

Primary Research Paper

Predation in a temporary pond with special attention to the trophic role of *Triops cancriformis* (Crustacea: Branchiopoda: Notostraca)

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Received 12 December 2005; in revised form 5 May 2006; accepted 4 June 2006; published online 7 August 2006

Key words: *Triops cancriformis*, diet, Mediterranean temporary pond, sex-biased predation, hydroperiod length, life-history strategy

Abstract

Temporary ponds are described as environments with a low predation pressure. Notostracans inhabit these types of ponds, and some populations acquire a high proportion of larger individuals, whose feeding behaviour is mainly predatory. The predation nature of *Triops cancriformis* is not widely accepted, because its diet is still partly controversial. We analysed the diet of one population of *T. cancriformis* in a Mediterranean temporary pond (Espolla pond, NE Iberian peninsula) to evaluate its predation behaviour. The gut content of the individuals bigger than 10 mm is mainly composed of detritus, plant fibres and microcrustaceans (cladocerans, ostracods and copepods). The prey number increases with the body size of individual *T. cancriformis* as previously described. Sex-biased predation was observed for one copepod prey, but not for the other. Predation pressure in that community was monitored along six hydroperiods as the percentage of predator biomass (not only *T. cancriformis*) in relation to the non-predator biomass. The proportion of predator biomass is high, and this contrasts with the low predation pressure expected for a temporary system with short hydroperiods.

Introduction

Several myths have been attributed to the temporary ponds and pools such as that their faunas are constrained due to the drying-out (Biggs et al., 1994; Williams, 1996). Similarly, they were considered refuges where fauna was protected from predation (Kerfoot & Lynch, 1987; Wellborn et al., 1996). Although it is true that predation plays a different role in permanent and temporary waters (Zimmer et al., 2001; Brucet et al., 2005), mainly due to the absence of fish, predation can also determine the community composition and structure in temporary waters (e.g. Blaustein, 1990; Blaustein et al., 1995; Brendonck et al., 2002).

Temporary ponds with short hydroperiods do not always exhibit low predatory pressure, because some predator taxa have high dispersal capacities

(e.g. *Notonecta*; Blaustein et al., 1995), or resting stadia to overcome the dry phase (e.g. *Mesostoma* or *Agabus*; Wiggins et al., 1980; Blaustein, 1990). The latter is also the case of *Triops*, whose populations could reach high densities (MacKay et al., 1990; Boix et al., 2002). The predation effects of *Triops* over invertebrate and vertebrate populations (Knoepffler, 1979; Dodson, 1987; Walton et al., 1991), or over the community composition and structure (Walton, 2001), its selective feeding on species or size (Fry et al., 1994; Tietze & Mulla, 1989), and even its use as a biological control agent of mosquitoes (Tietze & Mulla, 1991) have been reported. However, the predation nature of *Triops cancriformis* (Lamarck) is not widely accepted, because its diet is still partly controversial (Dumont & Negrea, 2002). Field and laboratory observations of dipteran prey captured by *Triops*

(Maynar, 1923; Margalef, 1951; Dodson, 1987; Fry et al., 1994), and gut contents analyses (Margalef, 1948; Pont & Vaquer, 1986) are in agreement with the predatory nature of *Triops*. In contrast, Thiéry (1991) considered that *Triops* species are filter feeders and several studies considered *Triops* species herbivorous (Dumont & Negrea, 2002 and references therein).

There was a double aim to this work. First, the predatory nature of one population of *Triops cancriformis* was studied, by means of the analysis of the diet and the factors that affect it, and if they showed a preferential consumption of some prey species or their developmental stages. Second, the predation pressure over the community of one Mediterranean temporary pond was analysed.

Material and methods

Espolla temporary pond (42° 09' 06" N, 02° 46' 01" E; surface = 3.13 ha, maximum depth = 4 m) is located in the Banyoles karstic area (NE Iberian peninsula). It has the same groundwater supply as Lake Banyoles and the other ponds in the area. The flooding dynamics of this pond are irregular. Some years there are two complete hydroperiods (autumn and spring) separated by a dry period. It is not uncommon to have only a single hydroperiod in a year, in late autumn or winter, and occasionally no flooding at all. The animal community richness is dominated by insects, with 82 out of 118 taxa, followed by

crustaceans (14 taxa) and amphibians (11 taxa). The remainder is made up of turbellarians, nematodes, oligochaetes, bryozoans and gastropods (Boix et al., 2001).

Sampling was conducted weekly during seven hydroperiods occurring between 1996 and 1999 (Table 1). In the last hydroperiod sampled, the species composition was analysed, but not the abundances. Complete flooding events in which most of the pond area was flooded, (hydroperiods H1, H2 and H3) were distinguished from those in which only the lower parts of the basin were flooded (hydroperiods Ha, Hb, Hc and Hd). Complete flooding events were characterised by rapid flooding (less than 24 h) and drying (approx. 15 days), and a high water turnover rate except during drying phase (Boix et al., 2004). The pond was divided into seven areas by bathymetry, hydrology and vegetation. A modified Elster beam trawl (Schwoerbel, 1966) was pulled along a 20 m transect in each area (Fig. 1). This sampling device had an opening of 50 × 30 cm and a mesh size of 250 µm. Samples were preserved *in situ* with 4% formalin.

The diet study was carried out during one hydroperiod and the effect of three factors on the gut contents was analysed (size and sex of *T. cancriformis*, and sampling day). Two categories of *T. cancriformis* sizes were created: small size (10–14 mm of central carapace length, hereafter CCL) and big size (14–18 mm CCL). Two sampling days were selected, with different microcrustacean composition, in order to assess the potential selectivity of animal prey. The days

Table 1. Characteristics of the sampled hydroperiods at Espolla temporary pond, and species richness and percentage of predator species for each hydroperiod

	Beginning	Hydroperiod length (days)	Number of samples	Species richness	% Predator species	% Predator species of group 4
<i>Hydroperiods</i>						
H1	11-01-1996	100	17	67	33	55
H2	02-05-1996	46	7	54	37	70
Ha	21-11-1996	10	2	11	18	100
H3	09-12-1996	96	15	73	32	61
Hb	06-06-1997	3	1	7	0	0
Hc	04-07-1997	18	5	34	38	77
Hd	13-11-1999	14	4	18	28	60

The percentage of predators that belong to group 4 of the life-history strategy (Wiggins et al., 1980) is also shown.

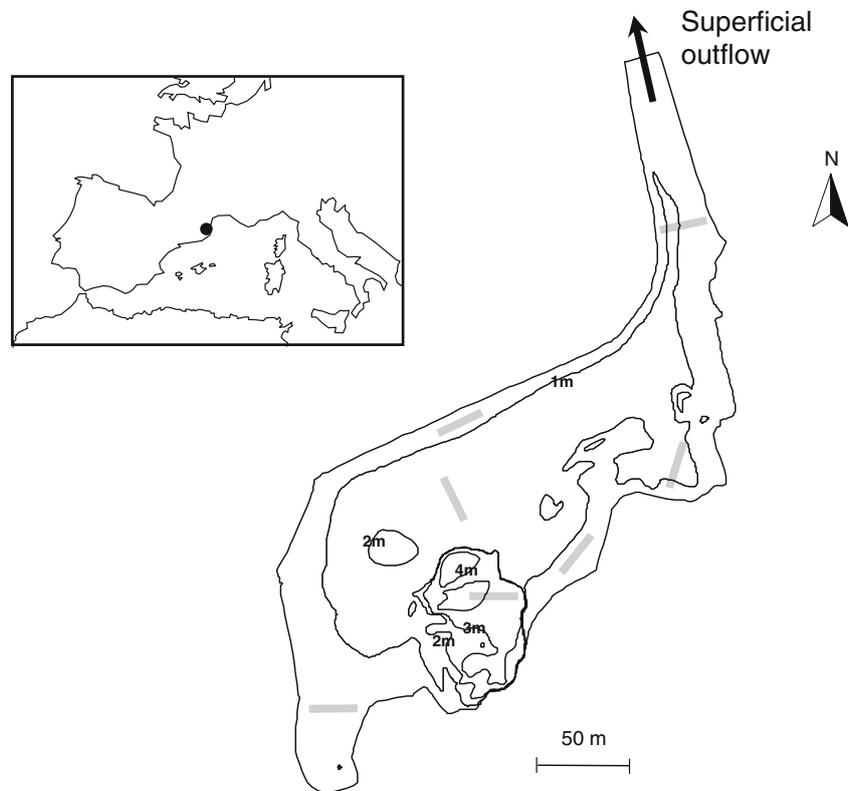


Figure 1. Bathymetric map of Espolla temporary pond showing the location (in grey) of the 7 transects.

selected belonged to hydroperiod 3 (6th February 1997 and 04th March 1997), and they corresponded to different community succession phases (middle and drying phases; Boix et al., 2004). Ten individuals were selected in each category, so a total of 80 individuals were dissected, and its gut content analysed under a stereomicroscope. All animal content was transferred to a slide, counted and identified to species level under a microscope. For copepods, sex was determined in adult individuals, and all non-adult stages were considered copepodites (no naupliar stages were found in gut contents).

Three analyses were used to study *T. cancriformis* predation. First, an electivity index was used to check if *T. cancriformis* has a diet dominated by determinate species, following Vanderploeg & Scavia (1979):

$$E_i = \frac{[W_i - (1/n)]}{[W_i + (1/n)]}; W_i = \frac{r_i/p_i}{\sum r_i/p_i}$$

where r_i is the relative (proportional) abundance of prey i in the diet, p_i is the relative abundance of

prey i in the environment and n is the number of prey types included in the analysis. This index ranges from +1 (positive selection, i.e. the prey is found in a higher proportion in the gut than in the environment) to -1 (negative selection, i.e. the prey is found in a lower proportion in the gut than in the environment) and values near zero indicate neutral selectivity.

A full factorial ANOVA test was performed in order to find out if the number of prey was different between sex (male vs. female), size (small vs. big), and sampling day (middle vs. drying). Finally, the comparison between the frequencies of copepod males, females and copepodites in gut contents and in the pond was done by means of a chi-square test. Analyses were performed using SPSS 11.5.1 for Windows.

The total number of individuals for each taxon on a given day was estimated as the sum of abundances in each area. Area abundance was calculated as density (individuals m^{-2}) multiplied by flooded area on the day. The biomass of each species was obtained by means of the abundance

of each species and the dry weight estimated by length according to existing equations for microcrustaceans (Dumont et al., 1975; Bottrell et al., 1976; Malley et al., 1989; Johnston, 1995), and macroinvertebrates (Smock, 1980; Lafont, 1987; Meyer, 1989; Mitchell, 1991; Traina & Ende, 1992; Quintana, 1995). For *T. cancriformis*, larval *Agabus nebulosus* Forster, adult *Berosus signaticollis* (Charpentier), larval Alleculidae, *Physella acuta* (Draparnaud), *Fossaria truncatula* (Müller), and all amphibian larvae (*Triturus marmoratus* (Latreille), *Discoglossus pictus* (Otth), *Pelobates cultripipes* (Cuvier), *Pelodytes punctatus* (Daudin), *Hyla meridionalis* (Boettger), and *Bufo calamita* (Laurenti)), dry-weight-to-length equations were determined as part of this study because they were the most abundant species. In the case of gastropods, biomass was estimated as ash-free dry weight to counter shell weight.

According to Wiggins et al. (1980), each taxon was assigned to a life-history strategy group. Group 1, 2 and 3 include species that are dormant during the unfavourable season, but they differ in the dispersion capacity and the moment of oviposition. Group 1 includes species with passive dispersal, group 2 includes species with active dispersal which need water for oviposition, and group 3 includes species with active dispersal which do not need water for oviposition. Group 4 includes species that cannot remain in the basin during the unfavourable season. Only *T. cancriformis* individuals with CCL greater than 10 mm were considered predators, since it is only from this size upwards on that their diet is animal-based (Pont & Vaquer, 1986).

Results

Gut content analysis of T. cancriformis

Almost 100% of guts analysed comprised detritus, plant fibres and animal prey (Fig. 2). Among animal prey, copepods and cladocerans were the most abundant, whereas ostracods and notrostracans were only found occasionally. The number of animal prey was significantly higher in big-sized animals than in small-sized animals, and it decreased in both small- and big-sized animals on the second sampling day (Table 2). Significant

differences were also found between males and females predation, although its size effect was lower than in the other factors (Table 2). The interaction of the factors was explained by the fact that smaller males in the second day had the lowest numbers of animal prey in the gut content, and even several individuals had not any animal prey.

In terms of abundance, *Megacyclops viridis* Jurine and *Cyclops* sp. were the main animal prey of *T. cancriformis*, both being the most abundant microcrustaceans in the pond (Table 3). *Daphnia pulicaria* Forbes, *Simocephalus vetulus* (Müller), *Alona elegans* Kurz, *Heterocypris incongruens* (Ramdohr) and *T. cancriformis* metanauplius were also found in the gut contents. Although electivity indexes were calculated separately for male, female, big-sized and small-sized individuals of *T. cancriformis*, no relevant differences were found among them. The most relevant result obtained from electivity indexes were the positive selectivity found both days towards *Alona elegans*. Positive selectivity was also found towards *T. cancriformis*, *M. viridis* and *H. incongruens*. However, they are not relevant results due to their low presence in the guts analysed, or to the contrasting electivity indexes found between days (Table 3).

Similar proportions of *Cyclops* sp. males, females and copepodites were found in the gut contents of *T. cancriformis* and in the pond (Fig. 3). In contrast, significant differences were found on both days between the frequencies of male, female and copepodites of *M. viridis* in *T. cancriformis* gut contents and pond (6th February 1997: $\chi^2_2 = 1251.787$, $p < 0.001$; 4th March 1997: $\chi^2_2 = 207.401$, $p < 0.001$). While the frequency of *M. viridis* females was similar in pond and gut contents, *M. viridis* males were twice as abundant in the gut contents. In contrast, copepodites were significantly more abundant in the pond than in the gut contents. This result was not an artefact, because the high proportion of males was not due to one or very few guts with a high number of copepods (Fig. 3).

Predation at community level

The community was characterised by its high richness of predators: 3 turbellarians, 1 notostracan, 2 odonates, 10 heteropterans, 14 coleopterans,

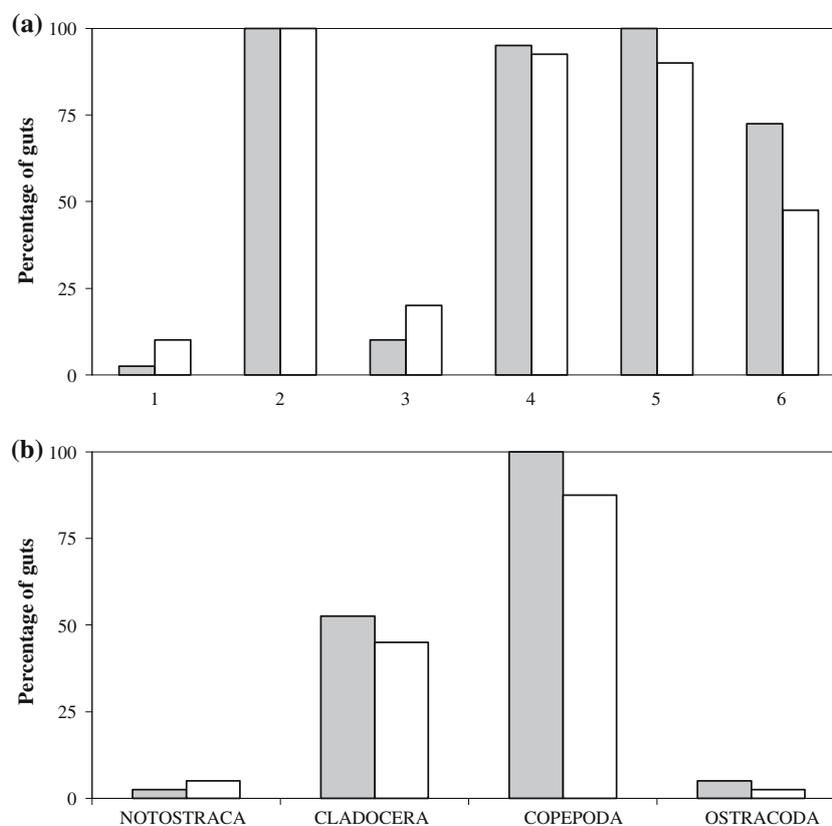


Figure 2. Percentage of guts which contain the different food items. Above (a), the percentage of presences of filamentous algae (1), detritus (2), notostracan exuviae (3), plant fibres (4), animal prey (5), and bryozoan statoblasts (6) found in *T. cancriformis* guts. Below (b), the frequency (percentage of guts) of several animal items found on *T. cancriformis* guts. Grey bars correspond to the first sampling day (6th February 1997), and the white ones to the second sampling day (4th March 1997).

6 dipterans and 1 amphibian. In spite of this richness, few species were abundant and only *T. cancriformis* and *Agabus nebulosus* were present in high numbers. Most days, the predator taxa proportion was 20–30%, with a much lower proportion at the beginning of the hydroperiod.

The last days of the hydroperiod, on the other hand, showed a higher proportion of predators, due to a large number of predatory heteropterans (Fig. 4a).

The number of predator species was correlated to the number of non-predator species ($r = 0.724$;

Table 2. Analyses of Variance (ANOVA) for number of animal prey, using sex, size group (SIZE) and sampling day (DAY) as factors

Source of variation	df	<i>F</i>	<i>p</i>	Partial eta squared
SEX	1	5.789	0.019	0.074
SIZE	1	33.897	<0.001	0.320
DAY	1	32.184	<0.001	0.309
SEX × SIZE	1	3.145	0.080	0.042
SEX × DAY	1	5.905	0.018	0.076
SIZE × DAY	1	2.442	0.122	0.033
SEX × SIZE × DAY	1	7.719	0.007	0.097
Error	72			

Partial eta squared values, as a measure of size effects, are also shown.

Table 3. Percentages of prey species in the pond, and in *T. cancriformis* gut content by sampling day

Sampling day	Prey species	Relative Abundance (%)		Relativised Electivity Index
		POND	GUT	
06.02.1997 middle phase	<i>Triops cancriformis</i> (CCL < 5)	0.01	0.08	+ 0.20 (1)
	<i>Daphnia pulex</i>	0.02	–	–
	<i>Simocephalus vetulus</i>	1.7	0.23	–0.41 (2)
	<i>Alona elegans</i>	0.01	2.29	+ 0.35 (20)
	<i>Heterocypris incongruens</i>	2.4	0.15	–0.98 (2)
	<i>Eucypris virens</i>	0.8	–	–
	<i>Megacyclops viridis</i>	95.1	97.25	–0.50 (40)
04.03.1997 drying phase	<i>Triops cancriformis</i> (CCL < 5)	negligible (< 0.01)	0.42	+ 0.50 (2)
	<i>Daphnia pulex</i>	23.8	4.18	–0.56 (14)
	<i>Simocephalus vetulus</i>	2.6	1.67	–0.03 (7)
	<i>Moina brachiata</i>	0.03	–	–
	<i>Alona elegans</i>	0.4	0.84	+ 0.52 (4)
	<i>Heterocypris incongruens</i>	0.5	0.21	+ 0.30 (1)
	<i>Megacyclops viridis</i>	28.4	64.93	+ 0.02 (30)
	<i>Cyclops</i> sp.	44.3	27.77	–0.46 (29)

Mean values of Vanderploeg and Scavia's Relativised Electivity Index for each prey. The number of guts that contained the prey item are shown in parentheses.

$p < 0.001$; $n = 47$), despite the variation observed in proportion (range = 0.00–0.71, mean \pm SD = 0.33 ± 0.18). An asymptotic increase of the number of predator species with hydroperiod length, or with the number of samples, was observed (Fig. 5), since both variables were related. On the other hand, if we exclude the very short hydroperiods (less than 10 days), the spring–summer hydroperiods (H2 and Hc) had the highest proportion of predator species, which were explained by the high proportion of predator species of the group 4 of life-history strategy (Table 1). In these sense no significant Pearson and Spearman correlations were obtained between hydroperiod length and percentage of predator species.

In relation to biomass, the proportion of predators was higher in mid-hydroperiod (Fig. 4b). The lower proportion of predator biomass at the end was explained by the high biomass of different species of amphibians, principally *Pelobates cultripes* and *Pelodytes punctatus*, both collectors (Díaz-Paniagua, 1987). Predator biomass was clearly dominated by *T. cancriformis* (individuals of CCL > 10 mm); apart from the short hydroperiods, they accounted for 90% of total predator biomass.

The time pattern of predators classified according to Wiggins et al. (1980) showed complete hydroperiods dominated by group 1, group 4 individuals gaining importance toward the end, and group 2 reaching maximum relative abundance in the middle (Fig. 6a). The incomplete hydroperiods, however, were characterised by group 4 predator dominance. This increase in relative importance of group 4 toward the end of the complete hydroperiods and peaking of group 2 in the middle was also visible in the time pattern of the number of predatory species in each group (Fig. 6b). Group 3 predators were scarce in number of species and abundance.

Discussion

T. cancriformis predation

T. cancriformis in Espolla pond is a predator species, since animals have been found in almost all guts dissected. This is in agreement with diet studies made by Pont & Vaquer (1986), which also reported the increase of the predatory nature of *T. cancriformis* with their size. An effect of the

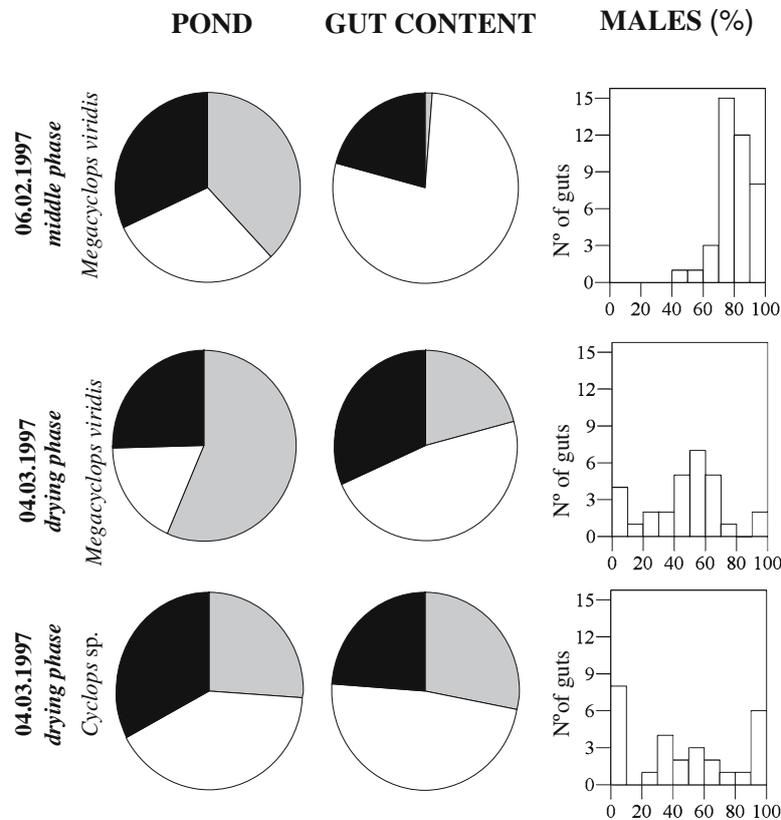


Figure 3. Relative abundance of copepodites, males and females of the two copepod species (*Megacyclops viridis* and *Cyclops sp.*) in the pond and in the gut content. It is also shown for each species and sampling day the number of guts with a determinate percentage of copepod males. Females appear in black, males in white and copepodites in grey.

drying process has also been detected. In the drying phase, where stressing conditions exist, the number of prey found in gut contents were significantly lower than in middle phase, where environmental conditions were less stressing (Boix et al., 2004, and references therein). Stressing conditions at Espolla pond during the drying process have been reported to affect both abundances and faunal composition. Microcrustacean abundances decrease due to an increase of predator density by concentration (Boix et al., 2004), and this corroborates to the lower number of prey found on *T. cancriformis* guts during the drying phase. The decrease of prey (microcrustacean density) and the increase of individuals with a high potential predatory impact (*T. cancriformis* individuals with CCL > 14 mm) are shown by means of the change in value of the prey:predator ratio, from close to 5600 to close to 800, between the two days analysed.

In relation to the feeding behaviour, only one microcrustacean species seems to have been selected: *Alona elegans* (the smallest and more benthic species; Margalef, 1983). Among copepod species (the main prey of Espolla population of *T. cancriformis*), *M. viridis* is selected more often than *Cyclops sp.* *M. viridis* is a smaller (significant differences in size between both species: $F_{1,98} = 75.716$; $p < 0.001$) and a more littoral species than *Cyclops sp.*, which is a more euplanktonic species (Margalef, 1983). Thus, the diet of the *T. cancriformis* is rich in small microcrustacean species, which have a lower escape capacity (Buskey, 1994; Mauchline, 1998), and also in species with less planktonic habit.

Furthermore, a sex-biased predation was observed for one prey species of copepod (*M. viridis*) but not for the other (*Cyclops sp.*). Bias in sex ratio due to predation has been observed in several prey-predator relationships, and the sexual

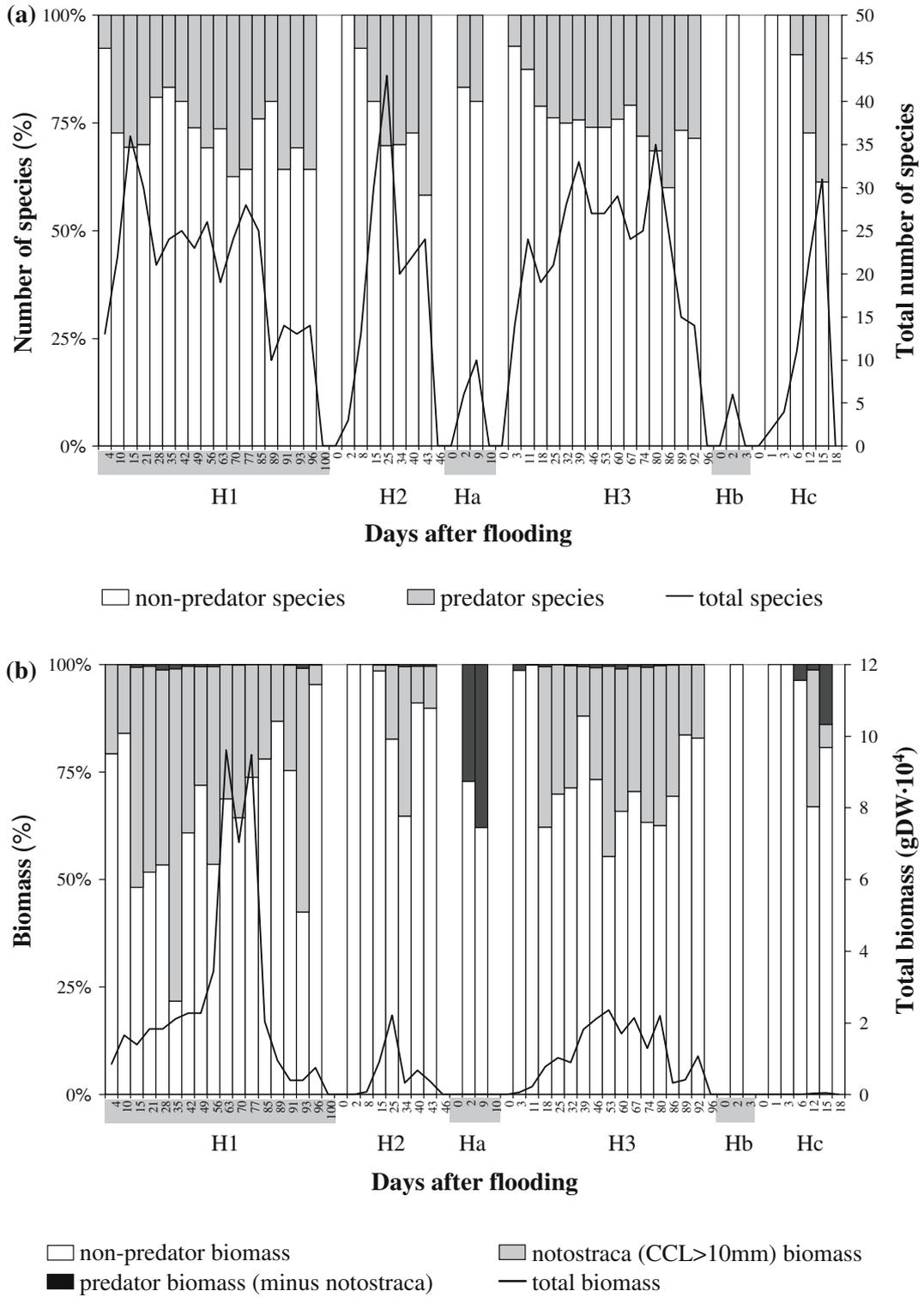


Figure 4. Above, predator/non-predator species ratio and total number of species throughout the hydroperiods (a). Below, predator/non-predator biomass ratio and total biomass throughout the hydroperiods (b).

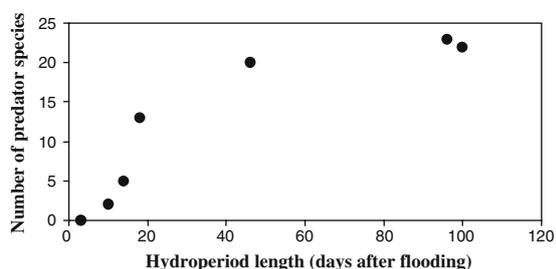


Figure 5. Number of predator species in relation to the hydroperiod length in Espolla temporary pond.

dimorphism in size is the generalised explanation (Britton & Moser, 1982; Hairston et al., 1983; Scabetsberger & Jersabek, 2004). For copepod prey, selective predation was described for both sexes (Maly, 1970). The possible causes for selective predation of female copepods are the size (because predator selects big sizes, or because big sizes are more easily to be detected) and the slower movement of the ovigerous individuals (Brooks & Dobson, 1965; Maly, 1970; Hairston et al., 1983; Winfield & Townsend, 1983). The selective predation of male copepods are scarcer and have been related to their more active behaviour, because some predators detect the prey by means of prey movements (Maly, 1970; Saito & Kiørboe, 2001). The latter may be the case for the prey–predator relationship between *T. cancriformis* and *M. viridis* in Espolla pond. The non-biased predation observed for *Cyclops* sp. could be due to a less different natatory behaviour between males and females, or for a lower number of encounters between prey (*Cyclops* sp.) and predator (*T. cancriformis*) due to a more spatial segregation of them (*Cyclops* sp. is more planktonic, while *T. cancriformis* is more benthic). It is interesting to note that the predator population (*T. cancriformis*) could be, at the same time, sex-biased under predation by herons (Boix et al., 2002).

Predation at community level

In Espolla, differences can be observed between the temporal pattern of the proportion of predators, according to the number of species and to biomass (Fig. 4). Thus, while the proportion of predator species is highest at the end of the hydroperiod, predator biomass is highest in the

middle. This may be explained by reference to the biology of the groups giving the maxima: heteropterans, Wiggins et al. (1980) group 4, mainly account for the maxima in predator-species proportions; *T. cancriformis* and *Agabus* spp., groups 1 and 2, respectively, are mainly responsible for the maxima in predator-biomass proportions. Increases in predator percentages during a hydroperiod have also been observed in other temporary (Lake et al., 1989) and semi-permanent habitats (Closs & Lake, 1994). Moreover, Schneider & Frost (1996) described the increase in predator numbers that occurred alongside an increase in water permanence of an aquatic temporary system.

The relationship between prey species and predator species is in agreement with the idea that the number of predator species is determined by the number of prey in aquatic environments, and that prey species are limited by the number of predators (Jeffries & Lawton, 1985; Warren & Gaston, 1992). It is assumed that hydroperiod length or pond size determines the number of predator species or its proportion (Schneider & Frost, 1996; Spencer et al., 1999), but other aspects have to be taken into account such as the season in which the flood occurs (Jeffries, 2002). The dispersion and the colonisation of temporary habitats by predators of group 4, mainly aerial colonisers, are strongly determined by season characteristics such as air and water conditions or life cycles (Landin & Stark, 1973; Landin, 1976; Nilsson, 1986; Wissinger, 1997; Velasco & Millán, 1998; Wilcox, 2001). As a consequence, the ecological role of these species is more important in spring and summer. The scientific literature on temporary aquatic environments has been developed mainly in systems that fill or keep water during spring (e.g. Williams, 1983; Lake et al., 1989; Bazzanti et al., 1996; Moorhead et al., 1998; Lahr et al., 1999). In these environments in which the predator guild is dominated by species of group 4, the arrival of predators at the temporary pond is related to the hydroperiod length. But in those environments where the predators of group 4 have less presence (for example, if the flood occurs in winter), the increase of predator species according to the hydroperiod length is less evident. In Espolla pond, the fact that the highest proportions of predator species, due to group 4 predators, are in the

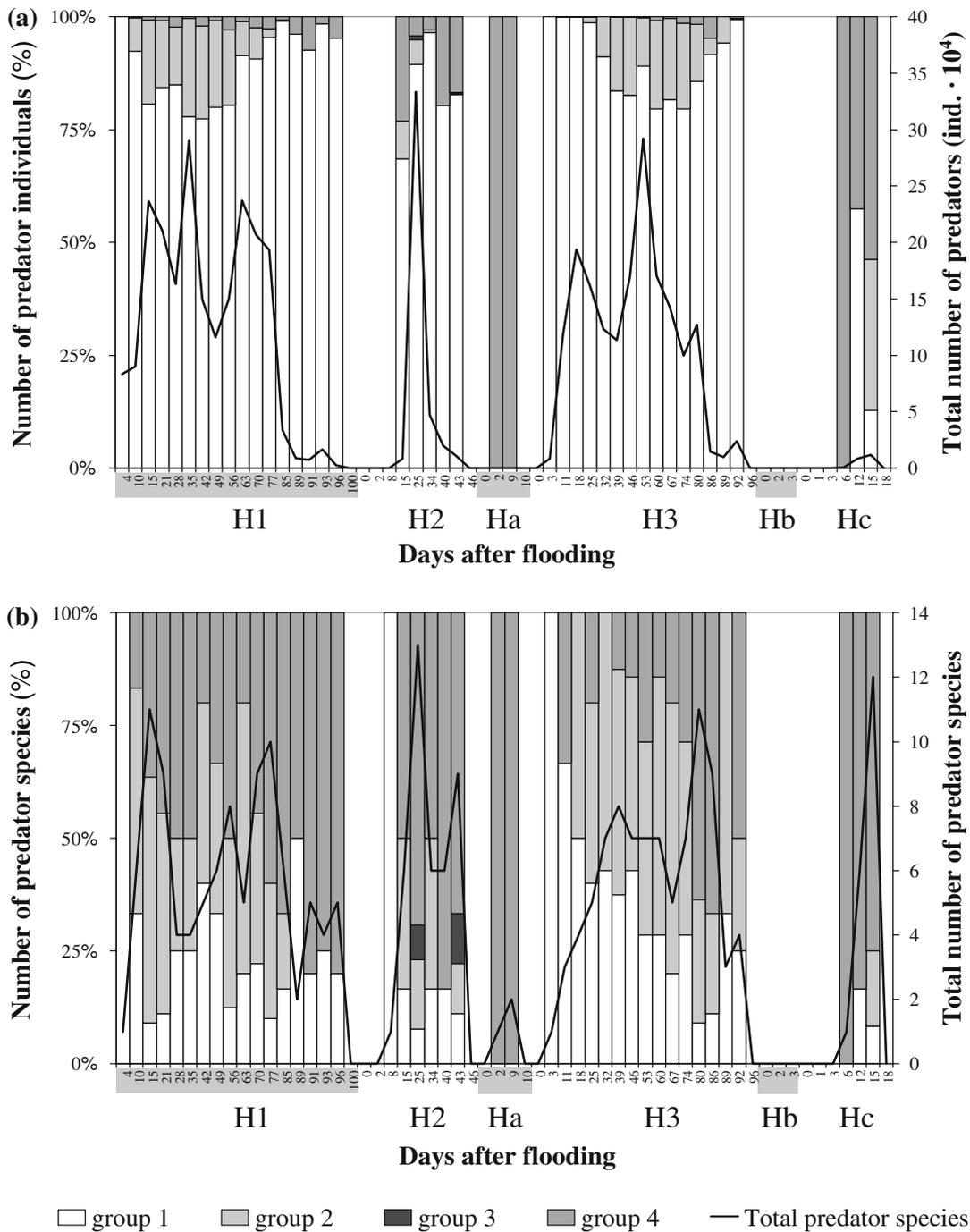


Figure 6. Above, number of predator species assigned to Wiggins et al. (1980) groups (a). Below, abundance of predators assigned to Wiggins et al. (1980) groups (b).

spring–summer hydroperiods could be interpreted in that way. Note that in other environments such as Mediterranean rock pools where the predators

appear as quickly as the non-predators, the proportion of predatory species are not related to water permanence (Spencer et al., 1999).

Observed values in the proportion of predator biomass to community biomass (range = 0.00–0.78, mean \pm SD = 0.25 ± 0.18) suggest that predatory pressure in Espolla is high, in spite of the shortness of the hydroperiods. Also, the role of the principal predator, *T. cancriformis*, has been described in relation to its control of invertebrate populations (Walton et al., 1991) and of vertebrates (Knoepffler, 1979). It is considered that temporary environments are subject to less predation pressure (Wellborn et al., 1996; Schneider & Frost, 1996). This is especially true where the main community predators are Wiggins et al. (1980)'s group 4, because longer duration increases the probability of migrant species entering the system. Note also that having group 4 species as main predators is common in temporary environments (e.g. Schneider & Frost, 1996; Higgins & Merritt, 1999). However, the relationship between degree of predation and length of hydroperiod may be modulated if the system's principal predators differ biologically. For example, Higgins & Merritt (1999) comment that *Agabus* spp. can survive the dry phase in egg form, and thus take advantage of more abundant prey early in the hydroperiod. Although Schneider & Frost (1996) considered that in systems with hydroperiods of 50–100 days predation had no "substantial influence" on community structure, temporary environments where major populations of group 1, 2 and 3 predators develop, as in Espolla pond, may suffer high predation pressure even in short hydroperiods. The diversity of invertebrate predators' biology is not sufficiently borne in mind in one-dimensional or schematic conceptual models of the structuring process in aquatic communities.

Acknowledgements

We thank Carles Alcaraz for his advice on electricity indices. Financial support was provided by a grant from the Ministerio de Ciencia y Tecnología of the Spanish government, Programa Nacional de Biodiversidad, Ciencias de la Tierra y Cambio Global (ref. CGL2004-05433/BOS).

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