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Cannibalistic behaviour of rock-pool copepods: An experimental approach for space, food and kinship

Fabiane Gallucci ^{a,*}, Emil Ólafsson ^b

^a Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany

^b Menntun Consultoría Científica, C/Cava Alta 9 2ºC, 28005 Madrid, Spain

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Abstract

Studies on cannibalism in harpacticoid copepods are restricted to predation on naupliar larvae in rock-pool harpacticoids of the genus *Tigriopus*. An earlier experimental study on the Mediterranean copepod *Tigriopus fulvus* indicated that females recognized their own larvae and preferentially preyed on nauplii other than their own. In a series of laboratory experiments, we tested if there were differences in naupliar predation as a function of crowding, food level and sex in *Tigriopus brevicornis* and *T. fulvus*. Results show that cannibalism was restricted to the first larval stages (N1 and N2). Both food availability and adult density significantly affected the predation rate. Contrary to earlier suggestions, adult males also preyed on the nauplii. We found no evidence that adults spare their own offspring, for neither *T. fulvus* nor *T. brevicornis*. This is in accordance with what one would expect for species having the life history characteristics of *Tigriopus*, i.e.: multiple broods and large number of offspring. Earlier results indicating parental care in *Tigriopus* must be taken with caution.

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1. Introduction

Cannibalism, defined as intraspecific predation, is a behaviour trait found in a variety of animals, from protozoa to birds and mammals (e.g. Fox, 1975; Polis, 1981; Elgar and Crespi, 1992a). This behaviour is a major strategy in the biology of many species and may influence population structure, life history, competition for mates and resources, and other behaviours (Polis, 1981). Often it develops at ecological time scales as a reaction to food scarcity (Fox, 1975) but other factors

such as population density (Fox, 1975; Polis, 1981), predator size and sex, and size or moult stage of the prey (Luppi et al., 2001) may affect this behaviour.

Cannibalism of newborn animals is widespread and common in nature (Polis, 1981). Seizing a similarly sized victim may be a highly energy consuming and rather risky way of acquiring nutrients. To minimize the risk, individuals from many cannibalistic taxa preferentially cannibalize on small and vulnerable stages (Schausberger, 2003). Intraspecific predation on smaller immature life stages has been observed in several marine and estuarine crustacean species and can be the main cause of juvenile mortality in size-structured populations (Sparrevik and Leonardsson, 1995; Luppi et al., 2001; Moksnes, 2002). It can also result in age-

* Corresponding author. Tel.: +49 471 4831 1731; fax: +49 471 4831 1776.

E-mail address: Fabiane.Gallucci@awi.de (F. Gallucci).

specific habitat segregation as already reported for isopods (Leonardsson, 1991; Sparrevik and Leonardsson, 1995), crabs (Kurihara et al., 1989), fishes (Foster et al., 1988) and aquatic insects (Robinson et al., 1991; Sih and Krupa, 1992). In the terrestrial environment, preferential cannibalism on larvae has been well reported for adult phytoseiid mites (Croft et al., 1996; Schausberger, 1997; Walzer and Schausberger, 1999; Schausberger and Croft, 2001).

The most intriguing costs of cannibalism are the potential loss of inclusive fitness when a cannibal kills and consumes a genetically related individual (Elgar and Crespi, 1992b). Negative fitness, consequences of consuming one's own young, has resulted in the evolution of prey discrimination in a number of cannibalistic taxa (Anthony, 2003). Animals from various groups appear to be able to recognize their kin and display favouritism to relatives (Komdeur and Hatchwell, 1999; Schausberger and Croft, 2001; Anthony, 2003). For many species, this nepotism is expressed as differential cannibalism of kin and non-kin (Elgar and Crespi 1992a; Pfennig, 1997). Nevertheless, although kinship has been considered a fundamental factor in the evolution of cannibalism (Fox, 1975; Polis, 1981; Elgar and Crespi, 1992b), the indirect inclusive benefits of kin recognition must be substantial for this behaviour to be maintained by natural selection.

Intraspecific predation of nauplii by adults has been reported for several calanoid copepods (Landry, 1981; Conley and Turner, 1985; Daan et al., 1988). So far, no evidence exists of nauplii recognition by mothers or/and preferential cannibalism. When it comes to harpacticoids, this subject is restricted to only two studies, which reported a cannibalistic behaviour in the rock-pool genus *Tigriopus* (Lazzaretto and Salvato, 1992; Lewis et al., 1998). The species of this genus are found in the supralittoral fringe of almost every ocean (Damgaard and Davenport, 1994; Davenport et al., 1997) and since its earliest descriptions, its congeners have become familiar subjects in a variety of mensurative and manipulative studies of harpacticoid copepod biology (Powlik, 1999). Lewis et al. (1998) described *T. californicus* as cannibalistic, often ingesting their own nauplii or even younger copepodite stages. Lazzaretto and Salvato (1992) also reported the existence of cannibalistic behaviour in laboratory-reared *T. fulvus*. However, this cannibalism was restricted to females and non-related nauplii since mothers were found to spare their own offspring. Lazzaretto and Salvato (1992) also suggested that males do not exhibit this cannibalistic behaviour and that predation is limited to the first larval stages.

In this study, a series of experiments was carried out using the Mediterranean *Tigriopus fulvus* and the

Atlantic *Tigriopus brevicornis* to see if there is a cannibalistic behaviour of these harpacticoid copepods on their own nauplii and what the major regulating factors are. We tested specifically the following hypothesis: H₁: Adult females of *T. brevicornis* and *T. fulvus* prey on their own nauplii and hence do not exhibit kinship recognition; H₂: Naupliar predation is both food and density dependent H₃: Adult males cannibalize on nauplii larvae to the same extent as females; H₄: Predation on naupliar larvae by adults is restricted to the first larval stages.

2. Materials and methods

All animals used in the experiments came from cultures reared from *T. brevicornis* and *T. fulvus* individuals collected in the west coast of Sweden (Atlantic Ocean) and Mallorca, Spain (Mediterranean Sea), respectively. The diatom *Phaeodactylum tricornutum* was cultured in f2 medium (Guillard, 1975) and used as food in the experiments. At the onset of each experiment density estimates of the microalgae were calculated by counting cells from a known volume of culture medium under high power microscope. All the experiments were carried out at temperatures ranging from 21 to 24 °C, with a photoperiod of 12:12 h light/dark and in artificial seawater.

2.1. Experiments

2.1.1. Food effect

To test the effect of food availability on the cannibalistic behaviour, 128 small Petri-plates (962 mm²) were used as experimental units allowing 8 treatment levels (4 food levels and 4 respective controls) for each copepod species of 8 replicates each. Each Petri-plate contained 4.5 ml of artificial seawater, supplied with no diatoms, low (2×10^2), medium (8×10^2) or high (16×10^2) numbers of diatom cells mm⁻² and one ovigerous female with its first egg sac. After nauplii hatched, females were left in the plates for 72 h before the number of survivors was counted. Control treatments consisted of identical set-up apart from that females were removed as soon as nauplii hatched. The experimental units were randomly distributed on the incubation shelves.

2.1.2. Crowding effect

To test the effect of crowding of adults on larval predation intensity, females of *T. brevicornis* were left with their nauplii for 72 h in Petri-plates of 4

different sizes (254, 962, 1963 and 5674 mm²) with either the same density of diatoms per unit area of each plate (8×10^2 mm⁻²) or the same total amount of diatoms in each plate (2×10^5) independently of its area, i.e. decreasing amount of diatom mm⁻² with increasing size of the dish (8×10^2 , 2×10^2 , 1×10^2 , 0.3×10^2). Each treatment was replicated ten times resulting in 80 experimental units.

2.1.3. Sex effect

Females of *T. brevicornis* carrying developed egg sacs (ca 3 days old) were killed by pressing a dissecting needle against their cephalothoraxes. The egg sacs were then detached from the females and each transferred to a 254 mm² Petri-dish containing 3×10^2 diatom cells mm⁻². As soon as the nauplii hatched, a male or a female was added to the dish, while controls remained without addition of adults. Nauplii were counted 72 h after hatching. Altogether, 30 experimental units allowed ten replicates of each treatment.

2.1.4. Naupliar stages

To establish if predation by adults was confined to certain naupliar stages the size distribution of nauplii with time was established for 44 nauplii of *T. brevicornis* over more than 100 h. Nauplii were fixed in 4% formalin and transferred to polyvinyl lactophenol on microslides before measuring maximum width and length under a high power light microscope.

To verify if females preferred any particular naupliar stage, developed egg sacs were incubated in 962 mm² Petri-dishes containing 5000 µl of medium with 2×10^5 diatom cells and females added at certain time intervals after naupliar hatching (e.g. 1 h, 2 h, ..., 72 h). The numbers of nauplii were counted upon female addition and 72 h later.

2.2. Data analyses

Differences in nauplii density estimates were assessed by using either 1- or 2-way ANOVA, followed by Tukey *a posteriori* tests in case of significant differences. Cochran's *C* test was used to test homoscedasticity and when necessary, data were log ($x+1$) transformed. In a few cases some replicate samples had to be discarded since we were unable to determine exact hatching of nauplii during nights. In two-way ANOVAs with unequal subclass sizes, the computational procedures are considerably more complicated so that sometimes it is better to reduce sample size of subclasses (Sokal and Rohlf, 1997). To equalize sample sizes here,

we randomly removed some replicates so that we ended up with a total of 8 replicates for each treatment.

3. Results

3.1. Food effect

There was a significant decrease in predation rates with increasing amount of food ($p < 0.01$, HSD: $16 \times 10^2 > 8 \times 10^2 > 2 \times 10^2$, 0; Fig. 1a). The results from the two-way ANOVA showed no significant interaction between the factors 'species' and 'food level' ($p > 0.05$). Still, at each resource level and for both copepod species, numbers of nauplii were significantly higher ($p < 0.05$) in the control plates without females than in plates with females. Results from a 2-way ANOVA performed only for control plates showed a significant interaction ($p < 0.05$) between the factors 'species' and 'food level'. While for *T. fulvus* there were no significant

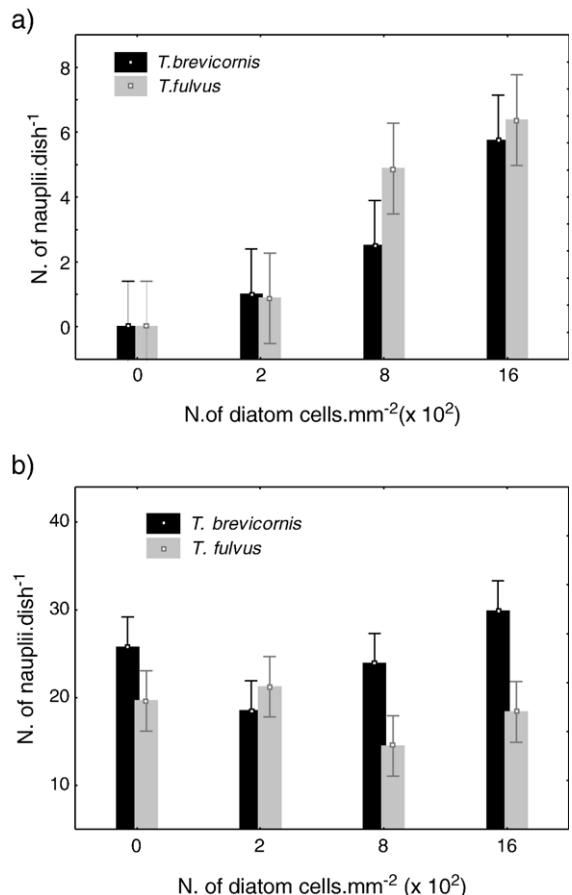


Fig. 1. Mean and confidence interval of number of nauplii dish⁻¹ for *T. brevicornis* and *T. fulvus* at 72 h after hatching for the different food levels in the presence of an adult female (a) and in the absence of females (b).

differences in the number of surviving nauplii between resource levels, for *T. brevicornis* nauplii survival was significantly higher at the ‘high food level’ when compared to ‘low food’ ($p<0.05$, Fig. 1b). However, ‘high food’ did not differ from the ‘no food’ treatment ($p>0.05$). Number of surviving nauplii at ‘medium’ and ‘high food’ levels was significantly higher for *T. brevicornis* than for *T. fulvus* ($p<0.05$, Fig. 1b).

3.2. Crowding effect

There was a significant increase in the number of remaining nauplii with increased size of the dish ($p<0.01$, HSD: $((254<1963)=962<5674$; Fig. 2). The results from the two-way ANOVA showed no interaction ($p>0.05$) between the combined effect ‘dish size’ vs. ‘food concentration’ illustrating that the differences in predation rate on nauplii at different dish sizes did not depend on the concentration of resource.

3.3. Sex effect

There was no significant difference (1-ANOVA, Tukey test, $p>0.05$, Fig. 3) in the average number of nauplii 72 h after the hatching between the female and male treatments. In contrast, the number of nauplii vial^{-1} in the control was significantly higher ($p<0.05$) than in both the female and male treatments (Fig. 3).

3.4. Nauplii stages

Measurements of nauplii lengths and widths from hatching until copepodite I are shown in Fig. 4. From

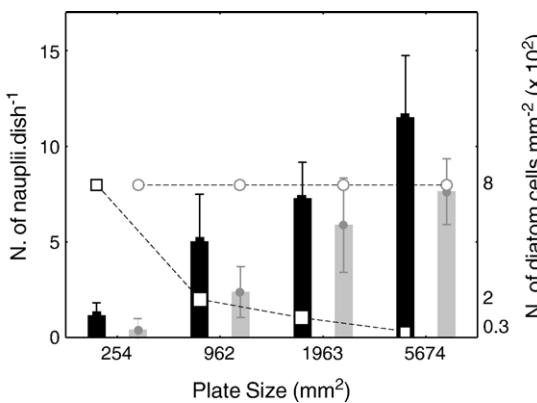


Fig. 2. Results from the ‘crowding effect’ experiments. On the left y-axis, mean and confidence interval of number of nauplii dish^{-1} for *T. brevicornis* at 72 h after hatching (bars) and on the right y-axis the concentration of diatoms per mm^2 (open symbols). Black bars and square symbols represent one of the experiments and grey bars and circle symbols represent the other.

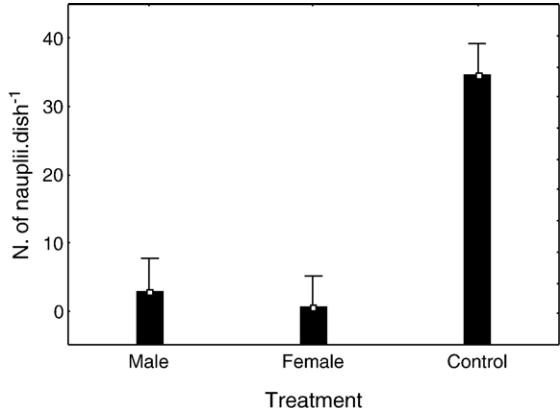


Fig. 3. Mean and confidence interval of number of nauplii dish^{-1} of *T. brevicornis* at 72 h after hatching.

length and width measures, 6 nauplii stages could be identified (Fig. 4a). Fig. 4b shows the size distribution of nauplii with time.

Fig. 5 shows the relative number of surviving nauplii 72 h after addition of females. There was a sharp

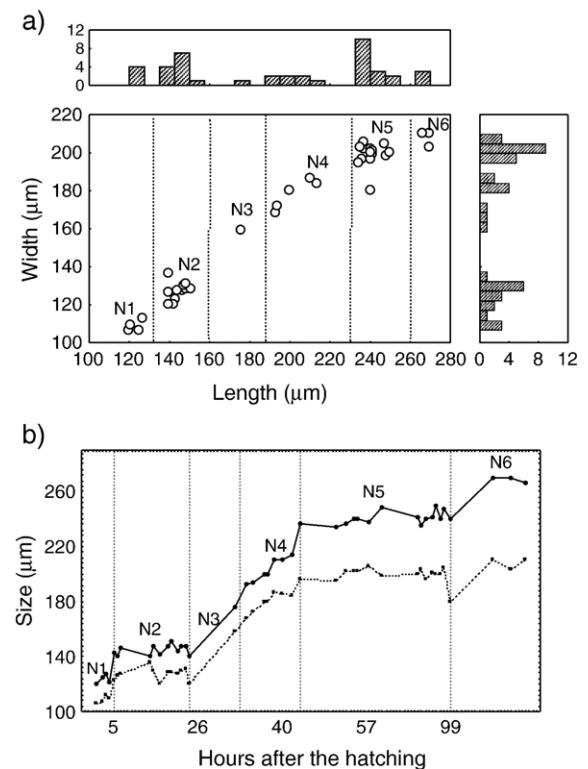


Fig. 4. Scatterplot with histogram for nauplii length and width of *T. brevicornis*, measured from hatching to copepodite I, indicating six nauplii stages (a) and size distribution of nauplii with time (b): nauplii length (full line) and width (interrupted lines).

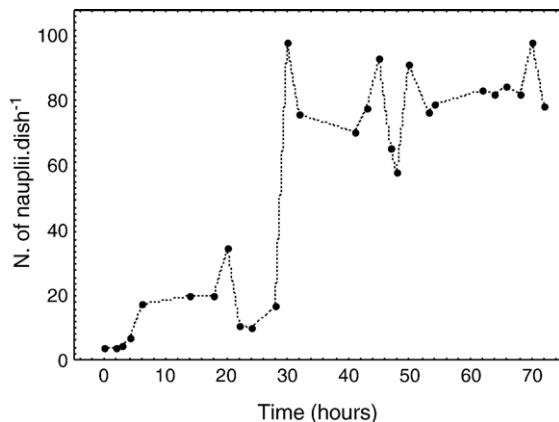


Fig. 5. Relative number of surviving nauplii of *T. brevicornis* in 72 h after adding a female to the dish. Time stands for the amount of hours after nauplii hatching at which the female was introduced into the vessel.

increase in the relative number of survivals when nauplii were ≥ 30 h old.

4. Discussion

The results of the present study clearly show that adult *T. brevicornis* and *T. fulvus* feed on their own nauplii. Besides, when comparing the food effect (with mothers) and the sex effect (with non-related females) experiments at equivalent food levels, we saw no significant differences ($p > 0.05$) in predation rates indicating that females ate their own larvae to the same extent as they ate non-kin. These observations are in sharp contrast to what was described by Lazzaretto and Salvato (1992) who reported that females avoid preying on their own nauplii whilst eating unrelated, and therefore suggested a mother/offspring recognition mediated by chemical compounds. We find it difficult to explain the discrepancy between our results and those of Lazzaretto and Salvato (1992) especially in the light of our finding that crowding was a major factor affecting naupliar predation. Lazzaretto and Salvato found no predation by mothers at more than 5 times higher densities than in some of our treatments where we found mothers preying significantly on their offspring.

Inclusive fitness theory (Hamilton, 1964) suggests that cannibalistic individuals should preferentially cannibalise non-kin. However, kin recognition mechanisms also mean energy costs and to be maintained by natural selection, its benefits must be substantial. Besides, a surprisingly widespread occurrence of filial cannibalism suggests a strong adaptive base for such behaviour (Polis, 1981). Progeny are sometimes used as a food source during periods of food scarcity increasing the survival probability

and fitness of either the parent or the remaining offspring (Hrdy, 1979). The genus *Tigriopus* is characterized by numerous brood (~ 10–14 per copulation) containing large numbers of offspring (~ 30 eggs, Harris, 1973; ~ 58 eggs, Comita and Comita, 1966; up to 150 eggs, Brown, 1991), which, in agreement to our findings, suggests a reproductive strategy without parental care. In addition, while *Tigriopus* populations can be decimated by sudden changes in the habitat, the organisms possess an innate ability to flourish from a very small initial population to *in situ* densities virtually without equal in coastal or offshore assemblages of microcrustacea (Powlik, 1998). In evaporated pools, individuals of *Tigriopus* can remain dormant within the hollow thalli of the seaweed *Enteromorpha intestinalis* or buried under loose sediment on the rock-pool bed (McAllen, 1999) until more favourable conditions return to the rock-pool by tidal inundation or freshwater runoff. Thus, for adult females, cannibalism on immatures of their own progeny may be a mechanism to regain energy, which can be reinvested into offspring production when conditions improve.

Often cannibalism is a reaction of adults to food scarcity and/or overcrowding or high population density. Foraging theory predicts that the intensity of cannibalism usually increases when quality and/or quantity of alternative food decreases (Fox, 1975; Polis, 1981). In this study, food availability clearly showed to be an important factor regulating the cannibalistic behaviour in *Tigriopus*. For both *T. fulvus* and *T. brevicornis*, predation on nauplii by adult females significantly decreased with increasing amount of diatoms. However, even for the highest concentration of diatom cells, cannibalism still occurred. Starvation may increase cannibalistic tendencies, but it is not essential for initiating this behaviour. Many animals will cannibalise as soon as all other food items are removed, but they may also respond simply to a reduction in the relative availability of alternatives (Fox, 1975). The consumption of con-specifics can also be attributed to specific nutritional deficiencies, e.g. of protein, glycogen, vitamins, minerals, etc. (Polis, 1981). Not only food quantity itself but also its quality may have influenced the cannibalistic behaviour observed here. The copepods in our experiment were fed with only one species of diatom and this is probably a reason for a high ingestion of nauplii even at high food levels (adult female consumed an average of 81% of total nauplii at the highest food level).

The effects of crowding are not always so clear since they are often linked to food shortage with increasing size of the population (Fox, 1975). However, regardless of resource availability, increasing the number of organisms increases the probability of encounter and frequency of subsequent cannibalism (Polis, 1981). Our results show

an example of enhanced cannibalism due to increased density independent of the resources available. Under both experimental conditions, predation rates decreased with lower prey densities. However, in one of the experimental set ups, we increased diatom concentration by as much as 20 times for an increase in nauplii density of 5 times and still predation on nauplii was higher than in treatments where food was scarcer but densities lower. The crowding effect observed on the cannibalistic behaviour was not a result of less food availability with increasing size of the population but clearly illustrates the influence of space in the predation on nauplii by adult females of *T. brevicornis*. In the field, evaporation concentrates the individuals retained in the pool basins to extremely high densities (up to 20 ind. ml^{-1} ; Powlik, 1998) and this can potentially enhance cannibalism.

As observed for planktonic copepods (Landry, 1978a; Lonsdale et al., 1979; Daan et al., 1988), cannibalism in *T. brevicornis* was dependent on the nauplii stage offered, with a declining rate of capture with ascending developmental stage. Indeed, predation by adult females seemed to be restricted to the two first naupliar stages while survival was close to 100% from nauplius stage 3 (30 h old) onwards. Studies on calanoid copepods support the idea that the more rapid swimming of older naupliar stages makes them less vulnerable to cannibalistic predation, rather than their size (Conley and Turner, 1985; Daan et al., 1988). The additional swimming legs, which develop as a copepod matures, could be important in limiting the stage-specific susceptibility to predation (Landry, 1978b). In our experiments we observed that newly hatched nauplii of *Tigriopus* did not swim but rather crawled around the bottom of the Petri plates, while older stages typically after 2 days made frequent excursions into the water column. This may explain why older nauplii were not taken, since the adults clearly foraged on food particles on the bottom. However, invertebrate predators are generally limited by the maximum size of prey they can successfully capture or handle (Landry, 1978b). We believe that this is not the case with *Tigriopus* since in cross-breeding experiments *T. brevicornis* has been observed to grasp juveniles of *T. fulvus*, as they typically do for copulation purposes, and shortly after eat them (Ólafsson unpublished data).

Some authors have suggested that cannibalism may be an artefact of laboratory systems or that it occurs only in cases of severe stress, especially when alternatives, such as dispersal, are not possible (Fox, 1975). Although cannibalistic behaviour has not yet been investigated in the natural habitat of *Tigriopus* species, several conditions appear to favour this behaviour: (1) a relatively small habitat, (2) a high population density and (3) food shortages

of short duration (Fraser, 1936). Normally the copepods live in shallow pools (2–10 cm depth, Davenport et al., 1997), some often being extremely small i.e. ~ 10 cm diameter (an extreme of 1 cm diameter and 1 cm depth was reported for *T. brevicornis* by Damgaard and Davenport, 1994). Besides, enhanced evaporation and sustained isolation from replenishment end up in population densities as high as 20 ind. ml^{-1} (Powlik, 1998). Finally, the genus *Tigriopus* lives in pools at and above the high-water mark (Damgaard and Davenport, 1994) being exposed to extreme changes in environmental conditions in very short periods of time (Fraser, 1936) which are likely to result in drastic changes in food availability. So, it seems very much likely that the cannibalistic behaviour reported from laboratory experiments occurs in nature.

Despite our relatively small experimental units compared to most natural rock pools, our experimental nauplii densities (from 0.6 to 3 nauplii ml^{-1}) correspond to densities reported for *T. brevicornis* in the field (see Johnson, 2001). Adult densities we used (from 0.02 to 0.3 adult female ml^{-1}) were at the lower end of densities recorded by Johnson (2001) and the ratio (nauplii female $^{-1}$) ml^{-1} is also in accordance to such a field report. Therefore, the cannibalism magnitude reported in this study (from 81% of total nauplii at higher food levels to 99% at no food treatment) may be relevant to field conditions. Habitat complexity, however, is generally considered to decrease rates of intra-specific predation (Jormalainen and Shuster, 1997; Sparrevik, 1999) and further investigations should focus on the effects of habitat heterogeneity on cannibalism by adults on nauplii.

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