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Population dynamics and tolerance to desiccation in a crustacean ostracod adapted to life in small ephemeral water bodies

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ABSTRACT

Given their small size, isolation and unpredictability, temporary rockpools present high environmental stress and impoverished communities of species that have adapted to such stressful conditions. Special adaptations of the invertebrates living in these habitats include tolerance to desiccation and fast ontogenetic development in order to maintain stable populations and face high risk of extinction. Dozens of small rockpools (mostly with Ø < 1 m) can be found in east Spain on limestone substrate, where the only known Iberian populations of *Heterocypris bosniaca* Petkovski et al. (2000), an ostracod species with geographic parthenogenesis, have been recently found. In this survey, two of these rockpools have been monitored during the main hydroperiod between the fall of 2005 and summer 2006 to test the ability of *H. bosniaca* parthenogenetic populations to face unpredictable hydroperiod dynamics. Pools were visited weekly, and limnological data and ostracod samples were obtained from either water or substrate in dry periods. Ostracod individuals were counted and assigned to growth instars to monitor population changes. In the laboratory, experimental cultures allowed the estimation of survival dependence on the substrate desiccation rate. Throughout the hydrological cycle studied, several hatching periods were observed, usually preceded by desiccation, followed by substrate hydration and water dilution by rain. The demographic changes observed indicate that *H. bosniaca* populations are able to persist in intermittently inundated environments and produce several generations per annual hydrological cycle. In addition, adult individuals were able to survive in the wet mud of dry pools for longer than five weeks. The experimental data suggest a lower average survival time when exposed to desiccation processes, and that the velocity of substrate water loss is a determining factor for the survival rate of ostracods resisting dry events in temporary ponds. As shown by ostracods' life histories in temporary aquatic environments undergoing unpredictable desiccation events, a combined strategy of adult tolerance to short periods of water scarcity and rapid hatching from resting egg banks can be advantageous for the monopolization of small-sized ephemeral habitats.

Introduction

Temporary pools are small-sized systems with particular environmental traits and functioning dynamics compared to other water bodies like lakes or rivers (Williams et al. 2003; Declerck et al. 2006). Although they are small, their special ecological setting helps them contribute significantly to regional biodiversity as they usually harbor taxa that are uncommon in other habitats (Eitam et al. 2004; Scheffer and van Geest 2006). The small areas of temporary pools involve high vulnerability to environmental degradation and local hydrological changes (Nicolet et al. 2004), resulting in impoverished communities which encompass species adapted to the particularly stressing conditions there (Bayly 1997). Despite the scientific interest shown in temporary pools, their functioning is poorly known, although they are recognized as being very valuable water bodies for biodiversity conservation. Furthermore, they provide stepping stones for the spread of aquatic species among larger water bodies (Oertli et al. 2002; Nicolet et al. 2004).

The shorter the inundation period, the poorer the species richness of temporary pools (Jocque et al. 2007). This is because extinction due to pool drying greatly affects community structure (Eitam et al. 2004). Despite this pattern, species respond individually to the environmental conditions in these habitats (Jeffries 2003). Particular adaptations to life in temporary environments include migration to other habitats during the dry season or the survival during this period in arrested physiological stages, chiefly as dormant eggs (Wiggins et al. 1980; Wissinger 1999). Apart from these traits, a fast developmental rate is essential in short hydroperiod pools (Boven 2009; Jocque et al. 2010), and egg bank formation and erratic hatching are essential to help avoid extinction locally (Williams 1998).

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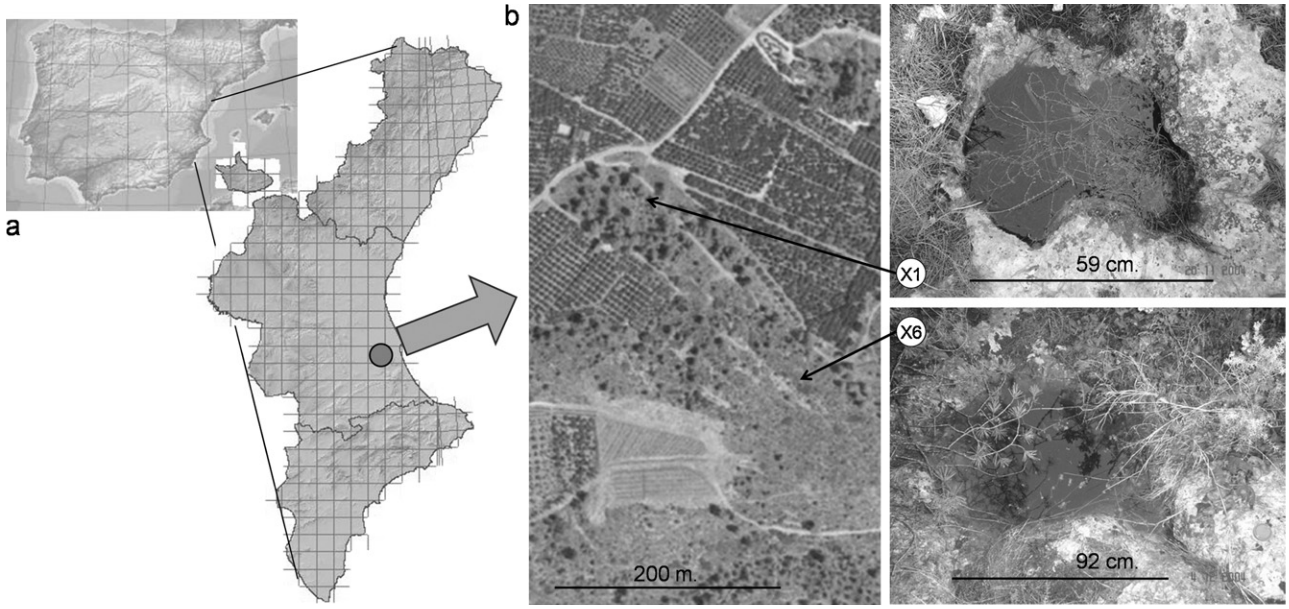

Fig. 1. (a) Location of the sampling area in the Valencian region of Spain, (b) aerial view of the sampling area and detail of the two sampled pools.

On the limestone rocky substrate of the Mediterranean shrublands of Racó de Rius (east Spain), we found 119 rainy rockpools over an area covering 65 ha. Of these, 35 harbor asexual populations of the ostracod crustacean *Heterocypris bosniaca* Petkowski et al. (2000) (Aguilar-Alberola and Mezquita 2008a), which was recently discovered in the Iberian Peninsula (Aguilar-Alberola and Mezquita 2005, 2008b). In 2004, we carried out initial sampling campaigns and selected two rockpools to start a monitoring survey on *H. bosniaca* populations (Aguilar-Alberola and Mezquita 2008b). Surprisingly by the end of the hydroperiod we observed many individuals living in these rockpools which were already dry. They were grouped in compact packs below a mixture of pine needles and mud substrate, which shows an adaptive behavior in response to desiccation (Williams 2006). Shortly after rehydrating a small sample of the substrate from these pools, hundreds of actively swimming ostracods could be seen. This amazing capacity to tolerate desiccation in mud may prove extremely beneficial to ostracods and other invertebrates living in such ephemeral and unpredictable environments (Delorme and Donald 1969; Williams 2006).

In order to understand how *H. bosniaca* population dynamics respond to short-term environmental changes that have a great impact on rockpools (e.g., rain, temperature variability, desiccation), we initiated a full hydroperiod, high-resolution monitoring program which commenced after the summer of 2005 when all the previously studied ponds had been dry over a long period. In addition to field information, our aim was to test tolerance to the reducing water content in the substrate and the effect of the velocity of desiccation on the ostracod survival rate under controlled laboratory conditions, which could potentially allow us to decipher how some invertebrates can withstand repeated short desiccation events in small temporary pools.

Methods

Field sampling

The two studied rockpools, X1 and X6, are located in a limestone mountain area with Mediterranean shrublands in Rafelguaraf (Spain), and are separated by a distance of approximately 210 m (Fig. 1). Both pools dry up in summer for several months, and in dry years, they probably have a very short hydroperiod. The two pools differ in size as X1 is smaller (32 cm × 59 cm max. diameter, and max. depth of 13 cm) than X6 (92 cm × 120 cm, max. depth 20 cm), in illumination terms, and in some hydrochemistry and hydroperiod aspects (Aguilar-Alberola and Mezquita 2008b). The organic substrate in rockpool X1 accumulates pine needles, while fig (*Ficus carica*) leaves are dominant in X6, which also harbors an anostracan, *Branchipus schafferi*, population. A previous work showed that the dominant ostracod species in these pools, *H. bosniaca*, has a relatively short life cycle in these environments (Aguilar-Alberola and Mezquita 2008b), similarly to that of *Heterocypris incongruens* (Latifa 1987). In this work, we once again found high density populations of this species, demonstrating that *H. bosniaca* has established stable populations in the study area. Aguilar-Alberola and Mezquita (2008b) discuss these and other initial observations on the hydrological cycle of these pools and the dynamics of their *H. bosniaca* populations.

In order to study a whole inundation period, we waited for a significant rainy event that would fill rockpools X1 and X6 (which had been dry since January 2005), and this event took place after summer 2005. We started sampling on the day immediately after the event, this being 18/09/05. From this date onward, we sampled both ponds weekly, even if they were dry (i.e., without free water) until no living individuals were observed. The sampling campaign lasted 30 weeks and ended on 9/04/06. When free water was available, we measured water temperature, electric conductivity and pH using a Hanna Instruments® portable probe, and oxygen content with a WTW® oxymeter. At the same time, a water sample was obtained in a PE bottle to analyze chloride concentration and alkalinity using standardized volumetric tests (Aquamerck® kits 1.11106.0001 and 1.11109.0001, respectively). If no free water was present, none of these variables were measured. Daily information on maximum and minimum air temperatures and precipitation was obtained from the data available online on the Spanish Ministry of the Natural, Rural and Marine Environment's web site (2008) from the nearest meteorological observatory located in Carcaixent, Valencia. The field sampling area and the meteorological observatory are 8.6 km apart, and both sites belong to the same climatic region (Pérez 1994). Therefore, no major differences in precipitation and temperature patterns are expected.

Ostracod samples were collected with a 100 mL, 5 cm Ø PE bottle which was directly introduced into the water of the pool and