Biotic interactions affect the colonization behavior of aquatic detritivorous macroinvertebrates in a heterogeneous environment

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ABSTRACT

It has previously been suggested that macroinvertebrates actively search for suitable patches to colonize. However, it is not well understood how the spatial arrangement of patches can affect colonization rates. In this study, we determined the importance of the environmental factors (distance, connectivity and resource availability) for patch colonization in an experimental system using *Gammarus aequicauda* (Amphipoda), *Lekanesphaera hookeri* (Isopoda) and *Ecrobia ventrosa* (Gastropoda). Furthermore, we also assessed how the relative importance of each of these environmental factors differed in interactions between the three species. The single species experiments showed that distance was the most important factor for *G. aequicauda* and *E. ventrosa*. However, while *E. ventrosa* preferred patches close to the release point, *G. aequicauda* strongly preferred patches further from the release point. High resource availability was a strong determinant for the patch colonization of *G. aequicauda* and *L. hookeri*. Connectivity was only of moderate importance in the study system for *L. hookeri* and *E. ventrosa*. The effects of the environmental factors were strongly affected by interspecific interactions in the multispecies experiments. For *G. aequicauda*, the distance preference was lowered in the presence of *E. ventrosa*. Moreover, while for *L. hookeri* the effect of resource availability was ruled out by the species interactions, resource availability gained importance for *E. ventrosa* in the presence of any of the other species. Our results suggest a strong link between environmental factors and biotic interactions in the colonization of habitat patches and indicate that the effect of biotic interactions is especially important for species sharing similar traits.

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1. Introduction

Assessing how species distribute through their environment has long been among the fundamental issues of community ecology (MacArthur, 1972; Cody and Diamond, 1975). However, the interaction between abiotic and biotic factors determining species-specific space-use behavior and recourse patch colonization are complex and require more empirical evidence (Wiens and Milne, 1989; HilleRisLambers et al., 2012). An example of a system where interactions between abiotic and biotic factors are poorly understood is that of aquatic systems in which coarse detrital material (i.e. any form of non-living organic matter) provides sources of food and physical shelter for macroinvertebrates (Mancinelli and Rossi, 2002; Winemiller et al., 2010). Although

short-term patch colonization behavior has been observed for detritivorous macroinvertebrates on these detrital patches (Mancinelli et al., 2005, 2007), there is a lack of empirical evidence on the underlying mechanisms (Swan and Palmer, 2000; Boyero et al., 2012).

The colonization of macroinvertebrates enhances the temporal variability of the detrital accumulations as they play an important role in the degradation of the coarse material (Rossi, 1985; Gessner and Chauvet, 1994; Swan and Palmer, 2000). The degradation of their own habitat forces the organisms to continuously accommodate the changing conditions (Moore et al., 2004). As the arrangement of the detrital accumulations (hereafter referred to as patches) is relatively unstable it is likely that connectivity between the detrital patches is of importance in the patch dynamics (Hanski, 1999; Snäll et al., 2003). Murphy et al. (1998) found that aquatic macroinvertebrates actively select patches differing in size (e.g. amount of detrital material) and quality (e.g. leaf mass, water flow and depth), with favorable conditions for establishment. The

specific conditions which a species selects for during establishment are expected to be affected by the species traits (Weiher and Keddy, 1999; Leibold et al., 2004).

Body size has been linked to the use of space by an organism and strength in biotic interactions. For example, body size is able to affect ingestion energetics as it has been shown that larger individuals leave patches sooner than smaller individuals (Brown, 1988; Brown et al., 1994) suggesting that the perceived resource availability in a patch depends on a species body size (Basset et al., 2012). Furthermore, interspecific differences in body size have been suggested to control interspecific coexistence (Basset, 1995; Wilson et al., 1999) and stabilize consumer–resource interactions (Basset et al., 2002, 2012). Additionally, the realized abundance of a species within dynamic or fragmented environments is expected to be restricted by dispersal limitation (Hanski, 1999; Palmer et al., 2000; Jenkins et al., 2007) and biotic interactions (Åström and Bengtsson, 2011).

To elucidate the use of detrital patches by detritivorous macroinvertebrates we tested the importance of both abiotic and biotic factors under controlled laboratory conditions. We used an experimental aquatic system in which three detritivorous macroinvertebrate species were able to move among and select patches that were characterized by different environmental factors (i.e. distance, patch connectivity and resource availability). We explored how the different patch types affected the density of individuals of the different colonizing species. Afterwards we determined whether biotic interactions between the species affected the colonization behavior. Additionally, we measured species traits (i.e. body mass and movement speed) in order to derive a functional explanation of the results from the colonization experiments.

We formulated two questions to determine the patch use of the three species that naturally compete for resources. Firstly, do species differ in their short-term responses to the environmental conditions characterizing the experimental environment? Our hypothesis is that differences in dispersal capacities will determine the relative importance of distance and connectivity between patches for the different species (Hanski, 1999; Jenkins et al., 2007; Åström and Bengtsson, 2011), while differences in body mass will determine the importance of resource availability (Basset and DeAngelis, 2007; Basset et al., 2012). Secondly, does the response to different patch types depend on the presence of competing species? Here we expect that resource competition between the species will result in a shift of the relative importance of each environmental factor (Basset, 1995; Weiher et al., 2011). We expect changes in the relative importance of an environmental factor due to exclusion of species from their preferred patches due to the presence of a stronger competitor (Chesson, 2000; Amarasekare, 2003).

2. Material and methods

2.1. Sampling site and study species

All organisms were collected in a fresh water channel (Giammatteo channel) connected to a small micro-tidal coastal basin (Acquatina Lagoon; 40°26′54.6″N, 18°13′55.5″E) located in Puglia, southeast Italy on the Adriatic coast. This freshwater channel (salinity 1.72 ± 0.020‰; pH 7.52 ± 0.022 measured with YSI 556 MPS multiprobe during April–June 2012) with a depth of 30–70 cm is characterized by a benthic habitat that consists of rocky boulders and dense accumulations of leaf detritus. The leaf detritus mainly consists of *Phragmites australis* (Cav.) Trin. ex Steudel (Poaceae) and *Posidonia oceanica* (L.) Delile (Posidoniaceae) and accumulates in between the empty spaces of the rocky boulders where it provides

habitat for macroinvertebrates. Depending on the arrangement and the sizes of the rocks (diameter ±10–20 cm) the distances between the patches range from a minimum of 10 cm up to 1 m. The build-up of detritus in between the boulders shows much temporal variability and patch size can range from 2 cm to 20 cm (personal observation). The number of species characterizing this benthic habitat is low and mainly consists of the three studied detritivorous species that compete for resources and space, namely *Gammarus aequicauda* (Martynov) (Amphipoda: Gammaridae), *Lekanesphaera hookeri* (Leach) (Isopoda: Sphaeromatidae) and *Ecrobia ventrosa* (Montagu) (Gastropoda: Hydrobiidae). The dense accumulations of leaf detritus and submerged macrophytes in the middle of the channel are normally dominated by *G. aequicauda* and *E. ventrosa*, while *L. hookeri* is mainly found in detritus patches at the shallow edges of the channel. Although these species compete for the same resources, differences in feeding habits and mobility allow them to utilize the resources in close proximity to each other. While *G. aequicauda* is able to shred and scrape the surface of the resources (Mancinelli, 2012), *L. hookeri* and *E. ventrosa* are only able to feed by scraping the surface (Lopez and Levinton, 1978; Mancinelli, 2010). Moreover, the species differ in locomotion and substrate relation. Both *L. hookeri* and *E. ventrosa* are mainly substrate surface crawlers. Additionally, *L. hookeri* is also able to actively swim in a reversed position (Mancinelli, 2010) giving it the possibility to move quickly between spatially separated resource patches. However, *G. aequicauda* is a full water swimmer (Mancinelli, 2012) and has the highest capacity to move between resource patches compared to the other species.

The organisms were collected with leaf packs filled with dried *Phragmites australis* leaf fragments (±50 cm long, 15 cm wide, 1.0 cm mesh), which we kept in between the rocky boulders for three days. We maintained laboratory stocks of each species in a multi compartment channel system filled with water originating from our field location (constant temperature of 18 °C, salinity <2.0) and a diet of dried *P. australis* leaf fragments supplemented with fresh macrophyte material from April to August 2012. All animals were kept in the channel system for at least three days to acclimatize to the laboratory conditions before using them in any experiment.

2.2. Interspecific trait variation

To quantify interspecific differences in body mass we randomly selected 100 individuals per species from the laboratory stock. Each animal was dried individually in microtiter plates placed in a stove at 60 °C for 72 h. The dry weight of each specimen was weighted to the nearest 0.001 mg (Sartorius ME5) and subsequently the specimens were burned in an oven for 5 h at 450 °C to acquire the ash free dry weight. Additionally, we determined interspecific differences in dispersal capacities by measuring the movement speed of 10 individuals per species. The animals were randomly selected from the laboratory stock and starved for a period of 24 h prior to the experiments. Their movement was monitored with a webcam (640 × 480 VGA resolution) in an enclosed Petri dish (Ø 14.5 cm; 8 mm water layer) for 15 min with a rate of 4 frames per second in Cocoa – SGDataProc (V. 1.0, Apple Developer Connection). The coordinates of the trajectories followed by the animals during the trial were classified following Jeanson et al. (2003). The coordinates within a distance of 5 mm from the wall were considered to be wall following paths and were discarded from the data analyses. The remaining paths were considered to be exploratory paths and were used to calculate average movement speed of each individual animal as reported in Mancinelli (2010). Between experiments the arena was cleaned with deionized water to remove any residual chemical cues.