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Crustacean assemblages of coastal wetlands from fragmented and scarcely isolated islands compared with the mainland

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The present study compared crustacean assemblages from coastal wetlands between a fragment archipelago and a landmass. The study included four typical crustacean taxonomic groups (i.e. Cladocera, Copepoda, Ostracoda and Malacostraca) from the Balearic Archipelago region as an example of a fragment island ('Archipelago') and the Catalonia region as the landmass ('Mainland'; Spanish Mediterranean coast). We tested null hypotheses based on the expected similarity between Archipelago and Mainland in terms of crustacean assemblages and biodiversity. Similar relationships of those community attributes with environmental variables were also expected in both regions. The results partially met the null hypotheses. We found that crustacean taxonomic composition varied between Archipelago and Mainland, likely due to peculiar biological and biogeographical processes acting in the Archipelago. The relationship between crustacean assemblages and the environmental variables was mostly similar between Archipelago and Mainland, as expected. Both regions also showed similar patterns of species distribution (i.e. Archipelago and Mainland coastal wetlands were characterised by a

few dominant species). This result could be masked by the ‘filter’ effect exercised by the harsh conditions of coastal wetlands. Moreover, the total diversity values (gamma biodiversity) in the Archipelago were similar to the values for the Mainland, supporting the hypothesis that fragment islands can be of substantial value for the conservation of global biodiversity.

Additional keywords: crustacean diversity, fragment islands, island biogeography, Mediterranean ecoregion.

Introduction

The study of island biogeography has produced an extensive number of theories, models and tests, not only for biogeography, but also for evolution and ecology (e.g. MacArthur and Wilson 1967; Diamond 1975; Whittaker and Fernández-Palacios 2007). Different categorisations of islands, depending on the geological mechanism of their origins, are possible, for example oceanic islands, continental fragments, continental shelf islands, land-bridge islands (Darwin 1859; Wallace 1902; Whittaker and Fernández-Palacios 2007). In the present study, we followed the more generalised ‘Darwinian’ and ‘fragment’ island concepts suggested by Gillespie and Roderick (2002). Darwinian islands include those islands formed *de novo*, and the best known are the oceanic islands. In addition, some mangrove islands and rock pools could be included within this category (Gillespie and Roderick 2002). Fragment islands include those islands that are separated fragments from continents or mainland landmasses. The best known fragment islands are the continental islands, although we could also include isolated habitats within this category (Gillespie and Roderick 2002). In the present study, when we refer to ‘Darwinian’ and ‘fragment’ islands, we are only considering the case of oceanic and continental islands respectively.

Fragment and Darwinian islands are expected to have different roles in key ecological processes, such as immigration. For example, communities that are nearly saturated with species and have well-established biotic interactions can reduce the risk of potential colonisers (e.g. alien species; Shurin 2000; De Meester et al. 2002). In this sense, fragment islands should have a biota similar to their continental sources and the ecological niches would be filled to the point that the establishment of new species was hampered. Nevertheless, the magnitude of the effects of these ecological processes and, consequently, the expected assemblage characteristics and community structure will be ultimately determined by the isolation level of the island. Distance from the continent, the level of habitat dissimilarity and the dispersion capacity of the colonisers are main aspects to consider in establishing the scale of isolation (Gillespie and Roderick 2002). Three scales of isolation can be generally described, namely low, intermediate or high, which can be applied to both Darwinian and fragment islands (Gillespie and Roderick 2002). Evidence of the ecological processes that took place in Darwinian islands (or high-intermediate isolated fragmented islands) is widely known (e.g. Darwin 1859; Simon 1987; Gillespie et al. 2008),

whereas empirical studies in fragment islands are scarce, probably because it is less appealing to find no significant differences between island and mainland ecological dynamics, as could be expected.

Coastal wetlands are naturally stressed environments (Barnes 1989; Basset et al. 2006; Pérez-Ruzafa et al. 2011). This environmental stress is caused by the effects of variable physical factors, such as tides, storms, winds or flows (Quintana et al. 1998; Pérez-Ruzafa et al. 2005; Ciavatta and Pastres 2011), as well as the intermediate position between freshwater and marine, and between freshwater and land interfaces (Kjerfve 1994; Comín et al. 2004; Dauvin 2007). In this context, it is interesting to highlight that the Mediterranean region is characterised by a high seasonality, accompanied by sharp changes in water regimens (Alvarez Cobelas et al. 2005; Beklioglu et al. 2007). This unstable hydrological regimen has been related to strong changes in community composition and in population dynamics (e.g. Guelorget and Perthuisot 1983; Gascón et al. 2007). In the present study, we examined the crustacean assemblages of coastal wetlands from a fragmented and scarcely isolated archipelago and compared them with the crustacean assemblages of a mainland landmass. We selected the best represented groups occurring in coastal wetlands (Cladocera, Copepoda, Ostracoda and Malacostraca). In particular: (1) Cladocera, Copepoda, Ostracoda and Malacostraca are considered key groups for wetland food webs (Jeppesen et al. 2007; Brucet et al. 2010; Jensen et al. 2010); (2) they represent a high proportion of the metazoan biodiversity (Boix et al. 2007; Brucet et al. 2009); (3) some species are physiologically well adapted to these stressful environments (e.g. Kevrekidis et al. 2000; Brucet et al. 2009); and (4) some groups have a high dispersal capacity (Louette and De Meester 2005; Frisch et al. 2006) through different vectors that could act at different geographical scales (Havel and Shurin 2004), such as amphibians or wind (Vanschoenwinkel et al. 2008), birds (Green et al. 2008), fish (Beladjal et al. 2007) and even humans (Rossi et al. 2003; García-Berthou et al. 2007).

As a case study of fragment islands, we selected the Mediterranean Balearic Archipelago (Mediterranean Spain), located less than 100 km from the mainland (i.e. Catalonia). The response of crustacean assemblages to the main environmental variables was compared between the Balearic Archipelago and Catalonia. The main aim of the present study was to evaluate differences in crustacean diversity and structure between the mainland and fragment island at the species and assemblage levels, contributing to the limited literature published regarding fragment islands scarcely isolated. The main hypothesis tested was that crustacean assemblages and their responses to environmental variables are expected to be similar between the Balearic Archipelago and the mainland landmass (Catalonia; hereafter 'Mainland'). Moreover, partial null hypotheses that supported the main hypothesis were tested, namely: (1) the environmental variables that best fit the species variability in the crustacean assemblages will not vary between

the Archipelago and Mainland; (2) different diversity values measured at different scales (α , β and γ) will not be found between the Archipelago and Mainland; and (3) the relationships between the number of crustacean species and the environmental variables will not vary between the Archipelago and Mainland.

Material and methods

Areas of study

The study was performed in coastal wetlands from two Spanish Mediterranean regions: Catalonia (north-eastern Iberian Peninsula; Mainland) and the Balearic Archipelago (Western Mediterranean sea; 'Archipelago') located ~100 km from the Spanish east coast (Fig. 1). Coastal wetlands from the four principal islands of this Archipelago (i.e. Majorca, Minorca, Ibiza and Formentera) were sampled in the present study. Both the Mainland and the Archipelago sites belong to the Mediterranean ecoregion, characterised by dry summers and mild winters, with rainfall occurring mainly during autumn and spring (Britton and Crivelli 1993). All coastal wetlands studied were permanent and brackish. Although the Mediterranean Sea has a microtidal range (<2 m; Davies 1964), all the coastal wetlands studied were marine influenced and shallow (maximum depth <6 m).

Sampling procedure

Mainland data were obtained from surveys conducted at 32 coastal wetlands (one sampling site per wetland, yielding 32 sites). In the Archipelago, surveys were conducted at 23 coastal wetlands. In three of the wetlands, more than one sampling site was established due to the size and within-habitat heterogeneity, yielding 32 sampling sites. The study was performed during winter (February–March) and spring (May–June) in 1996, 1997, 2000, 2003 (Mainland) and 2006 (Archipelago) to reflect temporal variability.

Water temperature, electrical conductivity, percentage oxygen saturation and pH were measured *in situ*, whereas dissolved inorganic nutrients (ammonium, nitrite, nitrate and phosphate) and chlorophyll-*a* (Chl-*a*) content were analysed in the laboratory. Details of the analytical protocols for these variables can be found in Boix et al. (2008) for the Mainland sites and Lucena-Moya et al. (2009) for the Archipelago sites. The coastal wetland surface area (size) was calculated using freely available aerial photographs (Departament de Política Territorial i Obres Públiques 2005; Ministerio de Agricultura Pesca y Alimentación 2006). Additional information on the characterisation of the coastal wetlands (chemistry of the water and size) is summarised in Table 1.

Crustacean samples were collected accounting for the possible different microhabitats within each sampling site (e.g. shores with and without vegetation, submerged vegetation, bare sediment). Thus, a sampling effort proportional to the representativeness of each microhabitat

was performed at each site. A hand net with a mesh size of 250 μm was used. A fixed number of ‘sweeps’ (10 and 20 in the Archipelago and Mainland respectively) was undertaken at each sampling site. The abundance data were calculated as catch per unit effort (CPUE; i.e. individuals per sweep). Each ‘sweep’ consisted of a rapid push through the water column and on the bottom.

Data analysis

Environmental characterisation

To test the significance of differences in the environmental characterisation of the coastal wetlands over space and time, comparisons were made between the following groups: Group 1, Mainland-winter; Group 2, Mainland-spring; Group 3, Archipelago-winter; Group 4, Archipelago-spring. A multivariate approach based on principal components analysis (PCA) coupled with between-group analyses was used (Dolédec and Chessel 1989). The between-group analysis allowed us to obtain the centroid of each group. Differences among groups were checked using a Monte Carlo permutation test (999 unrestricted permutations under a reduced model). The PCA was performed by applying the function ‘*duddi.pca*’, centroids were calculated by means of the function ‘*between*’ and a Monte Carlo test was performed using the function ‘*randtest.between*’. These three functions can be found in the *ade4* library written in the R language (R Foundation for Statistical Computing, Vienna, Austria) (Dray and Dufour 2007). Variables were log transformed ($\log(x + 1)$) when necessary and standardised (by the maximum). The dataset analysed contained a total of 128 data samples (32 sites \times 2 seasons = 64 samples for each region of study) and eight environmental variables (water temperature, electrical conductivity, percentage oxygen saturation, pH, dissolved inorganic nitrogen (DIN; obtained by summing nitrogen fractions: ammonium + nitrite + nitrate), phosphate, Chl-*a* and water body size).

Composition of crustacean assemblages and environmental variables

Similarity percentage analysis (SIMPER) was used to detect characteristic crustacean species on coastal wetlands. This analysis examines the contribution of individual species to the average dissimilarity between pairs of groups (Archipelago *v.* Mainland) and resemblances within a group (Archipelago and Mainland) using Bray–Curtis similarities. Absence and presence data per site were used and the region of study (Archipelago *v.* Mainland) was included as a factor. The SIMPER analysis was performed using PRIMER 6 (PRIMER-E Ltd.) (Clarke and Warwick 2001).

Canonical correspondence analyses (CCAs) were performed to identify the environmental variables that best fit the species variability in the crustacean assemblages. A combined CCA (i.e. Mainland and Archipelago together) was first performed to quantify the regional effect

through their conditional effect. Another two CCAs were performed for each separate region (i.e. one for Mainland and another for Archipelago) to identify whether the environmental variables related to the crustacean assemblages were similar across regions. All the species abundance matrices used (93 taxa for Archipelago and Mainland combined; 66 taxa for Mainland; 58 taxa for Archipelago) were square root transformed. We downweighted for rare species to reduce their influence in the analysis (ter Braak and Šmilauer 1998). All environmental variables ($n = 8$) were log transformed ($\log(x + 1)$), except pH and region. Season (spring and winter) was taken into account as a covariate. The forward selection procedure was used to obtain the conditional effect (λ) for each variable, and expressed as a percentage. Two significance tests for canonical axes were performed using the Monte Carlo test (499 permutations). The first test shows whether the first canonical axis is sufficient to explain species variation. The second permutation test (with all canonical axes) verifies the existence of a relationship between environmental parameters and species matrix. CCAs were performed using CANOCO 4.5 (ter Braak and Šmilauer 1998).

Crustacean diversity and environmental variables

We used three approaches to analyse values of diversity in the Archipelago and Mainland for each taxonomic group of crustaceans (Cladocera, Copepoda, Ostracoda and Malacostraca), as detailed below.

1. α Diversity as mean species richness per site. Significant differences in α diversity values between the Mainland and Archipelago were tested for each crustacean taxonomic group using either Kruskal–Wallis H test or one-way analysis of variance (ANOVA) tests depending on whether the parametric assumptions were met.
2. β Diversity as multiple-site similarity measures independent of patterns of richness (Baselga et al. 2007; Baselga 2010). Because β diversity may be caused by two different phenomena, namely nestedness (reflecting a process of species loss) and species turnover (implying the replacement of some species by others; Harrison et al. 1992; Baselga et al. 2007; Baselga 2010), we assessed the overall multiple-site dissimilarities, considering total β diversity (Sørensen-based multiple-site dissimilarity; β SOR), spatial turnover (Simpson-based multiple-site dissimilarity; β SIM) and nestedness (nestedness-resultant multiple-site dissimilarity (β NES), which is inferred: β NES = β SOR – β SIM) components. Calculations were performed using the free software R (R Foundation for Statistical Computing, Vienna, Austria) and followed functions and scripts described in Baselga et al. (2007) and Baselga (2010).
3. γ Diversity as the total richness for each region, calculated using the Chao2 estimator (EstimateS: statistical estimation of species richness and shared species from samples,

version 8.2; <http://viceroy.eeb.uconn.edu/estimates/>, accessed 15 January 2015). This estimator is a highly recommended measure of total richness because it is independent of possible differences in the sampling effort (Magurran 2013). The bias-corrected formula of the Chao2 estimator was used when Chao's estimated CV for abundance distribution was <0.5 ; otherwise, a classic Chao2 estimator was used. To determine whether the results obtained with the Chao2 estimator were significantly different ($P < 0.05$), the criterion used was the absence of overlap among the 95% confidence intervals (CIs) of the coastal wetlands (Colwell et al. 2004).

The relationships between species richness and the environmental variables were explored by means of linear mixed effects (LME) models. The categorical spatial variable region (i.e. Archipelago or Mainland) was introduced as a dummy variable. The model was mixed because the explanatory variables are a mixture of fixed (regions of study) and random (season: winter and spring) factors. Residual plots were checked for model assumptions. We started with the most complex model taking into account the double interactions with the 'region' factor. The residual maximum likelihood (REML) method was used to find the fittest and most parsimonious model (see Venables and Ripley 2002). All models were estimated by the LME function in the lme library written in the R language (Pinheiro and Bates 2000).

Results

Environmental characterisation

A comparison of centroids from the PCA ordination showed no significant differences between Mainland-winter and Archipelago-winter groups ($P > 0.05$) or between Mainland-spring and Archipelago-spring groups ($P > 0.05$) in the environmental characterisation of the coastal wetlands (Fig. 2; Table 1). However, significant differences were found between seasons within the same region (e.g. Archipelago-winter v. Archipelago-spring), reinforcing the importance of seasonality in Mediterranean areas.

Composition of crustacean assemblages and environmental variables

In all, 93 crustacean species were recorded in the Archipelago ($n = 58$) and Mainland ($n = 67$) systems (see Table S1, available as Supplementary Material to this paper). Furthermore, 27 crustacean species were found exclusively in the Archipelago, whereas 35 were found in the Mainland (Table S1). Ostracods and copepods had the highest occurrence among all the crustaceans; specifically, copepods were present in every sample from the Mainland (Table 2). Malacostracans showed a high occurrence, but only in the Archipelago, and cladocerans had the lowest occurrence in both regions (Table 2). The percentage of common species was always higher (Cladocera and Copepoda) or slightly higher (Ostracoda) in the Archipelago than in the Mainland, except for Malacostraca (Table 2).

SIMPER analysis showed a high dissimilarity (>80%) between the regions (Archipelago v. Mainland) for the crustacean composition (Table 3). Furthermore, a low similarity within Mainland (~20%) and Archipelago (~25%) should be noted because it indicates a high variability within regions. Taxa that best characterised the crustacean assemblages of the Archipelago were the ostracod *Cyprideis torosa* (25.91%) and the two malacostracans *Gammarus aequicauda* and *Lekanesphaera hookeri* (22.14% and 19.63% respectively; Table 3). The crustacean assemblages of the Mainland were characterised by the copepod *Acanthocyclops* gr. *robustus* (32.99%) and the malacostracan *Gammarus aequicauda* (25.55%). Moreover, the Mainland included characteristic crustacean species missing from the Archipelago (two copepods (*Diacyclops bicuspidatus* and *Eurytemora velox*), one ostracod (*Cypridopsis vidua*) and one cladoceran (*Daphnia pulicaria*); Table 3).

In relation to the explanatory variables that best fit the species variability in the crustacean assemblages, the factor 'region' explained the highest percentage (24.66%) of the crustacean variability for the combined CCA (i.e. Archipelago and Mainland together; Table 4). Conversely, analysis for each region separately (i.e. Archipelago CCA and Mainland CCA) showed that ~50% of the variability in the crustacean assemblages was explained by the same variables in both regions (i.e. electric conductivity, size and DIN; Table 4).

Crustacean diversity and environmental variables

Significant differences were observed for the α diversity. Specifically, the mean richness of Cladocera and Copepoda was significantly higher in the Mainland than in the Archipelago ($H = 5.98$ (d.f. = 1, $P = 0.0145$) and $H = 44.98$ (d.f. = 1, $P < 0.001$) respectively; Fig. 3a). Conversely, the mean richness of Malacostraca and Ostracoda was significantly higher in the Archipelago than in the Mainland ($F_{1,126} = 10.6$ ($P = 0.001$) and $H = 8.67$ (d.f. = 1, $P = 0.0032$) respectively; Fig. 3a). β Diversity did not differ between the Archipelago and Mainland for all groups of crustaceans (Fig. 3b). It was observed that β diversity was due to the replacement of species (β_{SIM}) rather than species loss (β_{NES}) in both regions. Regarding γ diversity, there was no significant difference in the total estimated species richness between the Archipelago and the Mainland (Fig. 3c).

The relationships between crustacean species richness and environmental variables were not significantly different between regions, except for Malacostraca and Cladocera, for which the interaction with the factor 'region' was significant (Fig. 4; Tables S2, S3). The relationship between Malacostraca richness and electrical conductivity was positive in both regions, albeit almost ninefold stronger in the Archipelago than in the Mainland sites (Fig. 4a). There was a significant positive relationship between nutrient content (phosphate and DIN) and Malacostraca richness in the Archipelago, whereas in the Mainland this trend was reversed (Fig.

4b, c). The relationship between Cladocera richness and DIN was region dependent, but the trend was similar in both regions (i.e. negative, although markedly stronger in the Archipelago than in the Mainland; Fig. 4d).

Discussion

Recognising the characteristic features of different islands types (e.g. Darwinian *v.* fragment islands, according to Gillespie and Roderick 2002) is important for understanding emerging patterns, in particular speciation, biodiversity and conservation (Whittaker and Fernández-Palacios 2007; Watson 2009). Although studies on Darwinian islands are widely reported in the literature (Sauer 1969; Cowie and Holland 2006; Whittaker et al. 2008; Caujapé-Castells et al. 2010), fragment islands have received less attention. This may be related to the anticipated similarity expected between fragment islands and the mainland landmass from where they originate, being less appealing for the researchers to investigate. Because we found significant differences in the species composition of the crustacean assemblages, we are not able to confirm the null hypothesis that assumed the similarity of the crustacean assemblages between the Archipelago (Balearic Islands) and Mainland (Iberian Peninsula). Such a difference was supported by the results of the combined CCA, which determined the regional effect as the best predictor of species variability. Considering the type of variables and analyses performed in the present study, we did not have enough information to single out the causes of these differences. Nevertheless, we can think of two possible causes, the first being the effect of stochastic ecological drift and evolutionary processes at local (e.g. community level) or regional (e.g. meta-community level) scales (Hubbell 2001). The current isolation of the Archipelago began at the end of the Messinian salinity crisis, 5.3 Myr ago (Clauzon et al. 1996; Krijgsman et al. 1999), although the Archipelago suffered another regrouping during the Quaternary glaciations (Melendez-Hevia 2004). This is a sufficient time gap, biologically and geologically, so that the composition of the crustacean assemblages could differ from their source because of those processes related to the evolution and ecological drift (Lomolino et al. 2010). The second possible cause is the proximity of the coastal wetlands from the Archipelago to several land masses other than the Mainland site (e.g. by recruitment or dispersion; Barnes 1995). For example, in the present study, the Archipelago crustacean assemblage had 27 species that were not shared with the Mainland. This number of 'exclusive species' could be attributed to the potential influences of other regions and mainland landmasses. In fact, crustacean fauna of African origin have been found in temporary ponds in the Balearic Islands (Jaume 1989; Zamora et al. 2005).

Beyond the regional effect, most of the variability of crustacean assemblages in both regions was explained by the same environmental variables, including electrical conductivity, size and DIN. These results support other studies that found that these three variables were related to the

turnover rate of the water body (Guelorget and Perthuisot 1983; De Kroon et al. 1985). In particular, wetland size and electrical conductivity have been identified as the main drivers of the fauna in coastal wetlands throughout the world (Joyce et al. 2005; Nielsen et al. 2007) and especially the Mediterranean area (Quintana et al. 1998; Anton-Pardo and Armengol 2012). Therefore, despite the dissimilarity in the composition of the crustacean assemblages between the Archipelago and the Mainland, we can assert that their responses to environmental variables were comparable.

A marked dissimilarity in crustacean assemblages (~80%) between the Archipelago and Mainland was observed. Furthermore, a high dissimilarity was detected within regions, which reflects the variability among coastal wetlands within the Archipelago and Mainland. These results are in accordance with studies conducted in transitional waters of the Mediterranean and Black seas (Barbone and Basset 2010). These authors found that there was a patchy distribution of macroinvertebrate taxa and a low average similarity in taxa composition (~10%) among lagoons within the same region. We observed a similar pattern in both the Archipelago and Mainland consisting of the dominance of the assemblages by very few species: three species dominated in the Archipelago (*Cyprideis torosa*, *Gammarus aequicauda* and *Lekanesphaera hookeri*) and two species dominated in the Mainland (*Acanthocyclops gr. robustus* and *Gammarus aequicauda*). This pattern is typically expected in highly restrictive or ‘filtered’ environments. Thus, harsh conditions can act as a ‘filter’ for the community structure, causing the reduction of the community to a few species (Poff 1997; Strange and Foin 1999). Similar conclusions have been made for other Mediterranean coastal ecosystems (e.g. Barbone et al. 2007; Barbone and Basset 2010). Certainly, the Mediterranean coastal wetlands can be considered highly ‘filtered’ ecosystems, where the ‘filter’ is partly imposed by harsh and changeable environmental conditions (e.g. abrupt changes between seasons, variations in water level and salinity) and variable physical factors (e.g. storms, wind, flows) of this ecoregion (Statzner et al. 2001; Elliott and Quintino 2007). Therefore, regardless of the mainland or fragment island region, a similar pattern of crustacean community structure was observed, in accordance with our null hypothesis.

The instability and harshness of the environmental conditions of coastal wetlands can also constrain crustacean diversity in both the Mainland and Archipelago. The second proposed partial null hypothesis of equal diversity between regions was applicable to β and γ diversity. The comparable values of the among-systems (i.e. β) and total (i.e. γ) diversity between the Archipelago and the Mainland can be explained by a high temporal or spatial (among wetlands) turnover of species (Chalcraft et al. 2004; Anderson et al. 2011). This is supported by the high taxa occurrence, elevated dissimilarity within the wetlands and high rate of replacement of the crustacean species observed in both regions. However, within the equilibrium theory of island

biogeography, it would be expected that the turnover rate would be lower in the islands than on the continent (MacArthur and Wilson 1967; Walter 2004). However, our results support the hypothesis of similarity between fragment islands and mainland. The crustacean assemblage of the Archipelago can be supplied by the migration or colonisation from mainland landmasses, as well as migration among islands, favouring the maintenance of levels of diversity. Conversely, the Balearic Archipelago is old enough to have probably reached a fairly stable total biodiversity level. However, this scenario is different from what is happening on a smaller scale, because the α diversity values differed significantly between regions. It is expected that in fragment islands, over time and with isolation, the number of species (α diversity) on islands created by fragmentation will, if anything, decline (Gillespie and Roderick 2002). Based on this premise, it could be expected that the Mainland, being the principal source, would exhibit higher α diversity values than the Archipelago. However, this expectation was not always met, because the α diversity values were higher in the Archipelago for two taxonomic groups (Malacostraca and Ostracoda). As argued previously for the crustacean assemblage, various causes could be responsible for differences in the diversity values for those crustacean groups between regions, including environmental conditions, biological processes and biogeographical events. Furthermore, we considered crustaceans with a high component of microcrustaceans (cladocerans, ostracods, copepods), characterised by small body size, high fecundity and large geographic ranges. In previous studies, crustacean species meeting these traits were less prone to extinction following fragmentation (e.g. Cardillo 2003; Cooper et al. 2008), which could contribute to the maintenance of high levels of α diversity also in the islands. Although, we are not able to confirm the specific causes of the differences in biodiversity between the Archipelago and Mainland, it is of note that fragment and scarcely isolated islands may hold similar or even higher values of local diversity than the Mainland.

Finally, the third proposed null hypothesis regarding the relationships between environmental variables and species richness was partially met. Thus, the relationships were similar across regions, although not for all cases (i.e. Malacostraca and Cladocera responded differently to environmental variables). The similar environmental relationships observed in the present study for copepods, cladocerans and ostracods have also been found in other studies, such as a reduction of copepod diversity with an increase in water temperature (e.g. Frisch and Green 2007), decrease in diversity (cladocerans, copepods) with salinity (Boix et al. 2008; Brucet et al. 2009) and an increase of ostracod diversity with Chl-*a* (Allen and Dodson 2011). Malacostraca and Cladocera showed different patterns between the two regions. Different factors could be responsible for those differences. For example, a higher eutrophication range (nutrients and Chl-*a*) in the Mainland and a higher sea connectivity of the coastal wetlands in the Archipelago may favour the α diversity of typical littoral taxa such as malacostracans, as well as their positive

relationships with nutrients and electrical conductivity in the Archipelago. This is a hypothesis that needs to be tested experimentally. However, high eutrophication and sea connectivity would not be favourable environmental conditions for typical freshwater crustaceans, such as cladocerans, in the Archipelago.

Conclusion

The Balearic Archipelago, as an example of fragment islands, met some of the proposed null hypotheses based on the expected similarity to the Mainland. These results are consistent with the fact that fragment islands are half-way between the mainland and oceanic islands (which are expected to be the most dissimilar to the mainland) and so they have characteristics of both (Novosolov and Meiri 2013). However, it is remarkable that despite the short geographic distance that separates the Balearic Archipelago from the closest mainland, these islands are the most isolated islands in the Mediterranean (Bover et al. 2008). Indeed, the Balearic Islands have been described by some as ‘oceanic-like islands’ (Alcover *et al.* 1998) because of their isolation and their ancient fragmentation from the mainland. Although our data showed significant differences in species richness and assemblage structure between the Archipelago and Mainland, similar environmental patterns could be identified regardless of the regional effect. Thus, we should consider that the similarity between the fragment island and mainland may be somehow cofounded by the effect of a ‘filter’ exerted by the ecosystem itself (i.e. coastal wetlands). The fact that fragment islands can support a diverse crustacean fauna comparable to the mainland, or even higher in some cases, provides evidence that islands in general contribute a more significant portion of global biodiversity than is commonly recognised (Walter 2004). Therefore, fragment islands are ecosystems of substantial conservation interest, although they have been less ecologically considered than oceanic islands. Fragment islands, with stable population dynamics, can be considered important faunal reservoirs that can feed back to their original sources.

Supplementary material

Supplementary material includes a species list identified in the present study for Archipelago and Mainland (absence and presence) and two tables containing a summary of the LME results that supports Figure 4. The Supplementary material is available from the journal online (see http://www.publish.csiro.au/?act=view_file&file_id=MF15457_AC.pdf).

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Table 1. Environmental variables from the studied coastal wetlands

The mean \pm s.d. are shown for each season and for each region of study. DIN, dissolved inorganic nitrogen

Environmental variables	Archipelago		Mainland	
	Winter	Spring	Winter	Spring
Size (ha)	251 \pm 240		29 \pm 16	
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	5.60 \pm 1.40	9.16 \pm 1.94	9.64 \pm 2.41	18.65 \pm 3.28
pH	8.17 \pm 0.09	8.22 \pm 0.09	8.04 \pm 0.11	8.05 \pm 0.12
Water temperature ($^{\circ}\text{C}$)	13.79 \pm 0.88	24.34 \pm 0.65	11.41 \pm 0.41	25.29 \pm 1.08
Conductivity (mS cm^{-1})	7.41 \pm 1.03	18.69 \pm 3.06	11.19 \pm 2.34	12.75 \pm 2.63
Dissolved oxygen (%)	95.73 \pm 4.42	73.23 \pm 5.72	81.45 \pm 4.44	91.66 \pm 12.05
Phosphate (μM)	3.92 \pm 0.56	1.93 \pm 0.81	3.11 \pm 1.67	4.37 \pm 1.93
DIN (μM)	123.16 \pm 32.48	30.58 \pm 13.87	136.94 \pm 42.75	148.67 \pm 53.35

Table 2. Descriptive parameters of the crustacean assemblage in the coastal wetlands from the Archipelago and the Mainland

Occurrence is given as the percentage of samples in which the crustaceans were found

	Cumulative species richness		Common species (%)		Occurrence (%)	
	Archipelago	Mainland	Archipelago	Mainland	Archipelago	Mainland
Cladocera	13	18	53.80	38.90	40.60	62.50
Ostracoda	12	13	58.30	53.80	90.60	81.30
Copepoda	17	24	76.50	54.20	81.30	100.00
Malacostraca	16	12	31.30	41.70	93.80	62.50

Table 3. Summary of similarity percentage analysis (SIMPER)

The contribution to the average resemblances within sample groups (Contrib%) and the cumulative percentage (Cum.%) of characteristic species are given. The average dissimilarity between groups (Mainland v. Archipelago) was 85.29%. Asterisks indicate exclusive species (i.e. those that only appear in one region of the study). CLA, Cladocera; OST, Ostracoda; COP, Copepoda; MAL, Malacostraca.

Species	Contrib%	Cum.%
Archipelago (average similarity: 24.25%)		
<i>Cyprideis torosa</i> (OST)	25.91	25.91
<i>Gammarus aequicauda</i> (MAL)	22.14	48.04
<i>Lekanesphaera hookeri</i> (MAL)	19.63	67.67
<i>Loxoconcha elliptica</i> (OST)	5.55	73.22
<i>Heterocypris salina</i> (OST)	3.36	76.58
<i>Palaemonetes varians</i> (MAL)	2.59	79.17
<i>Simocephalus vetulus</i> (CLA)	2.57	81.73
<i>Sarscypridopsis aculeata</i> (OST)	2.52	84.25
<i>Calanipeda aquaedulcis</i> (COP)	2.29	86.54
<i>Daphnia magna</i> (CLA)	1.66	88.2
<i>Megacyclops viridis</i> (COP)	1.39	89.59
<i>Corophium acherusicum</i> (MAL)	1.08	90.67
Mainland (average similarity: 9.50%)		
<i>Acanthocyclops</i> gr. <i>robustus</i> (COP)	32.99	32.99
<i>Gammarus aequicauda</i> (MAL)	25.55	25.55
<i>Chydorus sphaericus</i> (CLA)	7.87	42.78
<i>Calanipeda aquaedulcis</i> (COP)	6.9	49.68
<i>Diacyclops bicuspidatus</i> (COP)*	5.84	55.52
<i>Eucyclops serrulatus</i> (COP)	4.79	60.31
<i>Heterocypris salina</i> (OST)	4.25	64.56
<i>Lekanesphaera hookeri</i> (MAL)	4.01	68.57
<i>Macrocyclus albidus</i> (COP)	3.05	71.62
<i>Cyprideis torosa</i> (OST)	2.75	74.37
<i>Cypridopsis vidua</i> (OST)*	2.48	76.85
<i>Simocephalus vetulus</i> (CLA)	2.27	79.12
<i>Eucypris virens</i> (OST)	2.18	81.3
<i>Tropocyclops prasinus</i> (COP)	1.97	83.27
<i>Daphnia magna</i> (CLA)	1.75	85.03
<i>Daphnia pulicaria</i> (CLA)*	1.6	86.62
<i>Eurytemora velox</i> (COP)*	1.35	87.98
<i>Pleuroxus adundus</i> (CLA)	1.28	89.25
<i>Loxoconcha elliptica</i> (OST)	1.27	90.53

Table 4. Results from canonical correspondence analyses (CCAs): combined (Archipelago and Mainland) and for each region separately

The order of the significant explanatory variables that had the best fit for species variability are indicated with numbers from 1 to 6. Variance explained by the first two axes is also shown. % λ , conditional effect expressed as percentage. DIN, dissolved inorganic nitrogen; Chl-*a*, chlorophyll *a*

Explanatory variables	Combined CCA		Archipelago CCA		Mainland CCA	
	Best fit	% λ	Best fit	% λ	Best fit	% λ
Region	1	24.66				
Conductivity	2	19.73	1	24.58	1	20.08
Temperature	3	10.31	2	16.20		
Size	4	9.42	4	11.17	2	16.47
DIN	5	8.52	3	13.97	3	15.26
Chl- <i>a</i>	6	8.07			4	14.06
Phosphate					5	11.24
Variance explained (%)						
Axis 1		4.3		5.6		5.0
Axis 2		7.1		8.9		9.7

Fig. 1. Location of the coastal wetlands sampled (black dots) on the Catalonian mainland ('Mainland') and on the Balearic Islands ('Archipelago'): 1, Minorca; 2, Majorca; 3, Ibiza; 4, Formentera.

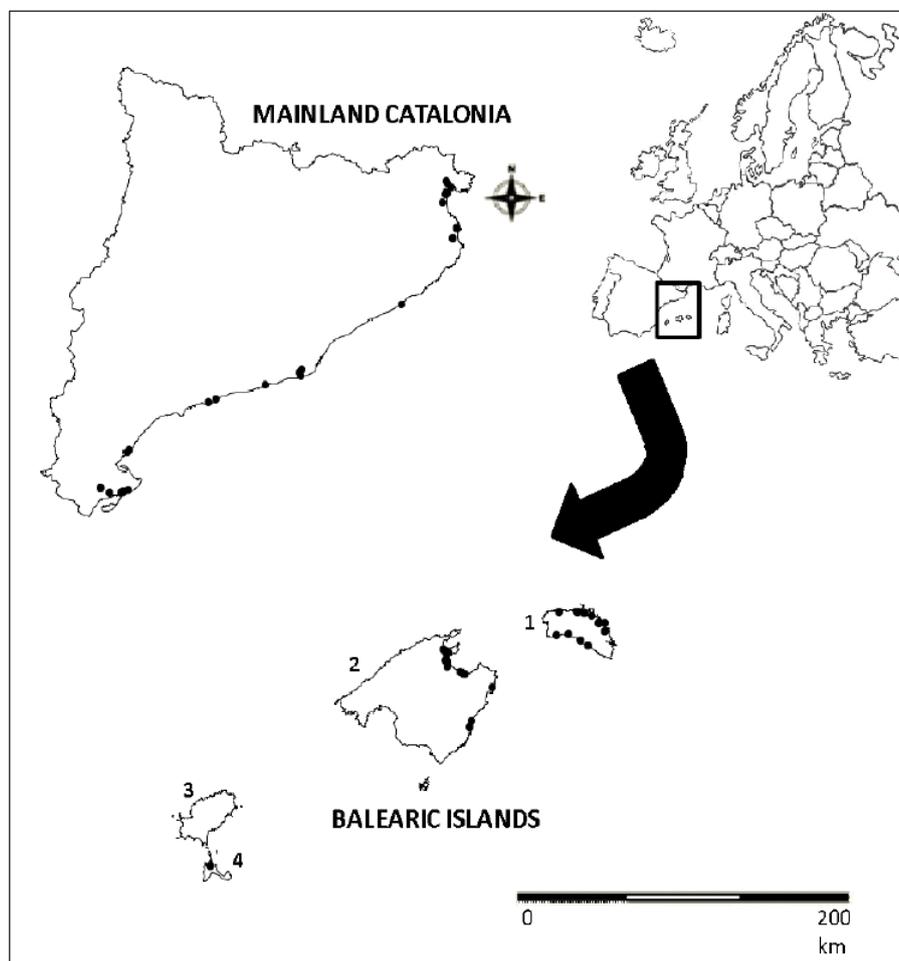


Fig. 2. Plot showing the centroids for the Mainland (MAIN) and the Archipelago (ARCH) regions in spring and winter taking into account all the environmental variables (see Table 1).

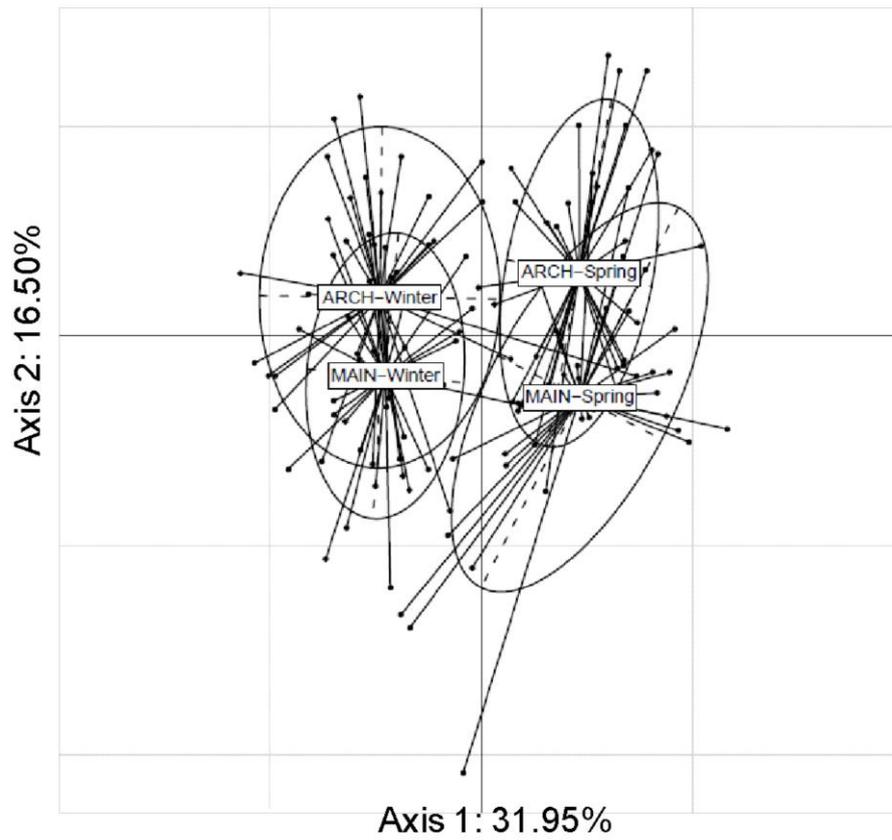


Fig. 3. Representation of the three diversity levels considered: (a) α diversity as mean species richness (mean \pm s.d.), (b) β diversity as Simpson-based multiple-site dissimilarity (β_{SIM}) and nestedness-resultant multiple-site dissimilarity (β_{NES}) and (c) γ diversity as total species richness estimated using Chao2. Data are the mean \pm 95% confidence intervals. *, $P < 0.01$; **, $P < 0.001$. CLA, Cladocera; OST, Ostracoda; COP, Copepoda; MAL, Malacostraca.

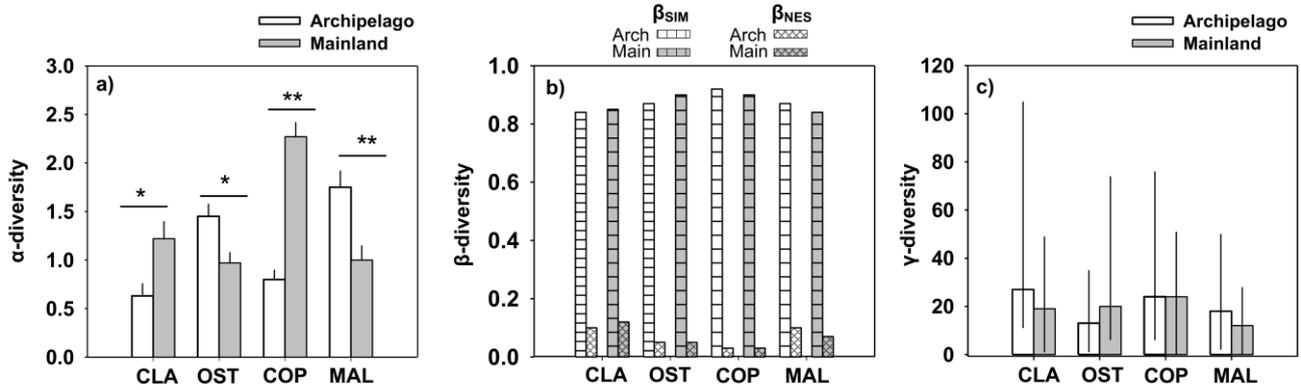
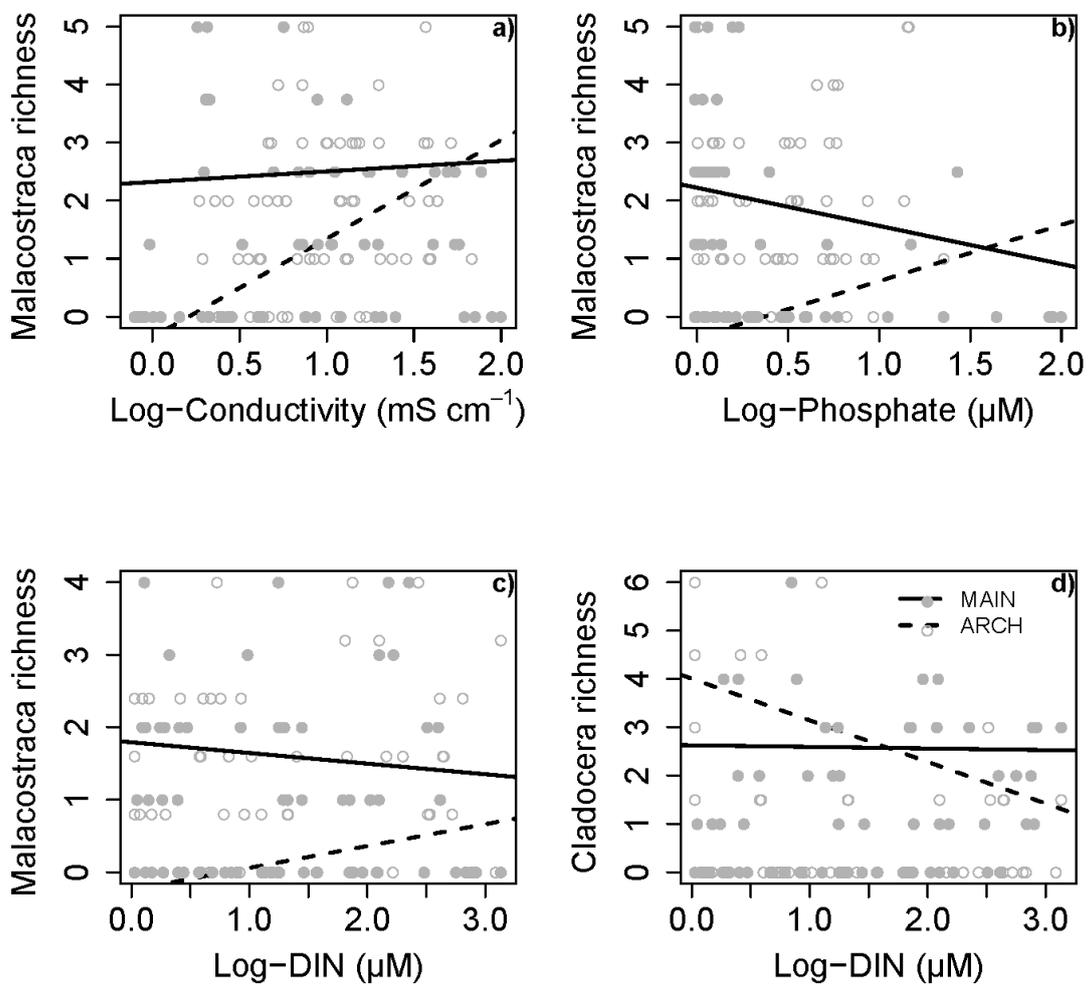


Fig. 4. Biplots showing the results of the linear mixed-effects models for those cases where a significant interaction with the regional factor (Archipelago (ARCH) or Mainland (MAIN)) was detected. DIN, dissolved inorganic nitrogen.



Supplementary material

Table S1. List of crustaceans species identified in the Archipelago and Mainland

+ indicates presence; – indicates absence. CLA, Cladocera; OST, Ostracoda; COP, Copepoda; CAL, Calanoida; CYC, Cyclopoida; HARP, Harpacticoida; MAL, Malacostraca; MYS, Mysidacea; AMPH, Amphipoda; ISO, Isopoda; TAN, Tanaidacea; DEC, Decapoda

Species	Taxonomic Group	Archipelago	Mainland
<i>Alona guttata</i> Sars, 1862	CLA	+	–
<i>Bosmina longirostris</i> (O.F. Müller, 1776)	CLA	–	+
<i>Camptocercus rectirostris</i> Schoedler, 1862	CLA	–	+
<i>Ceriodaphnia laticaudata</i> P.E. Müller, 1867	CLA	–	+
<i>Ceriodaphnia reticulata</i> (Jurine, 1820)	CLA	–	+
<i>Chydorus sphaericus</i> (O.F. Müller, 1785)	CLA	+	+
<i>Coronatella rectangula</i> (Sars, 1861)	CLA	+	+
<i>Daphnia curvirostris</i> Eylman, 1887	CLA	+	–
<i>Daphnia magna</i> Straus, 1820	CLA	+	+
<i>Daphnia pulicaria</i> Forbes, 1893	CLA	+	+
<i>Leydigia acanthocercoides</i> (Fischer, 1854)	CLA	+	–
<i>Leydigia leydigii</i> (Schödler, 1862)	CLA	–	+
<i>Megafenestra aurita</i> (Fischer, 1849)	CLA	–	+
<i>Moina micrura</i> Kurz, 1874	CLA	–	+
<i>Ovalona</i> cf. <i>anastasia</i> (Frenzel and Alonso 1988)	CLA	+	–
<i>Oxyurella tenuicaudis</i> (Sars, 1862)	CLA	–	+
<i>Pleuroxus aduncus</i> (Jurine, 1820)	CLA	+	+
<i>Pleuroxus denticulatus</i> Birge, 1879	CLA	–	+
<i>Pleuroxus laevis</i> Sars, 182	CLA	–	+
<i>Scapholeberis mucronata</i> (O.F. Müller, 1776)	CLA	–	+
<i>Scapholeberis rammneri</i> Dumont and Pensaert, 1983	CLA	+	–
<i>Simocephalus exspinosus</i> (DeGeer, 1778)	CLA	+	+
<i>Simocephalus vetulus</i> (O.F. Müller, 1776)	CLA	+	+
<i>Tretocephala ambigua</i> (Lilljeborg, 1900)	CLA	+	–
<i>Bradleystrandesia reticulata</i> (Zaddach, 1844)	OST	–	+
<i>Candona angulata</i> G. W. Müller, 1900	OST	+	–
<i>Candonocypris</i> sp. Sars, 1894	OST	–	+
<i>Cyprideis torosa</i> (Jones, 1850)	OST	+	+
<i>Cypridopsis hartwigi</i> G. W. Müller	OST	+	–
<i>Cypridopsis vidua</i> (O. F. Müller, 1776)	OST	–	+
<i>Cypris bispinosa</i> Lucas, 1849	OST	+	–
<i>Cypris subglobosa</i> Sowerby, 1840	OST	–	+
<i>Eucypris virens</i> (Jurine, 1820)	OST	+	+
<i>Herpetocypris brevicaudata</i> Kaufmann, 1900	OST	–	+
<i>Herpetocypris chevreuxi</i> (Sars, 1896)	OST	+	–
<i>Heterocypris incongruens</i> (Ramdohr, 1808)	OST	+	+

<i>Heterocypris salina</i> (Brady, 1868)	OST	+	+
<i>Ilyocypris getica</i> Masi, 1905	OST	+	-
<i>Ilyocypris gibba</i> (Ramdohr, 1808)	OST	-	+
<i>Loxococoncha elliptica</i> Brady, 1868	OST	+	+
<i>Plesiocypridopsis newtoni</i> (Brady & Robertson, 1870)	OST	+	+
<i>Sarscypridopsis aculeata</i> (Costa, 1847)	OST	+	+
<i>Arctodiaptomus salinus</i> (Daday 1885)	COP (CAL)	+	-
<i>Arctodiaptomus wierzejski</i> (Richard, 1888)	COP (CAL)	+	-
<i>Calanipeda aquaedulcis</i> Kritschagin, 1873	COP (CAL)	+	+
<i>Eurytemora velox</i> (Lilljeborg, 1853)	COP (CAL)	-	+
<i>Mixodiaptomus kupelwieseri</i> (Brehm, 1907)	COP (CAL)	-	+
<i>Acanthocyclops</i> gr. <i>robustus</i> (Sars, 1863)	COP (CYC)	+	+
<i>Cyclops</i> sp. O. F. Müller, 1776	COP (CYC)	-	+
<i>Diacyclops bicuspidatus</i> (Claus, 1857)	COP (CYC)	-	+
<i>Diacyclops bisetosus</i> (Rehberg, 1880)	COP (CYC)	-	+
<i>Ectocyclops phaleratus</i> (Koch, 1838)	COP (CYC)	-	+
<i>Eucyclops macruroides</i> (Lilljeborg, 1901)	COP (CYC)	-	+
<i>Eucyclops serrulatus</i> (Fischer, 1851)	COP (CYC)	+	+
<i>Halicyclops rotundipes</i> Kiefer, 1935	COP (CYC)	+	+
<i>Macrocyclops albidus</i> (Jurine, 1820)	COP (CYC)	+	+
<i>Megacyclops viridis</i> (Jurine, 1820)	COP (CYC)	+	+
<i>Microcyclops rubellus</i> (Lilljeborg, 1901)	COP (CYC)	+	+
<i>Paracyclops fimbriatus</i> (Fischer, 1853)	COP (CYC)	-	+
<i>Thermocyclops dybowskii</i> (Landé, 1890)	COP (CYC)	+	+
<i>Tropocyclops prasinus</i> (Fischer, 1860)	COP (CYC)	+	+
<i>Canthocamptus staphylinus</i> (Jurine, 1820)	COP (HAR)	+	+
<i>Canuella perplexa</i> T. and A. Scott, 1893	COP (HAR)	+	+
<i>Cletocamptus confluens</i> (Schmeil, 1894)	COP (HAR)	+	+
<i>Cletocamptus retrogressus</i> Schmankevitsch, 1875	COP (HAR)	+	-
<i>Eudactylopus</i> sp. cf. Scott, 1909	COP (HAR)	+	-
<i>Harpacticus littoralis</i> Sars, 1910	COP (HAR)	-	+
<i>Nitocra lacustris</i> (Shmankevich, 1875)	COP (HAR)	-	+
<i>Schizopera</i> sp. (cf. <i>compacta</i>) Lint, 1922	COP (HAR)	-	+
<i>Tisbe longicornis</i> (T. and A. Scott., 1895)	COP (HAR)	+	+
<i>Atyaephyra desmarestii</i> (Millet, 1831)	MAL (DEC)	-	+
<i>Corophium acherusicum</i> Costa, 1857	MAL (AMP)	+	-
<i>Corophium insidiosum</i> Crawford, 1937	MAL (AMP)	+	-
<i>Corophium orientale</i> Schellenberg, 1928	MAL (AMP)	+	+
<i>Corophium sextonae</i> Hurley, 1954	MAL (AMP)	+	-
<i>Cyathura carinata</i> (Kroyer, 1847)	MAL (ISO)	+	-
<i>Echinogammarus pacaudi</i> (Hubault and Ruffo, 1956)	MAL (AMP)	-	+
<i>Echinogammarus stocki</i> Karaman, 1969	MAL (AMP)	+	-
<i>Gammarus aequicauda</i> (Martyinov, 1931)	MAL (AMP)	+	+
<i>Gammarus insensibilis</i> Stock, 1966	MAL (AMP)	+	-

<i>Heterotanais oerstedii</i> (Kroyer, 1842)	MAL (TAN)	–	+
<i>Lekanesphaera hookeri</i> (Leach, 1814)	MAL (ISO)	+	+
<i>Leptocheirus pilosus</i> Zaddach, 1844	MAL (AMP)	–	+
<i>Mesopodopsis slabberi</i> (Van Beneden, 1861)	MAL (MYS)	–	+
<i>Microdeutopus</i> sp. Costa, 1853	MAL (AMP)	+	–
<i>Orchestia gammarellus</i> (Pallas, 1766)	MAL (AMP)	+	–
<i>Orchestia platensis</i> Hayat, 1998	MAL (AMP)	+	–
<i>Palaemon elegans</i> Rathke, 1837	MAL (DEC)	+	–
<i>Palaemon longirostris</i> Milne-Edwards, 1837	MAL (DEC)	–	+
<i>Palaemonetes varians</i> (Leach, 1814)	MAL (DEC)	+	–
<i>Palaemonetes zariquieyi</i> Sollaud, 1939	MAL (DEC)	–	+
<i>Proasellus coxalis</i> (Dollfus, 1892)	MAL (ISO)	+	+
<i>Procambarus clarkii</i> (Girard, 1852)	MAL (DEC)	+	+
Total species	93	58	67
Exclusive species		26	35

Table S2. Summary of the LME results for the variable species richness

The significance between regions was assessed using the conditional *F*-test of the intercept values (see Table S3), while the slopes inform about the relationship between the dependent variable (species richness) and the independent variables (continuous environmental parameters). Slope values of independent variables retained in each mixed effects model are shown for each region; when non-significant differences were detected for the slopes of each region (i.e., the same slope for both regions) then ‘overall slope’ is shown. The *t*-test obtained from each mixed effects model, indicating the significance of the slopes, is shown. The regional effect (‘Region’, i.e. Archipelago *v.* Mainland) is highlighted in bold. Cond, conductivity; Pho, phosphate; DIN, dissolved inorganic nitrogen; Chl-*a*, chlorophyll-*a*

Species richness	Variable	Slopes			<i>t</i> -Student	<i>P</i> -value
		Archipelago	Mainland	Overall		
Cladocera d.f. = 121	Phosphate			0.74	3.24	0.002
	Conductivity			-1.81	-7.93	0.000
	Region × DIN	-0.66	-0.03		3.31	0.001
Ostracoda d.f. = 123	Size			0.29	4.12	0.000
	Chl- <i>a</i>			0.41	2.17	0.032
	Region					
Copepoda d.f. = 123	Conductivity			-0.58	-2.75	0.007
	Temperature			-1.18	-2.27	0.025
	Region					
Malacostraca d.f. = 118	Chl- <i>a</i>			-0.59	-2.15	0.034
	Region × DIN	0.43	-0.15		-2.18	0.032
	Region × Pho	0.97	-0.63		-2.56	0.012
	Region × Cond	1.70	0.20		-2.51	0.014

Table S3. Complementary table to Table S2, where intercept values are shown
P-values < 0.05 show significant differences in the intercept values of Mainland and Archipelago, i.e. significant differences of species richness between both regions

Species richness	Intercept		<i>F</i>	d.f.1	d.f.2	<i>P</i> -value
	Archipelago	Mainland				
Cladocera	2.75	2.63	0.19	1	121	0.667
Ostracoda	-0.03	-0.48	6.8	1	123	0.010
Copepoda	2.86	4.25	62.51	1	123	<0.0001
Malacostraca	-0.36	1.79	6.5	1	118	0.012