



Facing predation risk in aquatic systems: differential response of zooplankton and habituation to the *false alarm*

María Florencia Gutierrez^{1, 2, *}, Victoria Andrade³, Noelia Fantón³ and Ana María Gagneten³

With 7 figures and 3 tables

Abstract: In aquatic systems, physical and chemical alarm signals favor early detection of predators and promote the development of antipredation behaviors in prey. However, further studies are needed to understand how different antipredation behavior could be among different species coexisting in a natural assembly. In this study, we conducted an indoor experiment with a zooplankton assemblage from a natural subtropical system to experimentally analyze their evasion behavior when exposed to an enclosed visual predator. We aimed to assess whether such behavior was different depending on the species within the assemblage and if they habituate to the alarm signals released by the predator after a certain period of time without receiving any real attack. Ostracods, cladocerans and copepod nauplii evaded the predator, but differed in the magnitude of the response as well as in the response time. However, the evasion behavior was not maintained through time and most organisms returned to an even distribution as time passed, suggesting that zooplankters may habituate to alarm signals. Adult copepods and copepodites (here analyzed together) did not evade fish and showed an almost homogeneous distribution over time. Rotifers moved over time, independently of fish presence. Differential responses to the same alarm signals may contribute to determining the spatial distribution of zooplankton in natural aquatic ecosystems.

Keywords: antipredation behavior; experiments; fish predation; freshwater microcrustaceans; rotifers

Introduction

Predation pressure is one of the major selective forces in nature that promotes the so-called “arms race” in which predator and prey interact by adjusting strategies to optimize performance (Ohman 1988; Jamieson 2005; Kondoh 2007; Aránguiz-Acuña et al. 2010). In aquatic systems, zooplankton is a key group whose organization and dynamics are strongly related to this selection force (Brooks & Dodson 1965; Hall et al. 1976). While size selective consumption has been considered as the main influencing factor determining

the structure of communities (Iglesias et al. 2011), the development of antipredation mechanisms may also play an important role (Lass & Spaak 2003).

In order to minimize the possibility of being consumed, some zooplankton organisms are able to establish morphological (e.g. cyclomorphosis), life cycle or behavioral (e.g. DVM-DHM) changes (Ohman 1988; Ślusarczyk 1995; Chang & Hanazato 2003; Lass & Spaak 2003). It has been shown that these adjustments are, in part, triggered as a response to the early detection of chemical and mechanical signals released by predators (Singarajah 1969; Ślusarczyk 1995; Lau-

Authors' addresses:

¹ Instituto Nacional de Limnología (CONICET-UNL) Ciudad Universitaria, 3000 Santa Fe, Argentina

² Escuela Superior de Sanidad (FBCB-UNL) Ciudad Universitaria, 3000 Santa Fe, Argentina

³ Facultad de Humanidades y Ciencias (UNL) Ciudad Universitaria, 3000 Santa Fe, Argentina

* Corresponding author: fgutierrez@inali.unl.edu.ar

ridsen & Lodge 1996; Pijanowska & Kowalczewski 1997; Titelman 2001). Antipredation strategies imply an unavoidable energy cost in association with other attributes of the organism life cycle such as survival, physiology and/or behavior that will ultimately determine the assemblage's composition in nature (Ohman 1988; Lind & Cresswell 2005; Vos et al. 2006).

During the last decades, the interest in further studying the responses of zooplankton to alarm signals in relation to the individual tradeoffs has increased (see Lass & Spaak 2003 for a review). However, most studies have focused on a few species generally concentrated in the cladoceran genus *Daphnia* (Roozen & Lüring 2001; Weber & Vesela 2002; Stabell et al. 2003; Sakwinska & Dawidowicz 2005). Although approaches considering a few isolated species allow recognizing the diversity of defense mechanisms and estimating the individual energy costs, they hardly represent realistic scenarios because *Daphnia* is not always the dominant or most representative species. Therefore, studies on other groups are required to better understand the variety of possible responses to the same stimuli and ultimately, the functioning of ecological systems. Moreover, as the real risk of any species in a natural system will depend on several factors including the number of predators present, prey availability and the strength of interactions between them (Viitasalo et al. 1998; Kiørboe et al. 1999; Titelman 2001), studies on natural assemblages and coexisting species are also required.

While the kind and magnitude of any antipredation response are of particular interest, the reaction times as well as the persistence of the response once triggered are also important aspects from an energy perspective (Aránguiz-Acuña et al. 2010). In this vein, rapid responses can be beneficial if the real risk is high, but harmful if the risk is low because exhibiting an unnecessary change implies a high energy cost (Lind & Cresswell 2005). Conversely, slow reactions can prevent maladaptive responses (*sensu* Hülsmann et al. 2004), but they imply staying vulnerable in a potentially hostile environment until the response is effectively developed.

The objective of this study was to experimentally analyze the response of a zooplankton assemblage to physicochemical signals of a zooplanktonophagous fish, taking into account the time factor. Among the antipredation strategies, we focused on the evasion behavior because it is a rapid response and can be simultaneously measured in several species within an assemblage (Lass & Spaak 2003).

In this study, we used an assemblage from a subtropical system, where the dominant zooplankton species are small in comparison to the size of *Daphnia* and cover a wide range of functional groups (Iglesias et al. 2011; Jose de Paggi et al. 2014). Although there are some field researches that document zooplankton evasion responses to visual and tactile predators in subtropical systems (Meerhof et al. 2007; Jose de Paggi et al. 2012), experimental conditions may help to understand the actual cause of such behavior and are appropriate for isolating the effect of alarm signals from other interacting abiotic (e.g. light, temperature, dissolved oxygen) and biotic (e.g. direct pressure from predators) factors. Accordingly, in our study, we hypothesized that (1) animal behavior in facing alarm signals is different depending on the species, (2) animals may habituate to the signal after a certain period of time if not attacked and (3) the evasive animals respond immediately after the exposure but not persistently in time.

Methods

Species collection

Zooplankton and fish (*Cnesterodon decemmaculatus*) samples were collected from a shallow lake of the Paraná River floodplain (31° 37' S, 60° 41' W), Argentina. A 200- μ m plankton net was used for zooplankton collection, while fish individuals were collected with a manual net. In the laboratory, animals were kept for several days in glass containers with dechlorinated and permanently aerated water to facilitate their acclimation. Laboratory conditions remained constant (photoperiod: 18 L: 6 D; temperature: 20 \pm 1 °C). Zooplankton organisms were fed *ad libitum* every other day with a mixture of *Chlorella* sp. and *Scenedesmus* sp. Fish were fed with commercial pellets and zooplankton organisms from our stock culture.

Experimental set-up

The experiment was conducted in the laboratory under the same environmental conditions mentioned above (Fig. 1). The zooplankton assembly was placed in 3 L (20 cm diameter and 9.5 cm high) plastic containers ("buckets") after being gently homogenized. Another 6 cm diameter perforated container was placed in the center of each bucket. Two treatments were performed: the Control treatment and the Fish treatment. In the Control treatment, the central containers remained empty, while in the Fish treatment, one fish was placed inside the central container (Fig. 1). The fish used in the experiment had an average size of 4.25 (\pm 0.45) cm. The perforations of the central container were sealed with a 45- μ m mesh, which prevented the entry of zooplankton and the exit of fish, and allowed the passage of chemical (e.g. kairomones) and mechanical (e.g. fish movement) signals from the central container to the periphery of the bucket that zooplankters perceived as an alarm signal.

Three replicates per treatment were carried out. To ensure similar conditions among replicates, the three buckets of each

treatment were drilled, sealed with a 45- μm mesh and placed inside plastic trays (Fig. 1). Dechlorinated and aerated tap-water was used as the culture media for this experiment. Environmental variables (temperature, pH, conductivity and dissolved oxygen) were measured daily using Hanna portable probes.

To evaluate the zooplankton behavior, samples were taken from the center (i.e. near the central cylinder) and the periphery of the buckets (i.e. next to the inner wall) by using a tubular glass sampler. Five samplings were carried out: at 2, 4, 6, 24 and 48 h from the beginning of the experiment. To estimate the sampling error, the variation coefficient of all samples was calculated ($\text{VC \%} = (\text{SD}/\text{average}) * 100$).

Statistical analyses

For each replica, species richness and abundance of organisms were quantified, and the diversity (Shannon & Weaver 1964) and evenness indices were calculated. To evaluate the evasion behavior of zooplankton, the percentage of evaders was calculated as follows: $\text{Evaders (\%)} = (\text{EI} * 100)/(\text{II} + \text{EI})$, where EI (External Individuals) was the total number of individuals sampled in the periphery of the buckets, and II (Internal Individuals) was the total number of individuals sampled in the center of the buckets.

The data thus obtained were analyzed with two-way repeated measures ANOVA (RM) on one factor ($\alpha = 0.05$) and the Dunnett's post hoc test (Sokal & Rohlf 1969): Factor 1 = treatment, two levels (Control and Fish), Factor 2 = Time, five levels (2, 4, 6, 24 and 48 h). The Bonferroni correction was applied to control the error rate. Before the analysis, the normal distribution of data (Kolmogorov-Smirnov's test), homoscedasticity (Levene's test) and sphericity (Mauchly's test) were verified.

In order to measure the magnitude of the responses, Control treatment values (in %) were subtracted from values obtained in the Fish treatment (in %). Thus, values under zero represent the species that did not evade the fish and values above zero represent the organisms that evaded the fish. The absolute value of this formula represents the magnitude in which they responded to the fish alarm signal. The reaction time was estimated by measuring the time in which the animals belonging to the Fish treatment exceeded the evasion of animals of the Control treatment.

Results

During the experiment, all the environmental variables remained constant as no differences were found

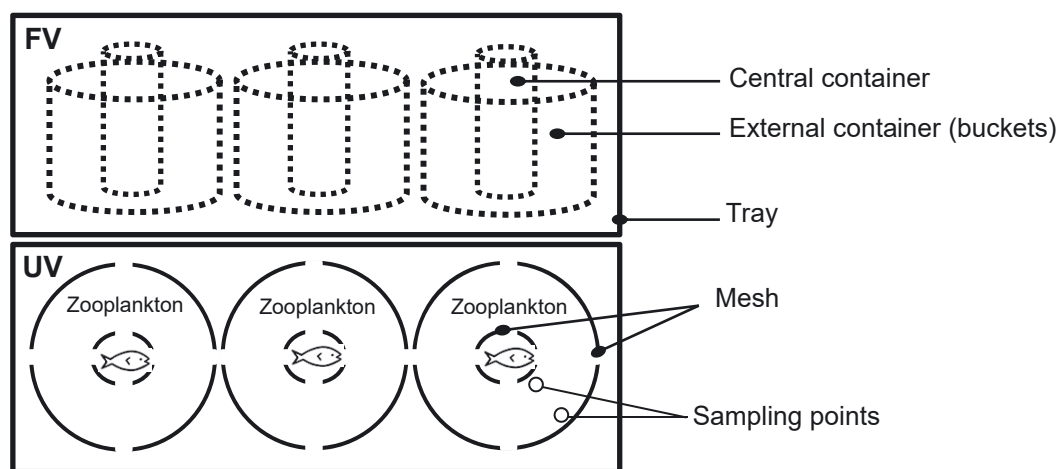


Fig. 1. Experimental design carried out to analyze the evasion behavior of a zooplankton assemblage from fish alarm signals. FV: Frontal view; UV: Upper view. One fish was located in the central container (6 cm diameter) of each replicate. The zooplankton assemblages were placed in the external container (20 cm diameter). The three replicates of each treatment were placed inside a big tray so as they share the same culture water.

Table 1. Main environmental variables measured in each treatment (Control and With Fish) during the entire experimental period (48 h). The table shows the range values obtained and the significance value from RM-ANOVA ($\alpha = 0.05$).

	Treatment	Value (range)	Sig. (RM-ANOVA)
Conductivity	Control	194.5–197	0.3258
	With Fish	192–193	0.5734
pH	Control	7.68–7.82	0.3494
	With Fish	7.46–7.48	0.6201
DO	Control	8.67–9.45	0.1656
	With Fish	9.32–9.35	0.5196

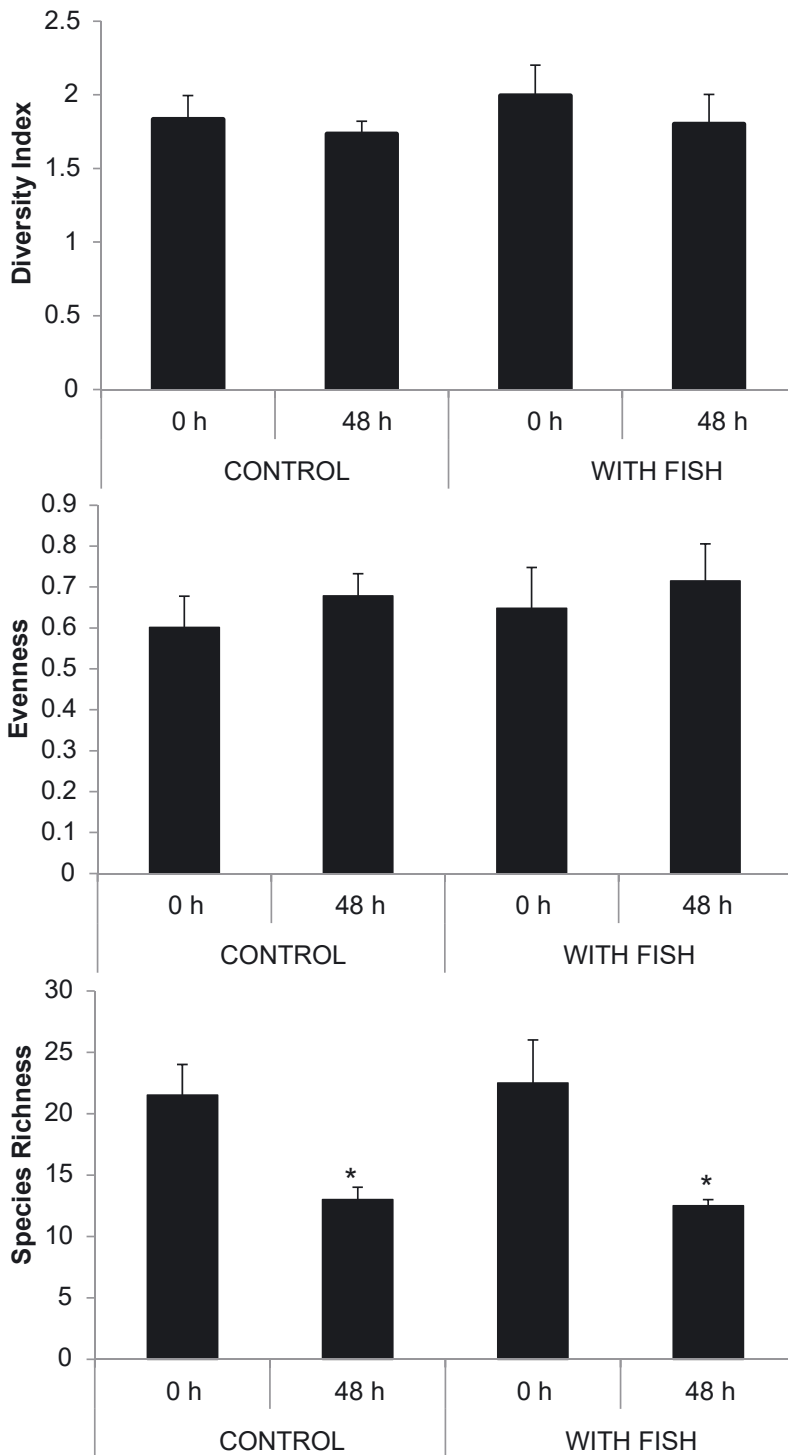


Fig. 2. Zooplankton community variables measured at the beginning (2 h) and at the end (48 h) of the experiments.

through time (Table 1). The variation coefficient (VC %) of organism abundance between samples remained below 20%, which is the maximum acceptable for zooplankton counts (Frontier 1981). In relation to fish, a passive behavior was observed throughout the 48 h of the experiments, which allow us to discard any mechanical entrainment effect on zooplankton.

The zooplankton assemblage was composed of different biological groups: Ostracoda, Cladocera, Copepoda and Rotifera (Table 2). Both Diversity and Evenness indices remained constant during the experimental period and between treatments ($p > 0.05$ in both cases; Fig. 2). Species richness slightly decreased in both treatments at the end of the experiment ($p < 0.05$), but remained in the same proportion (Fig. 2).

Table 2. List of taxa registered during the experiments.

Ostracoda	<i>Ostracoda</i> sp.
Cladocera	<i>Ceriodaphnia cornuta</i>
	<i>Ceriodaphnia dubia</i>
	<i>Chydorus eurynotus</i>
	<i>Chydorus pubescens</i>
	<i>Diaphanosoma fluviatile</i>
	<i>Guernella raphaelis</i>
	<i>Ilyocryptus spinifer</i>
	<i>Latonopsis brevireme</i>
	<i>Macrothrix elegans</i>
	<i>Macrothrix squamosa</i>
	<i>Moina reticulata</i>
	<i>Moinodaphnia macleayii</i>
<i>Simocephalus vetulus</i>	
Copepoda	Calanoida
	Cyclopoida
	Nauplio
Rotifera	<i>Brachionus</i> spp.
	<i>Cephalodella</i> spp.
	<i>Euchlanis</i> spp.
	<i>Keratella</i> spp.
	<i>Lecane</i> spp.
	<i>Lepadella</i> spp.
	<i>Platias</i> spp.
	<i>Polyarthra</i> spp.

In analyzing the entire zooplankton assemblage, we observed that individuals from the Fish treatment evaded this predator during the first 2 hours of the experiment, as more than 66% of them were found in the external area of the buckets (Fig. 3). After 4 hours, they acquired a relatively homogeneous distribution, which remained constant over time (Fig. 3). In contrast, individuals from the Control treatment acquired a homogeneous distribution in the buckets during the entire study period (Fig. 3). The interaction between time and treatment was significant, indicating that the position of individuals depended on both interacting factors: time and fish presence (Table 3).

When analyzing each particular group, we observed that, generally, ostracod position in the buckets did not differ within treatments or over time (Table 3). However, when comparing ostracod position between the two treatments, ostracods of the Control treatment tended to vary their position, moving toward the central zone after 4 hours [showing a statistically significant difference at this time compared to the other sampling times (Fig. 4)], while 60–80% of ostracods of the Fish treatment remained in the outer zone (Fig. 4).

Cladocerans exposed to the presence of fish displayed a statistically significant avoidance behavior (Table 3). Considering the entire group, the difference between treatments was recorded 2 hours after the beginning of the experiment (Fig. 4). Within this group, 9 out of 12 species exposed to the predator presence effectively remained further away from the central area

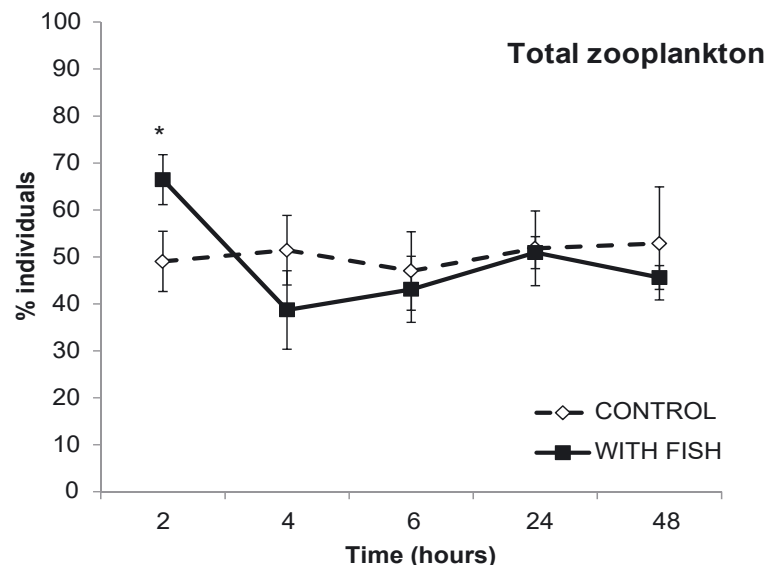


Fig. 3. Percentage (average and \pm SD) of evasive individuals (i.e. collected next to the outer wall of the pails) in the control (dotted lines) and treatments With Fish (continuous lines). The asterisk denotes a significant difference between treatments.

Table 3. Results of the RM-ANOVA testing for the effects of fish presence/absence (Treatment) and Time on the evasion behavior of the total zooplankton assemblage and each taxonomic group. Statistically significant values are highlighted in bold.

	<i>df</i>	Mean square	F	<i>p</i>
Total zooplankton				
Time	4	166.164	2.811	0.060
Time*Treatment	4	195.815	3.313	0.037
Treatment	1	16.537	2.057	0.224
Ostracoda				
Time	4	4.041	0.22	0.089
Time*Treatment	4	1265.66	6.766	0.060
Treatment	1	124.906	0.318	0.603
Cladocera				
Time	4	159.943	1.419	0.272
Time*Treatment	4	586.277	5.200	0.007
Treatment	1	1124.763	11.842	0.026
Copepoda (adults and copepodites)				
Time	4	91.520	0.722	0.589
Time*Treatment	4	97.860	0.772	0.559
Treatment	1	168.322	0.704	0.448
Copepoda (nauplii)				
Time	4	4336.532	13.293	0.021
Time*Treatment	4	50.958	0.156	0.712
Treatment	1	1474.376	3.439	0.137
Rotifera				
Time	4	1166.010	5.930	0.004
Time*Treatment	4	130.605	0.664	0.625
Treatment	1	206.411	3.601	0.131

when compared to the Control (without fish): *Ceriodaphnia dubia*, *C. cornuta*, *Macrothrix elegans*, *Guerinella raphaelis*, *Latonopsis brevireme*, *Chydorus pubescens*, *Moina reticulata*, *Simocephalus vetulus* and *Moinodaphnia macleayii* (Fig. 5). Among this evasive group, *C. cornuta*, *L. brevireme* and *G. raphaelis* manifested the strongest response, followed by *C. dubia* and *M. elegans* (see the magnitude of each response in Fig. 5). In addition to the differences observed in the magnitude of each response, cladocerans also showed differences in the period of time in which they exhibited the evasive response. While most cladoceran species responded with an evasion behavior within the first two hours of the beginning of the experiment, *S. vetulus* and *C. pubescens* responded later and at different times: the former species at 2 and 24 h from the beginning of the experiment, and the later, after 6 and 48 h of being exposed to the fish alarm signals (Fig. 6).

Adult copepods and copepodites maintained a homogeneous distribution in both Control and Fish treat-

ments, and no significant differences in their position in the buckets were observed between treatments or over time (Fig. 4). Conversely, nauplii manifested a general trend towards evading fish presence, since at all observation times, the percentage of evaders in the Fish treatment exceeded the percentage of evaders in the Control treatment (Fig. 7). The position of rotifers in the buckets varied significantly over time, practically in the same direction in both Control and Fish treatments (Fig. 4, Table 3).

Discussion

Zooplankton is a heterogeneous community with different taxa interacting among them, with other biological groups and with abiotic factors in the water column. Since the direct and indirect effects of predation are the major driving force in shaping this heterogeneity (Hanazato & Yasuno 1989; Gliwicz 1994), the de-

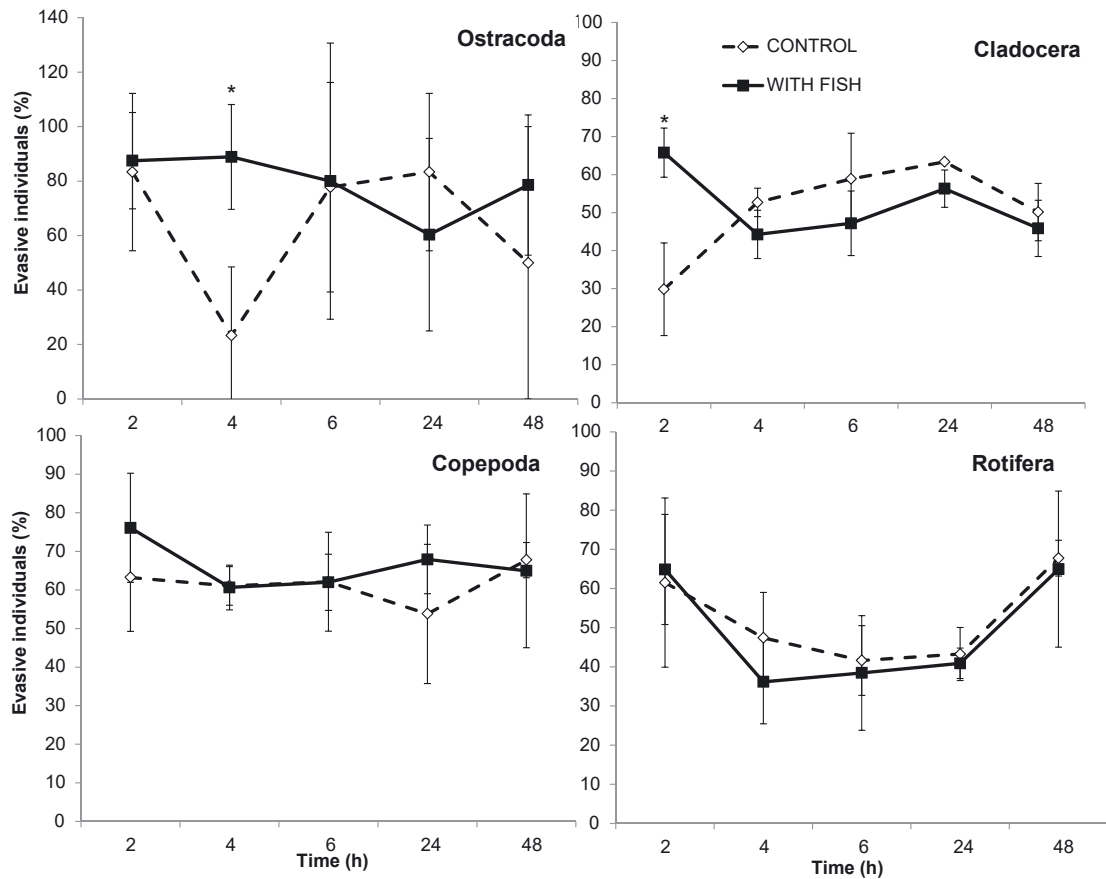


Fig. 4. Percentage (average and \pm SD) of evasive individuals of each taxonomic group (i.e. collected next to the outer wall of the pails) in the control (dotted lines) and treatments With Fish (continuous lines). Asterisks denotes a significant difference between treatments in the respective observation time.

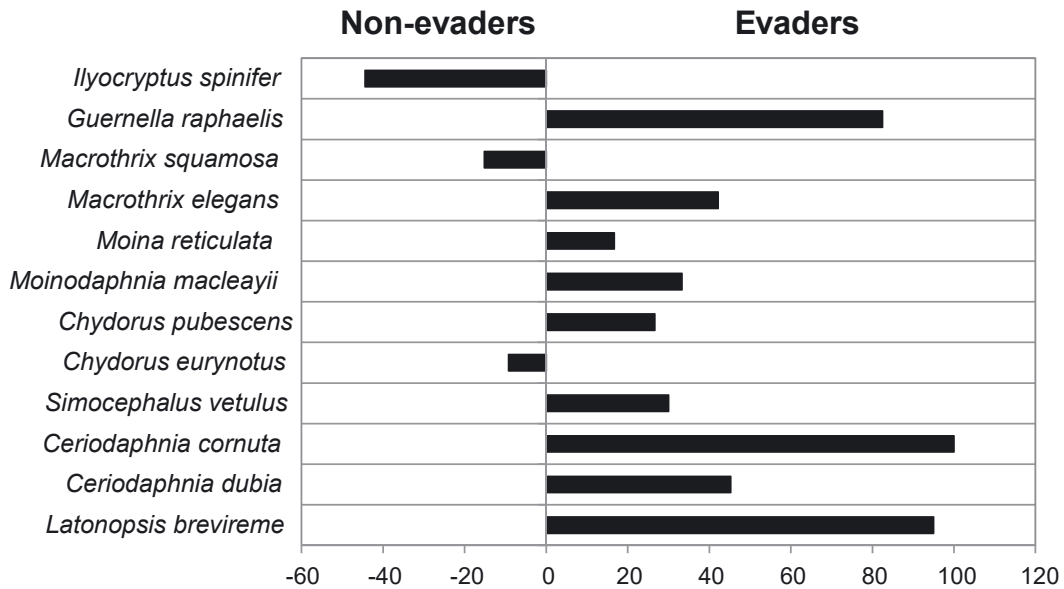


Fig. 5. Evasive and non-evasive cladocerans at two hours of starting the experiment. Control values (in %) were subtracted to values observed in the treatment With Fish (in %). Thus, values under zero (in the left of the panel) represent the species that did not evade the fish and values above zero (in the right of the panel) represent the organisms that evaded the fish. The length of each bar represents the proportion in which they moved with respect to the control (magnitude).

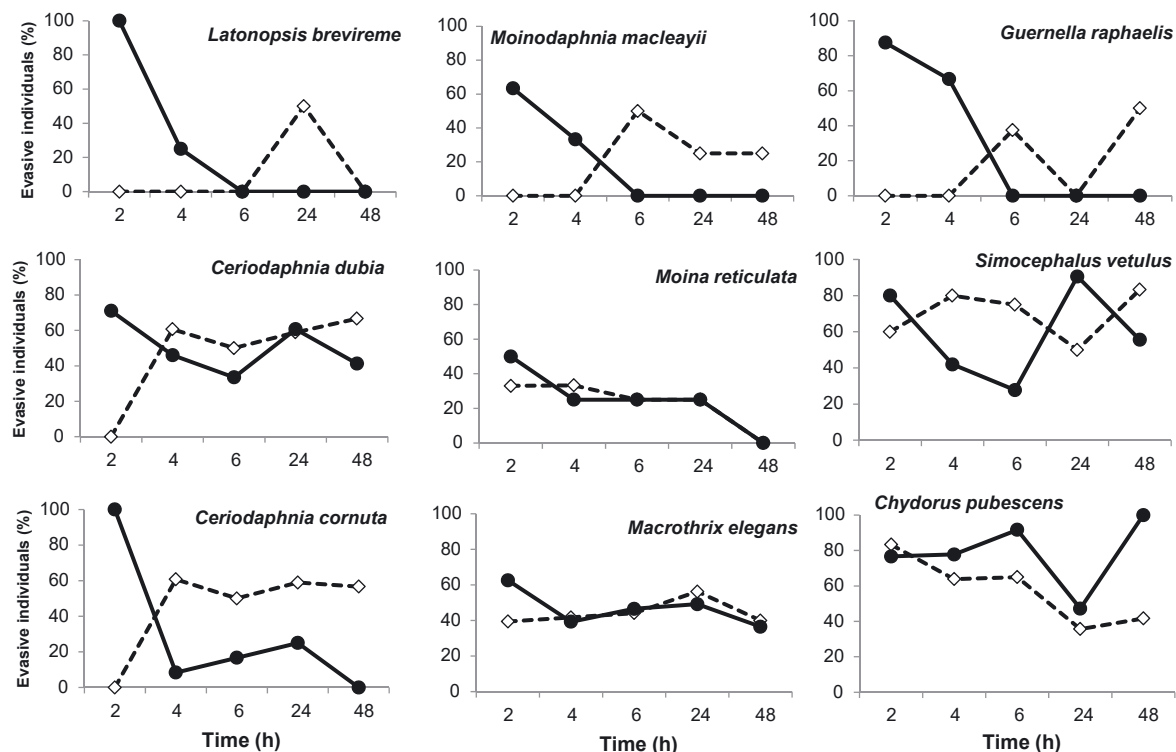


Fig. 6. Percentage (average) of evasive individuals of each cladoceran species (i.e. collected next to the outer wall of the pails) in the control (dotted lines) and treatments With Fish (continuous lines). The time in which the evasion of animals belonging to the treatment With Fish exceeded the evasion of animals of the Control was considered as the reaction time.

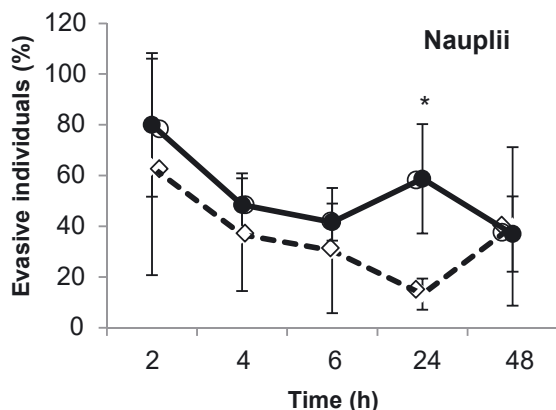


Fig. 7. Percentage (average \pm SD) of evasive nauplii (i.e. collected next to the outer wall of the pails) in the control (dotted lines) and treatments With Fish (continuous lines). Asterisks denote a significant difference between treatments in the respective observation time.

fense strategies acquired by each taxon play a key role for their persistence in the community. In this study, we found that different zooplankton taxa showed different responses to the alarm signals released by the fish *C. decemmaculatus*, as predicted before the be-

ginning of the experiment. Differential responses of zooplankton to the alarm signals may involve differences in their specific vulnerability in nature, which in turn may depend not only on their swimming speed (Kjørboe et al. 1999; Titelman 2001), but also on their life history traits that were evolutionarily determined through their interactions with other components of the systems in which they actually live (i.e., predators, environmental variables, shelters, etc.). This result concurs with field observations in which both the horizontal and vertical movements of different species within zooplankton were different, although the main "purpose" was the same for all the species (i.e., reducing mortality from predation) (De Meester 1996; Ramos-Jiliberto et al. 2004; José de Paggi et al. 2012). Moreover, in this study, behavioral differences were found at species level for cladocerans, and at the developmental stages level for copepods, indicating that the differential sensitivity could be more associated to an ecophysiological condition than to a taxonomic level. Accordingly, previous laboratory studies have shown that different clones of the same species of *Daphnia* manifested different ethological responses to fish kairomones (Brewer et al. 1999; Boeing et al.

2006), and large species responded differently to the same predators than small ones (Dodson 1989).

In particular, we found that most ostracods exposed to the alarm signals remained away from the “dangerous area” (i.e. central zone of the buckets), while those of the Control treatment varied their distribution throughout the experimental time. This response is in accordance with a previous experimental study, where the ostracod *Cypridopsis vidua* moved from uncovered areas into a vegetated area, safe from the risk of being eaten, when exposed to low quantities of water containing fish infochemicals (i.e. chemical signals: kairomones) (Roca et al. 1993). Cladocerans showed different evasive responses depending on the species. For instance, *C. cornuta*, *L. brevivireme* and *G. raphaelis* showed the strongest evasive response, while *M. reticulata* and *C. pubescens* developed the weakest one. Moreover, while most species responded within the first observation times to the alarm signals, *S. vetulus* and *C. pubescens* expressed late responses. These weak and delayed responses suggest that some species are more reticent than others in developing defense strategies, requiring greater certainty of the presence of a predator, which can be reached after the infochemical (kairomones) concentration exceeds a certain threshold in the surrounding media. This result is in accordance with Aránguiz-Acuña et al. (2010) who found that the reactivity of two rotifer species (*Brachionus calyciflorus* and *B. havanaensis*) to the alarm signal of their predator depended on the accumulation of signal in the environment. However, since this study only focused on the avoidance response, we recommend that other behavioral traits should be studied in the future to confirm other predictions since, in some cases, the concentration of kairomones does not affect the responses as the mere presence of the predator produces immediate defensive responses (Castro et al. 2007).

In contrast with the behavior of ostracods and cladocerans, rotifers remained in a similar position in both Control and Fish treatments over time. Similar findings have been obtained in field researches in which rotifers do not migrate in the horizontal plane despite the presence of visual predators (Iglesias et al. 2007; González Sagrario & Balseiro 2010). The fact that rotifers are usually consumed by predators other than fish, mainly invertebrates (e.g., *Asplanchna*), and that rotifers may constitute patches of low energy for *C. decemmaculatus*, could explain why rotifers behave independently of the presence of fish. Continuing the analysis and experimentally testing these differences is of high importance as it would allow us to

understand and predict how assemblies constitute in nature and the extent to which they can be modified by natural selection (e.g. under high predation pressure) (Brewer et al. 1999).

Accordingly to previous expectations, we also found that evasion responses were not maintained through time. This means that organisms did not remain so far away from the fish position, and returned to an even distribution as time was passing, acquiring, in some cases, a similar distribution as to that of the Control treatment. The most notorious behaviors in this line were those of *L. brevivireme*, *M. macleayii*, *G. raphaelis*, *C. cornuta* and *M. reticulata*. This contradicts the results of Dodson (1989), who found that *Daphnia* expressed a consistent predator response over two days in enclosure experiments, indicating that this Holarctic species does not habituate to predator alarm signals. However, Dobson (1989) later clarifies that such persistence may be the result of the extremely high concentration of chemical signals used in the experiments. Our findings were based on an experiment in which a single predator was present in the system, so that zooplankton organisms were exposed to alarm signals released at a natural rate. Moreover, as fish were not fed with living organisms during the experiment, the intensity of the chemical alarm signals might have been reduced over time in the absence of injured conspecifics (Gliwicz 1994; Pijanowska & Kowalczewski 1997).

In conclusion, our experiment demonstrated that avoidance behavior can be different for different species within a zooplankton assemblage. While ostracods, cladocerans and copepod nauplii evaded the presence of fish, adult copepods, copepodites and rotifers were indifferent to the alarm signals. Moreover, we observed that each species responded with different intensity and speed when exposed to the same predator and, confirming our suspicion, avoidance responses were not persistent over time, thus suggesting the possibility that the animals experienced a habituation to the alarm signals. To our knowledge, this is the first study in which a zooplankton assembly is simultaneously exposed to the presence of alarm signals from the same predator to assess their ethological responses in time, under laboratory conditions.

In conclusion, in aquatic systems, zooplankton is a key group whose organization and dynamics are strongly related to direct and indirect effects of predation. In this line, our results suggest that one of the mechanisms by which predation pressure structures the zooplankton community refers to the differential response of each species to the same risk, and not

only through selective consumption. Therefore, the results obtained in this study add information to better understand both the variety of possible responses to the presence of a feasible predator within zooplankton and how the interaction of predator and prey modulate aquatic communities. Further experimental studies including natural assemblages are needed for understanding the relationship between predators and native zooplankton and, more generally, the signals that determine the spatial distribution of such groups in aquatic ecosystems.

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