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On the occurrence of the tropical caprellid *Paracaprella pusilla* Mayer, 1890 (Crustacea: Amphipoda) in Europe

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Abstract

Paracaprella pusilla Mayer, 1980 is a tropical caprellid amphipod species. It was first described from Brazil and is found to be very common along the Atlantic coast of Central America. Since its original description, *P. pusilla* has been found in prolific volumes at numerous widespread locations in tropical and subtropical seas around the world, and is primarily associated with fouling communities in harbors. A well established population of *P. pusilla* was recently found in Cádiz, southern Spain, which is both the northernmost collection and the first recorded finding of this species in European coastal waters. Ship fouling is the most probable vector for its introduction. The species was always found in association with the native hydroid *Eudendrium racemosum* (Cavolini, 1785) and appeared to display a mutualistic relationship with this host.

Keywords*:* Alien species, Non native amphipod, Facilitation.

Introduction

Caprellid amphipods, commonly known as skeleton shrimps, are small marine crustaceans that are found in plenty in many littoral habitats. Here they form an important trophic link between primary producers and higher trophic levels (Woods, 2009). *Paracaprella pusilla*, originally described by Mayer (1890) from Brazil (type locality: Rio de Janeiro), is one of the most abundant caprellid species found along the Caribbean coast of Venezuela and Colombia (Díaz *et al.*, 2005; Guerra-García, 2006). The species' natural distribution is along the Atlantic coasts of Central and South America (Mayer, 1903), with most of the records from the coasts in the Gulf of Mexico and the Caribbean (Fig. 1). It appears to be a strongly Caribbean species (Carlton & Eldredge, 2009).

P. pusilla has since been reported from numerous locations in tropical and subtropical seas around the world, and is primarily associated with fouling communities in harbors (Table 1). Subsequent to its first reported occurrence in India (Sivaprakasam, 1977), the species has become the most abundant among the caprellids found along the entire coast of India, both in harbors and in natural intertidal rocky shores (Guerra-García *et al.*, 2010). An established population of *P. pusilla* has recently been reported from northern Australia (Montelli and Lewis, 2008), possibly introduced via biofouling on vessels. In spite of having direct development, caprellids can also disperse over large distances by 'rafting' on detached aquaculture buoys and other natural or artificial floating structures (Thiel *et al.*, 2003; Guerra-García *et al.*, 2011).

Although *P. pusilla* is distributed around the globe (Fig. 1), to date it has only been recorded in tropical and subtropical coastal waters. This study contributes to the knowledge of the alien amphipods in the Iberian Peninsula by documenting the presence of this tropical caprellid in the Strait of Gibraltar, southern Spain, very close to highlights the northernmost location of the species, and the first record made in European coastal waters.

Material and Methods

Numerous individuals of *P. pusilla* (including mature males, ovigerous females and juveniles) were collected from a floating pontoon at the Cadiz marina, southern Spain (36º32'29"N, 6º17'61"W) during a survey of peracarid crustaceans from harbors along the Strait of Gibraltar. This region experiences intense maritime traffic and is considered as a hotspot for biological invasions (Drake & Lodge, 2004). All specimens were found to be associated with the hydroid *Eudendrium racemosum* (Cavolini, 1785). The first discovery made was in September 2010,

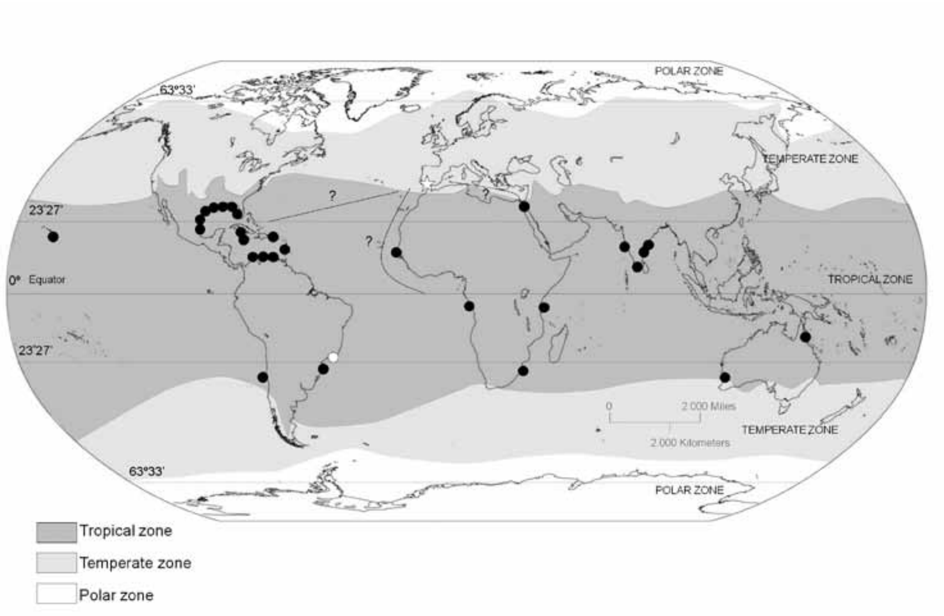

Fig. 1: Current global distribution of P. pusilla. Black circles indicate the records where the species has been found (all references are shown in Table 1); the white circle indicates the type locality (Rio de Janeiro, Brazil); the star symbol indicates the locality that was recorded during the present study, and represents the first record made in European waters. Possible pathways of introduction are indicated with question marks.

although it is not known as to how long they have been in existence at the site. Individuals were subsequently collected between October 2010 and July 2011 by detaching hydroid colonies at the base, and preserving them in 70% ethanol. Throughout this period, artificial substrates such as ropes, buoys and other arborescent organisms, including the bryozoans *Bugula neritina* (Linnaeus, 1758), *Tricellaria inopinata* D'Hondt and Occhipinti Ambrogi, 1985, *Zoobotryon verticillatum* (Della Chiaje, 1822) and the hydroid *Halocordile* sp., were sampled and examined in the laboratory for the presence of *P. pusilla.* In the laboratory, the epibionts on the hydrozoans were separated, identified under a stereomicroscope (Motic K-400L), photographed with a Nikon D90 digital camera and counted. An abundance of caprellids was expressed as the number of individuals/ml of substrate because of the different structures of the substrate species (Pereira *et al.*, 2006; Guerra-García *et al.*, 2010). The volume of substrates was estimated as the difference between the initial and final volumes when placed in a graduated cylinder with a predetermined quantity of water (Pereira *et al.*, 2006). Measurements of the total body length (from the front of the head to the end of the pereonite VII) of *P. pusilla* were taken using software Scion Image Alpha 4.0.3.2© (2000–2001, Scion Corporation). Water temperature and salinity were measured every month at the collection site using a conductivity meter CRISON MM40. Twentyfive hydroid colonies were studied during this period. In addition, five colonies were taken to the laboratory alive, where each colony was placed in separate aerated aquaria of 2.5 l supplied with an aquarium air pump. For observation, each colony was placed in small glass containers of 120 ml with a diameter of 6.5 cm and a height of 6 cm under a stereomicroscope to study the behavior of epibionts, especially the relationships between *P. pusilla*, *E. racemosum* polyps, the aeolids nudibranchs *Flabellina affinis* (Gmelin, 1791) and *Cratena peregrina* (Gmelin, 1791), which are hydroid predators associated with *E. racemosum.*

Results

Seawater temperatures ranged from 13.4 ºC (January 2011) to 24.8 ºC (July 2011), and salinity was from 32.4 psu (March 2010) to 36.6 psu (July 2011) in the Cádiz marina. *P. pusilla* was present from September 2010 to November 2010 and disappeared in December 2010 along with *E. racemosum* colonies. Shortly after the first *E. racemosum* colonies reappeared in the summer of 2011, the caprellid epibiont was once again recorded in July 2011. The most abundant population of *P. pusilla* was recorded in October 2010 ($\bar{X} \pm SD = 40.94 \pm 37.6$ ind/ml hydroid).

P. pusilla was only found associated with the hydroid *E. racemosum*, and not on any artificial substrates, nor on any other arborescent organisms at the Cadiz marina. Epibenthic peracarids were found to be commonly associated with *P. pusilla* within the hydroid colonies, including the amphipods *Caprella scaura* Templeton, 1836, *C. equilibra* Say, 1818, *Apocorophium acutum* (Chevreux, 1908), *Stenothoe monoculoides* (Montagu, 1815), the isopod *Dynamene edwardsi* (Lucas, 1849) and the tanaid

Table 1: Global distribution records of *Paracaprella pusilla* including date of reporting, site of collection (if known) and possible mechanism of introduction.

Date	Country	Localities	Collected from	Vector	Author of record
1890	Brazil	Rio de Janeiro	Ascidians		Mayer, 1890
1903	Brazil	Desterro	Unknown		Mayer, 1903
1903	Martinique	Fort de France and St. Anne	Unknown		Mayer, 1903
1903	Jamaica	Kingston harbour	Sides of a lighter	SF	Mayer, 1903
1928	Tanzania	Dar es Salaam	Unknown		Schellenberg, 1928
1928	Egypt	Suez Canal	Unknown	SF	Schellenberg, 1928
1937	Congo	Malembe	Algae and bryozoans	RF	Schellenberg, 1939
1937	USA	Hawaii (Honolulu harbour)	Intake water pipe	SF,BW	Edmonson and Mansfield, 1948
1941	USA	Hawaii (Honolulu harbour)	Hydroid (*Pennaria*)	SF,BW	Edmonson and Mansfield, 1948
1951	Gambia	Off Bathurst	Ships and buoys	SF, RF	Reid, 1951 (as *Caprella nigra*)
1955	South Africa	Durban harbour	Ship hull fouling	SF	Barnard, 1955; Day and Morgan, 1956
1957	USA	Texas	Fishing pier	SF,BW	Steinberg and Dougherty, 1957
1968	USA and Caribbean coast	Florida, Luisiana, Texas, Virgin Islands, Guadaloupe, Margarita, Curaçao	Mangrove roots, sea grass, hydroids and ascidians		McCain, 1968
1977	India	Kerala	Algae		
1977	India	Madras harbour, Tamil Nadu, Kerala and Pondicherry	Hydroids	SF	Sivaprakasam, 1997 (as *Paracaprella banardi* [a])
1978	USA	Gulf of Mexico	Bryozoans (*Amanthia* sp., *Bugula neritina*)		Caine, 1978
1987	USA	Gulf of Mexico	Barnacles on petroleum platforms	RF, SF	Lewbel *et al.,* 1987
1994	USA	Gulf of Mexico	Muddy sediments at 498 m depth		Winfield *et al.,* 2006
1997	USA	Florida	Artificial reefs	RF	Martin and Bortone, 1997; Camp, 1998
1998	Cuba	Sabana-Camagüey	Algae and stones		Ortiz and Lalana, 1998
1998	USA	Gulf of Mexico	Muddy sediments at 21m depth		Borja, 1998
2000	USA	Coast of Georgia	Soft bottom		Cooksey *et al.,* 2004
2001	Chile	Coquimbo	Detached aquaculture buoys	RF,AQ	Astudillo *et al.,* 2009
2003	USA	Alabama, Mississippi	Navigational buoy	RF	Foster *et al.,* 2004
2005	Venezuela	Caribbean coast	Gravel bottoms, ropes, mussels, oysters, sabellariid worms, hydroids (*Halocordyle*) associated with mangrove roots		Díaz *et al.,* 2005
2006	Colombia	Caribbean coast	Fouling communities of light-exposed pillars	RF	Guerra-García, 2006
2008	Australia	Port of Cairns	Boats	SF	Montelli and Lewis, 2008
2009	India	Vasai creek	Hydroid on an anchoring rope	SF	Bhave and Deshmukh, 2009
2009	Mexico	Gulf of Mexico	Drifting detached seaweeds	RF	Baeza-Rojano (pers. comm.)
2010	India	From Mumbai to Visakhapatnam harbour	Boats, seaweeds (*Gracilaria*) culture, coral rubbles, bryozoans *(B. neritina)* and hydroids from natural rocky shores	SF,RF, AQ	Guerra-García *et al.,* 2010

Likely vectors: SF - ship fouling; BW- ballast water; RF - rafting; AQ - aquaculture. [a]See Guerra-García *et al.* (2010)

Tanais dulongii (Audouin, 1826).

The morphological characteristics used to define *P. pusilla* were: (1) the large anterolateral projection of pereonite 2; (2) the small dorsal tubercle on pereonite 2; (3) the proximal knob on the basis of gnathopod 2; and (4) the lateral pleura in pereonites 3 and 4, more specially developed in pereonite 3 (shown in plate 2, figures 36 and 37 from Mayer, 1903). The specimens collected in Cadiz were found to display these features. The largest total body length for mature males was 7.97 mm, and for mature females it was 6.65 mm. Drawings of *P. pusilla* from different areas of the world, as well as our own examination of the specimens taken from the Gulf of Mexico, India and the Strait of Gibraltar showed little intraspecific variation in morphology.

Behaviorally, *P. pusilla* was found to hold an 'upright' posture on its native host (*E. racemosum*), and seemed to be able to switch between predatory and filter-feeding behaviors (Takeuchi and Hirano, 1995; Guerra-García *et al.*, 2002). *P. pusilla* frequently grazed on the settled detritus from the hydroid branches and, in some mature specimens the body was covered with detritus, possibly as a form of camouflage. We also observed that *P. pusilla* was commonly found in proximity of the polyps of *E. racemosum*. Occasionally, the caprellid placed its mouthparts into a polyp, appearing to feed on it, but a few seconds later the polyp returned to its former position with tentacles extended, without apparent damage. However, when a hydroid nudibranch predator (*Flabellina affinis* or *Cratena peregrina*) was added to the colony and moved toward the caprellid, *P. pusilla* displayed a deterrent behavior that triggered a change in the direction of the nudibranch, which then moved away from the area where the caprellids were present. This behavior was more common when the nudibranch was smaller than the caprellid, and we did not observe any differences between the two nudibranch species.

Discussion

Relationships between the introduced epibiont and its native host

P. pusilla, as with many other caprellid species, is reported to be relatively unselective with respect to substratum (Table 1). In different locations, this caprellid has been collected from *Bugula neritina* (Caine, 1978; Guerra-García *et al.*, 2010), a bryozoan, also commonly present in the Cadiz marina's fouling community. However, in this location, *P. pusilla* was only found within colonies of the hydroid *E. racemosum*. Indeed, the occurrence of *P. pusilla* in the Cadiz marina seems to relate directly to the presence of this substrate, which prompts us to assume the existence of a direct relationship between the introduced epibiont and its native host. In this sense, several aspects of the caprellid behavior could favor the establishment of the species in the area. First, *P. pusilla* seems to display an occasionally clepto-commensalist behavior by stealing captured prey from the polyps of *E. racemosun.* This peculiar trophic strategy was also observed by Bavestrello *et al.* (1996) to exist in other caprellid species (*Pseudoprotella phasma* and *Caprella* sp.) on *Eudendrium glomeratum* polyps. Second, *P. pusilla* is able to deter predator nudibranchs which feed on *Eudendrium* polyps by diverting them to areas of the colony devoid of caprellids. This mutualistic relationship was observed by Caine (1998) for *Paracaprella tenuis* on the hydrozoan *Bougainvillia rugosa* Clarke, 1882. Furthermore, the caprellid actively cleaned detritus from the hydroid branches. Dewey (1970) found that *Caprella equilibra* functioned as a defouling agent that promoted the survival of the hydroid *Aglaophenia pinquis*. In summary, the caprellid receives a suitable substratum for attachment, which also serves as camouflage from predators, and access to edible items including detritus, diatoms or copepods while living on the hydroid. In return, the hydroid is defouled and protected from predation. Several studies have suggested that some caprellids may feed directly on hydroids, but when Guerra-García and Tierno de Figueroa (2009) analyzed the stomach contents of *P. pusilla* they did not find any remnants of hydroids. These authors considered *P. pusilla* as a detritivore species. However, Caine (1978) did observe that ambush predation was the most frequently used strategy for obtaining food by this species, although it did commonly utilize alternate feeding modes. *P. pusilla*'s association with the hydroid *E. racemosum* may be either facultative, since it is found on numerous substrates in others localities, or obligatory (in this new range) as it is seemingly restricted to living in association with this hydroid in this area. Di Camillo *et al.* (2008) studied the interactions between *Eudendrium* and its epibionts, and emphasized the role of the *Eudendrium* colonies as a hotspot of coevolutionary relationships and life histories. This facilitation of the non-native caprellid by the native hydroid could have contributed to the successful establishment of *P. pusilla* in this new habitat.

Remarks on distribution and possible mechanism of introduction

P. pusilla is commonly reported from anthropogenic disturbed habitats where it has colonized a variety of artificial structures such as ropes, buoys, pontoons and oil platforms (Table 1). Lewbel *et al.* (1987) report the highest population density for this species, with 7948 caprellids/m^2 on an oil platform in the Gulf of Mexico (Woods, 2009). This ability to colonize a wide range of substrates suggests that this species may be capable of disperse by rafting on floating substrates. Thiel *et al.* (2003) reported the importance of rafting for the distribution of caprellids over long distances along the coast of Chile. Both rafting and biofouling communities on ships could explain the distribution of this species and the low morphological variation among specimens from different areas of the world. Further morphological and molecular studies are necessary to explore if the small morphological variation among populations in different geographic regions of the world correspond with low genetic structure.

One possible hypothesis in explaining the current global distribution of *P. pusilla* is that the species had spread from its natural range along the tropical eastern coast of the Americas, first to Africa and the Suez Canal (1920–1930s) and then to India (1980–1990s). The species has not yet been found in the Mediterranean, so the presence in the Strait of Gibraltar by entrance through the Suez Canal and the Mediterranean seems uncertain. However, knowledge of alien amphipods in this area is far from thorough (Zenetos *et al*., 2010), and it is therefore possible that the species is present in the Mediterranean but has yet to be detected there. Another possibility is that the species in Cadiz came from the West African coasts or from the Caribbean. Cadiz is one of Europe's busiest cruise destinations, with many cruise ships from the Caribbean and West Africa arriving at the international port of Cadiz, located a few kilometers from the Cadiz marina. The first introduction of *P. pusilla* into European coastal waters has possibly been through this international port via shipping or ballast water, with local secondary spreading to the Cadiz marina by rafting or recreational boating. Once introduced to a marina, there is a high probability that a species would be spread further via recreational yacht hulls; most likely to habitats of similar environmental conditions where the species can successfully establish itself (Ashton *et al*., 2006).

Although the abundance and species richness of caprellids in many areas of the world's oceans are still poorly known (Thiel *et al*., 2003), Laubitz (1970) pointed out that surface water temperature is an important factor determining the distribution of littoral caprellids. Evidences of changes in the geographic distribution of nonindigenous species are increasingly accompanied by observations of warming in particular areas of the seas (Occhipinti-Ambrogi, 2007). Further information about the potential warming in regions within temperate latitudes, and some details of the ecology of the species, like temperature tolerance studies, is still necessary to determinate if climate change could be involved in the successful establishment of this Caribbean species in temperate ecosystems.

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