Behavior is a major determinant of predation risk in zooplankton

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Abstract. Zooplankton exhibit different small-scale motile behaviors related to feeding and mating activities. These different motile behaviors may result in different levels of predation risk, which may partially determine the structure of planktonic communities. Here, we experimentally determined predation mortality associated with (1) feeding activity (ambush feeders vs. feeding-current vs. cruising feeders) and (2) mate-finding behavior (males vs. females). The copepods *Oithona nana*, *O. davisae* (ambush feeders), *Temora longicornis* (feeding-current feeder), and *Centropages hamatus* (cruising feeder) were used as prey for different predatory copepods. Copepods with "active" feeding behaviors (feeding-current and cruising feeders) showed significantly higher mortality from predation (~2–8 times) than similarly sized copepods with low motility feeding behavior (ambush feeders). Copepod males, which have a more active motile behavior than females (mate-seeking behavior), suffered a higher predation mortality than females in most of the experiments. However, the predation risk for mate-searching behavior in copepods varied depending on feeding behavior with ambush feeders consistently having the greatest difference in predation mortality between genders (~4 times higher for males than for females). This gender-specific predation pressure may partially explain field observations of female-biased sex ratios in ambush feeding copepods (e.g., *Oithonidae*). Overall, our results demonstrate that small-scale motile behavior is a key trait in zooplankton that significantly affects predation risk and therefore is a main determinant of distribution and composition of zooplankton communities in the ocean.

Key words: copepods; motile behavior; predation risk; trait-based approach; zooplankton.

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INTRODUCTION

More than 90% of the biological processes in the ocean are due to planktonic organisms, and attempts to understand ocean biogeochemistry and predict responses to climate change and other stressors require a mechanistic understanding of the biological processes in plankton food webs (Parsons and Takahashi 1973, Hays et al. 2005, Kiørboe 2008a). Among planktonic organisms, zooplankton occupy a key trophic position in marine food webs, playing a pivotal role in marine biogeochemical cycling and fish recruitment (Banse 1995, Castonguay et al. 2008, Alcaraz et al. 2010). Predation is a major cause of mortality in zooplankton (67–75% of total mortality, Hirst and Kiørboe 2002) and thus an important top-down control in marine plankton communities (Steele and Frost 1977, Frank et al. 2006, Daewel et al. 2014) and a major force of natural selection in the evolution of zooplankton morphology and behavior (Verity and Smetacek 1996). For example, the lack of physical refuges in the water column and the predation pressure have driven different zooplankton taxa to common strategies to reduce predation risk, such as vertical migration, reduced body size, and weak pigmentation to avoid visual predators and efficient escape responses (Brooks

and Dodson 1965, Ohman 1990, Hays et al. 1994, Brucet et al. 2010, Buskey et al. 2012). Knowledge of zooplankton predator–prey interactions is therefore essential for understanding the factors regulating the structure and dynamics of marine food webs.

Most animals are both predator and prey and have to face the challenge of feeding and evading predators simultaneously (Lima and Dill 1990, Tiselius et al. 1997, Kiørboe et al. 2010, Kiørboe 2013). Thus, survival (fitness) of most organisms is determined by their ability to find food and mates and avoid predation. These vital missions depend on encounter rates with prey, mate, and predators and, for most zooplankters, encounters rates are directly influenced by its small-scale motile behavior (Gerritsen and Strickler 1977, Visser 2007, Kiørboe 2008a). Models suggest that high swimming speeds can promote encounters with food and mates but also increase encounter rates with predators (Gerritsen and Strickler 1977, Visser 2007). Also, zooplankton swimming and feeding create fluid disturbances that may be perceived by rheotactic predators and further increase predator encounter rates (Kiørboe and Visser 1999, Visser 2001, 2007, Kiørboe and Jiang 2013). Therefore, there is a conflict (trade-off) between maximizing prey and mate encounter rates and simultaneously minimizing encounter rates with predators (Lima and Dill 1990, Tiselius et al. 1997, Kiørboe et al. 2010, Lasley-Rasher and Yen 2012).

Small-scale motile behavior is directly linked to feeding in zooplankton (Strickler 1982, van Duren and Videler 1995, 1996, Paffenhöfer et al. 1996, Titelman and Kiørboe 2003a, Seuront et al. 2004, Kiørboe 2008a, 2011). Zooplankton have developed three different ways of collecting food: They can be (1) ambush feeders that wait for prey to pass within their dining sphere, (2) feeding-current feeders that generate a feeding current and harvest prey that are entrained in the current, or (3) cruising feeders that capture prey that they encounter as they cruise through the water (Kiørboe 2011). Each of these different feeding behaviors involves different levels of motility and hydromechanical signals and consequently can result in different levels of predation risk (Paffenhöfer and Knowles 1980, Titelman 2001, Titelman and Kiørboe 2003b), and theoretical models predict ambush feeding to be the least risky, and

feeding-current feeding and cruise feeding to be the most risky behaviors (Kiørboe et al. 2010).

Planktonic copepods, the main components of marine zooplankton, have sexual reproduction, and copepod males commonly show a mate-seeking behavior and swim more and faster than females (Katona 1973, Uchima and Murano 1988, Buskey 1998, Doall et al. 1998, Strickler 1998, Bagøien and Kiørboe 2005a, b, Kiørboe et al. 2005). Mate-tracking and mate-searching behaviors of males increase their encounter rates with predators, making potentially males more susceptible to predation than females (Maier et al. 2000, Lasley-Rasher and Yen 2012). The difference in motile behavior between genders increases with increasing conflict between feeding and mate searching (Kiørboe 2008b). In ambush feeders, feeding is done from a stationary (non-moving) position, and therefore, ambush feeders have a low probability of encounter rates with mates when they are feeding. To compensate for this, ambush feeding males alternate between stationary feeding and extremely high-speed female-seeking motility (Kiørboe 2008b). We hypothesize that the differences in predation risk between copepod genders vary depending on the feeding behavior, with ambush feeders suffering the highest difference in predation mortality between males and females. In this context, predation has been proposed as one of the main factors controlling sex ratios and longevities in planktonic copepods (Hirst et al. 2010). However, empirical measurements of predation risk associated with sex behavior in copepods are limited (Hirst et al. 2010).

While theoretical models predict predation risk to depend strongly on the motile behavior related to feeding and mate finding in zooplankton, empirical evidence of the hypothesized relations is lacking. Here, we experimentally quantify the influence of motile behavior on predation risk in zooplankton, using planktonic copepods with differing feeding and mate-finding behaviors as our test case. Our hypotheses are that feeding behavior with less motility (ambush feeding) has a lower predation risk than more active feeding modes (feeding-current and cruising feeders) and that copepod males suffer a higher predation risk than females, particularly in cases where feeding and mate finding are conflicting activities (i.e., ambush feeders). Specifically, we test the quantitative predictions of the behavioral observations

and derived predation risk model (van Someren Gréve et al. 2017) developed for the species examined here.

Materials and Methods

We quantified predation risk associated with (1) feeding activity (ambush feeders vs. feeding-current feeders vs. cruising feeders) and (2) mating behavior (males vs. females) in bottle incubation experiments with the copepods *Oithona nana*, *O. davisae* (ambush feeders, Kiørboe 2011), *Temora longicornis* (feeding-current feeder; Kiørboe 2011), and *Centropages hamatus* (cruising feeder; Tiselius and Jonsson 1990, Kiørboe 2011) as prey for the predatory copepods *Aetideopsis armatus* (=*Chiridius armatus*), *Centropages typicus*, *Metridia longa*, and *Paraeuchaeta norvegica* (=*Euchaeta norvegica*).

Experimental organisms

Copepod species used as prey in this study were grown in continuous laboratory cultures in 30- and 100-L plastic tanks (~15–18°C). Specimens of *O. nana* and *O. davisae* were originally isolated from the Port of Gijon (Cantabrian Sea, Spain) and in coastal waters of Barcelona (NW Mediterranean, Spain), respectively. *T. longicornis* and *C. hamatus* were obtained from the Øresund strait (North Sea, Denmark) and Skagerrak strait (North Sea, Sweden). *O. nana* and *O. davisae* cultures were fed ad libitum the heterotrophic dinoflagellate *Oxyrrhis marina*. *T. longicornis* and *C. hamatus* cultures were fed with a mixed phytoplankton diet consisting of the cryptophyte *Rhodomonas* sp., the diatom *Thalassiosira weissflogii*, and the autotrophic dinoflagellates *Heterocapsa triquetra*, *Prorocentrum minimum*, and *Akashiwo sanguinea*, and in the case of *C. hamatus*, also with *O. marina*. Phytoplankton cultures were kept in exponential growth in B1 culture medium and maintained at 18°C and on a 12:12-h light/dark cycle in glass flasks. *O. marina* was fed the cryptophyte *Rhodomonas* sp and maintained at 18–20°C in 2-L glass bottles.

Copepod species used as predators were collected in Gullmar and Koster fjord on the Swedish west coast by oblique and horizontal plankton net tows (500-μm mesh). Adults of the larger predatory copepods *A. armatus* and *P. norvegica* were sorted on-board using a wide-mouth pipette and gently transferred to 20-L thermocontainers containing in situ deep water. We

isolated adults of the smaller predatory copepods, *C. typicus* and *M. longa*, from samples brought to the laboratory. Predatory copepods were kept in large plastic containers (30–200 L, depending on species) with in situ deep filtered sea water (0.2 μm) in temperature-controlled rooms (11°C for *A. armatus* and *P. norvegica* and 15°C for *C. typicus* and *M. longa*). All predatory copepod species were kept at The Sven Lovén Centre for Marine Sciences (Kristineberg, Sweden) and replaced with new specimens every 1–2 weeks, except for *C. typicus* specimens that were transported to the Centre for Ocean Life (Denmark) and kept continuously in culture as described for the copepods used as prey. To maintain large predatory copepods and avoid cannibalism, *A. armatus* and *P. norvegica* were fed with the copepod *Acartia tonsa* every 2 days. *M. longa* were fed with *A. tonsa* nauplii, *O. marina,* and *Rhodomonas* sp., and *C. typicus* was fed with *O. marina* and the mixed phytoplankton diet described above.

To obtain cohorts of *Oithona* spp., *T. longicornis*, and *C. hamatus*, we separated adults from the stock culture with 125- or 200-μm-mesh sieves and placed them in a new tank. After 48 h, adults were removed with a 100- or 200-μm-mesh sieve, and hatched nauplii were transferred to a new tank with food ad libitum. We let nauplii grow until the desired stage was reached (late nauplii or copepodites depending on the experiment, Tables 1 and 2).

Experimental procedures

We conducted 27 incubation experiments to estimate predation risk associated with feeding activity (Tables 1 and 2) and mating/gender behavior (Tables 3 and 4). In each experiment, we incubated two similarly sized prey species with contrasting foraging behaviors, or males and females of the same species, together with one predator species. We used different copepod developmental stages of different species to ensure prey with similar size but different feeding behavior (Tables 1 and 2). We used three to six concentrations of prey per experiment, with duplicate for each experimental bottle, and three to six controls for each experiment (one control per concentration). Prey concentration (prey/L) varied depending on the experiments (Figs. 1–7). At the beginning of the experiments, 20–30 individuals of each type of prey and 10

Table 1. Summary of the experiments conducted to determine predation risk associated with different feeding behaviors: ambush vs. feeding-current feeders (1A–1G).

Expt.	Species	Size ± SD (mm)	C	t (h)	Feeding behavior	Stage	I_{max} (CI)	β (CI)
1A†				48				
Predator	*M. longa*	2.3 ± 0.1	10					
Prey 1	*O. nana*	0.12 ± 0.02			Ambush	NV–VI	10.1 (16.0–6.4)	0.071 (0.031–0.163)
Prey 2	*T. longicornis*	0.13 ± 0.02			Feeding-current	NII–III		0.171 (0.096–0.305)
1B†				48				
Predator	*A. armatus*	3.0 ± 0.2	8					
Prey 1	*O. nana*	0.13 ± 0.01			Ambush	NV–VI	9.8 (12.2–7.9)	0.109 (0.065–0.182)
Prey 2	*T. longicornis*	0.14 ± 0.02			Feeding-current	NII–III		0.276 (0.188–0.405)
1C†				24				
Predator	*C. typicus*	1.1 ± 0.1	2–5					
Prey 1	*O. davisae*	0.15 ± 0.01			Ambush	NVI	71.4 (151–33.8)	0.056 (0.038–0.083)
Prey 2	*T. longicornis*	0.16 ± 0.01			Feeding-current	NIII		0.299 (0.212–0.422)
1D†				54				
Predator	*A. armatus*	3.1 ± 0.1	10					
Prey 1	*O. nana*	0.54 ± 0.02			Ambush	Female	—	0.022 (0.011–0.046)
Prey 2	*T. longicornis*	0.52 ± 0.03			Feeding-current	CI–II		0.169 (0.140–0.204)
1e†				42				
Predator	*A. armatus*	3.0 ± 0.2	10					
Prey 1	*O. nana*	0.54 ± 0.04			Ambush	Female	—	0.064 (0.031–0.135)
Prey 2	*T. longicornis*	0.57 ± 0.02			Feeding-current	CI–II		0.235 (0.124–0.444)
1F†				28				
Predator	*C. typicus*	1.1 ± 0.1	4–5					
Prey 1	*O. nana*	0.52 ± 0.05			Ambush	Female	10.1 (16.0–6.4)	0.086 (0.041–0.178)
Prey 2	*T. longicornis*	0.51 ± 0.07			Feeding-current	CI–II		0.183 (0.092–0.364)
1G†				43				
Predator	*P. norvegica*	5.1 ± 0.3	5–6					
Prey 1	*O. nana*	0.54 ± 0.05			Ambush	Female	2.6 (4.5–1.5)	0.056 (0.038–0.084)
Prey 2	*T. longicornis*	0.46 ± 0.04			Feeding-current	CI		0.138 (0.115–0.166)

Notes: Each experiment label in the table corresponds to its label in the figures. Size = average prosome length for predators and total length for prey; SD = standard deviation; C = concentration of predators per bottle (all experiments were conducted in 2-L bottles except for 1C and 2C where 1-L bottles were used), t = incubation time (hours); I_{max} = maximum ingestion rates (prey·predator^{-1}·d^{-1}, Eq. 5); β = maximum clearance rates (L·predator^{-1}·d^{-1}, Eqs. 3 and 4); CI = 95% confidence interval.
  † Indicates statistically significant difference in predation risk between prey (F-test, $P < 0.05$).
  "—" Indicates that saturation was not observed.

predatory copepods were fixed with Lugol's solution for sizing and staging. Number of predatory copepods per bottle ranged from 2 to 20 copepods depending on the experiment (Tables 1–4).

Prior to each experiment, copepods were acclimated to the experimental temperature (24 h) and predators were starved for 4–24 h (kept in 0.2 μm FSW). All experiments were conducted in 1- to 2-L bottles (Tables 1–4). Prey and predators were added at the desired concentrations and then incubated for 24–48 h in the dark in a temperature-controlled room (15°C except for *P. norvegica* at 11°C). For experiments with copepodites or adults as prey, specimens were picked individually under microscope, while for experiments with nauplii, individuals from each cohort were picked individually or, in the most of cases, we used aliquots from a concentrate of nauplii obtained using a 40-μm mesh. The bottles were not rotated during the experiments since this can negatively affect feeding of predatory copepods (Yen 1982). No phytoplankton was added to the experimental bottles. At the end of the experiments, entire bottle contents were filtered onto a 40-, 100- or 200-μm-mesh sieve, as appropriate. After determining the number of predators alive at the end of the incubation, all animals were preserved in 1% Lugol's solution and counted under a stereomicroscope.

Table 2. Summary of the experiments conducted to determine predation risk associated with different feeding behaviors: ambush vs. cruising feeders (2A–2E) and feeding-current vs. cruising feeders (3A–3B).

Expt.	Species	Size ± SD (mm)	C	t (h)	Feeding behavior	Stage	I_{max} (CI)	β (CI)
2A†				42				
Predator	*M. longa*	2.3 ± 0.1	6–9					
Prey 1	*O. nana*	0.12 ± 0.02			Ambush	NV–VI	12.7 (18.5–8.7)	0.080 (0.052–0.123)
Prey 2	*C. hamatus*	0.13 ± 0.02			Cruising	NII–III		0.210 (0.141–0.314)
2B†				39				
Predator	*A. armatus*	3.1.± 0.1	5					
Prey 1	*O. nana*	0.13 ± 0.02			Ambush	NV–VI	8.6 (12.1–6.1)	0.071 (0.031–0.162)
Prey 2	*C. hamatus*	0.12 ± 0.02			Cruising	NII–III		0.330 (0.165–0.657)
2C†				24				
Predator	*C. typicus*	1.0 ± 0.1	2–3					
Prey 1	*O. nana*	0.14 ± 0.02			Ambush	NV–VI	—	0.058 (0.035–0.098)
Prey 2	*C. hamatus*	0.14 ± 0.01			Cruising	NIII		0.305 (0.269–0.346)
2D†				43				
Predator	*C. typicus*	1.1 ± 0.1	5–7					
Prey 1	*O. nana*	0.56 ± 0.05			Ambush	Female	14.3 (68.2–3.0)	0.196 (0.110–0.350)
Prey 2	*C. hamatus*	0.50 ± 0.06			Cruising‡	CI–II		0.464 (0.246–0.874)
2E				46				
Predator	*A. armatus*	3.0 ± 0.1	10					
Prey 1	*O. nana*	0.52 ± 0.05			Ambush	Female	—	0.057 (0.040–0.082)
Prey 2	*C. hamatus*	0.47 ± 0.03			Cruising‡	CI		0.064 (0.046–0.088)
3A†				24				
Predator	*C. typicus*	1.0 ± 0.1	4–5					
Prey 1	*O. nana*	0.15 ± 0.02			Feeding-current	NIII	—	0.359 (0.298–0.432)
Prey 2	*C. hamatus*	0.13 ± 0.01			Cruising	NIII		0.258 (0.205–0.326)
3B†				24				
Predator	*C. typicus*	1.1 ± 0.1	3–6					
Prey 1	*O. nana*	0.46 ± 0.03			Feeding-current	CI–II	—	0.276 (0.163–0.467)
Prey 2	*C. hamatus*	0.46 ± 0.04			Cruising‡	CI–II		0.482 (0.297–0.782)

Notes: Each experiment label in the table corresponds to its label in the figures. Size = average prosome length for predators and total length for prey; SD = standard deviation; C = concentration of predators per bottle (all experiments were conducted in 2-L bottles); t = incubation time (hours); I_{max} = maximum ingestion rates (prey·predator^{-1}·d^{-1}, Eq. 5); β = maximum clearance rates (L·predator^{-1}·d^{-1}, Eqs. 3 and 4). CI = 95% confidence interval.
† Indicates statistically significant difference in predation risk between prey (*F*-test, *P* < 0.05).
‡ Indicates that the copepod can also create a feeding current.
"—" Indicates that saturation was not observed.

Calculations

Predation rates (I, prey·predator^{-1}·d^{-1}) of each predatory copepod on each prey type were calculated as

$$I = \frac{C_i - C_f}{N \times T} \quad (1)$$

where C_i is the initial prey concentration (average of initial and control bottles, prey/L), C_f is the final concentration of prey in the experimental bottle (prey/L), N is the average number of live predators during the incubation, and T is the incubation time in days.

The average concentration of each prey during the experiment (C, prey/L) was calculated assuming an exponential decline in prey concentration:

$$C = \frac{C_i - C_f}{\ln \frac{C_i}{C_f}} \quad (2)$$

Given that two prey were offered simultaneously, we fitted a two-species variant of Holling's disk equation (Holling 1959) to the observed predation rates to estimate maximum clearance rates (β, L·predator^{-1}·d^{-1}) on each type of prey and maximum ingestion rates (I_{max}, prey·predator^{-1}·d^{-1}). We assume that the two prey, 1 and 2, have similar handling times (τ = $1/I_{max}$, per day), but are cleared at different rates (β$_1$ ≠ β$_2$). Then:

Table 3. Summary of the experiments conducted to determine predation risk on males and females of ambush feeding copepods (4A–4F).

Expt.	Species	Feeding behavior	Gender	Size ± SD (mm)	C	t (h)	I_{max} (CI)	β (CI)
4A†						48		
Predator	A. armatus			2.7 ± 0.2	10			
Prey 1	O. nana	Ambush	Male	0.29 ± 0.02			4.7 (13.9–1.6)	0.196 (0.124–0.311)
Prey 2	O. nana	Ambush	Female	0.31 ± 0.02				0.054 (0.033–0.088)
4B†						48		
Predator	A. armatus			3.0 ± 0.2	5–8			
Prey 1	O. nana	Ambush	Male	0.31 ± 0.01			2.8 (4.8–1.6)	0.680 (0.192–2.412)
Prey 2	O. nana	Ambush	Female	0.32 ± 0.02				0.195 (0.060–0.631)
4C†						24		
Predator	P. norvegica			4.6 ± 0.6	2–4			
Prey 1	O. nana	Ambush	Male	0.28 ± 0.02			2.1 (6.9–0.6)	0.359 (0.045–2.860)
Prey 2	O. nana	Ambush	Female	0.29 ± 0.03				0.067 (0.004–1.008)
4D†						54		
Predator	P. norvegica			5.1 ± 0.3	5–6			
Prey 1	O. nana	Ambush	Male	0.29 ± 0.02			4.7 (13.9–1.6)	0.332 (0.193–0.571)
Prey 2	O. nana	Ambush	Female	0.30 ± 0.03				0.109 (0.061–0.196)
4E†						42		
Predator	C. typicus			1.1 ± 0.1	6–20			
Prey 1	O. nana	Ambush	Male	0.30 ± 0.01			13.7 (17.0–11.0)	1.105 (0.816–1.497)
Prey 2	O. nana	Ambush	Female	0.31 ± 0.02				0.407 (0.297–0.558)
4F†						28		
Predator	C. typicus			1.1 ± 0.1	4–5			
Prey 1	O. nana	Ambush	Male	0.30 ± 0.01			—	0.131 (0.108–0.158)
Prey 2	O. nana	Ambush	Female	0.31 ± 0.01				0.034 (0.019–0.062)

Note: Size = average prosome length for predators and prey; SD = standard deviation; C = concentration of predators per bottle (all experiments were conducted in 2-L bottles); t = incubation time (hours); I_{max} = maximum ingestion rates (prey·predator^{-1}·d^{-1}, Eq. 5); β = maximum clearance rates (L·predator^{-1}·d^{-1}, Eqs. 3 and 4); CI = 95% confidence interval.
  † Indicates statistically significant difference in predation risk between prey (F-test, $P < 0.05$).
  "—" Indicates that saturation was not observed.

$$I_1 = \frac{N_1}{T} = \frac{T_s\beta_1 C_1}{T_s + T_h} = \frac{T_s\beta_1 C_1}{\tau(N_1 + N_2) + T_s}$$
$$= \frac{T_s\beta_1 C_1}{\tau T_s(\beta_1 C_1 + \beta_2 C_2) + T_s} = \frac{\beta_1 C_1}{1 + (\beta_1 C_1 + \beta_2 C_2)\tau} \quad (3)$$

and similarly

$$I_2 = \frac{N_2}{T} \approx \frac{\beta_2 C_2}{1 + (\beta_1 C_1 + \beta_2 C_2)\tau} \quad (4)$$

where N_1 and N_2 are, respectively, the number of prey 1 and prey 2 captured; T is the total time ($T = T_s + T_h$), T_s is the searching time, T_h is the total handling time ($T_h = \tau(N_1 + N_2)$); and C_1 and C_2 are, respectively, the average concentration of prey 1 and prey 2.

The maximum ingestion rates (I_{max}, prey·predator^{-1}·d^{-1}) is

$$I_{max} = \frac{1}{\tau} \quad (5)$$

We consider the maximum clearance rate (β, L·predator^{-1}·d^{-1}) a measure of predation risk and computed the ratio between maximum clearance rates on prey with different behavior (β_1/β_2) to assess differences in predation risk. For each predation experiment, we conducted analysis of covariance (ANCOVA) to determine significant difference in predation rates (dependent variable) between prey types (independent variable) depending on prey concentration (covariate) using SPSS software. For each experiment, F-test was used to determine significant difference between the fitted models (Eqs. 3 and 4) and estimated maximum clearance rates (β_1 and β_2) using R software. A statistically significance level (α) of 0.05 was applied.

Table 4. Summary of the experiments conducted to determine predation risk on males and females of feeding-current feeding (5A–5D) and cruising feeding (6A–6C) copepods.

Expt.	Species	Feeding behavior	Gender	Size ± SD (mm)	C	t (h)	I_{max} (CI)	β (CI)
5A						44		
Predator	*A. armatus*			2.8 ± 0.1	10			
Prey 1	*T. longicornis*	Feeding-current	Male	0.80 ± 0.05			4.2 (57.0–0.3)	0.053 (0.026–0.109)
Prey 2	*T. longicornis*	Feeding-current	Female	0.81 ± 0.05				0.068 (0.033–0.139)
5B						46		
Predator	*A. armatus*			2.9 ± 0.1	10			
Prey 1	*T. longicornis*	Feeding-current	Male	0.80 ± 0.04			9.9 (84.1–1.2)	0.092 (0.054–0.156)
Prey 2	*T. longicornis*	Feeding-current	Female	0.78 ± 0.06				0.117 (0.070–0.197)
5C†						46		
Predator	*P. norvegica*			4.7 ± 0.6	6			
Prey 1	*T. longicornis*	Feeding-current	Male	0.74 ± 0.04			2.0 (3.1–1.3)	0.680 (0.165–2.807)
Prey 2	*T. longicornis*	Feeding-current	Female	0.75 ± 0.05				0.402 (0.095–1.700)
5D						49		
Predator	*P. norvegica*			4.8 ± 0.6	7			
Prey 1	*T. longicornis*	Feeding-current	Male	0.71 ± 0.05			4.5 (6.8–3.0)	0.558 (0.264–1.179)
Prey 2	*T. longicornis*	Feeding-current	Female	0.73 ± 0.05				0.642 (0.302–1.368)
6A†						44		
Predator	*A. armatus*			3.1 ± 0.2	10			
Prey 1	*C. hamatus*	Cruising‡	Male	0.80 ± 0.09			9.4 (162–0.5)	0.073 (0.045–0.120)
Prey 2	*C. hamatus*	Cruising‡	Female	0.91 ± 0.09				0.045 (0.027–0.073)
6B†						48		
Predator	*A. armatus*			3.0 ± 0.2	10			
Prey 1	*C. hamatus*	Cruising‡	Male	0.79 ± 0.07			—	0.035 (0.013–0.092)
Prey 2	*C. hamatus*	Cruising‡	Female	0.93 ± 0.07				0.023 (0.010–0.054)
6C†						46		
Predator	*P. norvegica*			4.7 ± 0.5	6–8			
Prey 1	*C. hamatus*	Cruising‡	Male	0.80 ± 0.08			4.8 (8.1–2.9)	0.292 (0.173–0.494)
Prey 2	*C. hamatus*	Cruising‡	Female	0.84 ± 0.09				0.190 (0.112–0.325)

Note: Size = average prosome length for predators and prey; SD = standard deviation; C = concentration of predators per bottle (all experiments were conducted in 2-L bottles); t = incubation time (hours); I_{max} = maximum ingestion rates (prey·predator^{-1}·d^{-1}, Eq. 5); β = maximum clearance rates (L·predator^{-1}·d^{-1}, Eqs. 3 and 4); CI = 95% confidence interval.
　† Indicates statistically significant difference in predation risk between prey (*F*-test, $P < 0.05$).
　‡ Indicates that the copepod can also create a feeding current.
　"—" Indicates that saturation was not observed.

RESULTS

Predation risk associated with feeding behavior

We found substantial differences in predation rates depending on feeding behavior of the prey. In almost all cases, the more active prey suffered much higher predation mortality than the less active prey at most prey concentrations (Figs. 1–3). When feeding-current feeders and ambush feeders were offered simultaneously as prey to predatory copepods, the predatory copepod fed on the feeding-current feeders at a significantly higher rate than for the ambush feeders (Fig. 1, ANCOVA, $P < 0.05$). This pattern was observed in all seven experiments conducted with these prey combinations, even though predation rates varied among predatory copepods and experiments (Fig. 1). When cruising and ambush feeders were offered simultaneously, predation rates were significantly higher on cruising feeders than on ambush feeders (Fig. 2, ANCOVA, $P < 0.05$) except for one experiment (Fig. 2E), where no significant difference between prey was observed (ANCOVA, $P = 0.658$). In contrast, there were no consistent differences in mortality risk between cruising and feeding-current feeders, although small but statistically significant differences were observed in individual experiments in favor of one or the other foraging strategy (Fig. 3, ANCOVA, $P < 0.05$).

Predation rates on both prey types generally increased linearly with increasing prey concentration, until, in some cases, reaching saturation (~functional response type II; Figs. 1–3). In cases where saturation was reached, estimated maximum ingestion rates (prey·predator^{-1}·d^{-1}) ranged from ~2.6 to 71 depending on prey type and predatory copepod species (Tables 1 and 2). Estimated maximum clearance rates (β), used as an estimator of predation risk for each prey type, ranged from 0.022 to 0.482 L·predator^{-1}·d^{-1} depending on prey feeding behavior, experiment, and predatory copepod species (Tables 1 and 2). Predation risk (β) on feeding-current feeders (in all cases) and cruising feeders (in four of five cases) was significantly higher than on ambush feeders (F-test, Tables 1 and 2). Differences in predation risk (β) between cruising feeders and feeding-current feeders were small but statistically significant (F-test, Table 2), and they were not in agreement between experiments.

Predation risk associated with gender behavior in copepods with different feeding behavior

Gender-specific predation risk differed depending on species/feeding mode (Figs. 4–6). When males and females of the ambush feeding copepod Oithona nana were offered simultaneously to predatory copepods (Table 3), predation rate on males was significantly higher than on females in all experiments, independent of the predatory copepod species (Fig. 4, ANCOVA, P < 0.05). In contrast, males and females of the feeding-current feeding copepod Temora longicornis had similar mortality risk due to predation across all the experiments (Fig. 5, ANCOVA, P > 0.05). In the case of the cruising feeding copepod Centropages hamatus, mortality from predation was higher for males than for females (Fig. 6, ANCOVA, P < 0.05), although the sex difference was much lower than in the ambush feeders (Fig. 4).

In most experiments, predation rates on males and females increased linearly with increasing prey concentration until reaching saturation (~functional response type II; Figs. 4–6), with maximum ingestion rates (prey·predator^{-1}·d^{-1}) ranging from 2 to 14 depending on the experiment and predatory copepod species (Tables 3 and 4). Estimated maximum clearance rates (β) on males and females of the ambush feeding copepod O. nana ranged from 0.131 to 1.105 and from 0.034 to 0.407, respectively, depending on the experiment (Table 3). In all cases, predation risk (β) on O. nana males was significantly higher than on females within a single experiment (F-test, Table 3). Predation risk (β) on males and females of the feeding-current feeding copepod T. longicornis was comparatively similar with no statistically significant differences in most cases (F-test, Table 4). In the case of the cruising feeder C. hamatus, males had a significantly higher predation risk (β) than females, although the difference in predation was low (F-test, Table 4).

Predation risk ratios between prey with different behavior (β$_1$/β$_2$)

Ratios between maximum clearance rates on prey with different behavior (β$_1$/β$_2$) differ among pairwise comparisons of feeding behaviors (Fig. 7A): The predation risk of feeding-current feeders was 2.1–7.7 times higher than that of ambush feeders and cruising feeders had a predation risk 2.4–5.3 times higher than ambushers, excluding one experiment where no difference between prey was observed (ratio ~1). In contrast, ratios between maximum clearance rates on cruising and feeding-current feeders were close to 1 (0.7–1.7), suggesting similar predation risk between these feeding behaviors (Fig. 7A). Ratios between maximum clearance rates on males and females (β$_1$/β$_2$) varied depending on feeding mode (Fig. 7B): The predation risk of males of the ambush feeding copepod O. nana was 2.7–5.4 times higher than for females, whereas difference in predation risk between genders of the feeding-current feeding copepod

Fig. 1. Predation rates of the predatory copepods Metridia longa (A), Aetideopsis armatus (B, D, E), Centropages typicus (C, F), and Paraeucheta norvegica (G) on feeding-current feeders (Temora longicornis) vs. ambush feeders (Oithona nana, O. davisae). Prey concentrations are average concentrations of each prey during the incubation (Eq. 2). Note that we used different copepod life stages within a single experiment (i.e., early T. longicornis nauplii vs. late Oithona nauplii and early T. longicornis copepodites vs. O. nana females) to ensure that prey have a similar size.
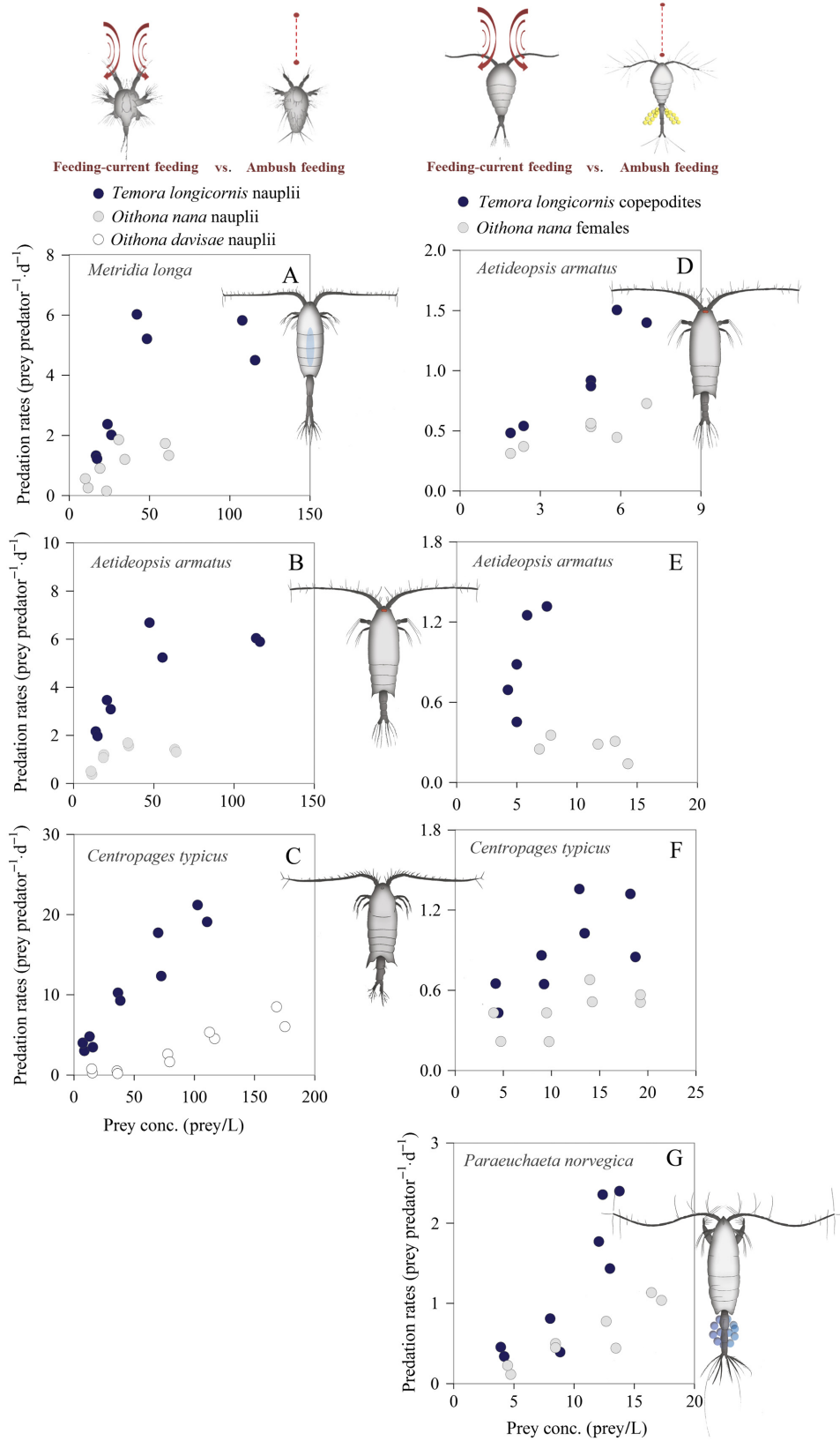
T. longicornis and cruising feeding copepod *C. hamatus* was lower (0.078–1.69 for *T. longicornis* and ~1.6 for *C. hamatus*) than for the ambush feeding *O. nana* (Fig. 7B).

DISCUSSION

The role of predation (top-down control) in structuring marine planktonic communities has received less attention by marine ecologists than that of bottom-up control (e.g., food/nutrient limitation, Verity and Smetacek 1996). However, increasing evidence suggests that predation plays an important role in determining the structure and dynamics of marine planktonic communities (Irigoien et al. 2005, Frank et al. 2006, Daewel et al. 2014). Among the factors affecting predation, the role of small-scale motile behavior of prey in defining predation risk has been understudied compared to other aspects of planktonic predator–prey interactions, such as prey size and abundance (Yen 1983, Munk 1997, Garrido et al. 2007). We have here demonstrated experimentally that small-scale motile behavior is a significant determinant of predation risk in zooplankton accounting up to nearly an order of magnitude variation in mortality risk. The feeding behaviors studied here transcend taxa, and therefore, the conclusions in terms of predation risk associated with feeding behavior apply not only for copepods but also for other planktonic organisms, allowing some generality on the role of prey behavior in predation risk in marine food webs. Our results are qualitatively consistent with predictions of theoretical models (Gerritsen and Strickler 1977, Visser 2007, Kiørboe and Jiang 2013, Uttieri et al. 2013). Moreover, the differences in mortality risk reported here are in reasonable quantitative agreement with the model predictions of behavior-dependent mortality risk in the species examined here (see van Someren Gréve et al. 2017). Our results also conform to the few previous experimental reports on prey motility and predation risk in zooplankton (Tiselius et al.

1997, Broglio et al. 2001, Titelman 2001), but our study is the first to systematically examine this dependency over the main foraging and mate-finding behaviors reported for zooplankton.

Both the sensory mechanisms of the predators and the motility of the prey need to be considered to account for the observed behavior-dependent predation risk. Although chemoreception can contribute to prey detection in some predatory copepods (Olsen et al. 2000), most predatory copepods, including the species used in this study, and other planktonic predators (e.g., chaetognaths) use mechanoreceptors to remotely perceive prey (i.e., rheotactic predators; Horridge and Boulton 1967, Yen et al. 1992, Kiørboe et al. 1999, Olsen et al. 2000, Kjellerup and Kiørboe 2012). The maximum distance at which rheotactic predators can detect prey depends on the hydrodynamic signal generated by the prey, which in turn depends on its size and motility behavior, that is, speed and propulsion mode (Tiselius and Jonsson 1990, Kiørboe and Visser 1999, Svensen and Kiørboe 2000, Kiørboe et al. 2014). Thus, for a similar prey size, a prey that actively moves (cruising feeders) and/or creates feeding currents generates high fluid disturbances (signals) that increase their probability of being detected by rheotactic predators. On the contrary, prey with low or reduced motility have decreased detection and encounter rates with rheotactic predators, making them less vulnerable to predation.

Prey motility not only increases predation risk from rheotactic predators but also increases the prey's susceptibility of being detected by visual predators (e.g., fish larvae, Buskey 1994, O'Keefe et al. 1998). In the context of trade-offs in zooplankton (Litchman et al. 2013), we assert that active motile behaviors, which are assumed to have higher feeding efficiencies, have the disadvantage/cost of a higher predation risk compared to less motile behaviors (e.g., ambush feeders). Among planktonic copepods, small ambush feeding copepods of the genus *Oithona* are considered the most ubiquitous and abundant

Fig. 2. Predation rates of the predatory copepods *Metridia longa* (A), *Aetideopsis armatus* (B, E), and *Centropages typicus* (C, D), on cruising feeders (*Centropages hamatus*) vs. ambush feeders (*Oithona nana*). Prey concentrations are average concentrations of each prey during the incubation (Eq. 2). Note that we used different copepod life stage to ensure a similar size of prey (i.e., early *C. hamatus* nauplii vs. late *Oithona* nauplii, and early *Temora* copepodites vs. *O. nana* female). *C. hamatus* copepodites also create a feeding current.
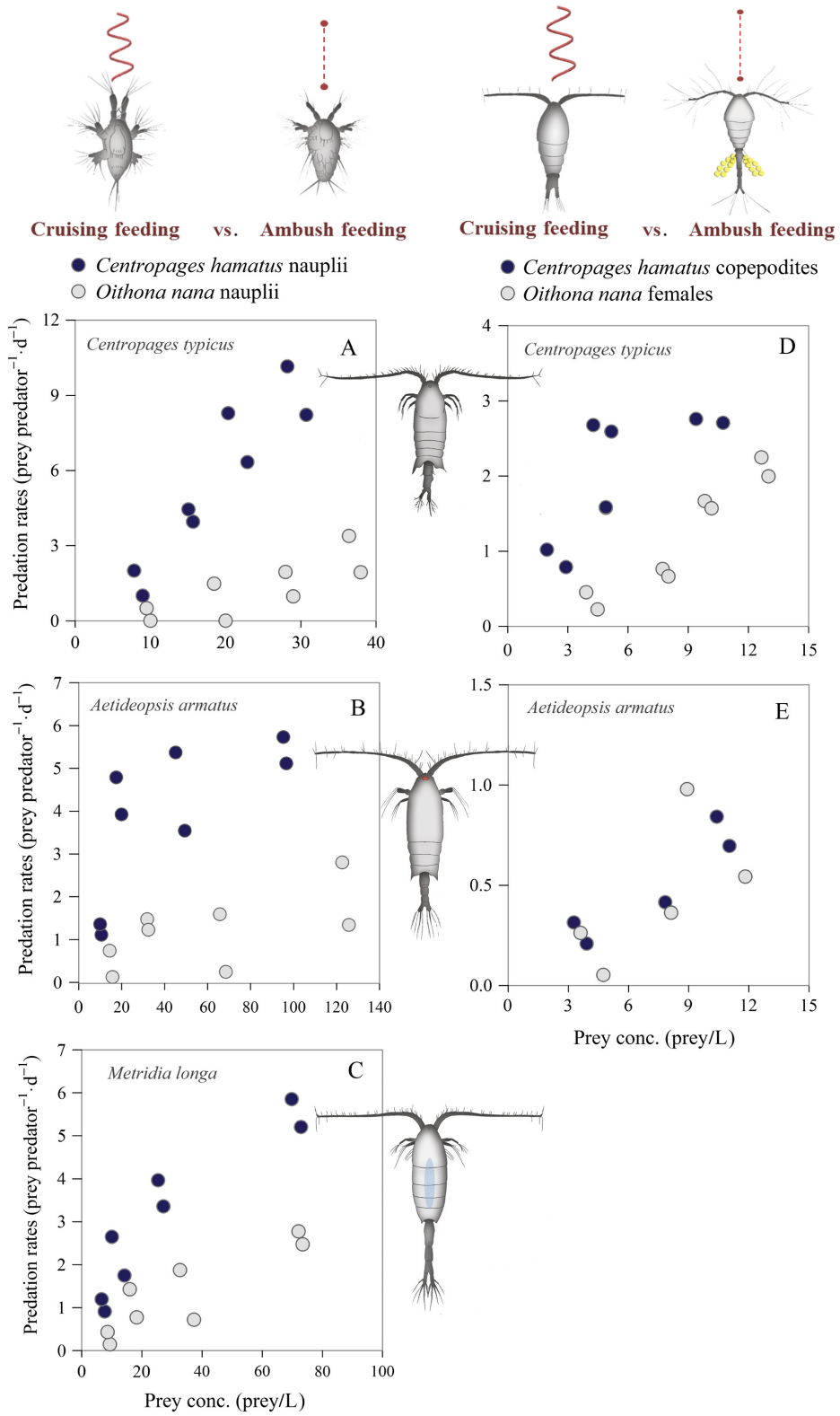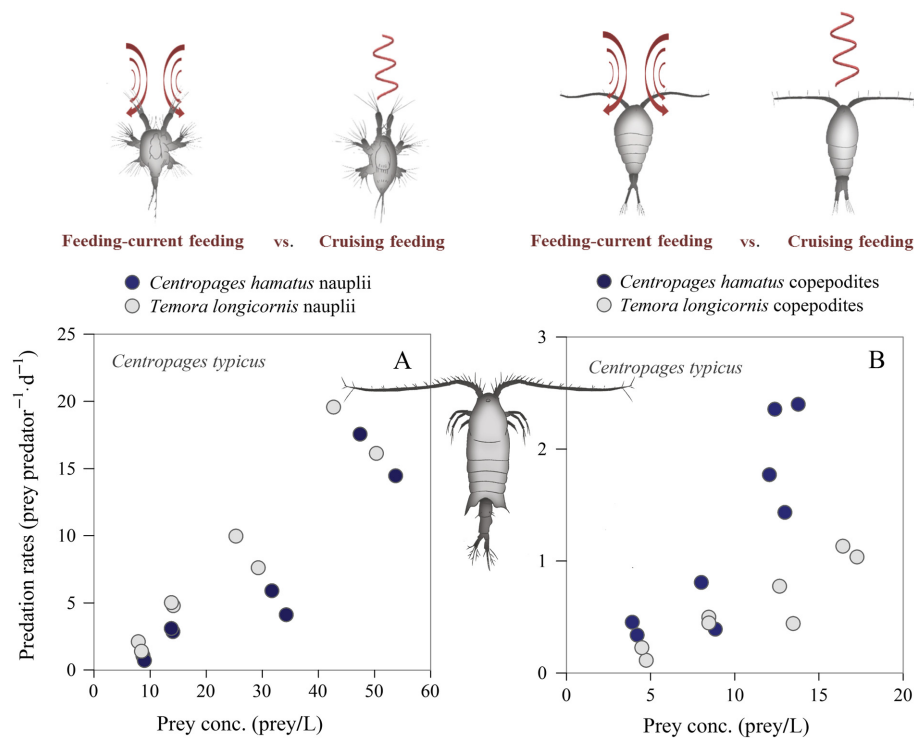
Fig. 3. Predation rates of *Centropages typicus* on nauplii of *Temora longicornis* (feeding-current feeder) and *Centropages hamatus* (cruising feeder) (A) and early copepodites of *T. longicornis* (feeding-current feeder) and *C. hamatus* (cruising feeder) (B). Prey concentrations are average concentrations of each prey during the incubation (Eq. 2). *C. hamatus* copepodites also create a feeding current.

copepods in the world's oceans (Gallienne and Robins 2001). The omnipresence and success of *Oithona* in marine environments can in part be due to their low motility foraging strategy, which likely results not only in lower metabolic costs and food requirements than other feeding modes (Paffenhöfer 1993, 2006, Almeda et al. 2010*a*, *b*, 2011) but also leads to a lower predation risk as demonstrated in this study.

Small-scale motile behavior is also closely associated with another crucial function of zooplankton: reproduction. Among planktonic pelagic copepods, males typically move more and faster than females (Kiørboe and Bagøien 2005, Kiørboe et al. 2005), and therefore, males are expected to have a higher predation risk than females (Kiørboe 2008*b*). Our results show that gender-specific predation risk depends on feeding behavior, with ambush feeders showing the highest difference in predation between males and females. These differences in predation risk

between genders are due to differences in motile behavior (e.g., % time moving, swimming speeds) between males and females depending on the feeding behavior (Kiørboe 2008*b*, van Someren Gréve et al. 2017). For example, males of the ambush feeding copepod *Oithona davisae* swim 15-fold faster than females (Kiørboe 2008*b*). Therefore, the strong difference in motile behavior between males and females of ambush feeders (*Oithona*) can explain the notable difference in gender predation risk observed in our study. On the contrary, copepods that move more during feeding (cruising feeders and feeding-current feeders) showed, in general, small differences in predation mortality between genders. In these feeding strategies, the difference in motile behavior (e.g., swimming speed) between genders is smaller than for ambush feeders (van Someren Gréve et al. 2017), which explains the small difference in predation risk between genders of active feeding modes.
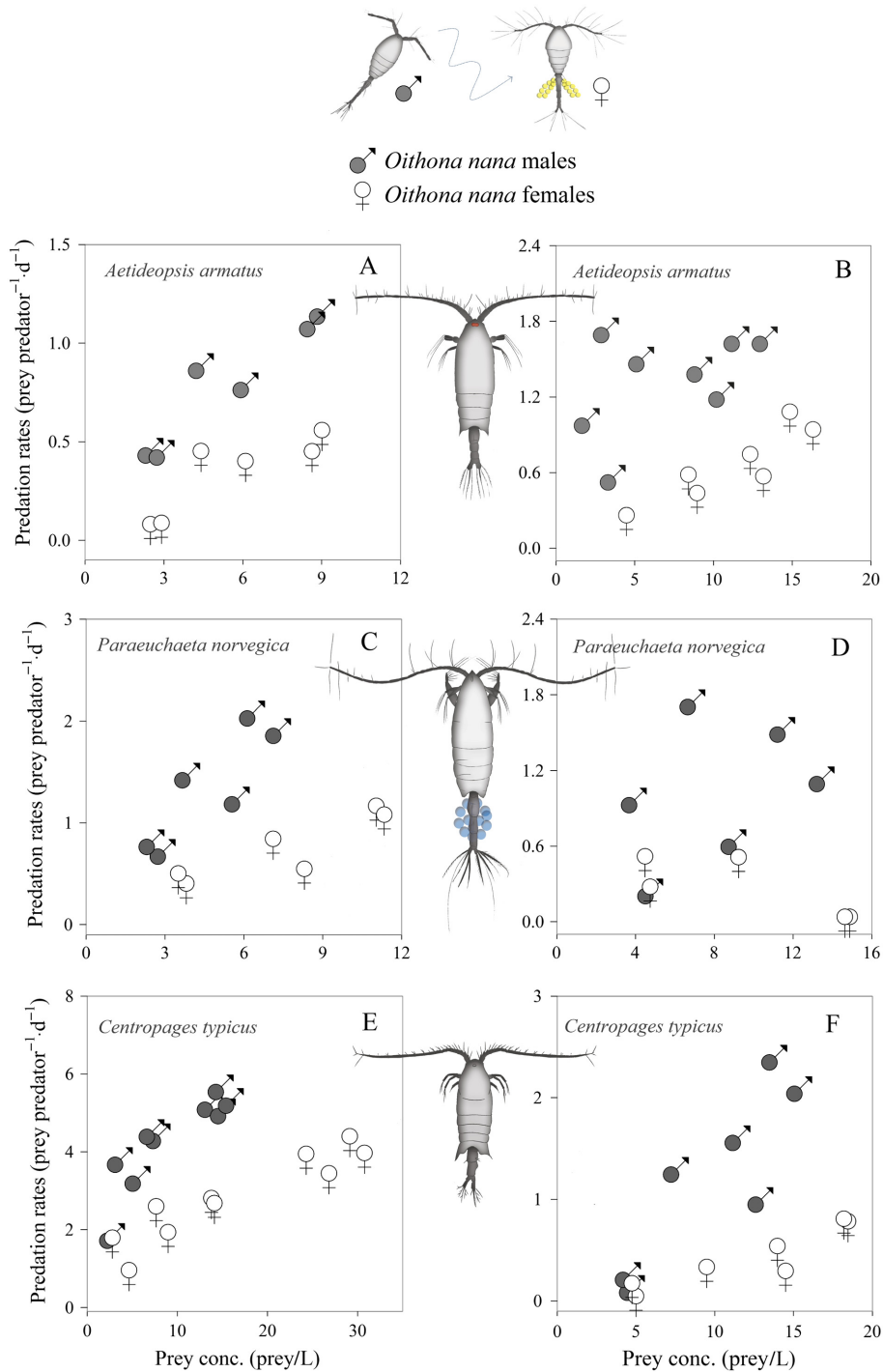
Fig. 4. Predation rates of *Aetideopsis armatus* (A, B), *Paraeucheta norvegica* (C, D), and *Centropages typicus* (E, F) on males and females of the ambush feeder copepod *Oithona nana*. Prey concentrations are average concentrations of each prey during the incubation (Eq. 2).
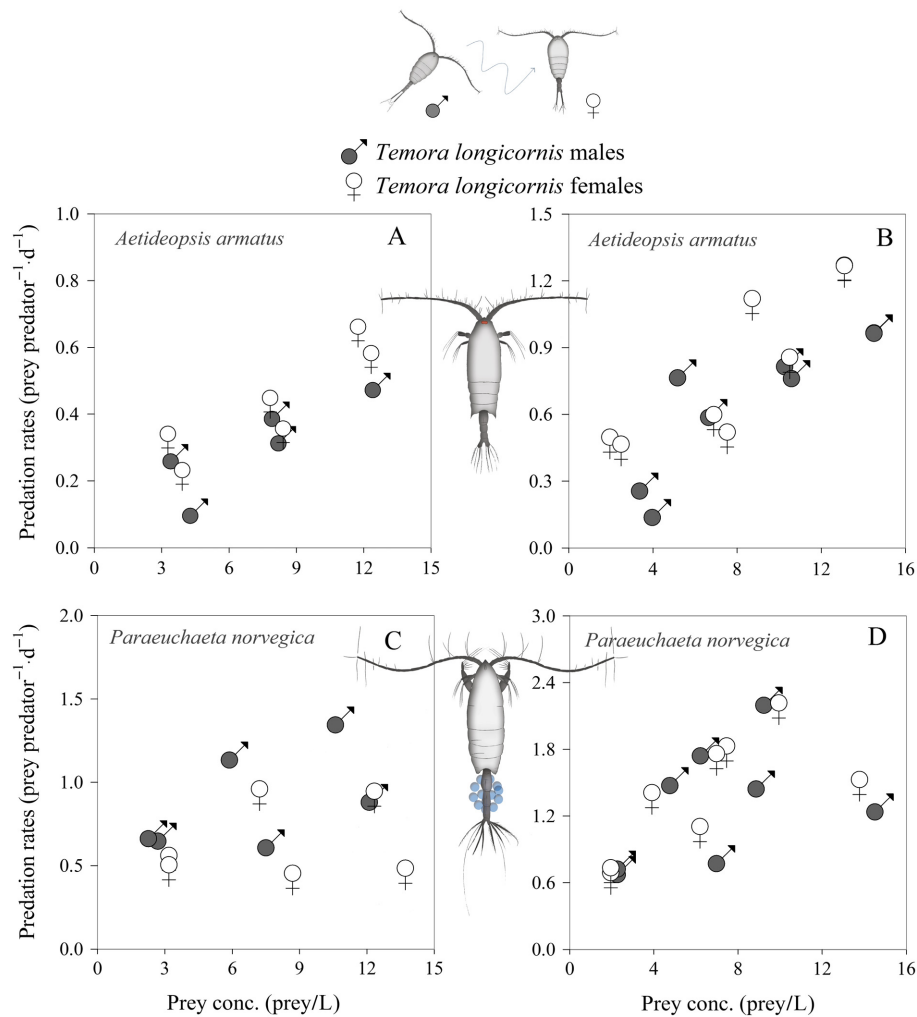
Fig. 5. Predation rates of *Aetideopsis armatus* (A, B), *Paraeuchaeta norvegica* (C, D) on males and females of the feeding-current feeder copepod *Temora longicornis*. Prey concentrations are average concentrations of each prey during the incubation (Eq. 2).

Copepod sex ratios are the result of multiple factors (e.g., physiological life span, environmental conditions, predation), and the relative contribution of each factor may vary among species. In a recent review, Gusmão et al. (2013) pointed out that there is little empirical evidence of predation causing female-biased sex ratios in marine pelagic copepods (Hirst et al. 2010). However, our experimental results suggest that the higher predation on males may partially explain field observations of high female-biased sex ratios in populations of ambush feeding copepods (0.16 for Oithonidae) and sex ratio close to 1 for more active species (Temoridae and Centropagidae;

Kiørboe 2006, Hirst et al. 2010). Our study demonstrates that gender-specific predation pressure can to some extent explain skewed sex ratios in *Oithona* and that behavior-dependent predation can decisively affect the population structure of planktonic copepods.

Copepods are able to distinguish between hydrodynamic signals created by themselves from those created by the motile behavior of prey or predators (Hwang and Strickler 2001, Bagøien and Kiørboe 2005*b*). This ability allows copepods to detect specific hydrodynamic disturbance generated by a moving predator (i.e., fluid deformation) and to escape (e.g., jumping) from this
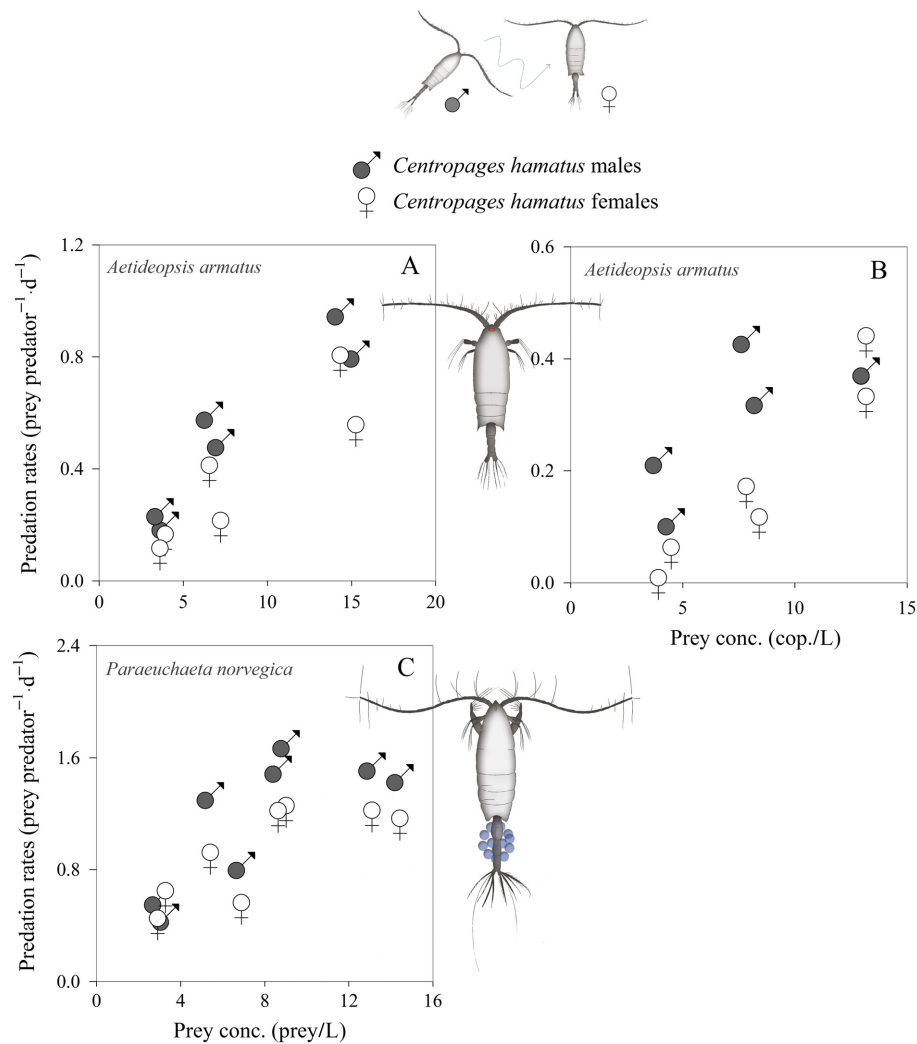
Fig. 6. Predation rates of *Aetideopsis armatus* (A, B), *Paraeuchaeta norvegica* (C) on males and females on the cruising feeder copepod *Centropages hamatus*. Prey concentrations are average concentrations of each prey during the incubation (Eq. 2).

predator to reduce mortality (Yen and Fields 1992, Buskey 1994, Buskey et al. 2012). The vulnerability of planktonic prey to predation depends on both the encounter rates with predators and the escape capabilities of the prey. Escape success can substantially differ among copepod species, and therefore, escape capabilities can partially explain difference in predation risk among copepods (Titelman 2001). However, in our parallel study on the behavior of the studied copepod species, we found that escape response parameters (e.g., jump distance, threshold deformation rates to elicit escape response) differ slightly among copepod stages of similar size with mostly non-statistically significant differences (van Someren Gréve et al. 2017). Even we found some significant differences in escape capabilities between species/stages (van Someren Gréve et al. 2017), escape response cannot explain the observed differences in predation risk between the planktonic copepods investigated here. For example, threshold deformation rates for males of *Oithona nana* are two times higher than for females, but predation on males was four times higher than on females (van Someren Gréve et al. 2017).
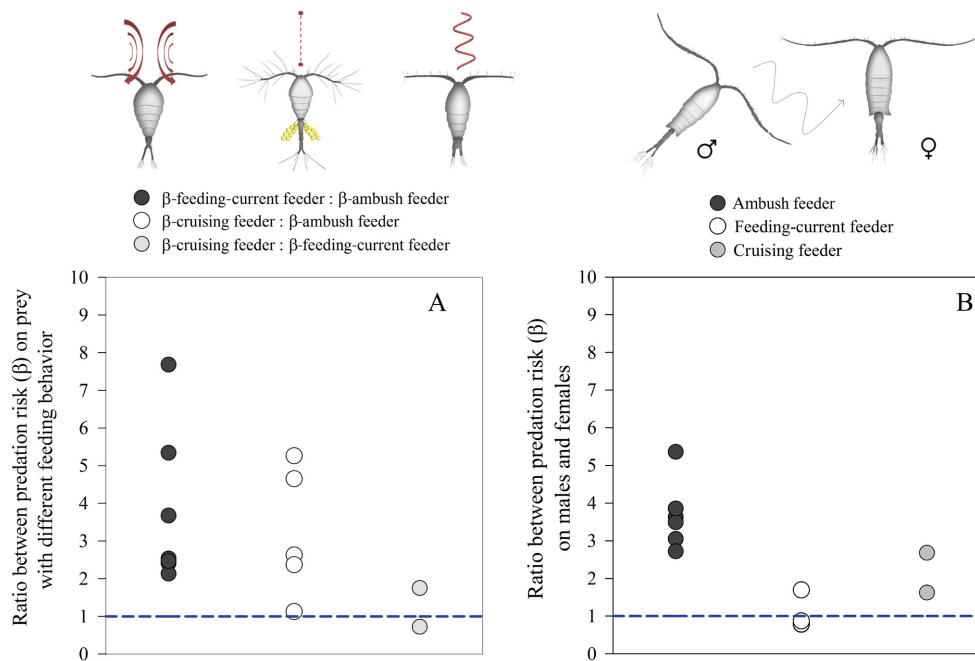
Fig. 7. Ratios between predator maximum clearance rates (β, L·predator^{-1}·d^{-1}) on prey with different feeding behaviors (A) and between maximum clearance rates (β) on males and females of copepods with different feeding behavior (B). The dashed line indicates a ratio = 1; that is, the predation risk is equal between prey types.

The predation rates found in this study are in the range of those from previous studies of studied predatory copepods feeding on copepods (Tiselius et al. 1997, Olsen et al. 2000) or nauplii (Sell et al. 2001, Titelman 2001). As expected, predation rates increase as prey concentration increases due to increased prey detection by predatory copepods (Gerritsen and Strickler 1977). In contrast to our model predictions (van Someren Gréve et al. 2017), we did not find a clear pattern between maximum clearance rates and body size of predatory copepods. This can be partially due to differences in predatory behavior among species, prey/predator size ratios, or bottle effects. For instance, the smaller predatory copepod, *C. typicus*, only feeds on certain body parts when capturing large prey (e.g., copepodites) and discards the rest. Also, clearance rates of the larger predatory copepods, which conduct large vertical migrations, can be more affected by limited incubation volume than those for the smaller species. Even though we conducted the experiments with the same methodology, predation rates can vary depending on individual variability (e.g., size, physiological state, age, starvation degree; Olsen

et al. 2000), which could partly explain the differences in predation rates of the same predator species among our experiments.

Laboratory experiments are an essential tool to investigate predator–prey interactions of plankton, but direct extrapolation to the field should be considered carefully. Extrinsic factors/environmental variability can affect the predation rates in the field. For example, small-scale turbulence may positively or negatively affect the ability of zooplankton to detect prey and predators (Rothschild and Osborn 1988, Gilbert and Buskey 2005). Ambush feeders that rely strongly on hydromechanical disturbances are more sensitive and respond differently to turbulence intensities than other feeding modes (Saiz et al. 2003). Also, food concentration can affect predation risk in zooplankton. Many planktonic copepods, including the species studied here, show a functional feeding response type III (Holling 1959). This type of functional response is characterized by the presence of a "feeding threshold," that is, a prey concentration below which the copepod stops feeding or reduces its clearance rates (Kiørboe et al. 1985, Wlodarczyk 1988). The presence of

lower feeding thresholds can be interpreted as an adaptation/strategy not only to conserve energy at low food concentrations (the energetic cost of collecting food at very low concentrations would not be compensated for the energetic gain) but also to reduce predation risk. Reduced feeding activity at low prey concentration may result in lower predation risk. Thus, other aspects of small-scale behavior may strongly influence mortality from predation in zooplankton.

Conclusions

In the context of trait-based approaches (Bruggeman and Kooijman 2007, Litchman et al. 2013), and in light of our results, small-scale motile behavior must be considered a key trait in zooplankton due to its strong influence on feeding, reproduction, and predation risk. Our results emphasize that feeding behavior–predation risk and mating behavior–predation risk are important trade-offs that defined optimal strategies in zooplankton and impact the structure and dynamics of copepod populations. Our empirical estimates of the predation risk associated with different motile behaviors in zooplankton help to quantify the gain over the risk associated with a specific behavior and to predict optimal zooplankton strategies depending on the environmental conditions (Visser 2007, Mariani et al. 2013). Overall, our results demonstrate that small-scale behavior associated with feeding and reproduction is a major determinant of predation risk in planktonic food webs.

Acknowledgments

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