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Feeding habits of amphipods (Crustacea: Malacostraca) from shallow soft bottom communities: Comparison between marine caves and open habitats

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ABSTRACT

Marine caves are environments of great interest since the organisms that inhabit them are forced to develop specific adaptations to high constraint conditions. Because of some of these particular conditions, such as light absence or oligotrophy, it can be expected that feeding strategies into caves differ from that present outside them. Nevertheless, no studies have been done to compare the trophic structure of marine caves and open habitats, at least for amphipod communities, considering their importance both inside and outside of the caves. In this study, the diet of the dominant amphipod species living on shallow sediments, both inside and outside of six marine caves in western Mediterranean, was characterized. Thereby, the gut content of 17 amphipod species was studied, being this study the first attempt to establish the feeding habit of most of these species. Analysis of digestive contents of the species showed that amphipod diet is less diverse in sediments than in other environments, such as algae and seagrasses. No herbivorous species were found in the sediment and carnivorous amphipods showed a little variety of prey, feeding mainly on crustaceans. Differences in the trophic structure were also found between marine caves and open habitats sediments: while outside the caves detritivorous was the dominant group (both in number of species and number of individuals), amphipods mainly play the role of carnivorous inside the caves. No detritivorous species were found into the caves, where carnivorous represents almost 60% of amphipods species and more than 80% of amphipod individuals. This pattern obtained in amphipods differ from the general trend observed in marine cave organisms, for which a generalist diet, such as omnivory, usually is an advantage in these oligotrophic conditions. The possible causes of this pattern are discussed.

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1. Introduction

Submarine caves constitute interesting ecosystems characterized by distinctive biological and ecological peculiarities (Gili et al., 1986). Despite the increased interest of the last decades in the study of these habitats (Benedetti-Cechi et al., 1996), many aspects remain almost unknown. Marine caves can be inhabited by specialized taxa, many of them restricted to live in caves (sometimes exhibiting extreme adaptations), or by more generalist taxa than can find temporal or permanent refuge there (e.g. Bussotti and Guidetti, 2009; Harmelin et al., 1985; Vacelet et al., 1994). In any case, from the feeding point of view, caves are usually poor environments that greatly condition their trophic webs, at a global scale, and the particular diet of the species present, at a low scale. Thus, the absence of light in marine caves (common fact to freshwater and terrestrial caves) avoids the presence of primary producers (except in some cases chemosynthetic bacteria) (e.g. Airoldi and Cinelli, 1996; Pohlman et al., 1997). Parravicini et al. (2010) pointed out that, because of the differences in water confinement and trophic depletion among different sectors inside marine caves, consistent variations in the trophic guild of sessile species can be found. Additionally for soft bottom communities, the existence of a lower hydrodynamism influences their habitat structure, usually offering a finer sediment substrate than the surrounding seabed (Bamber et al., 2008). Iliffe and Bishop (2007) note, at community levels, that the scarcity of food in anchialine caves drives organisms toward a generalist diet, being expected that detritus feeders, together with omnivorous, dominate in these environments. Nevertheless, the role of a particular taxon needs to be evaluated to really categorize it inside the trophic web. In fact, it is amazing how little is known about the ecology of caves in general, particularly when it comes to their trophic structure (Romero, 2009).

In soft-bottom marine substrates, amphipod crustaceans are one of the most important and diverse components of the fauna (Dauvin et al., 1994; Fincham, 1974; Lourido et al., 2008; Prato and Biandolino, 2005)

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structuring benthic assemblages (Duffy and Hay, 2000). Amphipods are frequent both inside and outside caves (Bamber et al., 2008; Iliffe, 2005; Navarro-Barranco et al., 2012). In relation with all the previously noted, the study of the feeding habits of amphipods can constitute an interesting tool to understand the trophic webs in the benthos of marine caves and their surroundings.

Thus, the aim of the present study is to describe the feeding habits of the most abundant species of amphipods inhabiting inside and outside of some marine caves in western Mediterranean, to compare the obtained results and to test the hypothesis that species and/or populations living inside the caves are more detritivorous or omnivorous than those living outside of the caves.

2. Material and methods

Six karstic marine caves were selected for this study (Fig. 1 and Table 1). All the caves presented similar length (10–25 m) and morphology, with a single submerged entrance followed by a rectilinear blind-ending tunnel without air chambers. The sampling was conducted during July and August of 2011. Two sampling stations were selected in each cave: one in the exterior area (outside the cave) and another inside the cave (each one approximately 10 m from the cave mouth). Samples were collected in each station using a hand-held rectangular core of 0.025 m² to a depth of 10 cm by SCUBA diving. Samples were washed using a 0.5 mm mesh sieve, fixed with ethanol (70%) stained with rose Bengal. Amphipods were sorted under binocular microscope. Additional samples were collected at each station for physicochemical analyses of the sediment. All samples were immediately stored frozen until the laboratory analyses. Granulometry was determined following the method proposed by Guitián and Carballas (1976). Organic matter was analyzed by dichromate oxidation and titration with ferrous ammonium sulfate (Walkley and Black, 1934).

To characterize the feeding habits of the amphipod community, we selected the species which contributed with at least 1% to the total abundance. In total, we studied 137 specimens of 7 species of amphipods living inside caves and 351 specimens of 13 species living outside caves. The whole list of analyzed material and details of provenance is included in Table 1, and the mean abundance of the amphipod species inside and outside the caves is included in Fig. 2.

For the diet study, individuals were analyzed following the methodology proposed by Bello and Cabrera (1999) with slight variations. This method has been successfully used to study the gut contents of different Table 1

Cave localities where amphipods were collected. Amb: Ampelisca brevicornis (Costa, 1853); Bag: Bathyporeia guilliamsoniana (Bate, 1857); Gaf: Gammarella fucicola (Leach, 1814); Haa: Harpinia antennaria Meinert, 1890; Hac: Harpinia crenulata (Boeck, 1871); Hap: Harpinia pectinata Sars, 1891; Him: Hippomedon massiliensis Bellan-Santini, 1965; Leh: Leptocheirus hirsutimanus (Bate, 1862); Mem: Megaluropus monasteriensis Ledoyer, 1976; Mef: Metaphoxus fultoni (Scott, 1890); Mog: Monoculodes griseus Della Valle, 1893; Pat: Pariambus typicus (Krøyer, 1884); Pel: Perioculodes longimanus (Bate & Westwood, 1868); PhI: Photis longipes (Della Valle, 1893); Phm: Phtisica marina Slabber, 1769; Sis: Siphonoecetes sabatieri De Rouville, 1894; Ure: Urothoe elegans (Bate, 1857).

Caves	Coordinates	Depth	Amphipod species	
		(m)	Outside	Inside
Gorgonias (GR) Cantarriján (CN) Treinta Metros (TM) Raja de la Mona	36° 44′ 17″ N, 3° 46′ 42″ W 36° 44′ 16″ N, 3° 46′ 41″ W 36° 43′ 12″ N, 3° 44′ 9″ W 36° 43′ 10″ N, 3° 44′ 6″ W	6 8 30 30	Bag, Mem Sis, Ure Hac Leh, Phl	Hap, Pel Hap, Pel Haa, Hac Gaf, Phm
(RM) Punta del Vapor (PV)	36° 43′ 22″ N, 3° 42′ 35″ W	12	Amb, Him, Mem, Pat, Pel, Phl, Sis	Hac
Calahonda (CL)	36° 42′ 46″ N, 3° 22′ 18″ W	19	Hap, Him, Mem, Mef, Phl, Pat, Sis, Ure	Hac, Hap, Mog

arthropod groups and other animals, both aquatic and terrestrial forms and both ethanol and formalin preserved samples, revealing that it is a very appropriate method for gut content analysis (e.g. Bo et al., 2012; Fenoglio et al., 2008; Tierno de Figueroa et al., 2006). Particularly, this method has been used previously in Amphipoda (Alarcón-Ortega et al., 2012; Guerra-García and Tierno de Figueroa, 2009; Vázquez-Luis et al., 2012). Each individual was introduced in a vial with Hertwig's liquid (consisting of 270 g of chloral hydrate, 19 ml of chloridric acid 1 N, 150 ml of distillated water and 60 ml of glycerin) and heated in an oven at 65 °C for approximately 3 h. After this, they were mounted on slides for its study under the microscope. The percentage of the absolute gut content (at $100 \times$), as the total area occupied by the content in the whole digestive tract, and the relative gut content (at $400 \times$), as the area occupied for each component within the total gut content, were estimated using the microscope equipped with an ocular micrometer. Mean and standard error of the mean were calculated. Amphipod species were assigned to their feeding group (detritivorous, carnivorous, and omnivorous) according to the diet. When the gut content included more



Fig. 1. Map of the study showing the location of marine caves where amphipods were collected. GR: Gorgonians, CN: Cantarriján, TM: Treinta Metros, RM: Raja Mona, PV: Punta Vapor, CL: Calahonda.

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