

Kin Recognition during Intraspecific Predation by *Harpacticus* sp. (Copepoda: Harpacticoida)

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Hans-Uwe Dahms and Pei-Yuan Qian (2006) Kin recognition during intraspecific predation by *Harpacticus* sp. (Copepoda: Harpacticoida). *Zoological Studies* 45(3): 395-403. Female predation on developmental instars of its own as well as on conspecific alien offspring is reported for a new species of *Harpacticus* sp. from Hong Kong waters. The intensity of predation by *Harpacticus* females on their own offspring compared to that on offspring of conspecific females did not differ which indicates that females do not spare their individual offspring. The nutritional status of females affected the intensity of their predation on nauplii. When starved, they consumed about twice as many nauplii as they did when being fed algae. Intraspecific predation was found to be density-dependent. Enhanced predation with increasing female/nauplius ratios could be explained by the increasing probability of female/nauplius encounters. Feeding ratios were determined and a functional ingestion response is discussed with findings from the literature. <http://zoolstud.sinica.edu.tw/Journals/45.3/395.pdf>

Key words: Kin recognition, Intraspecific predation, Density, Nauplius, Copepods.

Most information on food sources of harpacticoid copepods is anecdotal or vague, often relying on indirect observations, such as copepods being successfully reared on certain types of food. In an attempt to generalize these few findings, it seems as if most free-living harpacticoid copepods are opportunistic feeders and are known to feed on particulate organic material (POM) derived from living and/or decaying sources, as well as on prokaryotic bacteria and eukaryotic protists such as ciliates (Montagna 1984). Furthermore, there is evidence for the uptake of dissolved organic matter (DOM; Brown and Sibert 1977), and the diverse harpacticoid group taken as a whole may engage in the nutritional uptake of apparently any other organic source available in the aquatic environment (for a review see Hicks and Coull 1983). It appears that there are guilds in the Harpacticoida, and each harpacticoid taxon (not even considering ontogenetic and gender specificities) has its own

response to a given food item or substrate.

The first inference study on harpacticoid carnivory was made by Willey (1930) who observed representatives of *Tisbe* attached to decaying fish flesh or cephalopod eggs. Other reports on harpacticoid carnivory are more anecdotal. It cannot be excluded, however, that bacteria, which quickly cover organic surfaces, such as corpses of metazoa, are the predominant organic food source of harpacticoids that were found on carcasses (cf. Hicks and Coull 1983). As for carnivory, Kunz (1984) conducted a morphological inference study on predatory deep-sea harpacticoids. Later, Lehman and Reid (1992) observed that the limnetic *Phyllognathopus viguieri* did ingest nematodes belonging to 7 different genera. Seifried (1997) found an entire harpacticoid nauplius in the gut of *Ectinosoma tegula*; however, it remained unclear whether this was ingested as a dead larva or consumed when alive. Seifried and Durbaum (2000) showed by cinematographic techniques that *E.*

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carnivora was carnivorous and fed on immobilized ostracods or fish tissue.

Intra- and interspecific predation by adults has been reported for several copepod species, belonging to the Calanoida (e.g., Lonsdale et al. 1979, Yen 1988, Jonsson and Tiselius 1990, Uye and Liang 1998), Cyclopoida (e.g., Lampitt 1978, Williamson 1980, Brandl and Fernando 1981), and Harpacticoida (e.g., Lazzaretto and Salvato 1992). Predatory behavior on early developmental instars in the Harpacticoida has only been described for the harpacticoid taxon *Tigriopus*. Both, *Tigriopus* and *Harpacticus* sp., the latter studied here, belong to the Harpacticidae. *Tigriopus californicus* preys on early conspecific naupliar stages (Egloff 1966). *Tigriopus fulvus* preys on the offspring of conspecifics during shortages in the food supply (Lazzaretto and Salvato 1992). All representatives of *Tigriopus* studied in this respect can be regarded as opportunistic feeders, being facultative predators but can be sustained on POM or a microorganismic diet alone. Lazzaretto and Salvato (1992) postulated that harpacticoid females of *T. californicus* spare their offspring, by selectively predating on the nauplii of non-related conspecifics. This implies the presence of a recognition mechanism.

In the present study, we tested the hypothesis that adult females of *Harpacticus* sp. can differentiate between their own offspring and the offspring of conspecific females when predating on them. We also wanted to test the assumption that intraspecific predation on offspring varies with the abundance of other available food items and that intraspecific predation is density-dependent.

MATERIALS AND METHODS

Collection of harpacticoid copepods

All copepod specimens used in this study were derived from the stocks reared in the Coastal Marine Laboratory (CML) at Hong Kong University of Science and Technology (HKUST). They were isolated, maintained, and cultivated as follows. The laboratory populations were composed of hundreds of individuals, originating from 6 females obtained from macroalgae collected from a fish farm at Wong Chek, Hong Kong (22°25'N, 114°20'E) in early Apr. 2004. Females of *Harpacticus* sp. bearing egg sacs were collected using a beaker in which macroalgae (primarily *Ulva* sp.) from fish-farm rafts were stirred up and subse-

quently poured over a screen of 110 µm mesh size. The residue containing the harpacticoids was rinsed into smaller containers for transport to the laboratory.

Maintenance and cultivation of harpacticoid copepods

Adult females were placed in individual Petri dishes containing 25 ml of 0.45-µm-filtered seawater (FSW) with a salinity of 34 ppm. They were kept at 26°C in a light-dark cycle of 12: 12 h. The rate of seawater renewal was about 50%/wk. The copepods were fed exclusively with the chryso-phyte, *Isochrysis galbana*. Supplies of unicellular algae were renewed every 2 d, and excess food was always available. However, no food was added during the experiments that lasted for 48 h. For fecundity estimations, 20 females bearing egg sacs, from a laboratory population containing cohorts of different ages, were randomly chosen and fixed in 70% ethanol. Then, their egg sacs were removed, transferred to glycerine on a microscopic slide, and gently squeezed using a coverslip. The eggs were subsequently counted at 100x magnification.

Cultivation of algae

Monospecific algal cultures of the single-cell chryso-phyte, *I. galbana* (Tahitian strain), were semi-continuously grown in f/2-medium (Guillard and Ryther 1962) at 26°C and 34 ppm salinity under continuous illumination. Algae in the exponential growth phase were used to feed the copepods at densities of 1-2 x 10⁵ cells/ml.

Observations and experimental treatments

Observations of harpacticoid copepod behavior were made by placing glass culture bowls containing 250 ml of FSW and usually hundreds of harpacticoids and their developmental instars under a dissecting microscope. Experimental dishes were kept under the same conditions of water quality, temperature, light, and algal growth as the culture bowls in order to allow fast adaptation after the transfer of individual females or developmental instars.

Experiment 1: Predation dependent on starvation level and nauplii of different relatedness

Experiment 1 was designed to show 1)

whether females discriminate between their own naupliar offspring and that of other females (referred to as alien conspecific offspring), and 2) whether their discriminative power is dependent on their hunger level. Two treatments were used with either starved females or females provided with algal food ad libitum (10^5 cells/ml). The experimental setups were divided into treatments of female/nauplius combinations having different genetic relationships. In 1 treatment, which was labeled Own, mothers were combined with 20 individuals of their own early nauplii per dish, shortly after leaving the egg capsule cases which were still attached to the egg apertures of their mothers. In a 2nd treatment labeled Alien, females which had just released their nauplii were combined with 20 nauplii per dish derived from other females. Experiments were replicated 3 times. In each replicate, 5 nonovigerous females were added to 5 Falcon dishes (50 mm in diameter) that were filled with 4.5 ml of FSW or algal suspensions. Twenty nauplii were added to each dish (in total, 500 nauplii were used per replicate). Dishes with 20 nauplii but without females served as the controls. Naupliar mortality was estimated after 48 h, by counting the nauplii and subtracting this number from the original number of nauplii used. Natural mortality was estimated from the controls by counting dead specimens.

Experiment 2: Density-dependent predation

Experiment 2 was designed to examine whether the density of starved females enhanced naupliar mortality due to predation. In 3 separate treatments, 2, 3, and 5 nonovigerous females were added to 5 Falcon dishes (50 mm in diameter) that were filled with 4.5 ml of FSW. Twenty early naupliar stages were subsequently transferred to each dish; 400 nauplii were used per replicate). Dishes without females served as controls. Naupliar mortality was estimated after 48 h (see above).

Statistical analysis

The software package STATISTICA (StatSoft, Tulsa, OK, USA) was used for the statistical analyses. The normality of the data was substantiated by Shapiro-Wilk's W-test (Shapiro and Wilk 1965). Differences between treatments and controls were determined by one- and two-way analyses of variance (ANOVA) followed by a post-hoc (least square difference; LSD) test (Zar 1999).

RESULTS

It was inferred that adult females fed on early and advanced naupliar instars as well as on copepodids from the fact that certain instars were missing from the cultures.

If copepodids were fed upon, the females had a preference for younger individuals. It should be emphasized that representatives of *Harpacticus* sp. used here are not obligate predatory copepods. The laboratory populations of this species can readily be sustained solely on an algal diet, and can be fed other diets as well, so long as they are offered an organic food source, such as TetraMin, algal debris, boiled rice, or immobilized invertebrates). This opportunistic feeding mode may explain the rather moderate predation intensity on naupliar instars.

The assumptions mentioned above were not based on direct observations but rather were inferred from the fact that certain developmental stages were missing from the treatment populations, and disrupted body parts were occasionally found. Also, we were unable to determine if the ontogenetic instars were already dead when devoured. If this were the case, then no actual predation would have taken place. This reasoning was substantiated by the observation that *Harpacticus* sp. from Hong Kong waters feeds on carcasses of small invertebrates such as ostracods, tissue pieces of polychaetes or bivalves, and detached egg sacs.

Active pursuit of living conspecifics or offspring was not observed in females belonging to *Harpacticus* sp., except for a single case where an early nauplius was captured and seized by a *Harpacticus* sp. female.

Experiment 1: Was female predation effectively dependent on starvation and on the female's genetic relationship with the nauplii? In general, female predation on nauplii was assumed when naupliar mortality inferred from missing naupliar stages was significantly higher than that in the control. Dead naupliar corpses were occasionally found in the control but never in the experimental treatments where both dead and living nauplii were apparently ingested by the females. No significant difference was found between the level of predation on their own offspring by female *Harpacticus* sp. from Hong Kong waters and that of offspring by non-related conspecific females (Fig. 1). The results of 3 independent trials were consistent. It was found that females did not differentiate

between their closest relatives in the form of their own offspring and the offspring of other females.

Starvation affected the intensity of predation on nauplii (Fig. 1, one-way ANOVA results for replicate 1: $F_{3,15} = 3.178$, $p = 0.035$; replicate 2: $F_{3,15} = 4.211$, $p = 0.012$; and replicate 3: $F_{3,15} = 1.837$, $p = 0.161$). The pooled (replicates 1-3)

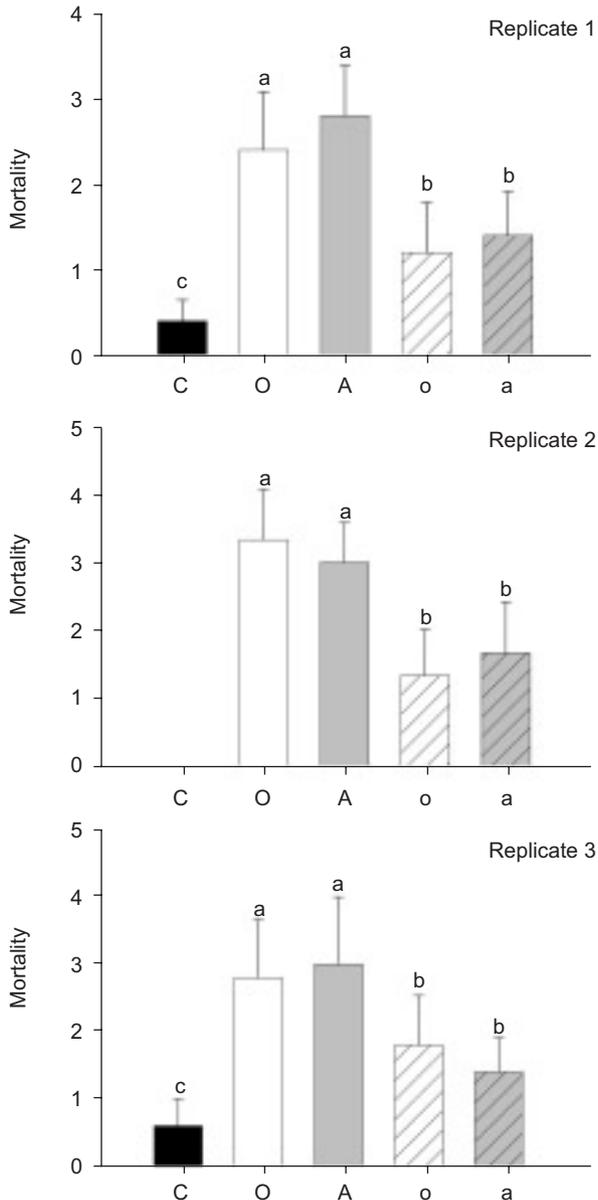


Fig. 1. Naupliar mortality ($n = 20$) of *Harpacticus* sp. in dishes with mothers (O/o=Own nauplii) or distantly related females (A/a=Alien nauplii), being either starved (unhatched) or fed ad libitum (hatched). Dishes without females served as controls (in 3 replicates). Means that do not significantly differ from each other are indicated by the same small letter above the error bars which represent the standard deviation (SD).

one-way ANOVA results were as follows: $F_{12,15} = 3.075$, $p = 0.074$. When starved, females devoured about twice as many nauplii as when fed ad libitum, irrespective of the relationship (own or alien) to the nauplii they were feeding on. Two-way ANOVA substantiated that only the feeding condition (starved or fed ad libitum) had a significant effect on the mortality of nauplii (not illustrated; two-way ANOVA results significant only for replicates 1 and 2 of 3 for the feeding condition; for replicate 1: $F_{3,15} = 4.82857$, $p = 0.043$ and replicate 2: $F_{3,15} = 4.736$, $p = 0.044$). There was no effect on naupliar mortality depending on whether it was their “own” or “alien” nauplii nor a discernible combined effect with the feeding condition.

Experiment 2: Was female predation effectively dependent on the density of females?

Higher female densities resulted in progressively higher mortality to nauplii than those at lower densities (Fig. 2, one-way-ANOVA results for replicate 1: $F_{3,15} = 23.126$, $p < 0.001$; replicate 2: $F_{3,15} = 61.221$, $p < 0.001$; and replicate 3: $F_{3,15} = 20.011$, $p < 0.001$). The pooled one-way ANOVA results were as follows: $F_{9,15} = 34.786$, $p < 0.001$. The results from the 3 independent trials were consistent.

From experiment 1, the daily per capita naupliar consumption by females was as follows: in a starved condition, a single female consumed 1.40 ± 0.327 (SD) nauplii/d; and when fed, a single female consumed 0.83 ± 0.245 nauplii/d. When all females were pooled from experiment 2 (effect of different female densities on naupliar predation), a single female consumed 1.54 ± 0.433 nauplii/d.

DISCUSSION

General considerations

Females of *Harpacticus* sp. exhibit no characteristic of obligatory predatory copepods. They can readily be sustained solely on an algal diet, and can survive and reproduce on other diets as well. This may explain the moderate predation intensity on naupliar instars. Even when females were starved, nauplii showed survival rates of about 25% after 24 h at the highest female densities of 5 females per Falcon dish. Even under high population densities, the pronounced fecundity of the new species of *Harpacticus* sp. compared to other representatives of the Harpacticidae (Table

1) allowed the survival of a substantial portion of nauplii.

Observations of mortality, which was not due to predation in the controls, showed that feeding on instars that had died, without actively preying on them when alive and moving, would have contributed only to a minor portion of the observed

decrease in naupliar abundances in the experimental treatments. The few cases of non-predation mortality among nauplii in the controls clearly show that the maintenance conditions were favorable for this species. Corpses were almost exclusively found in the control dishes. Some appeared whitish, probably due to internal microbial degradation. In the treatments with females, however, dead corpses were hardly ever recorded, suggesting that they were devoured before observations were made. The increase in consumed naupliar stages in the treatment dishes is most reasonably explained by active predation on the nauplii.

Ecological significance of intraspecific predation

Lazaretto et al. (1990) showed that arrested development of female copepodid stages I-II in *Tigriopus fulvus* occurred in a large proportion of females in laboratory cultures. The authors interpreted this delay in female maturation as a form of female dormancy. The dormancy phenomenon and the cannibalistic feeding behavior which occurs in this species were interpreted as mechanisms which negatively affect the rate of population growth under crowded conditions (cf. Dahms 1995). Therefore, dormancy and/or cannibalistic feeding will ultimately reduce the number of offspring and the population density.

According to Gabriel (1985) who studied freshwater cyclopoids, intraspecific predation can be expected to become an evolutionarily stable strategy (ESS) in fluctuating environments. The shallow marine phytoplankton habitat of *Harpacticus* sp. studied here can be interpreted as such a fluctuating habitat. It is noteworthy that this habitat is characterized by frequent changes in environmental conditions often for short periods of time, including electrolyte dilution due to precipitation and runoff, enhanced salinity due to evaporation, solar irradiation, oxygen reduction in zones of organic debris deposition, and the surge and shock of wave action. These events may offer unpredictable chances for opportunistic species at times. When population growth exceeds the carrying capacity of the environment, however, a storage function can be maintained by keeping material and energy within the assemblage of conspecifics by intraspecific predation.

Chemical recognition

The findings of Lazaretto and Salvato (1992)

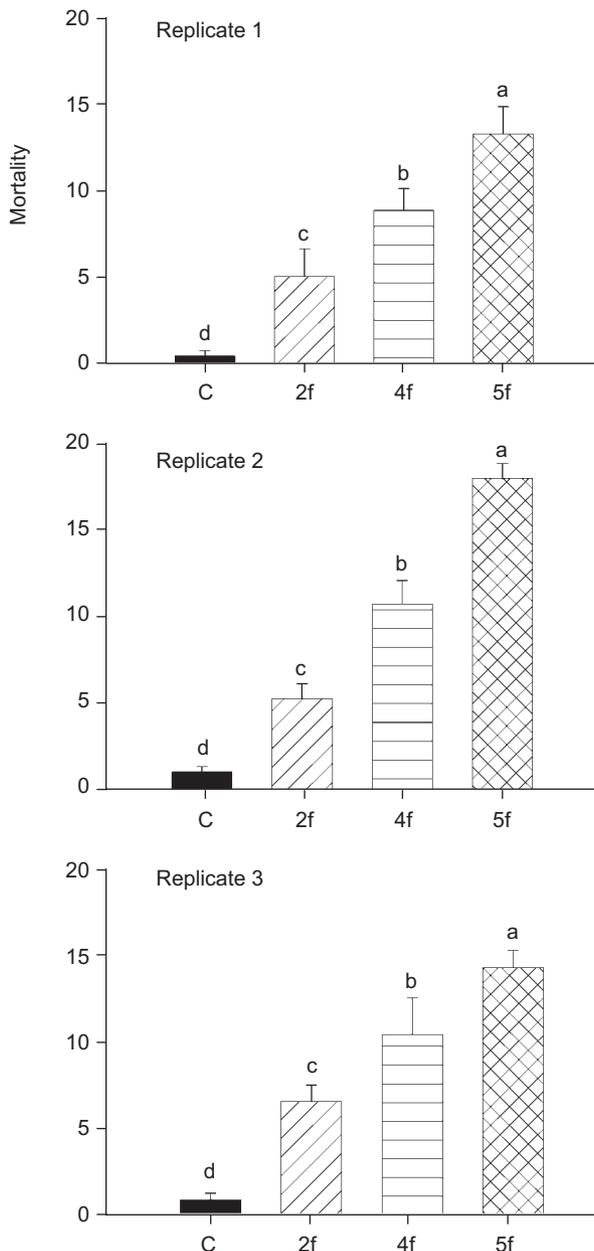


Fig. 2. Naupliar mortality ($n = 20$) of *Harpacticus* sp. in dishes with 2 (2f), 4 (4f), and 5 (5f) starved females. No food was added, and mothers are not included. Dishes without females served as the control (with 3 replicates). Means that do not significantly differ from each other are indicated by the same letter above the error bars which represent the standard deviation.

that mothers of the harpacticoid *T. fulvus* do not prey upon their own offspring (irrespective of adult densities with correlated variables like enhanced density stress, starvation, and the probability of an encounter) were not substantiated for *Harpacticus* sp. in this investigation. The females studied here did not discriminate between their own and more distantly related nauplii. Although not explicitly mentioned in previous studies, an underlying assumption is that mothers a) discern their offspring by some kind of chemical recognition, and b) will spare their offspring in order to maximize their fitness.

In terms of (a), one should consider the fact that all females used in previous studies were very likely closely related. They originated from the same sampling locality, and because only a few of them were used for rearing and subsequent experimental treatment would have produced a genetic bottleneck. Furthermore, they were initially or later raised under similar conditions, possibly in the same dish until the experiment started. This likely would have imparted a similar culture bowl-dependent odor to all individuals. Even if egg sacs had already been produced before they were isolated for the experiments, this odor would also likely have been imparted to the egg sacs and egg capsules of particular females. This would occur to their hatching nauplii, which would consequently provide similar cues for female olfactory recognition, irrespective of being their own or alien offspring.

In terms of (b), the evolutionary trend for mothers to spare their own offspring, as far as this phenomenon has been investigated for particular taxa at all, is not very pronounced among phylogenetically related taxa of the Harpacticoida or the

Copepoda in general (there are exceptions provided by brooding and brood-caring groups among other Crustacea though: see Vernberg and Vernberg 1983). It is likely that there is less of a selective advantage for kin recognition for r-strategists in general (see Dahms and Qian 2003). Also, mothers and offspring become separated very fast in these groups due to differential dispersal processes in their respective aquatic environments. Although the present study could not substantiate kin recognition by *Harpacticus* sp., it is reasonable to assume that the ability to recognize one's own offspring is most likely to have evolved in most harpacticoid copepods and be present in a planiform environment like the benthos or macroalgal blades from benthic or phytal habitats, respectively. Under such ecological conditions, individual or kin recognition may become an adaptive trait to avoid cannibalistic loss. In contrast, if planktonic cyclopoid and calanoid copepods release their eggs or nauplii freely into the water, then rapid dispersal of these instars will take place, and the probability of females encountering their own offspring will drop dramatically in this 3-dimensional environment (see Dahms and Qian 2003). Subsequent recognition of one's own offspring, in order to avoid cannibalistic behavior, is less of an adaptive advantage in such an ecological scenario.

In the rock pool-dwelling harpacticoid, *Tigriopus*, the release of chemical signals was reported by Bozic (1975) who verified the presence of "aggregation pheromones" in *T. brevicornis* which allowed specimens of this species to recognize previously colonized splash-pools. Kahan et al. (1988) hypothesized the possibility of chemical signal transmission in *T. japonicus* from moth-

Table 1. Number of egg-clutches (broods) per female and number of eggs per brood of females of selected laboratory populations of harpacticoid copepods belonging to the harpacticoid taxon Harpacticidae (x : average; - : not stated)

Taxon	Egg-clutch	Eggs	References
<i>Tigriopus californicus</i>	3	18	Huizinga 1971
<i>T. japonicus</i>	11	20-35	Takano 1971
<i>T. brevicornis</i>	10	x 30.1	Harris 1973
<i>T. brevicornis</i>	6	58	Comita and Comita 1966
<i>T. fulvus</i>	4	-	Fraser 1936
<i>Harpacticus uniremis</i>	11	119-229	Jewett and Fedder 1977
<i>Harpacticus</i> sp.	14	x 23.0	Walker 1982
<i>Harpacticus</i> sp.	>10	x 66.3	present study

ers to their offspring through an “umbilical cord” of egg-sac attachments, which may control egg maturation in relation to conditions of high experimental population density. Both these speculations, however, lack further substantiation.

Until now, the evidence for chemical signaling and communication that control different aspects of behavior in harpacticoids and copepods in general, is still largely indirect. Experimental evidence so far has mainly considered and hypothesized the presence of chemical compounds that are responsible for mate recognition and mating behavior in planktonic copepods (e.g., Lonsdale et al. 1998).

Intraspecific predation

Lazzaretto et al. (1990) were the first to show predation on intraspecific offspring for a harpacticoid copepod, namely the splash pool-inhabiting *T. fulvus* from the Mediterranean, which belongs to the same family (the Harpacticidae) as the *Harpacticus* sp. studied here from Hong Kong waters. The findings of Lazzaretto et al. (1990), that only 1st stage nauplii of *T. fulvus* were preyed upon by females, was not substantiated by the present study of *Harpacticus* sp., for which later instars were also affected. We also express doubt here that nauplii that were actually exposed to female predation in the study of Lazzaretto et al. (1990) were of the 1st naupliar stage. The 1st nauplius of egg sac-bearing harpacticoids as a rule develops to the 2nd stage while still being attached and clinging to the empty egg-sac capsules of their mothers (Dahms and Qian 2003). Initial demographic studies of *T. japonicus* from subtropical Hong Kong waters show that the duration of the nauplius I stage does not last longer than 6-12 h (after hatching through the egg membrane) at an experimental temperature of 26°C (unpubl. observ.). Assuming a similar physiological reaction norm for the congeneric *T. fulvus* from the Mediterranean studied by Lazzaretto et al. (1990), nauplii could have easily reached the 3rd or 4th naupliar stage after the 3-d experimental period used in that study. Therefore, it is more reasonable to assume that the intraspecific predation observed by Lazzaretto et al. (1990) might also have taken place at a later stage than the 1st nauplius.

In the experimental setup which examined density effects, an increase in naupliar mortality was correlated with an increase in the abundance of females. This is a reasonable prediction considering that the probability of female encounters with

nauplii becomes progressively higher with increasing female densities. Conversely, the casualties caused by the predatory behavior of females belonging to *Harpacticus* sp. were reduced with lower female densities. In this way, intraspecific predation reduces population density.

Feeding ratios

Feeding ratios were established as numbers of ingested nauplii per female in response to different densities used in the respective experiments. Feeding ratios of 0.7-1.5 nauplii/d/female will barely sustain the energy requirements of females. The low values reflect that carnivory, at least not carnivorous feeding on nauplii, is not the most important feeding mode of the species under consideration. However, we did not measure the carbon or biochemical content of females nor that of the nauplii of the particular *Harpacticus* species studied here. Due to allometric differences in representatives of *Harpacticus* sp. with copepods for which morphometry and carbon equations are provided in the literature (e.g., for copepodids by Uye 1982 and for nauplii of planktonic copepods by Torres and Escribano 2003), no “C” equivalents are provided. Also, nauplii as the single food source were used at certain densities only. Vanden Berghe and Bergmans (1981) observed a range of assimilation values of 0.18-0.39 µg C/copepod/d for other harpacticoid copepods, namely the sibling species pair *Tisbe holothuriae* and *T. battagliai*, whereas *T. furcata* consumed 0.05-0.12 µg C/copepod/d. As for the planktonic *Temora longicornis*, Harris and Paffenhöfer (1976) reported a body carbon ingestion of 146% (with the diatom *Thalassiosira rotula* at a concentration of 200 µg C/L as food at 12.5°C), and Klein Breteler et al. (1990) reported one of 170% (with the heterotrophic flagellate *Oxyrrhis marina* at 732 µg C/L density as food at 15°C). On the other hand, Dam and Lopes (2003) concluded for the same species *Tem. longicornis*, when all diets were considered (ca. 25-600 µg C/L), that the maximum daily carbon rations of around 70% body weight were the result. Lampitt (1978) employed an Ivlev curve in describing feeding as a function of naupliar-prey density, and showed that adults of the small planktonic cyclopoid, *Oithona nana*, obtained 25% of their nutritional requirements by predation on nauplii.

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