



Population dynamics of *Triops cancriformis* (Crustacea: Branchiopoda: Notostraca) of the Espolla temporary pond in the northeastern Iberian peninsula

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Abstract

The population dynamics of *Triops cancriformis* in Espolla temporary pond (NE Iberian peninsula) were studied during 1996 and 1997, which encompassed six flooded periods. Data were collected on each individual's size, sex, and, if female, on number of eggs in the oostegopodes. Male-biased sex ratios were found only in the drying-out phase and variations in fecundity were strongly related to hydroperiod duration. Sex ratio variation during the drying-out phase can be attributed to female mortality because the very low recruitment observed does not support the hypothesis of an increase of males. Two hypotheses are advanced to account for female mortality: (1) differential reproductive effort, and (2) size selective predation by herons. This population is characterised by low values of maximum densities compared with other notostracan populations, and by higher densities in the spring–summer hydroperiods than in the winter ones.

Introduction

In recent times, many notostracan and anostracan populations in the Iberian peninsula have disappeared (Armengol et al., 1975), because of the loss of many temporary aquatic environments (Seminario sobre Bases Científicas para la Protección de los Humedales en España, 1986), similar to that observed worldwide (Löffler, 1993; Franzén, 1996; Kuller & Gasith, 1996; Brown, 1998; Giudicelli & Thiéry, 1998). In addition, in the case of *Triops cancriformis* (Lamarck, 1801), rice-growing led to its elimination with pesticides (Font de Mora, 1923). Such treatment still occurs in rice cultivation, albeit with controlled application, to eliminate the exotic red swamp crayfish *Procambarus clarkii* (Girard). In the rice fields of València, where the presence of *T. cancriformis* is documented historically (Arévalo, 1915), reduction has been observed coinciding with a switch in treatment from organochlorates to organophosphates. Reduction has been such that in some areas, like the autonomous region of Catalunya (NE Iberian peninsula), *T. can-*

ciformis is now a protected species. In spite of this protection and *T. cancriformis*' local popularity (festival, street, rock group and shops all bear the name of this notostracan species), its population dynamics is poorly known.

In the northern half of the Iberian peninsula *T. cancriformis* populations are fewer than in the south. Northern populations, as the studied one, correspond to *simplex* form, while southern ones correspond to *mauritanicus* form. The *simplex* form is found in clayey or transparent waters, while the *mauritanicus* form is more frequent in clayey waters (Alonso, 1985). In contrast to the populations inhabiting clayey waters (Alonso pers. com.), the study population (Espolla temporary pond) is characterised by the overlapping of cohorts (Margalef, 1951; Vila & Abellà, 1990) and by an abundance of *T. cancriformis* throughout the hydroperiod, so that many die with drying out.

The aim of this work was to study the population dynamics of the tadpole shrimp *T. cancriformis* from the Espolla temporary pond in NE Iberian peninsula through the analysis of the fecundity, recruitment pat-



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

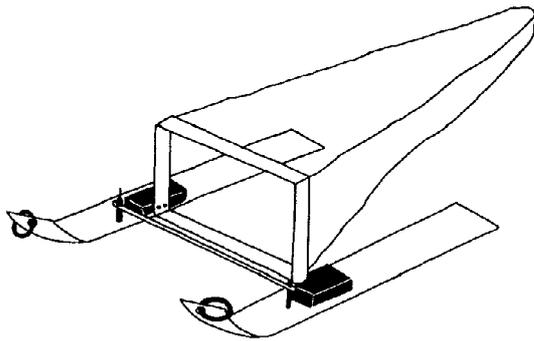


Figure 2. The modified Elster beam trawl (redrawn from Schwoerbel, 1966).

tern, sex ratio, and abundance of this crustacean in six consecutive hydroperiods.

Materials and methods

Espolla temporary pond ($42^{\circ}09'06''\text{N}$, $02^{\circ}46'01''\text{E}$; 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. Groundwater reaches

Table 1. Water characteristics of the Espolla temporary pond during 1996–1997. The median is included due to the high values of chlorophyll *a* and dissolved oxygen reached in the last days of the hydroperiod, when the pond was drying

	Range	Mean	Median
Temperature ($^{\circ}\text{C}$)	5.6 – 33.0	17.3	16.2
Conductivity ($\mu\text{S cm}^{-1}$)	212 – 1046	895.0	892.0
pH	6.5 – 8.7	7.7	7.7
Dissolved oxygen (mg l^{-1})	4.1 – 14.6	7.4	6.8
Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	0.14– 350.42	13.09	2.93

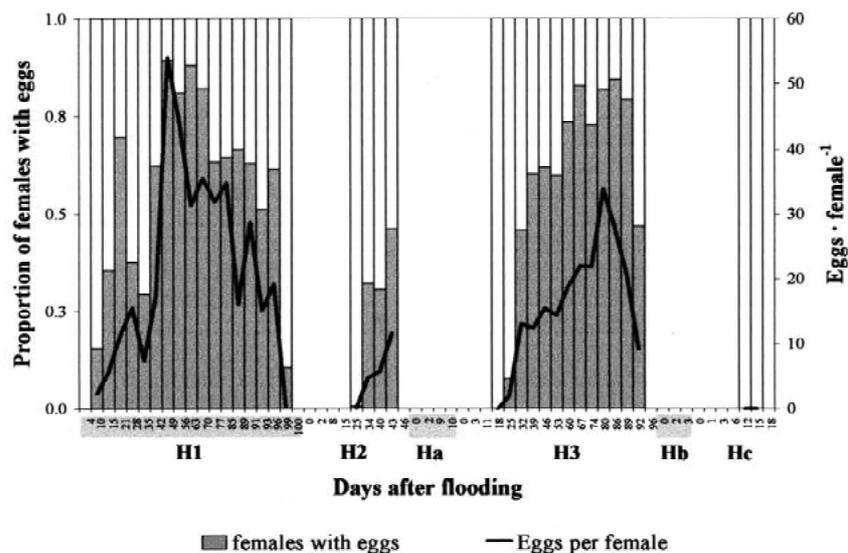
the pond at high temperature (19°C) and low oxygen concentration (3 mg l^{-1} approx.), but mean values of pond water are 17.3°C and 7.4 mg l^{-1} respectively (Table 1). The flooding dynamics of this pond are irregular. Some years there are two complete hydroperiods (autumn and spring) separated by a period of total desiccation. It is not, however, uncommon to have years with only one complete hydroperiod, 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). The ecological value of this ecosystem has been officially recognised since 1992 (Government of Catalunya, Decree 328/1992 of 14 December, by means of which approval is given to the Areas of Natural Interest Plan). Despite this, measures for its protection have still not been introduced.

Sampling was carried out during six hydroperiods between 1996 and 1997 (Table 2). Complete flooding events (hydroperiods 1, 2, and 3, in which almost the whole area of the pond was flooded) were distinguished from those in which only the lower parts of the basin were flooded (hydroperiods a, b and c). With the exception of hydroperiod 1, all flooding events began with the pond completely dry.

Sampling was conducted weekly except at the end of each hydroperiod when frequency was increased. 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 (Figs 1 and 2). This sampling device had an opening of $50 \times 30 \text{ cm}$ and a mesh size of $250 \mu\text{m}$. Samples were preserved 'in situ' with 4% formalin.

Table 2. Details of the hydroperiods sampled at the Espolla temporary pond

Hydroperiod	Start	End	Duration of inundation (days)	Number of sampling (days)	Maximum flooded area (m ²)
H1	11-01-1996	19-04-1996	100	17	28 131
H2	02-05-1996	16-06-1996	46	7	23 825
Ha	21-11-1996	30-11-1996	10	2	719
H3	09-12-1996	14-03-1997	96	15	26 175
Hb	06-06-1997	08-06-1997	3	1	125
Hc	04-07-1997	21-07-1997	18	5	2969

Figure 3. Proportion of females with eggs and eggs per female of *Triops cancriformis* throughout the hydroperiods.Table 3. Length-dry weight regressions for the *Triops cancriformis* population in Espolla temporary pond. Central carapace length was used to calculate biomass. Dry weight (DW) in mg and length (L) in mm

Lengths measured	n	r^2	DW+aL ^b	
			$a \pm SE$	$\pm SE$
Central carapace length	170	0.98	0.0111 \pm 0.0010	2.8960 \pm 0.0346
Maximum carapace length	170	0.98	0.0054 \pm 0.0005	3.0242 \pm 0.0341
Total length (furca excluded)	170	0.98	0.0034 \pm 0.0003	2.9678 \pm 0.0349

The total number of individuals 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. Three morphological lengths were measured in order to determine which weight-to-length equation gave the best

fit. These lengths were total length (furca excluded), maximum carapace length and central carapace length (from the anterior edge to the median carinal spine on the posterior sulcus). The three equations (Table 3) gave the same fit, so central carapace length (CCL) was chosen for its ease of measurement. Two different equations were used, one for *T. cancriformis* males and another for females, because of sexual dimorphism (Table 4). A side caliper (± 0.1 mm) was used to measure each specimen, except for the smaller ones (CCL < 10 mm) which were measured with a stereomicroscope ($\times 10$) with an ocular micrometer.

Females were identified primarily by the presence of oostegopod (egg sac) on the XIth thoracic appendage (Alonso, 1996), but also by the number of apodous body rings (Margalef, 1951) and the shape of the carapace (Cottarelli & Mura, 1983). Immatures were

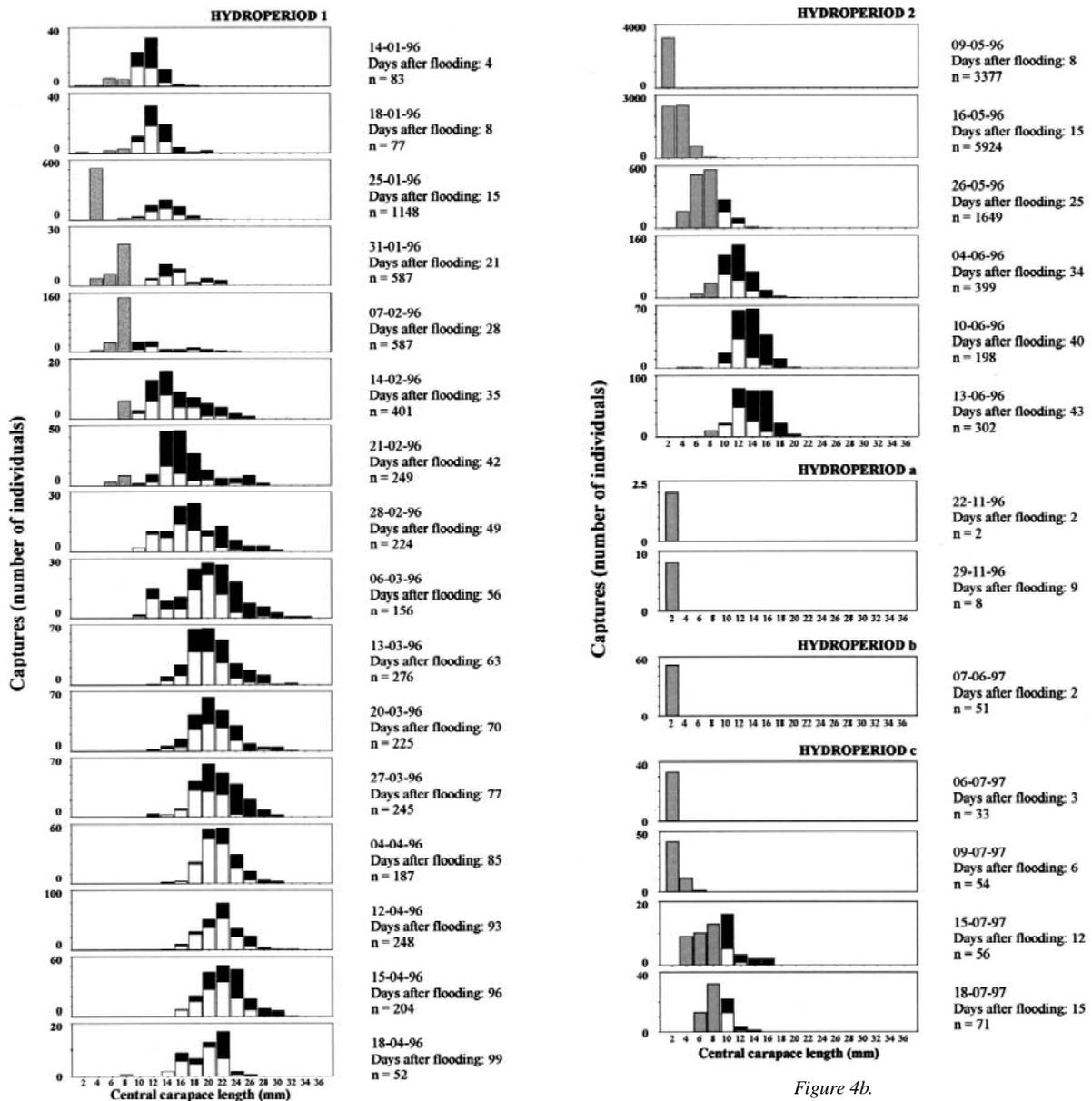


Figure 4a. Size structure of *Triops cancriformis* during all sampling days. Legend: Black columns are females, white columns are males, and grey columns are immature.

Figure 4b.

the population by means of two variables: percentage of females with eggs and number of eggs per female.

considered to be individuals with CCL less than 9 mm, because in small individuals the presence of oostegopod is more difficult to observe and mistakes are easier. Individuals with less than 4 mm CCL were considered recruits. The total number of eggs (from both oostegopods) for each female was counted with the aim to identify the temporal pattern of fecundity of

Results

Fecundity, as indicated by the proportion of egg-bearing females and the number of eggs per female, showed a bell-shaped pattern (Fig. 3) in the longer hydroperiods H1 and H3, while H2 showed a re-

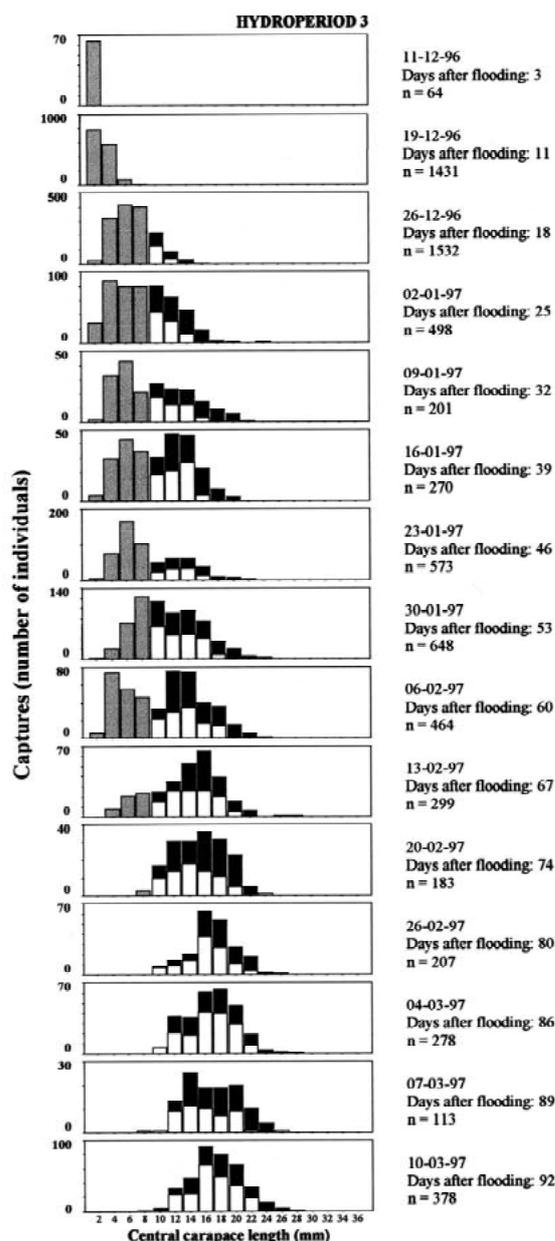


Figure 4c.

productive cycle truncated by the abrupt end of the hydroperiod.

Recruitment pattern differed in the three complete hydroperiods H1, H2 and H3. In H1 and H2, only one period of recruitment was observed, while the first 60 days after flooding of H3 showed at least three (Fig. 4). A coincidental point is the appearance of first recruits, around the 15th day after flooding. H2 and H3 exhibited population maxima at the start of the hy-

droperiod, but not H1, which unlike the others began when the pond was not completely dry. Its population maximum coincided with high relative abundance of smaller classes, when recruitment was considerable.

In the incomplete hydroperiods, due to their short duration, most individuals measured less than 9 mm CCL, and were therefore classified immature. Thus, population sex ratios were analysed only in the longer hydroperiods H1, H2 and H3, and most days showed a sex ratio of 1 male:1 female (Fig. 5). However, females became predominant in the middle days of H1 and H3 and throughout H2, and males toward the end of H1 and H3.

As shown in Table 5, in the complete spring hydroperiod (H2), the population reached higher densities than in complete winter hydroperiods (H1 and H3). The same relation is observed among incomplete hydroperiods: the spring (Hb) and summer (Hc) ones presented higher densities than the winter hydroperiod (Ha). The high density in Hb corresponds only to one value due to the short duration of the hydroperiod (3 days).

Discussion

The bell-shaped fecundity pattern could be interpreted as a consequence of female growth, maturity and senility. The decline at the end of the hydroperiod may be attributed to female ageing and to exhaustion from vigorous reproduction previously. An alternative explanation would attribute this decline to environmental cues, but the pattern observed in H2 does not corroborate this.

Size structure (Fig. 4) and the dynamics of population size (Fig. 6) in the long hydroperiods H1 and H3 suggest that if the duration is long enough, the Espolla population can produce more than one generation in each hydroperiod, as shown by Margalef (1951). The H3 recruitment pattern notwithstanding (Fig. 4), population maxima in H2 and H1 (Fig. 6) indicate that hatching, on a population level, is synchronic, as shown in other studies (Hempel-Zawitkowska, 1966; Hempel-Zawitkowska & Klekowski, 1968; Obregón-Barboza et al., 2001) and as previously observed in Espolla (Vila & Abellà, 1990). The lack of a maximum in H1 may be related to the fact that the shortness of the preceding dry period had left some water content because soil moisture may affect hatching (Fry & Mulla, 1992). The absence of recruitment in the second half of H1 and H2, in spite of high fecundity

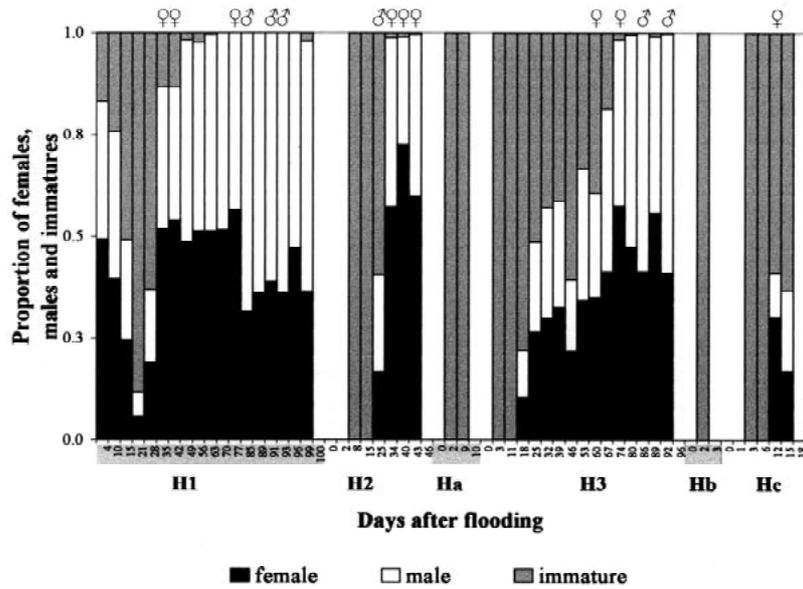


Figure 5. Proportion of females, males and immatures of *Triops cancriformis* throughout the hydroperiods. The days with a sex ratio significantly different from 1:1 ($P < 0.005$) are indicated (in the top of the figure) with the symbol of the dominant sex.

Table 4. Length-dry-weight regressions for females, males and immatures (CCL < 9 mm) of *Triops cancriformis*. Due to better fit, for females and males we used the regression obtained for males plus immatures, and females plus immatures. Dry weight (DW) in mg and length (L) in mm

<i>Triops cancriformis</i> (central carapace length)	size range (mm)	n	r^2	DW= aL^b	
				$a \pm SE$	$b \pm SE$
Immatures	1.1 – 8.9	50	0.92	0.0151±0.0023	2.6037±0.1078
Females	9.3 – 31.1	60	0.88	0.0117±0.0046	2.8914±0.1400
Males	9.9 – 26.4	60	0.82	0.0220±0.0102	2.6615±0.1624
Females + immatures	1.1 – 26.4	110	0.98	0.0111±0.0011	2.8924±0.0440
Males + immatures	1.1 – 31.1	110	0.98	0.0113±0.0010	2.8791±0.0401

levels, may be ascribed either to intraspecific relations (competition and even predation among adults) or to non-hatching of eggs.

In populations of *Triops cancriformis* sex ratios have been observed ranging from absence to dominance of males (Mathias, 1937; Zaffagnini & Trentini, 1980), as with other notostracan species (Sassaman, 1991). Also, variation in sex ratio in a given waterbody over different years has been documented (Desportes & Andrieux, 1944). The higher proportion of males in the final days has been described in other notostracan populations (Jézéquel, 1921; Ahl, 1991), whilst it is also true that the opposite scenario is known too, with females dominating at the end (Baudoin et al., 1937). Nevertheless, the latter case may be analogous to our H2, where the short duration does not permit old or

large individuals nor, by extension, differential mortality between sexes among older individuals. The lack of recruits in the middle and later hydroperiod phases and, proportionally, the greater reduction in larger sizes in the last days, suggests different mortality rates (greater for females) rather than birth rates (greater for males) as accounting for the change in sex ratio. We hypothesize that unlike other notostracan populations (Ahl, 1991) where the increase in males toward the end of the hydroperiod is ascribed to greater male recruitment, the population sex ratio at Espolla is determined by greater female mortality. This may be associated to ageing and exhaustion following reproduction increasing their vulnerability to stress: drying out leads to greater inter and intra-population competition because of greater density, and at the same time

Table 5. Minimum, maximum and mean densities of Espolla population (for each hydroperiod) and of other Notostraca populations found in different types of water bodies

Water body type	Sample	Min.	Max. (individuals m ⁻²)	Mean	Reference
<i>Triops cancriformis</i>					
Temporary pond	H1	3.0	25.5	8.9	This study
Temporary pond	H2	0.0	169.5	62.1	This study
Temporary pond	Ha	0.6	4.0	2.3	This study
Temporary pond	H3	3.3	44.1	11.8	This study
Temporary pond	Hb	–	–	121.9	This study
Temporary pond	Hc	0.0	39.8	11.3	This study
Rice field	station 1 (1976)	–	–	13	Pont & Vaquer (1986)
Rice field	station 2 (1976)	–	–	42	Pont & Vaquer (1986)
Rice field	station 2 (1977)	–	–	36	Pont & Vaquer (1986)
Rice field	station 3 (1978)	–	300	180	Pont & Vaquer (1986)
Ponds	–	–	2500	–	Langner (1985)
Carps pond	–	20	266	–	Barthelmes (1963) in Pont & Vaquer (1986)
<i>Triops longicaudatus</i>					
Playa	–	55*	295*	130*	MacKay et al. (1990)
Experimental pond	pond F3	5*	29*	15*	Walton et al. (1991)
Experimental pond	pond F5	10*	54*	29*	Walton et al. (1991)
Experimental pond	pond F6	18*	33*	28*	Walton et al. (1991)
<i>Lepidurus apus</i>					
Temporary pools in a ditch		–	58	1432	Burmeister (1982)

Legend: *estimated from bibliographical data.

increases the range of variation in environmental parameters (e.g., temperature and oxygen content) with the loss of water volume. Another hypothesis to account for the change in sex ratio at the end of the hydroperiod may be heron predation. Drying out leads to greater concentration and availability (in shallower water) of prey for these birds (such as *T. cancriformis* and anuran larvae). It is interesting to note that in the Camargue rice fields, *T. cancriformis* is one of little egret's (*Egretta garzetta* (L.)) main preys (Hafner et al., 1982). Herons are known for their capacity to adapt their diet and feeding behaviour to the resources available (Bredin, 1984; Erwin et al., 1985; Kersten et al., 1991) and for their selection of prey by size (Britton & Moser, 1982; Moser, 1986; Cezilly et al., 1988). Toward the end of H1 and H3 heron numbers rose considerably: the 20 or so cattle egrets (*Bubulcus ibis* (L.)) and the pair of grey herons (*Ardea cinerea* L.) present throughout the hydroperiod rose to about 50 and 6, respectively, while a group of about 35 little egrets also appeared. Selective predation of larger in-

dividuals could, then, lead to a bias in sex ratio, since female *T. cancriformis* are larger than the males. In fact, in the Camargue (Britton & Moser, 1982) there have been cases of changes in the sex ratio of mosquito fish (*Gambusia holbrooki* Girard) as a consequence of greater predation on the larger females by little egrets and grey herons.

Except in the case of Hb, the complete hydroperiods (H1, H2 and H3) reach higher densities than the incomplete ones (Table 5). An explanation could be that the recruitment is low in the deeper parts of the basin, the only ones flooded in incomplete hydroperiods. Only at the end of the hydroperiod does *T. cancriformis* reach high densities in these parts due to the reduction of the surface (which leads to the concentration of the population) but at these times the females are producing less eggs (Fig. 3). The low densities in the deepest area agree with the fact that *T. cancriformis* inhabits, preferably, the bottom of shallow waters and the duration of the trips to the surface implies a negative effect in the growth and in the reproductive success

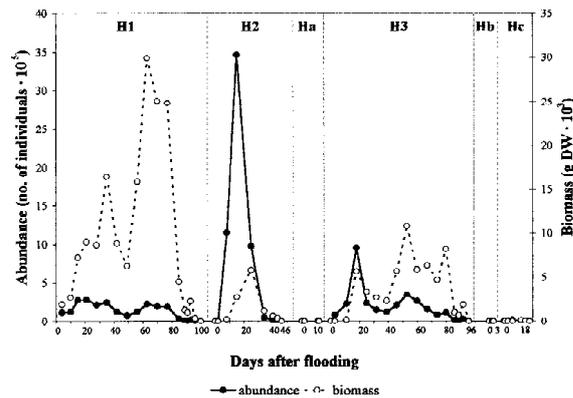


Figure 6. Abundance and biomass of *Triops cancriformis* through the hydroperiods.

(Scholnick & Snyder, 1996). The density value for the Hb is explained by two reasons: (1) the sampling day was near to the populational synchronic hatching, and (2) the flooded surface was diminishing and there was a concentration of the population. A relation between season and *T. cancriformis* density is observed as much in the complete hydroperiods as in the incomplete ones (Table 5). Thus, spring–summer hydroperiods show higher densities than the winter ones. This agrees with the fact that *T. cancriformis* is a thermophilic species (Kuller & Gasith, 1996, and references therein). The mean densities observed in the winter hydroperiods are lower than rice field populations with low density. On the other hand, the mean densities in spring–summer hydroperiods are between the densities of rice field populations with medium and high density (Table 5). In a wider comparison, the Espolla population has low population densities, being subequal to the densities of natural populations of *T. longicaudatus* in experimental ponds in California (Table 5). Although the population of Espolla temporary pond does not reach high densities, its abundance and presence in every hydroperiod indicate us that the population is successful.

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