Prey perception mechanism determines maximum clearance rates of planktonic copepods

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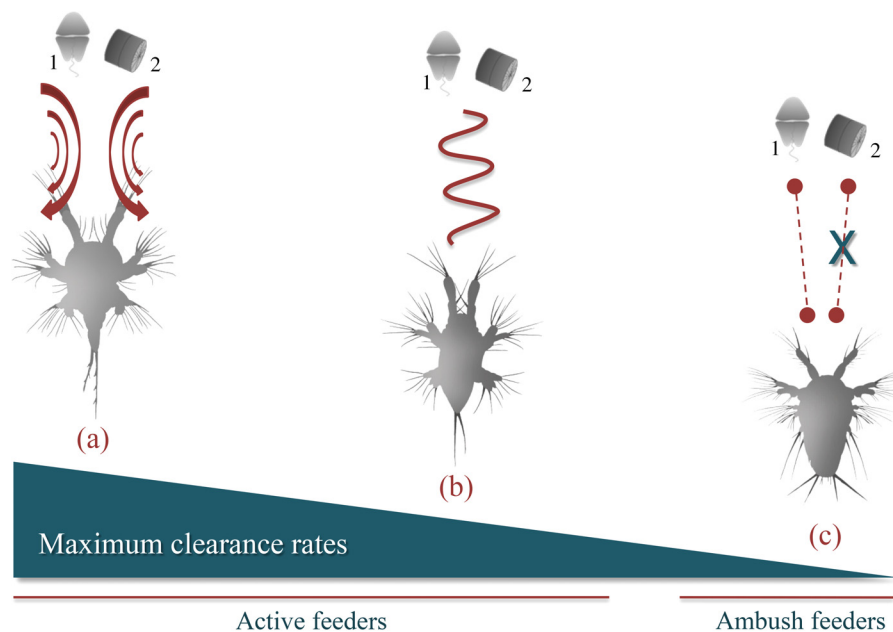
Abstract

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

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

Suspension-feeding zooplankton have three main ways of obtaining food: they can be (1) "ambush feeders" that wait motionless for motile prey to pass within their sensory reach or capture those prey that directly collide (Jiang and Paffenhöfer 2008; Kiørboe 2011, 2016), (2) "feeding-current feeders" that hover while generating a feeding current and harvest prey that are entrained in the current (Strickler 1982, 1985; Kiørboe 2011), or (3) "cruising feeders" that cruise through the water and capture encountered prey (Tiselius and Jonsson 1990; Kiørboe 2011). These feeding behaviors can be broadly classified into two main foraging strategies: "sit-and-wait" (ambushing) vs. "searching" (active feeding). Some copepod species can switch between feeding behaviors ("mixed feeding behaviour") depending on prey type and/or food availability (Landry 1981; Tiselius and Jonsson 1990; Kiørboe et al. 1996). This classification of feeding behaviors and foraging strategies applies across taxonomic groups, from small flagellates to large gelatinous zooplankton, and the different foraging modes are expected to have different benefits in terms of ability of obtaining food (foraging gain) and different costs in terms of mortality (predation risk) and metabolic expenses (Abrams 2003; Kiørboe et al. 2010). We have previously quantified the different costs associated with the main foraging behaviors in zooplankton through theoretical models and experimental testing, particularly mortality costs due to predation (Kiørboe

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Fig. 1. Graphic abstract showing the main hypotheses of this study: (i) ambush feeders are less efficient than active feeders (feeding-current and cruising feeders) in acquiring resources and (ii) that ambushers are particularly poor in collecting nonmotile prey. (**a**) Feeding-current feeder, (**b**) cruising feeder, (**c**) ambush feeder. 1: Motile prey, 2: Nonmotile prey. We used planktonic copepod nauplii and copepodites as model organisms. [Color figure can be viewed at wileyonlinelibrary.com]

et al. 2010, 2014; Almeda et al. 2017; van Someren Gréve et al. 2017*a*). Here, we aim at quantifying the benefits of the same foraging behaviors, specifically to quantify maximum clearance rates, to achieve a fuller understanding of the trade-offs of zooplankton small-scale foraging behaviors.

Zooplankton feeding has been extensively studied in both the laboratory and the field and experimental studies have focused mainly on the effect of grazer and prey size and food concentration (Harris and Paffenhöfer 1976; Ikeda 1977; Hansen et al. 1997; Saiz and Calbet 2007; Almeda et al. 2010*a*; Gonçalves et al. 2014; Helenius and Saiz 2017), while none have compared thoroughly the clearance efficiency of the different feeding behaviors/foraging strategies. Differences in methods and environmental conditions among previous studies complicate direct comparisons of maximum clearance rates in zooplankton feeding behaviors. Theoretical analyses by Kiørboe (2011) suggest that feeding-current feeding (hovering) is the most efficient behavior and ambush feeding the least efficient in terms of volume of water cleared. Specifically, ambush feeding is expected to be ~ 3–10 times less efficient than the active foraging behaviors, mainly because the predator–prey encounter is higher when due to the predator velocity than to a smaller prey velocity (Kiørboe 2011). In addition, ambush-feeding copepods depend on the fluid 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 nonmotile prey and prey that does not create a sufficiently strong hydromechanical signal (Henriksen et al. 2007; Jiang and Paffenhöfer 2008; Kiørboe 2011; Saiz et al. 2014).

Here, we experimentally test the hypotheses that (1) ambush feeders are less efficient than the active feeders (feeding-current and cruising feeders) in acquiring resources, and (2) that ambushers are particularly poor in collecting nonmotile 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 spatio-temporal 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.

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 Figs. 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*; and *A.s.*, *Akashiwo sanguinea*.

		Grazer					Prey			
Species	Feeding behavior	Exp. #	Stage	$L \pm SE$ (μm)	$W \pm SE$ (ng C ind.$^{-1}$)	D (ind. bt^{-1})	Species	ESD $\pm$ SD (μm)	$W \pm SE$ (pg C cell^{-1})	C (cells mL^{-1})
Oithona nana	**Ambush feeding**	1A	N	82 ± 1	26 ± 1	67-310	*R. s*	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	*T. w*	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	*O. m*	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	*A. s*	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				
Temora longicornis	**Feeding-current feeding**	2A	N	194 ± 7	112 ± 10	15-30	*R. s*	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	*T. w*	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	112 ± 10	14-30	*O. m*	14.3 ± 1.2	190 ± 0.1	10-468
		2I	N	281 ± 5	304 ± 13	10-25				
		2J	C	355 ± 9	551 ± 40	10-20				
		2K	N	187 ± 4	98 ± 5	14-30	*A. s*	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				
Centropages hamatus	**Cruising feeding**	3A	N	142 ± 1	74 ± 1	41-67	*R. s*	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	*T. w*	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	*O. m*	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	*A. s*	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				

The three experimental species were also selected because they are common and abundant in coastal waters (Razouls et al. 2005–2018; Martynova et al. 2011; Temperoni et al. 2011), play important ecological roles in food webs (Lampitt and Gamble 1982; Casini et al. 2004), and can be reared in the laboratory. Description of the motile behaviors of the experimental stages can be found in van Someren Gréve et al. (2017a). We used four different prey in the experiments: the cryptophyte flagellate *Rhodomonas salina*, the diatom *Thalassiosira weissflogii*, the heterotrophic dinoflagellate *Oxyrrhis marina*, and the mixotrophic dinofagellate *Akashiwo sanguinea* (Table 1). *R. salina*, *T. weissflogii*, and *A. sanguinea* cultures were kept in exponential growth in B1 culture medium (Hansen 1989) and maintained at 18°C and on a 12 : 12-h light/dark cycle in glass flasks. *O. marina* was fed on the *R. salina* and maintained at 18°C in 2-L glass bottles in dark.

The copepods were grown in continuous laboratory cultures in 30- and 100-L plastic tanks at ~ 15–18°C in dark. Specimens of *O. nana*, *T. longicornis*, and *C. hamatus* were originally isolated from the Port of Gijon (Cantabrian Sea, Spain), the Øresund strait (North Sea, Denmark), and the Skagerrak (North Sea, Sweden), respectively. *O. nana* cultures were fed on the heterotrophic dinoflagellate *O. marina* ad libitum. *T. longicornis* and *C. hamatus* cultures were fed with mixed cultured phytoplankton (*R. salina*, *T. weissflogii*, *Heterocapsa triquetra*, *Prorocentrum minimum*, *A. sanguinea* in a proportion of 1, 0.4, 0.2, 0.1, and 0.1, respectively), and in the case of *C. hamatus*, also with *O. marina*.

To obtain cohorts of *O. nana*, *T. longicornis*, and *C. hamatus*, we separated adults from the stock culture with 125- or 200-µm-mesh sieves and placed them separately in a new tank. After 48 h, adults were removed with a 100- or 200-µm-mesh sieve, and eggs/hatched nauplii were transferred to a new tank with food ad libitum. We let nauplii grow until the desired stage/length was reached (Table 1).

Functional feeding response experiments

We determined feeding rates of nauplii and copepodites with different feeding behavior using four 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-µm mesh to remove any cell aggregates. *O. marina* was not fed 4 d 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 the 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, µm) 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 µm 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, three bottles were used to determine the initial prey concentration ("initials"), three bottles were used to determine prey growth rates during the incubation without copepods ("control bottles"), and three bottles with copepods served as experimental treatments ("experimental bottles").

Nauplii and copepodites were either picked individually under a stereomicroscope or, in the most of cases, concentrated using a 40-µm 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 was chosen to ensure a reduction of ~ 30% in prey concentration during incubation according to previous studies (e.g., Almeda et al. 2010a; Saiz et al. 2014; Helenius and Saiz 2017). The experimental and control bottles were mounted on a rotating wheel (0.4 rpm) and incubated at 15°C for ~ 24 h in dark.

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

Calculations

Clearance rates, ingestion rates, and average prey concentration during the incubations were calculated according to Frost (1972). The functional feeding response of planktonic copepods commonly follow a type II or III model (Holling 1959; Kiørboe et al. 2018). The type III functional response differs from type II in the presence of a "feeding threshold", i.e., a prey concentration below which the copepod reduces its clearance rates (Kiørboe et al., 1985, 2018). The measured clearance rates (F, mL ind.$^{-1}$ d^{-1}) and ingestion rates (I, cells

ind.$^{-1}$ d^{-1}) in relation to prey concentration (C, cells mL^{-1}) were fitted to either a Holling functional response type II or type III model (Kiørboe 2008; Schultz and Kiørboe 2009):

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

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

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

$$I = \alpha\beta e^{1-\alpha/C} \quad (4)$$

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 Eqs. 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 behaviors 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 (β) = a + b log (W). Post hoc Bonferroni test was used for pairwise comparison. All statistical tests were conducted with IBM-SPSS software and a statistically significance level of 0.05 was applied.

Results

Clearance rates of nauplii and copepodites of *O. nana* (ambush feeders, Fig. 2), *T. longicornis* (feeding-current feeders, Fig. 3), and *C. hamatus* (cruising feeder, Fig. 4) varied depending on food concentration following mostly a type III and, in some cases, a type II functional feeding response (Figs. 2–4). Cruising feeders and feeding-current feeders showed type III functional response for all the prey (Figs. 3, 4, Table 2) except for *T. longicornis* feeding on *O. marina* (Fig. 3H–J, Table 2). In ambush feeders, we found both types II and III functional responses depending on the prey type and copepod stage (Fig. 2, Table 2). Except for nauplii feeding on *O. marina* (Fig. 2I–K), the decrease in clearance rates at the lowest concentration in ambush feeders was, however, relatively low, and even though a

functional response type III model was fitted to the data (Table 2), a type II model fitted the data almost equally well.

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

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

Discussion

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

Efficiency of zooplankton foraging strategies in terms of maximum clearance rates

We found that, in contrast to model predictions (Kiørboe 2011), maximum clearance rate in the three studied behaviors was similar for motile prey with a size range of 7–40 μm and, therefore, our first hypothesis was rejected. Our hypothesis was based on the fact that prey encounter velocities are higher in active than in ambush feeders, and that clearance rate scales with prey encounter velocity (Kiørboe 2011). However, clearance rates also vary with prey detection distance squared, and therefore even a relatively small increase in prey detection distances in ambushers compared with active feeders may compensate for the
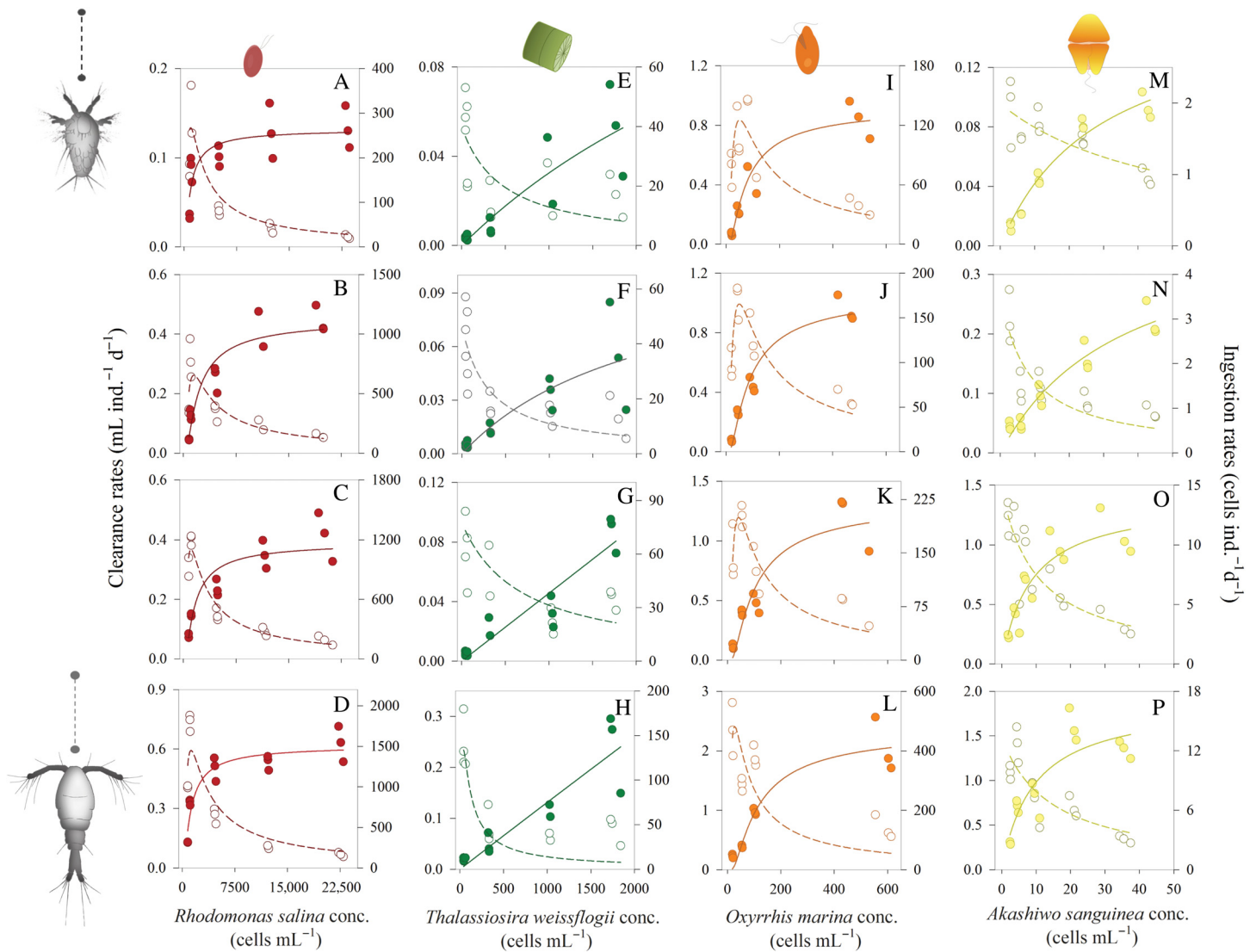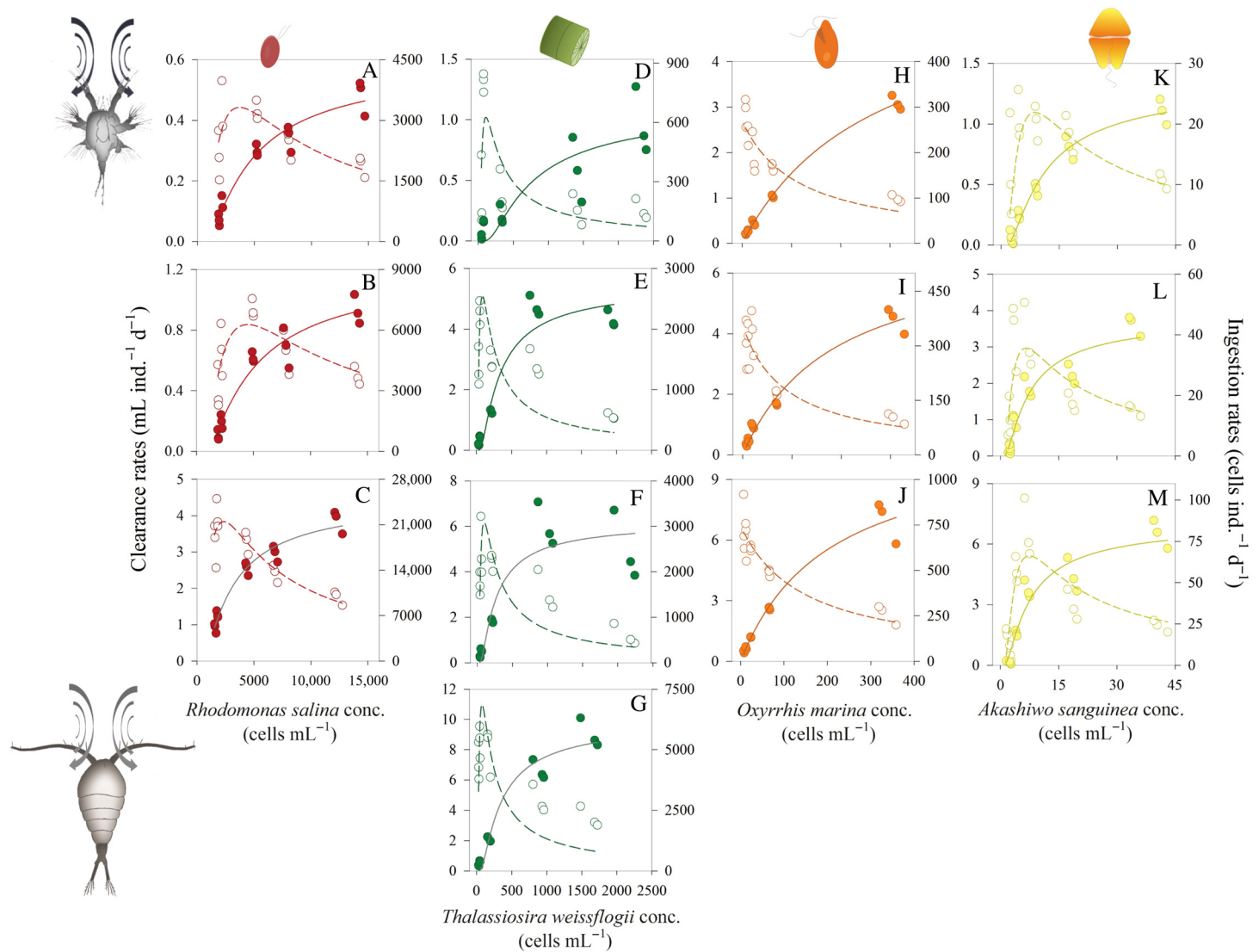
Fig. 2. Relationships between average food concentration during the incubation and clearance rates (empty circles; left axis) and ingestion rates (filled circles; right axis) of nauplii and copepodites of the ambush feeding copepod *O. nana* feeding on four different prey offered separately: *R. salina* (**A-D**), *T. weissflogii* (**E-H**), *O. marina* (**I-L**), and *A. sanguinea* (**M-P**). The discontinuous (for clearance rates) and continuous (for ingestion rates) curves correspond to the functional response models fitted to the data (Eqs. 1–4). Details about experimental organisms, incubation conditions, and model parameters are shown in Tables 1 and 2. [Color figure can be viewed at wileyonlinelibrary.com]

lower encounter velocities. Prey are perceived, captured, and handled individually by all three feeding behaviors (Price et al. 1983; Kiørboe 2011; Bruno et al. 2012) but ambush feeders perceive their prey differently than active feeders. Ambush feeding copepods respond to the fluid disturbance generated by motile prey and thus may perceive their prey at a considerable distance (Svensen and Kiørboe 2000; Kiørboe et al. 2009; Cheng et al. 2014) while active feeders appear rather to perceive their prey as they are touched, or nearly touched, by the setae on the feeding appendages (Uttieri et al. 2008; Tiselius et al. 2013; Gonçalves and Kiørboe 2015).

Our second hypothesis was confirmed as ambush feeding was clearly an inefficient foraging strategy for nonmotile prey-

like diatoms. This is in agreement with previous experimental field and laboratory studies and model predictions (Atkinson 1995; Kiørboe and Visser 1999; Paffenhöfer and Mazzocchi 2002; Henriksen et al. 2007; Vogt et al. 2013; Saiz et al. 2014; van Someren Gréve et al. 2017b). Prey motility can affect encounter rates by increasing the relative speed between predator and prey and by increasing prey detectability by a rheotactic predator. In active feeding behaviors (feeding-current and cruise feeders), the contribution of prey motility to predator–prey encounter rate is negligible due to the difference in swimming velocity between a large predator and a small prey (Kiørboe 2011). In ambush feeders, which wait motionless in the water column, prey velocity can affect encounter rates and
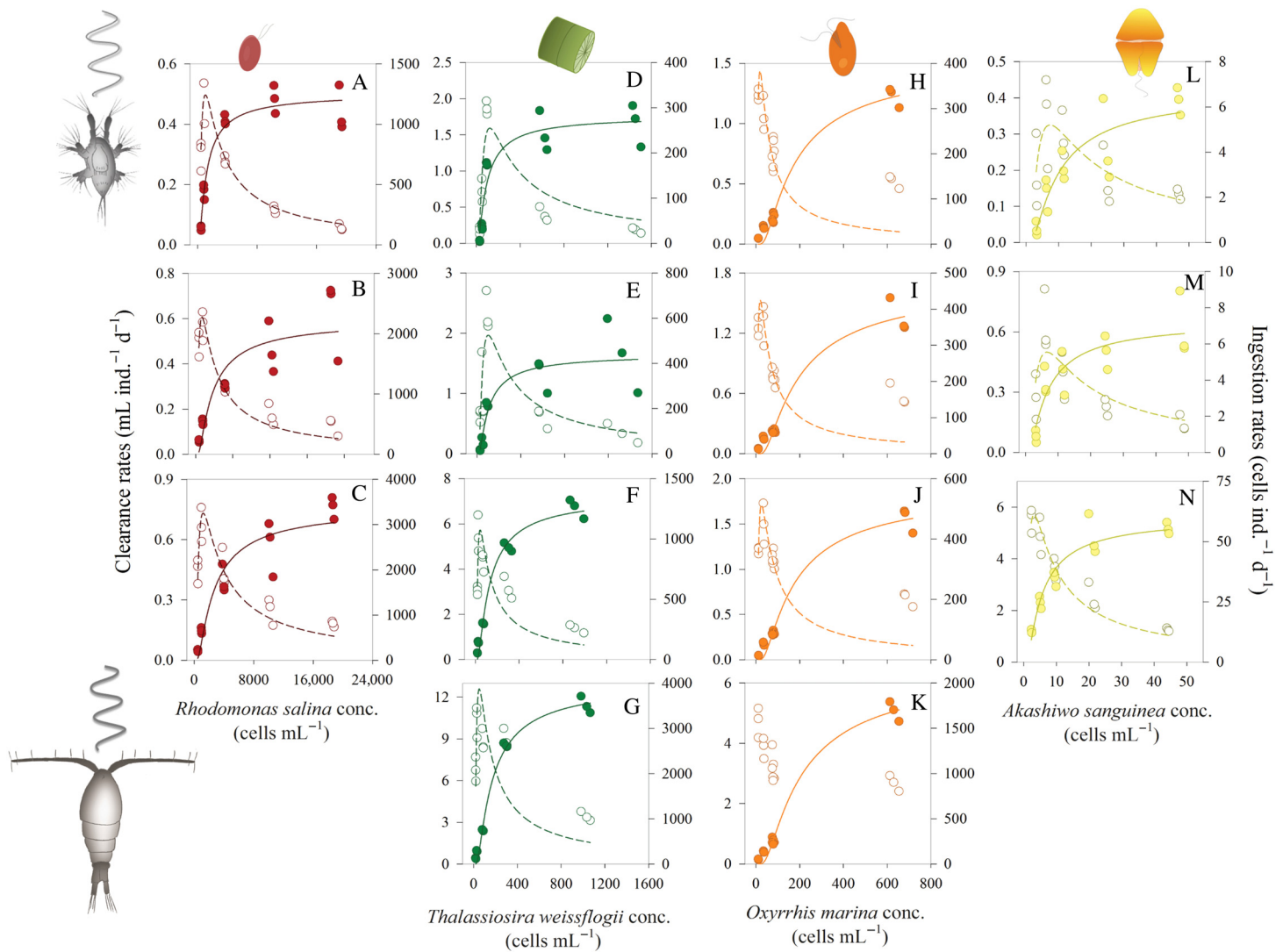
Fig. 3. Relationships between average food concentration during the incubation and clearance rates (empty circles; left axis) and ingestion rates (filled circles; right axis) of nauplii and copepodites the feeding-current feeder copepod *T. longicornis* feeding on four different preys offered separately: *R. salina* (**A-C**), *T. weissflogii* (**D-G**), the *O. marina* (**H-J**), and *A. sanguinea* (**K-L**). The discontinuous (for clearance rates) and continuous (for ingestion rates) curves correspond to the functional response models fitted to the data (Eqs. 1–4). Details about experimental organisms, incubation conditions, and model parameters are shown in Tables 1 and 2. [Color figure can be viewed at wileyonlinelibrary.com]

detectability (Kiørboe 2011). Thus, the strict ambush feeders *Oithona* have a very low clearance efficiency on nonmotile prey (diatoms) and a high clearance efficiency on the fast swimming prey *Oxyrrhis marina* (307–700 μm s^{-1}, Cosson et al. 1988). Rapidly sinking nonmotile prey, e.g., fecal pellets, may still be perceived by ambush feeders, and sinking particles may directly intercept/collide with the copepod feeding structures (Turner 1986; Hopkins and Torres 1989; González and Smetacek 1994; Atkinson 1995; Kiørboe and Visser 1999). This mechanism may account for the non-zero feeding on diatoms by ambush feeders in our experiments. The observed low feeding rates and lack of a saturation response in *O. nana* when fed on diatoms suggests that feeding rates remain encounter-limited rather

than digestion-limited simply because few diatom cells are encountered by chance, even at the highest prey concentrations examined. The differences in prey perception mechanism between active and ambush foraging also leads to the prediction that ambush feeders have a narrower prey size spectrum and a larger optimum prey : predator size ratio than active feeders, as observed in Kiørboe 2016.

Trade-off between foraging gain and predation risk and its ecological implications

Our results on behavior-dependent clearance rates help to understand the trade-offs of different feeding behaviors (foraging gain vs. predation risk) and to predict optimal feeding

Fig. 4. Relationship between average food concentration during the incubation and clearance rates (empty circles; left axis) and ingestion rates (filled circles; right axis) of nauplii and copepodites cruising feeder copepod *C. hamatus* feeding on four different preys offered separately: *R. salina* (**A-C**), *T. weissflogii* (**D-G**), the *O. marina* (**H-K**), and *A. sanguinea* (**L-N**). The discontinuous (for clearance rates) and continuous (for ingestion rates) curves correspond to the functional response models fitted to the data (Eqs. 1–4). Details about experimental organisms, incubation conditions, and model parameters are shown in Tables 1 and 2. [Color figure can be viewed at wileyonlinelibrary.com]

strategies in marine food webs depending on the environmental conditions (e.g., type of food resources: motile vs. nonmotile prey, low or high predation pressure). Ambush feeding is an inefficient behavior for nonmotile 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 behaviors are commonly dominant during diatom spring blooms (Kenitz et al. 2017). However, the presence of motile prey (e.g., ciliates and dinoflagellates) during diatoms blooms may also allow the occurrence of ambush feeding copepods (e.g., *Oithona similis*) in spring phytoplankton blooms (e.g., Atkinson, 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 behaviors for nonmotile prey. This is likely due to the stealth of ambush feeding compared with active feeding behaviors and the consequently lower predation risk. Estimates of predation risks of active vs. passive feeding strategies based on the motile behavior (van Someren Gréve et al. 2017*a*) 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 with active feeders. This estimate has been verified experimentally (Almeda et al. 2017) and is consistent with (rare) field

Table 2. Summary of the results from the functional feeding response experiments with copepods with different feeding behaviors. Each experiment label (Exp #) in the table corresponds to its label in the Figs. 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 (mL ind.$^{-1}$ d^{-1}), τ is the prey handling time (d), α is the prey concentration at the maximum clearance rate, $r^2(F)$ = coefficient of determination for clearance rate model Eqs. 1 and 3, I_{max} is the maximum ingestion rates (cells ind.$^{-1}$ d^{-1}), SE = standard error; $r^2(I)$ = coefficient of determination for ingestion rate model Eqs. 2 and 4. $^sI_{max}$ is the C-specific maximum ingestion rates (= maximum daily ration, % body C d^{-1}). The asteresitk (*) 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						
					$\beta \pm SE$	$\tau \pm SE$	$\alpha \pm SE$	$r^2(F)$	$I_{max} \pm SE$	$r^2(I)$	$^sI_{max} \pm SE$
Ambush feeding	1A	N	*R. s*	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	*T. w*	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	*O. m*	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	*A. s*	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	*R. s*	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	*T. w*	III	1.02 ± 0.15		109 ± 21	0.54	695 ± 349	0.75	113 ± 57
	2E	N		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	*O. m*	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	*A. s*	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	*R. s*	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	*T. w*	III	1.59 ± 0.15		122 ± 13	0.83	283 ± 63	0.89	54 ± 12
	3E	N		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	*O. m*	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	*A .s*	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
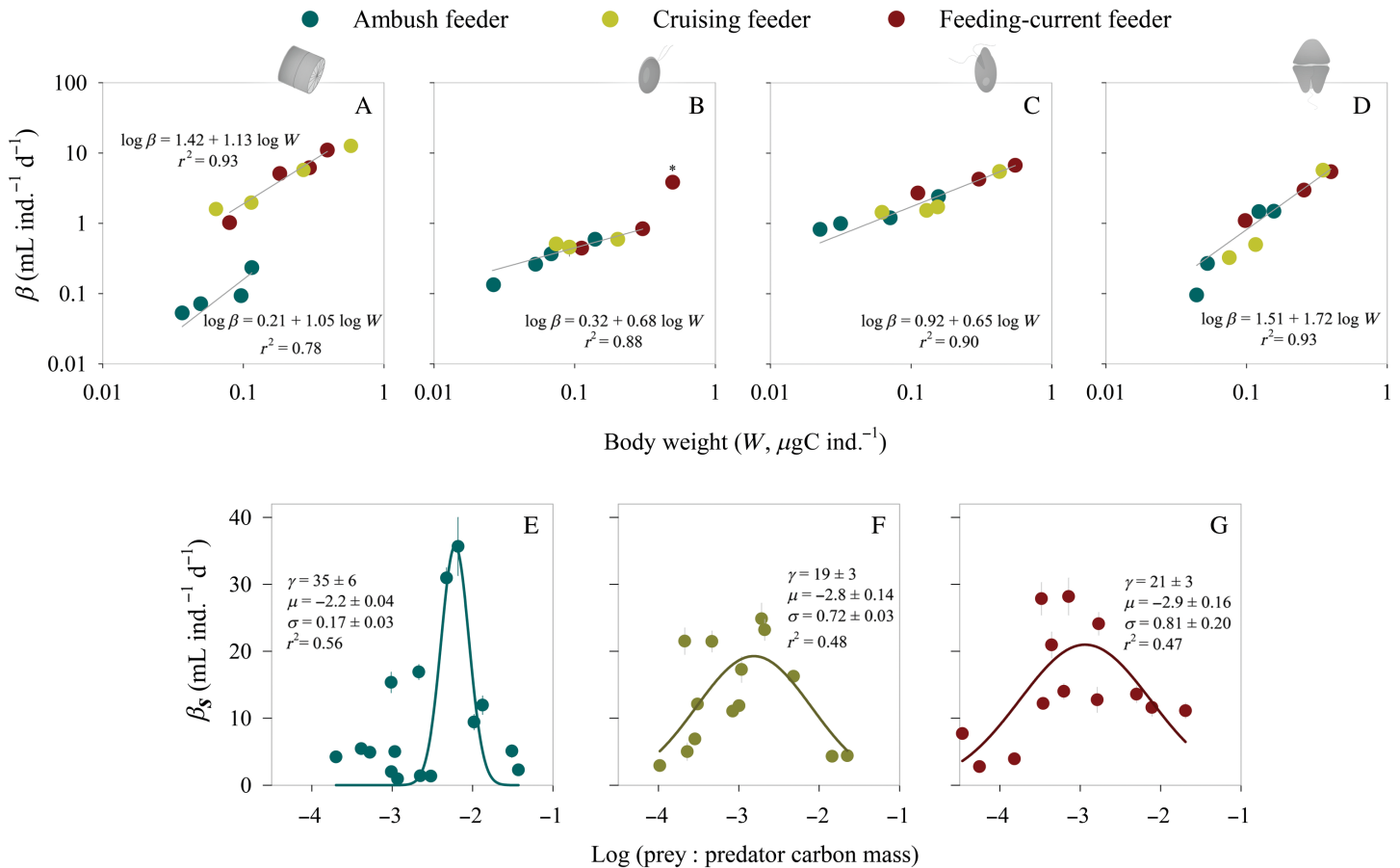
Fig. 5. Top panels: Maximum clearance rates (β) of nauplii and copepodites with different feeding behaviors as a function of grazer body weight for different prey: The nonmotile diatom *T. weissflogii* (**A**) and the motile prey the *R. salina* (**B**), *O. marina* (**C**), and *A. sanguinea* (**D**). Linear regression equations fitted to the logarithmically transformed data are indicated in each panel (**A-D**). Asterisk indicates an outlier (panel 5B). Bottom panels: Carbon-specific maximum clearance rates (β_s, mL μg C^{-1} d^{-1}) of copepod developmental stages with different feeding behaviors [ambush feeding (**E**), cruising feeding (**F**), feeding-current feeding (**G**)] as function of prey to predator body carbon mass ratios. Coefficients $\pm$ SE of parameters (γ, μ, σ) of the Gauss function fitted to the data (Eq. 5) are indicated in each panel (**E-G**). r^2 = coefficient of determination. [Color figure can be viewed at wileyonlinelibrary.com]

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

The trade-off between foraging gain and predation risk in planktonic copepods has at least two implications: First, it promotes species diversity as two different strategies can be equally fit in many environments. It allows coexistence of species that feed on very much the same resources and where the

more efficient feeder (competition specialist) would otherwise out-compete the less efficient (defense specialist) according to the competitive exclusion principle (Gause 1934; Hardin 1960). Generally, diversity is generated by co-existing species that distribute themselves along a gradient from competition to defense specialists (Thingstad et al. 2005; Winter et al. 2010). This idea is rather well-developed for prokaryotes competing for dissolved organics and defending themselves against virus attacks and grazing (Våge et al. 2013), but much less explored for other organisms such as copepods. We argue that the trade-off between feeding and survival is an important source of diversity in zooplankton communities. Second, some environments may favor one strategy over another, and whichever is the most "fit" foraging strategy in any particular environment depends on the presence and density of predators and on the availability and type of prey. This would imply a distinct feeding trait biogeography if such environments were recurrent (Visser 2007; Barton et al. 2013; Brun et al. 2016).

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

Data availability statement

The data from this work are archived at the Dryad repository: http://datadryad.org/review?doi=doi:10.5061/dryad.q0f5f

Author Contribution Statement

RA, TK, and HVSG conceived and designed the experiments. RA and HVSG performed the experiments, RA analyzed the data and all authors contribute to the data interpretation. RA wrote the paper with substantial input from TK and HSVG. All authors gave final approval for publication.

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Acknowledgments

Conflict of Interest

We have no competing interests.