.⁻¹ d⁻¹) in relation to prey
 186 concentration (C , cells mL⁻¹) were fitted to either a Holling functional response type II or type III
 187 model (Kiørboe, 2008a; Schultz and Kiørboe 2009):

$$188 \quad \text{Holling type II:} \quad F = \beta(1 + \beta\tau C)^{-1} \quad (1)$$

$$189 \quad I = \beta C(I + \tau\beta C)^{-1} \quad (2)$$

$$190 \quad \text{Holling type III:} \quad F = (\alpha\beta/C)e^{1-\alpha/C} \quad (3)$$

$$I = \alpha\beta e^{I-\alpha/C} \quad (4)$$

where β is the maximum clearance rate (mL ind.⁻¹ d⁻¹), τ is the prey handling time (d) and α is the prey concentration at the maximum clearance rate. Maximum ingestion rates ($I_{\max}$, cells ind.⁻¹ d⁻¹) were calculated as τ^{-1} (eq. 2) or $\alpha\beta e^1$ (eq. 4). A type III model was fitted to the data when a decrease in clearance rates was observed at the lowest prey concentration, which implies the presence of a “feeding threshold concentration”, (α in equation 3 and 4). When a feeding threshold concentration was absent or unclear, the type of model was chosen based on the best statistical fit by visually inspecting the fitted models on plotted data and by comparing the correlation coefficient (R^2) and standard error (SE) of the estimates from both fits.

Carbon-specific maximum clearance rates (β_s , mL μgC^{-1} d⁻¹) as a function of the prey: predator size ratio (x) were fitted to a Gaussian function:

$$\beta_s = \gamma e^{-0.5[(x-\mu)/\sigma^2]} \quad (5)$$

where γ is the value of maximum β_s (mL μgC^{-1} d⁻¹), μ is the prey: predator size ratio of maximum β_s and σ is the standard deviation.

To compare maximum clearance rates (β) among feeding behaviours depending on body weight (W), we used analysis of covariance (ANCOVA) to test for significant differences in slopes (b) and intercepts (a) among linear regressions fitted to the logarithmically transformed data i.e., $\log(\beta) = a + b \log(W)$. Post hoc Bonferroni test was used for pairwise comparison. All statistical tests were conducted with IBM-SPSS software and a statistical significance level of 0.05 was applied.

210

211 Results

212 Clearance rates of nauplii and copepodites of *O. nana* (ambush feeders, Fig. 2), *T. longicornis*
213 (feeding-current feeders, Fig. 3), and *C. hamatus* (cruising feeder, Fig. 4) varied depending on food
214 concentration following mostly a type III and, in some cases, a type II functional feeding response

215 (Figs. 2-4). Cruising feeders and feeding-current feeders showed type III functional response for all
 216 the prey (Fig. 3 and 4, Table 2) except for *T. longicornis* feeding on *O. marina* (Fig. 3 H-J, Table
 217 2). In ambush feeders, we found both type II and III functional responses depending on the prey
 218 type and copepod stage (Fig. 2, Table 2). Except for nauplii feeding on *O. marina* (Fig. 2 I-K), the
 219 decrease in clearance rates at the lowest concentration in ambush feeders was, however, relatively
 220 low, and even though a functional response type III model was fitted to the data (Table 2), a type II
 221 model fitted the data almost equally well.

222 Ingestion rates increased with increasing prey concentration until, in most cases, reaching saturation
 223 (Fig. 2-4). Saturation of ingestion rates was, however, not clearly observed in some experiments
 224 (Fig. 2 E-H; Fig. 3 H-J, Fig. 4 H-K) and, in these cases, the estimated maximum ingestion rates
 225 (Table 2) should be considered with caution. The lack of saturation was particularly evident in
 226 ambush feeders feeding on diatoms (Fig. 2, E-H). Functional response parameters and carbon-
 227 specific maximum ingestion rates for the different feeding behaviours and prey type are shown in
 228 Table 2.

229 Maximum clearance rates ($\text{mL ind}^{-1} \text{d}^{-1}$) increased with increasing grazer body weight for each of
 230 the four prey (Fig. 5). We did not find significant differences in maximum clearances rates (β)
 231 among feeding behaviours when prey was motile (ANCOVA, $p > 0.05$) (Fig. 5 B-C). However,
 232 maximum clearances rates (β) of ambush feeders were about one order of magnitude lower than for
 233 feeding-current and cruising feeders when non-motile diatoms were offered as food (ANCOVA,
 234 $p < 0.05$) (Fig. 5A). Carbon-specific maximum clearance rates (β_s , $\text{mL } \mu\text{g C}^{-1} \text{d}^{-1}$) varied with the
 235 prey to predator size ratio (Fig. 5 E-G) and the optimal prey to predator size ratio in ambush feeders
 236 (Fig. 5E) was higher and the prey size spectrum narrower than in feeding-current and cruising
 237 feeders (Fig. 5F-G).

238

239 Discussion

240 Since the first video observations of planktonic copepods in the 80s (Alcaraz et al. 1980; Koehl and
241 Strickler 1981; Paffenhöfer et al. 1982), several studies have emphasized the importance of
242 investigating small-scale individual behaviours to attain a better mechanistic understanding of
243 planktonic organisms' interactions and marine food webs dynamics (Henriksen et al. 2007;
244 Kiørboe, 2008, 2011; Kiørboe et al. 2014). Our previous research and others studies on behavioural
245 observations and feeding mechanisms of planktonic copepods (e.g., Price et al. 1983; Kiørboe et al.
246 2009; Kiørboe 2011; Bruno et al. 2012; Cheng et al. 2014; van Someren Gréve et al. 2017a;
247 Gonçalves et al. 2014) allow us to interpret the results obtained here from bottle incubations.

248 *Feeding efficiency of different zooplankton foraging strategies*

249 We found that, in contrast to model predictions (Kiørboe 2011), maximum clearance rate in the
250 three studied behaviours was similar for motile prey with a size range of 7-40 μm and therefore our
251 first hypothesis was rejected. Our hypothesis was based on the fact that prey encounter velocities
252 are higher in active than in ambush feeders, and that clearance rate scales with prey encounter
253 velocity (Kiørboe 2011). However, clearance rates also vary with prey detection distance squared,
254 and therefore even a relatively small increase in prey detection distances in ambushers compared to
255 active feeders may compensate for the lower encounter velocities. Prey are perceived, captured and
256 handled individually by all three feeding behaviours (Price et al. 1983; Kiørboe 2011; Bruno et al.
257 2012) but ambush feeders perceive their prey differently than active feeders. Ambush feeding
258 copepods respond to the fluid disturbance generated by motile prey and thus may perceive their
259 prey at a considerable distance (Svensen and Kiørboe 2000; Kiørboe et al. 2009; Cheng et al. 2014)
260 while active feeders appear rather to perceive their prey as they are touched, or nearly touched, by
261 the setae on the feeding appendages (Uttieri et al. 2008; Tiselius et al. 2013; Gonçalves and Kiørboe
262 2015).

263 Our second hypothesis was confirmed since ambush feeding was clearly an inefficient foraging
 264 strategy for non-motile prey like diatoms. This is in agreement with previous experimental field and
 265 laboratory studies and model predictions (Atkinson 1995; Kiørboe and Visser 1999; Paffenhöfer
 266 and Mazzocchi 2002; Vogt et al. 2013; Henriksen et al. 2007; Saiz et al. 2014; van Someren Gréve
 267 et al. 2017b). Prey motility can affect encounter rates by increasing the relative speed between
 268 predator and prey and by increasing prey detectability by a rheotactic predator. In active feeding
 269 behaviours (feeding-current and cruise feeders), the contribution of prey motility to predator-prey
 270 encounter rate is negligible due to the difference in swimming velocity between a large predator and
 271 a small prey (Kiørboe 2011). In ambush feeders, which wait motionless in the water column, prey
 272 velocity can affect encounter rates and detectability (Kiørboe 2011). Thus, the strict ambush feeders
 273 *Oithona* have a very low clearance efficiency on non-motile prey (diatoms) and a high clearance
 274 efficiency on the fast swimming prey *Oxyrrhis marina* ($307\text{-}700\text{ }\mu\text{m s}^{-1}$, Cosson et al. 1988).
 275 Rapidly sinking non-motile prey, e.g., faecal pellets, may still be perceived by ambush feeders, and
 276 sinking particles may directly intercept/collide with the copepod feeding structures (Turner 1986;
 277 Hopkins and Torres 1989; González and Smetacek 1994; Atkinson 1995; Kiørboe and Visser
 278 1999). This mechanism may account for the non-zero feeding on diatoms by ambush feeders in our
 279 experiments. The observed low feeding rates and lack of a saturation response in *O. nana* when fed
 280 on diatoms suggests that feeding rates remain encounter-limited rather than digestion-limited
 281 simply because few diatom cells are encountered by chance, even at the highest prey concentrations
 282 examined. The differences in prey perception mechanism between active and ambush foraging also
 283 leads to the prediction that ambush feeders have a narrower prey size spectrum and a larger
 284 optimum prey: predator size ratio than active feeders, as observed in Kiørboe 2016.
 285 *Trade-off between foraging gain and predation risk and its ecological implications.*

Our results on behaviour-dependent clearance rates help to understand the trade-offs of different feeding behaviours (foraging gain vs predation risk) and to predict optimal feeding strategies in marine food webs depending on the environmental conditions (e.g. type of food resources: motile vs non-motile prey, low or high predation pressure). Ambush feeding is an inefficient behaviour for non-motile prey as diatoms, that is the dominant prey during spring blooms in temperate latitudes. Then, active feeders, which are highly efficient feeding on diatoms, would have an advantage over ambush feeders during spring blooms. In fact, calanoid copepods with active feeding behaviours are commonly dominant during diatom spring blooms (Kenitz et al. 2017). However, the presence of motile prey (e.g., ciliates and dinoflagellates) during diatom blooms may also allow the occurrence of ambush feeding copepods (e.g., *Oithona similis*) in spring phytoplankton blooms (e.g., Atkinson, A. 1995; Castellani et al. 2007). Ambush feeding is a highly successful strategy and ambush-feeding copepods (*Oithona* spp) are considered among the most abundant copepods in the oceans (Gallienne and Robins 2001) even though they are less efficient than the other feeding behaviours for non-motile prey. This is likely due to the stealth of ambush feeding compared to active feeding behaviours and the consequently lower predation risk. Estimates of predation risks of active versus passive feeding strategies based on the motile behaviour (van Someren Gréve et al. 2017a) and fluid signals that feeding generates (Kiørboe et al. 2010) suggest that ambush feeders have up to an order of magnitude lower predation risk compared to active feeders. This estimate has been verified experimentally (Almeda et al. 2017) and is consistent with (rare) field estimates of mortality rates in copepods (Eiane and Ohman 2004). In addition, ambushers are expected to have a metabolic cost lower than actively feeding copepods (Castellani et al. 2005, Kiørboe 2010; Almeda et al. 2011). A lower energetic demand can allow a higher starvation tolerance. Thus, ambush feeding is expected to be less costly than active feeding also in terms of energy expenditure. This may explain why *Oithona* spp. (copepod species without resting eggs and low lipid content) can cope with food

310 limitation along the year in seasonal systems and be a dominant copepod in both oligotrophic and
311 eutrophic environments. An optimal foraging strategy is not necessarily the one that leads to the
312 highest feeding rate, but the one that optimizes the net gain over the risk/loss.

313 The trade-off between foraging gain and predation risk in planktonic copepods has at least two
314 implications: First, it promotes species diversity since two different strategies can be equally fit in
315 many environments. It allows coexistence of species that feed on very much the same resources and
316 where the more efficient feeder (competition specialist) would otherwise out-compete the less
317 efficient (defence specialist) according to the competitive exclusion principle (Gause 1934; Hardin
318 1960). Generally, diversity is generated by co-existing species that distribute themselves along a
319 gradient from competition to defence specialists (Thingstad et al. 2005; Winter et al. 2010). This
320 idea is rather well developed for prokaryotes competing for dissolved organics and defending
321 themselves against virus attacks and grazing (Våge et al. 2013), but much less explored for other
322 organisms such as copepods. We argue that the trade-off between feeding and survival is an
323 important source of diversity in zooplankton communities. Second, some environments may favour
324 one strategy over another, and whichever is the most ‘fit’ foraging strategy in any particular
325 environment depends on the presence and density of predators and on the availability and type of
326 prey. This would imply a distinct feeding trait biogeography if such environments were recurrent
327 (Visser 2007, Barton et al 2013, Brun et al. 2016).

328 Overall, feeding behaviour, prey perception mechanisms, and prey motility are main determinants
329 of predator-prey interactions in plankton food webs accounting for order of magnitude differences
330 in feeding rates and predation mortalities in planktonic copepods. These important differences are
331 not captured by models of pelagic systems operating with ‘functional types’ (e.g., Baretta et al.
332 1997), but are increasingly being built into trait-based models and may help to predict essential
333 features of the seasonal succession of plankton communities (Mariani et al. 2013).

334 **Data accessibility:** The data from this work are archived at the Dryad repository:

335 <http://datadryad.org/review?doi=doi:10.5061/dryad.q0f5f>

336

337 **Competing interests:** We have no competing interests.

338

339 **Authors' contributions:** RA, TK and HVSG conceived and designed the experiments. RA and
340 HVSG performed the experiments, RA analysed the data and all authors contribute to the data
341 interpretation. RA wrote the paper with substantial input from TK and HSVG. All authors gave
342 final approval for publication.

343

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547 **Figure legends**

548 **Figure 1.** Graphic abstract showing the main hypotheses of this study: i) ambush feeders are less
549 efficient than active feeders (feeding-current and cruising feeders) in acquiring resources, and (ii)
550 that ambushers are particularly poor in collecting non-motile prey. (a): feeding-current feeder, (b):
551 cruising feeder, (c): ambush feeder, 1: motile prey, 2: non-motile prey. We used planktonic copepod
552 nauplii and copepodites as model organisms.

554 **Figure 2.** Relationships between average food concentration during the incubation and clearance
555 rates (empty circles; left axis) and ingestion rates (filled circles; right axis) of nauplii and
556 copepodites of the ambush feeding copepod *O. nana* feeding on 4 different prey offered separately:
557 *R. salina* (A-D), *T. weissflogii* (E-H), *O. marina* (I-L) and *A. sanguinea* (M-P). The discontinuous
558 (for clearance rates) and continuous (for ingestion rates) curves correspond to the functional
559 response models fitted to the data (equations 1-4). Details about experimental organisms, incubation
560 conditions and model parameters are shown Table 1 and Table 2.

563 **Figure 3.** Relationships between average food concentration during the incubation and clearance
564 rates (empty circles; left axis) and ingestion rates (filled circles; right axis) of nauplii and
565 copepodites the feeding-current feeder copepod *T. longicornis* feeding on 4 different prey offered
566 separately: *R. salina* (A-C), *T. weissflogii* (D-G), the *O. marina* (H-J) and *A. sanguinea* (K-L). The
567 discontinuous (for clearance rates) and continuous (for ingestion rates) curves correspond to the
568 functional response models fitted to the data (equations 1-4). Details about experimental organisms,
569 incubation conditions and model parameters are shown in Table 1 and Table 2.

570

571 **Figure 4.** Relationship between average food concentration during the incubation and clearance
572 rates (empty circles; left axis) and ingestion rates (filled circles; right axis) of nauplii and
573 copepodites cruising feeder copepod *C. hamatus* feeding on 4 different prey offered separately: *R.*
574 *salina* (A-C), *T. weissflogii* (D-G), the *O. marina* (H-K) and *A. sanguinea* (L-N). The discontinuous
575 (for clearance rates) and continuous (for ingestion rates) curves correspond to the functional
576 response models fitted to the data (equations 1-4). Details about experimental organisms, incubation
577 conditions and model parameters are shown in Table 1 and Table 2.

578
579 **Figure 5.** Top panels: Maximum clearance rates (β) of nauplii and copepodites with different
580 feeding behaviors as a function of grazer body weight for different prey: the non- motile diatom *T.*
581 *weissflogii* (A) and the motile prey the *R salina* (B), *O. marina* (C) and *A. sanguinea* (D). Linear
582 regression equations fitted to the logarithmically transformed data are indicated in each panel (A-
583 D). Asterisk indicates an outlier (panel 5B). Bottom panels: Carbon-specific maximum clearance
584 rates (β_s , mL $\mu\text{g C}^{-1} \text{d}^{-1}$) of copepod developmental stages with different feeding behaviors (ambush
585 feeding (E), cruising feeding (F), feeding-current feeding (G)) as function of prey to predator body
586 carbon mass ratios. Coefficients $\pm$ standard error of parameters (γ , μ , σ) of the Gauss function fitted
587 to the data (eq. 5) are indicated in each panel (E-G). r^2 = coefficient of determination.

Table 1

Summary of the functional response experiments with copepods with different feeding behaviors. Each experiment label (Exp #) in the table corresponds to its label in the figures 2-4. N: nauplii, C: copepodite, *L*: average body length for nauplii and prosome length for copepodites, *W*: weight in carbon, SE: standard error, D: range of grazer concentration per experimental bottle, ESD: equivalent spherical diameter, SD: standard deviation, C: range of prey concentrations, *R.s*: *Rhodomonas salina*, *T.w*: *Thalassiosira weissflogii*, *O.m*: *Oxyrrhis marina*, *A.s*: *Akashiwo sanguinea*.

Species	Feeding behavior	Grazer					Prey			
		Exp. #	Stage	<i>L</i> ± SE (μm)	<i>W</i> ± SE (ng C ind ⁻¹)	D (ind. bt ⁻¹)	Species	ESD ± SD (μm)	<i>W</i> ± SE (pg C cell ⁻¹)	C (cells mL ⁻¹)
<i>Oithona nana</i>	Ambush feeding	1A	N	82 ± 1	26 ± 1	67-310	<i>R. s</i>	8.6 ± 1.1	28 ± 0.1	567-21618
		1B	N	113 ± 2	53 ± 2	39-258				
		1C	N	127 ± 3	68 ± 3	31-206				
		1D	C	183 ± 4	140 ± 4	20-85				
		1E	N	95 ± 2	37 ± 2	115-300	<i>T. w</i>	11.4 ± 1.2	112 ± 0.1	48-1904
		1F	N	110 ± 2	50 ± 2	99-298				
		1G	N	150 ± 3	96 ± 3	62-196				
		1H	C	162 ± 2	115 ± 2	30-86				
		1I	N	76 ± 1	23 ± 1	40-112	<i>O. m</i>	13.3 ± 1.2	152 ± 0.1	17-994
		1J	N	89 ± 2	32 ± 1	32-104				
		1K	N	131 ± 3	71 ± 3	21-80				
		1L	C	197 ± 3	157 ± 5	20-41				
		1M	N	104 ± 2	44 ± 2	84-362	<i>A. s</i>	39.4 ± 1.1	1635 ± 0.04	3-53
		1N	N	113 ± 3	53 ± 3	68-210				
		1O	C	169 ± 4	123 ± 5	34-102				
		1P	C	196 ± 3	157 ± 4	20-86				
<i>Temora longicornis</i>	Feeding-current feeding	2A	N	194 ± 7	112 ± 10	15-30	<i>R. s</i>	7.2 ± 1.1	17 ± 0.1	1916-16092
		2B	N	313 ± 7	304 ± 13	10-20				
		2C	C	339 ± 11	497 ± 52	10-20				
		2D	N	170 ± 1	80 ± 1	15-29	<i>T. w</i>	12.0 ± 1.1	130 ± 0.1	53-2660
		2E	N	245 ± 6	181 ± 9	12-19				
		2F	N	308 ± 7	295 ± 13	8-12				
		2G	C	321 ± 5	395 ± 20	6-10				
		2H	N	201 ± 6	114 ± 1	14-30	<i>O. m</i>	14.3 ± 1.2	190 ± 0.1	10-468
		2I	N	281 ± 5	236 ± 6	10-25				
		2J	C	355 ± 9	551 ± 40	10-20				
		2K	N	187 ± 4	98 ± 5	14-30	<i>A. s</i>	42.1 ± 1.1	1998 ± 0.04	3-54
		2L	N	289 ± 7	256 ± 12	10-25				
		2M	C	323 ± 5	399 ± 17	10-18				
<i>Centropages hamatus</i>	Cruising feeding	3A	N	142 ± 1	74 ± 1	41-67	<i>R. s</i>	7.8 ± 1.1	21 ± 0.1	566-21380
		3B	N	155 ± 3	92 ± 4	29-54				
		3C	N	216 ± 10	202 ± 20	23-33				
		3D	N	132 ± 3	64 ± 3	26-49	<i>T. w</i>	11.7 ± 1.2	123 ± 0.1	42-1692
		3E	N	170 ± 5	114 ± 7	20-46				
		3F	N	248 ± 7	267 ± 17	15-34				
		3G	C	358 ± 7	581 ± 30	6-10				
		3H	N	130 ± 3	62 ± 3	26-52	<i>O. m</i>	12.6 ± 1.2	130 ± 0.1	18-870
		3I	N	179 ± 5	129 ± 10	22-41				
		3J	N	196 ± 5	155 ± 8	18-29				
		3K	C	315 ± 7	426 ± 26	6-10				
		3L	N	143 ± 1	75 ± 2	23-45	<i>A. s</i>	39.8 ± 1.1	1679 ± 0.04	3-52
		3M	N	173 ± 3	116 ± 4	17-28				
		3N	C	226 ± 4	350 ± 13	5-8				

Table 2

Summary of the results from the functional feeding response experiments with copepods with different feeding behaviours. Each experiment label (Exp #) in the table corresponds to its label in the figures 2-4. N: nauplii, C: copepodite, SE: standard error, *R.s*: *Rhodomonas salina*, *T.w*: *Thalassiosira weissflogii*, *O.m*: *Oxyrrhis marina*, *A.s*: *Akashiwo sanguinea*. β is the maximum clearance rate ($\text{mL ind}^{-1} \text{d}^{-1}$), τ is the prey handling time (d), α is the prey concentration at the maximum clearance rate, $r^2(\text{F})$ = coefficient of determination for clearance rate model equations (1, 3) I_{max} is the maximum ingestion rates (cells $\text{ind}^{-1} \text{d}^{-1}$), SE=standard error,; $r^2(\text{I})$ = coefficient of determination for ingestion rate model equations (2, 4), $^sI_{\text{max}}$ is the C-specific maximum ingestion rates (=maximum daily ration, % body C d^{-1}). The asterisk (*) indicates that the maximum measured rate was used instead of the model prediction if predictions were unrealistic or no model (II or II) could be fitted to the data.

Feeding behaviour	Exp. #	Stage	Prey	FR type	Functional response model parameters						
					$\beta \pm \text{SE}$	$\tau \pm \text{SE}$	$\alpha \pm \text{SE}$	$r^2(\text{F})$	$I_{\text{max}} \pm \text{SE}$	$r^2(\text{I})$	$^sI_{\text{max}} \pm \text{SE}$
Ambush feeding	1A	N	<i>R. s</i>	III	0.13 ± 0.01		951 ± 312	0.76	264 ± 95	0.63	28 ± 10
	1B	N		III	0.26 ± 0.03		1485 ± 217	0.66	1132 ± 264	0.89	60 ± 14
	1C	N		III	0.37 ± 0.01		1083 ± 101	0.95	1178 ± 324	0.80	49 ± 13
	1D	C		III	0.59 ± 0.04		1250 ± 171	0.86	1512 ± 276	0.88	30 ± 6
	1E	N	<i>T. w</i>	II	0.05 ± 0.01	0.007 ± 0.011		0.37	149 ± 245	0.77	45 ± 74
	1F	N		II	0.07 ± 0.01	0.014 ± 0.011		0.64	74 ± 59	0.70	17 ± 13
	1G	N		II	0.09 ± 0.01	0.016 ± 0.015		0.54	$79 (*)$	0.87	$9 (*)$
	1H	C		III	0.23 ± 0.03		885 ± 341	0.63	210 ± 96	0.80	20 ± 9
	1I	N	<i>O. m</i>	III	0.82 ± 0.10		51 ± 6	0.65	140 ± 28	0.90	93 ± 19
	1J	N		III	0.99 ± 0.05		50 ± 4	0.83	180 ± 27	0.94	86 ± 13
	1K	N		III	1.20 ± 0.08		42 ± 4	0.68	225 ± 57	0.85	48 ± 12
	1L	C		III	2.41 ± 0.24		27 ± 5	0.73	478 ± 95	0.86	46 ± 9
	1M	N	<i>A. s</i>	II	0.10 ± 0.01	0.21 ± 0.06		0.61	3.4 ± 0.4	0.96	13 ± 1
	1N	N		II	0.27 ± 0.05	0.46 ± 0.13		0.66	5.3 ± 1.0	0.92	16 ± 3
	1O	C		II	1.47 ± 0.17	0.07 ± 0.02		0.77	14 ± 2	0.83	19 ± 3
	1P	C		II	1.48 ± 0.18	0.05 ± 0.01		0.72	17 ± 2	0.79	18 ± 2
Feeding-current feeding	2A	N	<i>R. s</i>	III	0.44 ± 0.02		3687 ± 315	0.50	4504 ± 620	0.94	68 ± 9
	2B	N		III	0.84 ± 0.05		4489 ± 361	0.58	9202 ± 1257	0.93	51 ± 7
	2C	C		III	3.83 ± 0.13		2338 ± 168	0.79	25234 ± 2450	0.95	86 ± 8
	2D	N		III	1.02 ± 0.15		109 ± 21	0.54	695 ± 349	0.75	113 ± 57
	2E	N	<i>T. w</i>	III	5.10 ± 0.50		85 ± 9	0.31	2753 ± 654	0.93	198 ± 47
	2F	N		III	6.18 ± 0.57		95 ± 10	0.42	3124 ± 1142	0.86	138 ± 50
	2G	C		III	11.00 ± 0.96		76 ± 8	0.25	6221 ± 1321	0.95	205 ± 43
	2H	N	<i>O. m</i>	II	2.70 ± 0.19	0.003 ± 0.001		0.76	588 ± 35	0.99	100 ± 6
	2I	N		II	4.26 ± 0.35	0.003 ± 0.001		0.77	588 ± 69	0.96	37 ± 4
	2J	C		II	6.72 ± 0.36	0.001 ± 0.000		0.83	1250 ± 156	0.97	43 ± 5
	2K	N	<i>A. s</i>	III	1.09 ± 0.11		8.7 ± 1.0	0.40	27 ± 3	0.97	55 ± 6
	2L	N		III	2.97 ± 0.33		6.6 ± 0.8	0.51	46 ± 8	0.90	36 ± 6
	2M	C		III	5.42 ± 0.50		7.5 ± 0.9	0.66	87 ± 15	0.92	44 ± 8
Cruising feeding	3A	N	<i>R. s</i>	III	0.51 ± 0.05		1050 ± 70	0.91	1256 ± 198	0.94	36 ± 6
	3B	N		III	0.46 ± 0.12		847 ± 57	0.91	2238 ± 905	0.80	51 ± 21
	3C	N		III	0.59 ± 0.10		1202 ± 74	0.85	3407 ± 970	0.90	35 ± 10
	3D	N		III	1.59 ± 0.15		122 ± 13	0.83	283 ± 63	0.89	54 ± 12
	3E	N	<i>T. w</i>	III	1.97 ± 0.22		101 ± 14	0.68	442 ± 140	0.82	48 ± 15
	3F	N		III	5.73 ± 0.42		43 ± 4	0.60	1354 ± 185	0.97	62 ± 9
	3G	C		III	12.5 ± 1.15		50 ± 5	0.06	3430 ± 379	0.98	73 ± 8
	3H	N	<i>O. m</i>	III	1.44 ± 0.10		18 ± 2	0.61	412 ± 42	0.97	86 ± 9
	3I	N		III	1.53 ± 0.10		19 ± 2	0.47	481 ± 66	0.96	48 ± 7
	3J	N		III	1.71 ± 0.11		25 ± 2	0.20	573 ± 59	0.97	48 ± 5
	3K	C		III	$5.16 (*)$		$(*)$	$(*)$	2203 ± 197	0.98	67 ± 6
	3L	N	<i>A. s</i>	III	0.33 ± 0.03		7.4 ± 1.0	0.51	6.8 ± 1.8	0.80	15 ± 4
	3M	N		III	0.50 ± 0.04		6.6 ± 1.0	0.62	7.3 ± 2.0	0.77	11 ± 3
	3N	C		III	5.69 ± 0.20		3.2 ± 0.2	0.92	61 ± 9	0.92	29 ± 4

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5