Exploring trophic strategies of exotic caprellids (Crustacea: Amphipoda): Comparison between habitat types and native vs introduced distribution ranges

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ABSTRACT

The trophic ecology of non-native species is a key aspect to understand their invasion success and the community effects. Despite the important role of caprellid amphipods as trophic intermediates between primary producers and higher levels of marine food webs, there is very little information on their feeding habits. This is the first comprehensive study on the trophic strategies of two co-occurring introduced caprellids in the Spanish coasts: Caprella scura and Paracaprella pusilla. The diet of 446 specimens of C. scura and 230 of P. pusilla was analyzed to investigate whether there were differences in the feeding habits in relation to habitat characteristics (natural vs artificial hard substrata), type of host substrata (bryozoans and hydroids) and native vs introduced distribution ranges (Brazil vs Spain). Results revealed differences in diet preferences of the two species that have important implications for their trophic behaviour and showed a limited food overlap, which may favour their coexistence in introduced areas. In general terms, P. pusilla is a predator species, showing preference by crustacean prey in all of its life stages, while C. scura feeds mainly on detritus. Although no sex-related diet shifts were observed in either of the species, evidence of ontogenetic variation in diet of C. scura was found, with juveniles feeding on more amount of prey than adults. No diet differences were found between native and introduced populations within the same habitat type. However, P. pusilla exhibited a shift in its diet when different habitats were compared in the same distribution area, and C. scura showed a flexible feeding behaviour between different host substrata in the same habitat type. This study shows that habitat characteristics at different scales can have greater influence on the feeding ecology of exotic species than different distribution ranges, and support the hypothesis that a switch between feeding strategies depending on habitat characteristics could favour invasion success.

1. Introduction

Biological invasions are one of the main conservation threats and have caused many species extinctions (Olden et al., 2004; Simberloff, 2010). Accordingly, they have become an important issue at a global scale (Zenetos et al., 2010) and a prominent object of study. Despite being a biogeographical phenomenon, most studies on invasive species have focused exclusively on their ecology in the communities to which they have been introduced, and have ignored the ecology of these species where they are native (Hierro et al., 2005). The trophic ecology of invasive species, which is necessary to understand the community-wide effects of invasions (Tillberg et al., 2007), has traditionally focused on the relationships between the trophic niche breadth and the invasion success or on the impact of the introduced species in the native community (Olden et al., 2004; Piscart et al., 2011). Thus, for
example, it is accepted that omnivorous species or those with a broad trophic niche have more success than those with a specialized diet, and often that invasive species prey on or compete with autochthonous (indigenous) taxa (Barbosa and Castellanos, 2005; Simberloff, 2010). However, a few studies assess the trophic changes between native and introduced distribution ranges for a particular species. For example, Tillberg et al. (2007) showed a shift in the diet of the ant invasive species after their establishment comparing its feeding habits between different distribution ranges.

Amphipods are a very important group in the aquatic benthic communities (Jazdzewski, 1980) being a fundamental trophic link between primary producers and higher trophic levels (Woods, 2009). They also are very successful colonizers of artificial hard substratum, reaching high densities in harbours and marinas (Buschbaum and Gutow, 2005; Ashton et al., 2010) including biofouling on ship hulls (Frey et al., 2009). Moreover, among crustaceans, their important role as invasive taxa has been indicated (Zenetos et al., 2010), and an increased number of introduced species belonging to this group have been recorded (Jazdzewski et al., 2002). Nevertheless, the invasive amphipod species, and especially in marine environments, are still poorly studied (Zenetos et al., 2010). For freshwater species, a wider bibliography demonstrating their role as invasive is available (e.g. Grabowski et al., 2007; Piscart et al., 2011). In general, most invasive crustaceans are omnivorous (Karatayev et al., 2009) and occasionally predators (Hänfling et al., 2011). However, the trophic ecology of these species in their introduced range in comparison with their native range has been almost ignored. Exploring differences in the feeding habits of exotic species in relation to habitat characteristic in different distribution areas can help to understand the factors involved in the invasion success by these species.

Caprella scaura Templeton, 1836 and Paracaprella pusilla Mayer, 1890 are the only two introduced caprellid amphipods in the Mediterranean Sea. Although the origin area of both species is unknown, as occurs with most fouling species which inhabits harbours (Carlton, 1996), Brazil is included in the potential native range of the two species (Ros et al., 2013a, 2014). P. pusilla was described for the first time in Brazil and C. scaura, although it was described for the first time in Mauritius, was also recorded in Brazil only two years later, in 1838. Both species are well established in Spanish coastal areas co-occurring in Cádiz (south Atlantic coast of Spain) and Mallorca (Balearic Islands) (Ros et al., 2013a). However, P. pusilla has only been found in Spain, being considered a recent introduced species in Europe, while C. scaura is widely distributed along the Mediterranean Sea and the southern Atlantic coast of the Iberian Peninsula, including Spain and Portugal, and it appears that it is displacing other native caprellids such as Caprella equilibra (Guerra-García et al., 2011; Ros, unpubl. obs.). Although their current distribution is well studied, little is known about their feeding strategies in their native and introduced distribution ranges. As the diet is the product of a feeding strategy (Kleppel, 1993), one may gain insight into the ways in which caprellid species respond to their food environments by measuring their diets. The only data on the feeding habits of C. scaura and P. pusilla, based on their diet, were reported by Guerra-García and Tierno de Figueroa (2009) from a few individuals in a general study of the caprellid diet. Moreover, it remains unclear whether these two species differ in dietary preferences or if they are able to shift their feeding pattern according to the habitat characteristics or with the sex and the development stage.

The aims of the present study are: (1) to describe in detail the diet of Caprella scaura and Paracaprella pusilla according to the different sex/age groups, and (2) to analyze the differences in the feeding pattern of both species in relation with native and introduced ranges, natural and artificial habitats and different host substrata which they inhabit. Finally, taking into account that the introduced range of C. scaura is not only restricted to Spain, the last aim (3) is to investigate the consistency of the diet preferences of C. scaura associated with the same host substratum and under similar habitat characteristics in different regions of the Mediterranean Sea.

2. Material and methods

2.1. Study area

The field survey was conducted from May 2011 to November 2012 in the native (south coast of Brazil) and in the introduced range (coastal localities of southern Iberian Peninsula and Balearic Islands, Spain) of Caprella scaura and Paracaprella pusilla. In the case of C. scaura, additional coastal localities of central and southern Italy, Corsica, Malta and Greece were sampled to investigate the homogeneity of the C. scaura diet in the introduced area.

2.2. Sampling collection

In the introduced (Spain) and native range (Brazil), two habitats, defined by hard substratum type (artificial vs natural), were selected for comparison. Selection of sampling localities was based on the abundance of caprellid populations. As artificial habitats we considered fouling communities associated to recreational marinas while intertidal and subtidal rocky coastal shores (1–5 m deep) were selected as natural habitats. In Brazil, both caprellid species were present in natural and artificial habitats while in Spain none of the species were found in natural habitats. In each locality, the host substrata (bryozoans and hydroids) where the caprellid species were more abundant were collected directly by hand. Each substratum was collected independently and all samples were fixed in situ in 90% ethanol. In the laboratory, caprellids were sorted and identified to species level. The studied species with the capture locations, host substrata and collection dates are given in Appendix 1.

2.3. Diet analyses

For the diet study, specimens were analyzed according to the method proposed by Bello and Cabrera (1999) and previously used in studies on Amphipoda gut content analyses (e.g. Guerra-García and Tierno de Figueroa, 2009; Navarro-Barranco et al., 2013; Vázquez-Luis et al., 2013). Individuals were placed in vials with Hertwig’s liquid and heated in an oven at 70 °C for ~6 h before mounting individuals on slides in Hertwig’s liquid for study under microscope. We used a compound microscope equipped with an ocular micrometre to estimate the percentage of absolute gut content (at 40× as % total area occupied by the contents in the whole digestive tract) and the relative abundances of food items in the gut content (at 400× as % area occupied by each component of the total gut contents).

2.4. Statistical analyses

To explore global differences among the diet of sex/age groups for each species (considering as variable the percentage of the dominant food items), one way ANOVA was used. To test possible diet differences for each species between native and introduced ranges in different substrata associated with artificial habitats, a two-way ANOVA was used with the following factors: ‘distribution range’, a fixed factor with two levels: native and introduced; ‘substratum’, a fixed factor and orthogonal, with two levels: the hydroid Eudendrium sp. and the bryozoan Bugula neritina for...
Paracaprella pusilla, and the bryozoans B. neritina and Zoobotryon verticillatum for Caprella scaura.

Taking into account that none of the species has been found in natural habitats in their introduced range, to test possible differences in the diet of each species between artificial and natural habitats, only the native range was considered (Brazil). For Caprella scaura, a two-way ANOVA was used with the following factors: ‘habitat’, a fixed factor with two levels: artificial and natural; and ‘substratum’, a fixed factor and orthogonal, with two levels: the bryozoans Bugula neritina and Zoobotryon verticillatum. For Paracaprella pusilla only one substratum was available for comparison in both habitats (Eudendrium sp.). Consequently, to test differences among habitats for this species, one-way ANOVA was used.

The total number of specimens available with detected digestive contents differed among samples. Therefore, to properly conduct balanced ANOVA designs, we always chose the lesser sample size for each treatment and we selected randomly the same number of specimens from each sample. Prior to ANOVA, heterogeneity of variance was tested with Cochran’s C-test. Data were transformed with the Ln (x + 1) if variances were significantly different at p < 0.05. Where variances remained heterogeneous, untransformed data were analyzed, as ANOVA is a robust statistical test and is relatively unaffected by heterogeneity of variances, particularly in balanced experiments (Underwood, 1997). In such cases, to reduce type I error, the level of significance was reduced to ≈0.01. Univariate analyses were conducted with GMA5 (Underwood et al., 2002). The affinities among species populations according to the dietary analysis were explored by MDS analysis using UPGMA and Bray–Curtis similarity index. Data of the area occupied for each component within the total gut content were considered (Guerra-García and Tierno de Figueroa, 2009). The multivariate analysis was carried out using the PRIMER v.5 package (Clarke and Gorley, 2001).

3. Results

We examined 446 specimens of Caprella scaura and 230 of Paracaprella pusilla. From these, digestive contents were found in 419 specimens of C. scaura (Tables 1 and 2) and 168 of P. pusilla (Table 1). Gut contents of the two studied exotic species included detritus, prey (crustaceans, polychaetes and hydroids), macroalgae, microalgae (e.g. diatoms) and dinoflagellates. The dominant component in C. scaura was detritus in all the sex/age groups, while crustacea (mainly harpacticoid copepods) were the dominant item in P. pusilla (Fig. 1). There were no significant differences in the diet of the different sex/age groups for both species, except for the juveniles of C. scaura, which showed lower values of detritus (F = 4.7, p < 0.01) and higher values of prey (F = 6.6, p < 0.01) than the remaining sex/age categories. The analysis of the gut contents of C. scaura in different localities of the Mediterranean Sea also showed that the diet was also clearly dominated by detritus, apart from the case of Malta where the percentage of crustaceans reached 45% (Table 2). This suggests that C. scaura is a primary detritivorous species, while P. pusilla is a primary carnivorous taxon, with more than 50% of prey in the gut content. In C. scaura, the average area occupied by the content in the whole digestive tract ranged from 46.1% to 81.5% in Bugula neritina and from 52.5% to 81.6% in Zoobotryon verticillatum. In P. pusilla, mean values ranged from 22.0% to 38.2% in B. neritina and 33.2–54.2% in Eudendrium sp.

When the influence of distribution range (native vs introduced) in the dietary composition was evaluated, no significant differences were found for any of the studied species within the same habitat characteristics (artificial habitats) (Table 3). However, the percentage of the main food items showed significant differences between substrata in both distribution ranges for Caprella scaura; the percentage of detritus in their gut was higher in Zoobotryon verticillatum (100 ± 0, mean ± standard error) than in Bugula neritina (93.4 ± 1.2) (Su, p < 0.05; Fig. 2, Table 3). In the native range, when the influence of the habitat (artificial vs natural) was tested, we found significant differences for Paracaprella pusilla (Fig. 3; Table 4), with higher percentages of prey in the artificial (87.6 ± 3.7) than in natural habitat (60.0 ± 9.9) (Fig. 4). These differences were also observed by MDS analysis in which P. pusilla collected from artificial habitat are clearly separated from the specimens collected from natural one (Fig. 5). This analysis also showed a limited food overlap based on a clear difference between the diets of the two exotic species.

4. Discussion

4.1. Feeding strategies of Caprella scaura and Paracaprella pusilla

In general, Caprella scaura is mainly a detritivorous species while Paracaprella pusilla is a carnivorous one, based on the dominant food item found in the gut content of all of the sex/age categories considered. However, both species feed on a high variety of items being able to display different feeding strategies. Although no sex-related diet shifts were observed in either of the species, an age-related diet shift was observed in C. scaura, where juveniles presented higher amount of prey and lower amount of detritus than the rest of sex/age groups considered. A diet shift during the development has also been observed in other amphipods such as Talitrus saltator (Olabarría et al., 2009) and has been reported as an important factor contributing to variation in diet within species (Hoeinghaus and Davis, 2007). Ontogenetic shifts in diet may occur in order to overcome physiological constraints (Hentschel, 1998; Rossi et al., 2004). For instance, when juveniles have physiological limitation in the maximum rate of food uptake, they might rely on higher quality sources of food to minimize the amount of food and maximize energy uptake (Hentschel, 1998). This could explain the observation that juveniles of C. scaura collected from Bugula neritina presented a higher percentage of prey items than juveniles of C. scaura collected from Zoobotryon verticillatum, since the last substratum retained more sediment than the former one (Ros et al., 2013b), providing an advantage to take detritus.

In addition, a biogeographical perspective is needed to establish the degree of specificity in the feeding strategy at different habitats and distribution ranges. In the case of Paracaprella pusilla, although we did not observe differences in its trophic habitats between its native and introduced distribution ranges, we observed a clear difference in the feeding strategy of this species when the diet of populations from artificial and natural habitats was compared. In the artificial habitat, P. pusilla fed mainly on crustacean prey, predominantly harpacticoid copepods (more than 80% of its gut content). In natural habitats prey represented only the 60% of its gut content, with a considerable amount of detritus. This could represent a potential adaptation to food resources. Detritus feeding may be important for carnivores when temporarily there is no available prey (Mayer et al., 2008), thus, the pycnogonid Ammothella longipes appears to be a carnivore during spring and early summer but seems to feed on detritus when availability of prey diminishes during winter (Soler-Membrives et al., 2011). With regard to Caprella scaura, the consistency of gut content found across different habitats, host substratum and distribution ranges suggests that detritus is a food type that remains available in the different habitats studied. Vázquez-Luis et al. (2013) studied the influence of the habitat type in the feeding habits on amphipods associated to macroalgae and found that detritivore species showed the least differences with respect to changes in habitats and substrata in...
which they inhabit. In our study, we observed a change in the proportion of detritus in the gut content of *C. scaura* when populations inhabiting different substrata were compared; particularly populations associated with *Zoobotryon verruculosum* fed practically only on detritus while populations associated with *Bugula neritina* fed also on other items but in low proportion. These small but significant differences could be related to the spatial structure of *B. neritina*, which host a high diversity of epiphytic fauna (Comardi, 1995), and may favour the occasional ingestion of small crustaceans or polychaetes by *C. scaura*, especially in the case of juveniles of this species. Despite this, detritus was the dominant item in all populations of *C. scaura* studied, including those that are invading different countries of the Mediterranean. Only in the case of the population of Malta, a high percentage of prey in its gut content (45%) was observed, reflecting that the species exhibits a plasticity feeding behaviour in its introduced range and possibly can adapt its diet regarding to the proportion of food items available.

### 4.2. Feeding ecology and invasion success

The different trophic strategies observed in the two caprellid species may have important consequences in their invasion success.
The trophic niches of Paracaprella pusilla and Caprella scura are segregated in their introduced range, since P. pusilla prefers to feed on crustaceans while C. scura feeds mainly on detritus. This could avoid an interspecific competition for the same food item and possibly favours the coexistence of both species in the same introduced areas and even the same substratum types. This coexistence was pointed out by Ros et al. (2013b) in the substratum Eudendrium racemosum in southern Spain.

Ship fouling and ballast water have been suggested as the most probable dispersal vectors for Paracaprella pusilla (Mead et al., 2011; Ros and Guerra-García, 2012). Taking into account that the main crustacean prey observed in its gut content were small harpacticoid copepods, and that copepods are the most abundant main crustacean prey observed in its gut content were small harpacticoid copepods, and that copepods are the most abundant crustacean of the invaded range (Mead et al., 2011; Ros and Guerra-García, 2012), this feeding habit could facilitate the dispersal of this species by these means. Predation is also an important part of food acquisition in the invasive amphipod Dikerogammarus villosus (Sowinsky, 1894), a very successful invader of freshwater ecosystems in Europe. Once in the introduced range, P. pusilla would need to be established in artificial habitats such as harbours or artificial marinas. The eutrophication that characterize these habitats due to anthropogenic activities may cause the replacement of large copepods with small ones (Uye, 1994). This could favours the increase of small harpacticoid copepod populations (the preferred diet item for P. pusilla) in the recipient habitat.

Table 2

<table>
<thead>
<tr>
<th>N/n</th>
<th>%Abs</th>
<th>Components (100%)</th>
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</thead>
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<td></td>
<td></td>
<td>%Det %Cru %Pol %Hyd %MAlg %Malg %Din</td>
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<tr>
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<td>19/18</td>
<td>56.7(6.1)</td>
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<tr>
<td>Civitavecchia</td>
<td>20/19</td>
<td>40.0(4.7)</td>
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<tr>
<td>Malta</td>
<td>23/21</td>
<td>58.8(4.5)</td>
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<tr>
<td>Ajaccio</td>
<td>20/15</td>
<td>49.3(8.2)</td>
</tr>
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</table>
Fig. 2. Diet preferences of *Caprella scaura* based on the percentage of each food item in populations collected in different host substrata, different habitat types and different distribution ranges.
Paracaprella pusilla and Caprella scabra, as with other fouling species, have the particularity that their dispersion usually takes place among artificial habitats. As we show here, substantial predation on small crustaceans, mainly harpacticoid copepods, supported a larger role in the trophic strategies of Paracaprella pusilla. Caine (1974), studying the particular trophic strategy was observed by Ros and Guerra-García (2013b) in P. pusilla and Caprella scabra, as with other fouling species, have the particularity that their dispersion usually takes place among artificial habitats. As we show here, substantial predation on small crustaceans, mainly harpacticoid copepods, supported a larger role in the trophic strategies of Paracaprella pusilla.

4.3. Trophic relationships between exotic caprellids and its preferred host substrata

We observed that individuals of Paracaprella pusilla collected from the hydroid Eudendrium sp. presented higher absolute gut content than those collected from the bryozoan Bugula neritina. This may be due to a clepto-commensalist behaviour developed by P. pusilla stealing captured prey from the polyps of the hydroid. This pecular trophic strategy was observed by Ros and Guerra-García (2012) in P. pusilla in Southern Spain and previously by Bavestrello et al. (1996) in other caprellid species (Pseudoproteus phasma and Caprella sp.) on Eudendrium gloriumat Picard, 1952, polyps. Alarcón-Ortega et al. (2012) studied the feeding habits of caprellids from the west coast of Mexico and found that Paracaprella sp. associated with hydroids also showed a significant amount of small copepods in the digestive tract, supporting the idea of clepto-commensalism. Therefore, the presence of hydroids in their gut may be an accidental intake of polyps when P. pusilla is stealing the captured prey from the hydroid. Mayer (1882) and MacKay (1945) stated that caprellids parasitize or eat hydroids, and McDougall (1943) reported that caprellids invaded hydroid colonies for food and shelter and concluded that while the substratum was eaten to some extent, the major food sources were the food items occurring on the hydroid stems.

In the case of Caprella scabra, although it was found in a wide variety of substrata in its introduced range, it seems to prefer the bryozoan Bugula neritina over other types of fouling substrata (Ros et al., 2013b). This bryozoan is a suspension feeder which creates a current bringing microscopic plankton and organic particles toward the animal. These currents may favour the intake of detritus by C. scabra.

In both cases, trophic relationships with its preferred substrata may favour the establishment and dispersal success of the species.

### 4.4. Functional morphology of feeding

A relationship among feeding modes, preferred food and mouthpart morphology has been noted for several feeding specialists among the amphipods (McCain, 1968; Caine, 1974; Mayer et al., 2008). Caine (1977) established that filter-feeder caprellids were those with molar and swimming setae but without mandibular palps. These are the features of Caprella scabra, as well as the other species of the genus Caprella. However, Guerra-García and Tierno de Figueroa (2009) only found that, in caprellids, obligate predators were characterized by the absence of molar process and swimming setae in the antennae 2. Caine (1977) previously established that caprellid predators were those with mandibular palps and molar processes but without swimming setae. P. pusilla has a rudimentary mandibular palp, the molar process is present but it is clearly less developed than in C. scabra, and it lacks the swimming setae. This implies that, in any of the cases, its morphology is not specialized for an exclusive feeding strategy. In fact, P. pusilla is able to prey on other items, although it is probably less efficient in the intake of detritus than C. scabra, which has a well-developed molar and swimming setae that create currents and act as a particle-collecting device.

### 4.5. Potential impacts on the recipient community

As we show here, substantial predation on small crustaceans, mainly harpacticoid copepods, supported a larger role in the trophic strategies of Paracaprella pusilla. Caine (1974), studying the magnitude of small copepods in the digestive tract, supporting the idea of clepto-commensalism. Therefore, the presence of hydroids in their gut may be an accidental intake of polyps when P. pusilla is

### Table 3

Results of ANOVA test on the influence of the distribution range (native vs introduced) and substratum (Bugula neritina vs Zoothyon verticillatum for C. scabra and Eudendrium sp. for P. pusilla) in the percentage of the dominant food items.*** P < 0.001. n.s. not significant.

<table>
<thead>
<tr>
<th>Caprellid species</th>
<th>Source of variation</th>
<th>df</th>
<th>%Detritus MS F</th>
<th>P</th>
<th>%Prey MS F</th>
<th>P</th>
<th>F vs. Res</th>
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<td>0.4661</td>
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<td>34.78</td>
<td>0.53</td>
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<td>Ln (x+1)</td>
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<td>Paracaprella pusilla</td>
<td>Distribution range – Ra</td>
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Fig. 3. Diet preferences of *Paracaprella pusilla* based on the percentage of each food item in populations collected in different host substrata, different habitat types and different distribution ranges.
Table 4
Results of ANOVA test on the influence of the habitat (artificial vs natural) and substratum (Bugula neritina vs Zoobotryon verticillatum) in the percentage of the dominant food items in C. scaura and only on the influence of the habitat (artificial vs natural) in the percentage of the dominant food items in P. pusilla.* P < 0.05.

<table>
<thead>
<tr>
<th>Caprellid species</th>
<th>Source of variation</th>
<th>df</th>
<th>% Detritus</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>% Prey</th>
<th>MS</th>
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Fig. 4. Different percentages of detritus and prey in the gut content of Paracaprella pusilla associated to Eudendrium sp. between artificial and natural habitats from its native range (Brazil). Values are mean and standard error of the mean.

Fig. 5. Two dimensional MDS plot based on the diet of the two species in different habitats, ranges and substrata. Data are taken from the total values of Tables 2 and 3. Eud: Eudendrium sp.; Bug: Bugula neritina; Zoo. Zoobotryon verticillatum; Pp: Paracaprella pusilla; Cs: Caprella scaura.
bioconcentration factor for TBT (Takeuchi et al., 2004), a toxic compound that was used in antifouling paintings during the 1980s and early 1990s (Stewart, 1996). Given that C. scaura reaches high densities in the introduced areas (Guerra-García et al., 2011) and it is able to survive throughout the year (Ros et al., 2013b), it plays an important role in the energy flow through food webs in introduced areas by accumulating pollutants and transmitting them to higher trophic levels. In fact, C. scaura is a common prey for many fishes and crabs (Dubiski-Silva and Masunari, 2008).

5. Conclusions

Dietary analysis of Paracaprella pusilla and Caprella scaura under a biogeographical approach has revealed that exotic caprellids in the Mediterranean present a limited trophic niche overlap. In general terms, P. pusilla exhibits a trophic preference by crustacean prey, particularly small copepods, while C. scaura feeds mainly on detritus. Although no sex-related diet shifts were observed in either species, there is evidence of ontogenetic changes in feeding mode of C. scaura, with juveniles feeding on more amount of prey than adults. This study supports three mechanisms that favour invasion success: (1) a switch between feeding strategies depending on the host substrata and/or habitat characteristics; (2) development of trophic relationships with the substrata in which they inhabit and are dispersed (by substrata attaching to the ship hulls), and (3) relative constancy on the diet between artificial environments in which the species spread out. It highlights the fact that the carnivorous species, P. pusilla, seems to change its feeding strategy in natural environments in comparison with artificial ones, alternating between a predatory/clepto-commensalist mode and a detritivorous feeding, while C. scaura, a primarily detritivorous species, does not need to change its feeding strategy. Further studies are necessary to show the implications of this shift in the population fitness and the spread success to natural environments.

Acknowledgements

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<th>Country</th>
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<th>Substrate</th>
<th>Caprellid species</th>
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References


