The shallow marine ostracod communities of the Azores (Mid-North Atlantic): taphonomy and palaeoecology

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This is the first palaeoecological and taphonomical study of the Recent marine ostracods from the Azores. The aims of this work were to address the following questions: i) to establish the typical ostracod assemblages from the shallow waters of the Azores; ii) to determine the bathymetric ranges for each ostracod species; iii) to investigate the time span and depth in which significant transport occurs; iv) to quantify the amount of out of habitat transport between sandy beaches, tide pools and the sublittoral; v) to determine distinctive taphonomic features that can be used to recognize the amount of temporal resolution in ostracod assemblages. Fifteen species were recovered, representing 8 families and 12 genera (*Loxoconcha*, *Neonesidea*, *Xestoleberis*, *Aurila*, *Urocythereis*, *Heterocythereis*, *Carinocythereis*, *Callistocythere*, *Leptocythere*, *Semicytherura*, *Lanceostoma* and *Cylindroleberis*). The living assemblages are dominated by specimens of the Loxoconchidae, Xestoleberidae and Hemicytheridae, whereas the dead assemblages are dominated by specimens of the Loxoconchidae, Hemicytheridae, Bairdiidae, Xestoleberidae and Trachyleberidae. The shift from life-dominated assemblages in the shallower depths to death-dominated assemblages at greater depths is a consequence of significant transport downwards. The abundance of ostracods is higher in the first 10-20 m depth, especially in fine to medium sandy substrates. Considerable differences among islands were supported by the Bayesian model, as a consequence of the physical and hydrodynamic factors that differently affect each of the Azorean islands. Large-scale (sea-surface currents, Holocene relative sea-level, storms) and small-scale processes are responsible for shaping the Azorean Recent marine ostracod communities. No living specimens were found in the samples collected at the beach faces, thus reinforcing former interpretations of one of the authors (S. Ávila) that advocate that at a global scale, sandy beaches in oceanic islands located at temperate latitudes are almost or even completely devoid of life due to historical reasons related with the sea level changes.

KEYWORDS | Ostracods. Recent. Oceanic islands. Taphonomic processes. Palaeoecology. Bayesian model.

INTRODUCTION

Ostracods are small crustaceans characterized by a bivalved carapace that totally encloses the body and appendages. Their bodies show reduced trunk segmentation and 5-8 pairs of limbs, which protrude from the gaping valves for locomotion. They are typically 0.5-2.0mm long in the adult stage (Horne *et al.*, 2002). Ostracods are one of the most diverse groups of living crustaceans, with over 20,000 estimated living species, of which, approximately 8,000 have been described (Morin and Cohen, 1991). Ostracods are particularly sensitive to environmental changes and are, thus, very useful in palaeoenvironmental interpretations (Whatley, 1983; Cronin *et al.*, 2002; Holmes and Chivas, 2002).

Ostracoda fauna differ in the number of families and species around the world, usually, with more species in continental margins than around insular habitats. Owing to their high level of isolation, far-away oceanic islands are a perfect place for the study of evolutionary processes and patterns of dispersal, colonization and speciation (*e.g.* Schornikov and Keyser, 2004; Wilson, 2007; Ávila *et al.*, 2012). As truly volcanic oceanic islands, the Azores have been the subject of several studies with a biogeographical perspective: molluscs (Ávila and Azevedo, 1997; Ávila, 2000; Ávila *et al.*, 1998, 2000, 2004, 2009a, 2009b; Janssen *et al.*, 2008; Ávila and Sigwart, 2013), sponges (Xavier and van Soest, 2012), algae (Tittley and Neto, 1995). As there are only few published studies on the marine Ostracoda of the Azores (Poulsen, 1972; Angel, 1973; Meireles *et al.*, 2012), this is an additional contribution to help deciphering the biogeographic puzzle of this region of the Atlantic. Moreover, this study provides important elements for untangling the relationships between different populations and how the environmental stress can determinate the biocenosis (living populations), thanatocoenosis (dead-assemblages, mostly made of disarticulated valves of ostracods, which may contain autochthonous and/or allochthonous elements, depending on the amount of transport) and taphocoenosis (fossil assemblages containing *in situ* and/or allochthonous fossil elements).

In this work we focused on the Recent shallow marine ostracod biodiversity and abundance, as well as on the taxon geographical and bathymetrical distribution around the archipelago of the Azores, relating the different assemblages with physical (geographical location, degree of exposure to the waves, depth, tidal range), ecological (habitat type, biodiversity) and sedimentological factors that may affect the ostracod communities.

As comparison of invertebrate abundance from recent and old strata depend on the sediment age and history, its granulometry, and the method and type of sample upon which these counts rely on (Kornicker, 1959), a comprehensive taphonomic, ecological, and sedimentological characterization of the study area was done in order to evaluate the influence of the environment and the effect of the depositional processes in shallow-water areas. Specifically, we addressed the following questions: i) is there a typical ostracod assemblage from the shallow marine depths of the Azores?; ii) which is the bathymetric range for each ostracod species?; iii) what is the depth and time span in which significant transport occurs?; iv) when transport occurs, is there a difference in the amount of out of habitat transport for sandy beaches, tide pools and the sublittoral?; v) do ostracod assemblages bear distinctive taphonomic features that can be used to recognize the amount of temporal resolution in other deposits?

Study area

The Azores archipelago is a group of young volcanic oceanic islands that are located in the mid-North Atlantic (Fig. 1) (25–32°W, 37–40°N), about 1,500km from the shores of mainland Portugal. The easternmost Santa Maria Island is the oldest island in the archipelago, having emerged during the Late Miocene (Abdel-Monem *et al.*, 1968, 1975; Féraud *et al.*, 1980, 1981; Ávila *et al.*, 2012) and is very rich in Neogene fossiliferous sediments, including Late Miocene marine ostracods (Meireles *et al.*, 2012).

Today, generally, the coastline of these islands has a NW-SE to WNW-ESE direction, coincident with the major tectonic trends of each of the islands (Borges, 2003). The climate is temperate, with low thermal amplitude, high precipitation, and high air humidity and persistent winds (Calado *et al.*, 2011). Annual average sea-surface temperature is about 19ºC, ranging from 14ºC in winter to 24ºC in the summer period (Whissak *et al.*, 2010). The pattern of the sea-surface currents in the North Atlantic is dominated by the Gulf Stream that flows from West to the East, that is, from the American coasts to Europe. One of the branches of the Gulf Stream, the Azores Current, is a meandering jet across the Atlantic at latitude 38ºN, just South of the Azores islands (Johnson and Stevens, 2000; Rogerson et al., 2004) (Fig. 1).

The long fetch that characterizes the Azores results in a high-energy wave climate, where both sea and swell are relevant sources of coastal energy, with the northern-facing shore of each island in general being more exposed (Borges *et al.*, 2002). The steep submarine slopes and the absence of large shallow shelves (Borges *et al.*, 2002; Ávila *et al.*, 2008; Quartau *et al.*, 2010, 2012) produce localized patterns of wave shoaling, refraction and diffraction which, especially during storms, occur just before they break, leading to coastal fragmentation into a number of dynamic
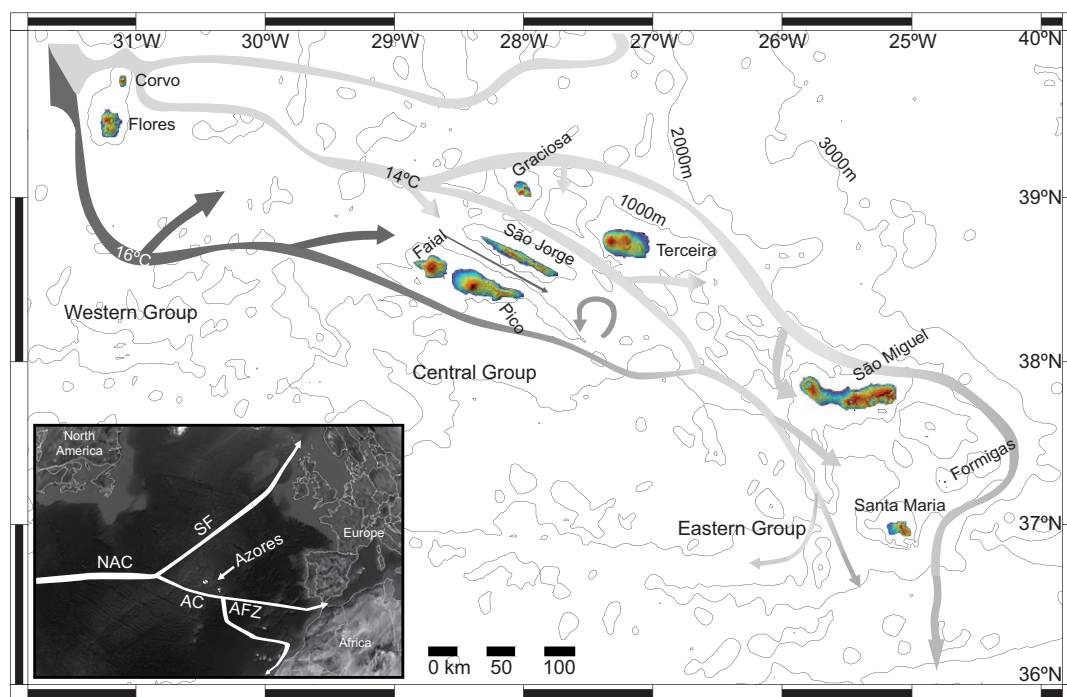
FIGURE 1. Geographical location of the Azores Archipelago (Western, Central and Eastern Groups), and the Azores Current (approximate position for the 30.6 meters depth and temperature; modified from Johnson and Stevens, 2000) around the archipelago. Insert: main oceanic currents of the North Atlantic Ocean; SF: Subpolar Front, NAC: North Atlantic Current, AC: Azores Current, AFZ: Azores Frontal Zone (adapted from Rogerson *et al.*, 2004; Storz *et al.*, 2009). The bathymetry of the Azores archipelago is from IOC IHO & BODC (2003).

cells, limited in terms of longshore sediment movement by virtually impermeable lateral boundaries (Borges *et al.*, 2002). The Azores littoral is microtidal to low mesotidal, with tides and tidal currents being minor contributors to coastal morphology and sediment dynamics (Borges *et al.*, 2002). The tides are semidiurnal, with a yearly average and maximum spring tidal range of 0.75-1m and 1.3m, respectively; the storm events are frequent and variable from year to year, with an average recurrent interval of 7 years for extreme events (Borges, 2003).

The transport processes of the coastal sediments are controlled by four main factors: i) steep submarine slopes and absence of large shallow shelves; ii) swell and coastal storms; iii) local sediment supply; and iv) littoral drift currents induced by the Atlantic surface waters. Coastal drift currents are residual, although influenced by the North Atlantic circulation, and have a small effect on the sediment redistribution of the Azorean littoral, being this role attributed mainly to stormy waves that have the capability of disturbing the dynamic cells previously mentioned (Borges, 2003).

Azores coastal forms range from low rocky coasts (some of them with tide pools) to bluffs, plunging cliffs, pocket beaches, dunes, and lagoons. Sandy beaches are not common coastal forms, are small, and do not occur in all islands. In plunging cliffs, the intertidal zone is also vertical, with a reduced area available for the settlement of the intertidal organisms. On the subtidal zone, lava rocky shores covered by algae dominate. Unconsolidated sediments are also common, ranging from boulders to sand environments, covering the marine rocky substrate.

MATERIALS AND METHODS

Collection and examination of specimens

Three field campaigns were done for this study. The first one was aimed to reveal the characterization and distribution of the beach surface sediments. A total of 600 samples were collected by one of the authors (P. Borges) from 1994 to 1999, which allowed establishing a general sedimentary composition, as well as charts of grain-sized fractions and carbonate contents (Borges, 2003). The second campaign was performed by a team from DOP (University of the Azores) from 1998 to 2008, and collected 20 samples in the inner shelf of the islands of the Central and Western groups, between 20 and 86m depth. For the sedimentary samples (first and second campaigns), a subsample of 100g of material was retrieved, washed and sieved (250μm, 120μm, 63μm) in the laboratory. Subsequently, all ostracod specimens from the same fraction were handpicked under a binocular stereomicroscope, sorted and counted. In accordance with

Whatley (1988), species with over 10 valves of adults and juveniles/sample, or adults and last moult stages/sample, were considered as autochthonous on that site.

The third campaign was done by the first author and collected 27 samples, all containing ostracods with soft parts, therefore assumed to have been living at the time of collection. All biotopes sampled were shallow (less than 15m depth), and included intertidal pools and intertidal rocky lava shore platforms. Live ostracods were also collected using a 180µm mesh hand dredge dragged over the bottom surface to a depth of 3–5cm. The sample was washed through a set of sieves with a mesh width of 1.0 and 0.25mm. All taxa from the same fraction were sorted, washed in fresh water and fixed in 70% alcohol in separate tubes.

Of the 647 samples collected, 60 were visually selected, encompassing biogenic carbonate samples from 7 out of the 9 islands of the Azores (only São Jorge and Corvo were not chosen) and of the isolated Formigas islets. These samples were screened for ostracods, which were found in 45 samples (Table 1). A total of 2,799 ostracods were handpicked, containing 586 living ostracods and 2,213 dead specimens (empty or disarticulated valves). Specimens picked from the samples were placed on standard micropalaeontological cavity slides for further examination, classification and counting. Only the autochthonous ostracods (sensu Whatley, 1988) were identified. The taxonomy and classification adopted follows Horne *et al.* (2002), and both were checked using the WORMS website (http://www.marinespecies.org). A detailed taxonomic description of the ostracod species is out of the scope of this paper and will be dealt with separately. The figured specimens (Fig. 2) are held in the collections of the Department of Biology, University of the Azores, Section of Ostracoda, under prefix "DBUA/OS". Other abbreviations used: RV=right valve, LV=left valve.

Statistical analysis

Several indices were calculated to describe the diversity of the ostracod assemblages: abundance (number of individuals), species richness, Shannon-Wiener diversity and evenness. All ostracod species/specimens were used in the statistical analyses. Data were analyzed using a Bayesian inference with the application WinBUGS (Spiegelhalter *et al.*, 2003). This methodology is an adequate tool for data analysis in ecology (McCarthy, 2007; Kéry, 2010; King *et al.*, 2010) as it allows testing different models in order to determine the possible differences in parameter estimates for different communities (Marcelino *et al.* 2013). We opted to use Bayesian inference, since all parameters are considered as random variables, thus uncertainty is included at all components of the models (Gelman *et al.*, 1995) which seemed as highly adequate to the type

of available data. The best models were selected based on their complexity and fit and also included, as derived quantities, comparisons between community types. They allowed a more comprehensive and easily interpretable approach than the more traditional analysis which usually imply sequential interpretation of multivariate, univariate, and post-hoc tests (Zuur *et al.*, 2007). We used the normal distribution as a prior for Shannon-Wiener diversity and for evenness, and the Poisson distribution for total abundance and species richness (Gelman *et al.*, 1995; McCarthy, 2007; King *et al.*, 2010). The following models were tested: i) island effect model, allowing different parameters for each of the islands; ii) habitat model, allowing different parameters for each habitat type (beach, sublittoral, tide pools); iii) depth model, allowing different parameters for each depth class ($\leq$10m, <30m, $\geq$30m); iv) geographical location model, allowing different parameters for location class (North, South, East, West, Southwest); and v) sediment model, allowing different parameters for sediment diameter size (fine sand, fine to medium sand, medium sand, medium to coarse sand, and coarse sand to gravel). A null model, considering that all the samples belong to the same community, was also calculated as a benchmark to compare the validity of the factorial models (we expect the fit of factorial models to be better than that of the null model). Besides estimating the different probability distributions for each community type (group.mean$_i$), we also calculated, as derived quantities, the differences in estimates (d_i) among islands, habitats types, depth classes, location classes and sediment sizes. In all cases we used three Markov chains and updated the model the required number of times to be clearly sufficient to reach convergence, by using normally accepted criteria (King *et al.*, 2010), including analysis of trace plots, the Brooks-Gelman-Rubin diagnostic, and the magnitude of Monte Carlo error, as provided by WinBUGS. To estimate model parameters, we only considered the estimates obtained after convergence. We used Deviance Information Criteria (DIC) as a measure of model complexity and fit (Spiegelhalter *et al.*, 2002). In general, we found that updating the model 100,000 times and using the last 30,000 updates to estimate model parameters and DIC was clearly sufficient to assure chain convergence.

In order to have a global vision of the effect of habitat type (beach, sublittoral, tide pools) on community composition and diversity, we applied a discriminant analysis to a data set including species abundances, total abundance and species richness (all log transformed), and Shannon-Wiener and Equitability diversity indices. The classification module of SPSS v.18 was used.

We used the R package *Indicspecies*, available through Cran (http://cran.r-project.org/web/packages/indicspecies/), to determine indicator species among the

TABLE 1. Characterization of the sampling sites. Grain size abbreviations, Fs: fine sand; Ms: medium sand; Cs: coarse sand; G: gravel; n.a.: not applicable

| Sample	Island	Code	Lat. (N)	Long. (W)	Depth (m)	Habitat	Location	Grain size	Date
1	Santa Maria	SMA_BE_S_5	36,930,066	-25,024,709	0	Beach	South	Fs to Ms	September 1998
2	Santa Maria	SMA_BE_S_9	36,949,994	-25,094,447	0	Beach	South	Fs to Ms	September 1998
3	Santa Maria	SMA_BE_S_10	36,949,994	-25,094,447	0	Beach	South	Fs	September 1998
4	Santa Maria	SMA_SU_S_13	36,941,454	-25,170,836	18	Sublittoral	South	Ms	July 2011
5	Santa Maria	SMA_TP_S_71	36,941,454	-25,170,836	4	Tide pool	South	Fs to Ms	July 2011
6	Formigas	FOR_SU_S_3	37,269,408	-24,781,723	20	Sublittoral	South	Ms to Cs	July 2008
7	São Miguel	SMG_BE_S_20	37,712,072	-25,495,147	0	Beach	South	Ms	May 1994
8	São Miguel	SMG_BE_S_50	37,741,653	-25,648,505	0	Beach	South	Ms to Cs	August 1994
9	São Miguel	SMG_SU_S_24	37,795,745	-25,795,512	10	Sublittoral	South	Ms	June 2010
10	São Miguel	SMG_SU_S_14	37,823,819	-25,864,477	10	Sublittoral	South	Fs	January 1995
11	São Miguel	SMG_SU_S_8	37,746,506	-25,625,782	20	Sublittoral	South	Fs	August 1995
12	São Miguel	SMG_SU_S_47	37,741,653	-25,648,505	20	Sublittoral	South	Fs to Ms	August 1995
13	São Miguel	SMG_TP_S_57	37,750,036	-25,629,902	1	Tide pool	South	Fs to Ms	June 2011
14	São Miguel	SMG_TP_S_59	37,744,614	-25,640,019	1	Tide pool	South	Fs to Ms	June 2011
15	São Miguel	SMG_TP_S_60	37,707,412	-25,508,177	2.5	Tide pool	South	Fs to Ms	June 2011
16	São Miguel	SMG_TP_S_66	37,749,984	-25,630,073	1	Tide pool	South	Fs to Ms	June 2011
17	São Miguel	SMG_SU_S_68	37,741,942	-25,647,754	15	Sublittoral	South	Fs to Ms	August 1995
18	São Miguel	SMG_SU_S_69	37,741,942	-25,647,754	9	Sublittoral	South	Fs to Ms	August 1995
19	Terceira	TER_BE_S_7	38,654,952	-27,237,167	0	Beach	South	Ms	August 1996
20	Terceira	TER_BE_E_6	38,718,599	-27,054,176	3	Beach	East	Ms	August 1996
21	Terceira	TER_SU_S_4	38,631,891	-27,146,873	23	Sublittoral	South	Cs	July 2002
22	Pico	PIC_TP_S_1	38,389,975	-28,251,514	1	Tide pool	South	Ms to Cs	August 2010
23	Pico	PIC_SU_E_42	38,413,920	-28,012,561	46	Sublittoral	East	Ms to Cs	November 2010
24	Pico	PIC_SU_E_45	38,412,710	-28,015,480	54	Sublittoral	East	Ms to Cs	November 2010
25	Pico	PIC_SU_W_55	38,525,070	-28,562,736	69	Sublittoral	West	Cs to G	July 2002
26	Pico	PIC_SU_N_56	38,496,056	-28,219,070	65	Sublittoral	North	Cs to G	June 2010
27	Faial	FAI_BE_S_16	38,524,935	-28,627,281	0	Beach	South	Fs	September 1997
28	Faial	FAI_SU_E_46	38,573,567	-28,596,550	30	Sublittoral	East	Fs to Ms	August 2009
29	Faial	FAI_SU_SW_40	38,524,197	-28,627,624	10	Sublittoral	Southwest	Fs	August 2009
30	Faial	FAI_SU_SW_41	38,560,117	-28,765,517	30	Sublittoral	Southwest	Cs	August 2009
31	Faial	FAI_SU_E_54	38,556,800	-28,596,533	30	Sublittoral	East	Fs to Ms	June 2011
32	Faial	FAI_SU_N_43	38,658,437	-28,712,081	85	Sublittoral	North	Ms	December 2011
33	Graciosa	GRA_BE_S_22	39,013,531	-27,953,134	0	Beach	South	Ms	March 1997
34	Graciosa	GRA_TP_S_52	39,012,523	-27,958,853	1	Tide pool	South	Fs to Ms	June 2011
35	Graciosa	GRA_TP_S_12	39,012,523	-27,958,853	1	Tide pool	South	Fs to Ms	June 2012
36	Graciosa	GRA_TP_S_51	39,012,523	-27,958,853	1	Tide pool	South	Fs to Ms	June 2013
37	Flores	FLO_SU_E_2	39,462,919	-31,127,994	20	Sublittoral	East	Fs to Ms	July 2002
38	Flores	FLO_TP_E_48	39,461,643	-31,118,602	3	Tide pool	East	Fs	June 2011
39	São Miguel	SMG_TP_W_64	37,893,415	-25,825,939	19	Tide pool	West	n.a.	June 2011
40	São Miguel	SMG_SB_S_85	37,795,745	-25,795,512	19	Sublittoral	South	Ms	August 2001
41	São Miguel	SMG_SB_N_86	37,849,103	-25,685,005	7	Sublittoral	North	Ms	August 2002
42	São Miguel	SMG_SB_N_87	37,836,903	-25,664,405	10	Sublittoral	North	Ms	August 2003
43	São Miguel	SMG_SB_N_88	37,842,054	-25,480,728	7	Sublittoral	North	Ms	August 2004
44	São Miguel	SMG_SB_S_89	37,707,412	-25,508,177	4	Sublittoral	South	Ms	August 2005
45	São Miguel	SMG_SB_S_90	37,750,036	-25,629,902	11	Sublittoral	South	Ms	August 2006

different habitat types sampled in this study. The package was written by De Cáceres *et al.* (2010) as a refinement of the IndVal method originally developed by Dufreen and Legendre (1997). The algorithm determines both fidelity (restriction to a site or group of sites) and consistency (consistent species occurrence among sites within site groups) and provides a statistic (IndVal) and an associated p-value. Only species significant at the p<0.05 level were selected as indicator species.

RESULTS

Live Ostracoda assemblages

Fourteen living species were found: *Loxoconcha rhomboidea* (Fischer, 1855); *Loxoconcha malcomsoni*

Horne and Robinson, 1985; *Neonesidea longisetosa* (Brady, 1902); *Aurila convexa* (Baird, 1850); *A. woutersi* Horne, 1986; *Xestoleberis rubens* Whittaker, 1978; *Heterocythereis albomaculata* (Baird, 1838); *Urocythereis britannica* Athersuch, 1977; *Leptocythere pellucida* (Baird,1850); *Carinocythereis whitei* (Baird, 1850); *Callistocythere* sp.; *Semicytherura* sp.; *Lanceostoma* sp., and *Cylindroleberis* sp. (Fig. 3; Table 2). Living shallow marine ostracod species were found in tide pools and sublittoral (inner shelf) zones, between 1 and 15-20m depth, in fine to medium sands, usually in association with algae and sponges. *Loxoconcha rhomboidea*, *Xestoleberis rubens*, *Heterocythereis albomaculata* and *Loxoconcha malcomsoni* were the most abundant species, ranging from 27.5% to 12.3% of the total abundance (*cf.* Table 3). In general, *Loxoconcha* rhomboidea; *L. malcomsoni*, *Neonesidea longisetosa*, *Xestoleberis rubens* and *Heterocythereis albomaculata*
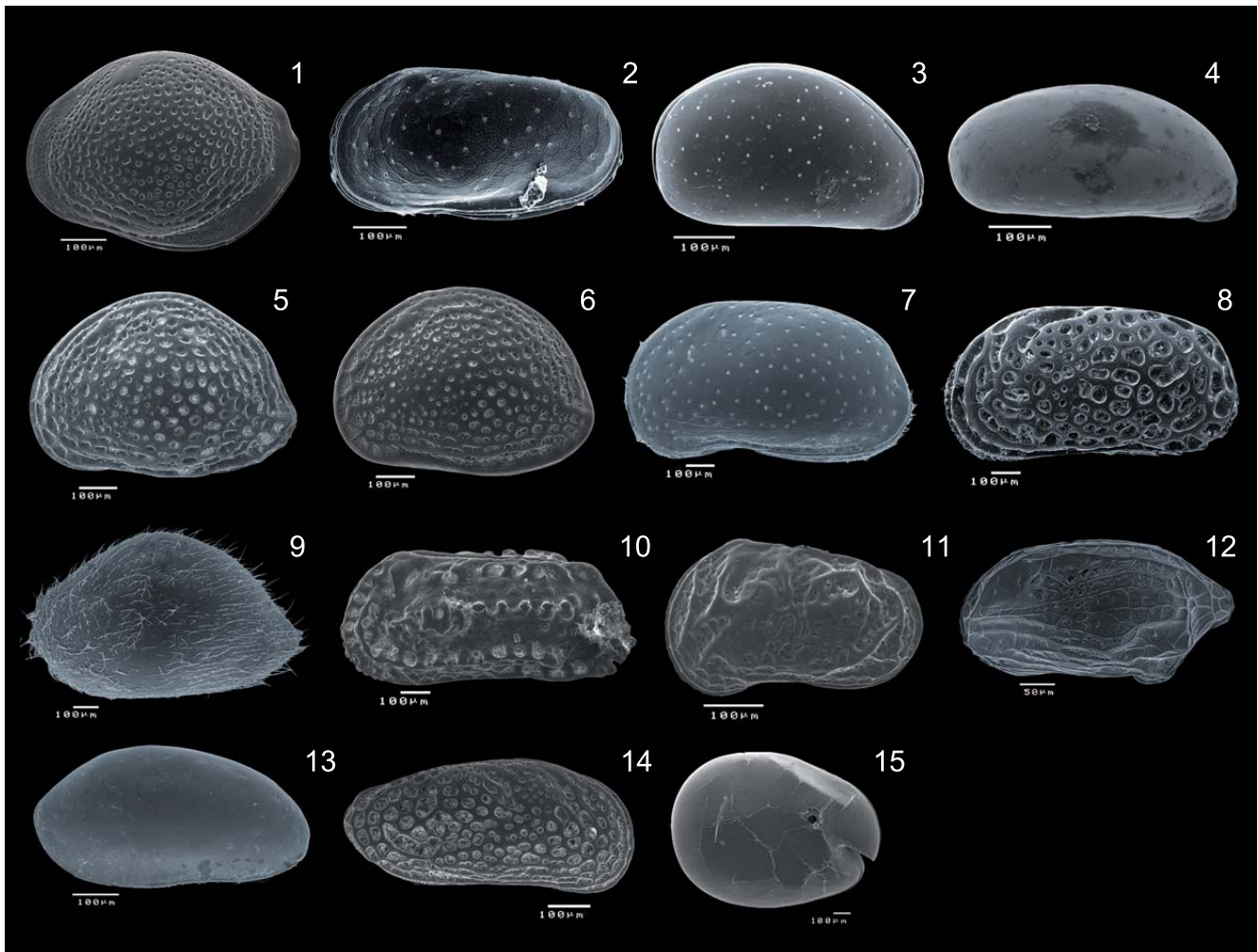
FIGURE 2. External view (SEM photographs) of the valves of the species of marine ostracods reported for the Azores archipelago. 1) *Loxoconcha rhomboidea* (Fischer, 1855). DBUA/OS 0144. L.V.; 2) *Loxoconcha malcomsoni* Horne and Robinson, 1985. DBUA/OS 0001. L.V.; 3) *Xestoleberis rubens* Whittaker, 1978. DBUA/OS 0118. L.V.; 4) *Xestoleberis* cf. *depressa* Sars, 1866. DBUA/OS 0181. L.V.; 5) *Aurila convexa* (Baird, 1850). DBUA/OS 0039. L.V.; 6) *Aurila woutersi* Horne, 1986. DB/OS 0120. L.V.; 7) *Heterocythereis albomaculata* (Baird, 1838). DB/OS 0113. L.V.; 8) *Urocythereis britannica* Athersuch, 1977. DBUA/OS 0017. L.V.; 9) *Neonesidea longisetosa* (Brady, 1902). DBUA/OS 0133. L.V.; 10) *Carinocythereis whitei* (Baird, 1850). DBUA/OS 0054. L.V.; 11) *Callistocythere* sp. DBUA/OS 0124. L.V.; 12) *Semicytherura* sp. DBUA/OS 0123. L.V.; 13) *Lanceostoma* sp. DBUA/OS 0117. L.V.; 14) *Leptocythere pellucida* (Baird, 1850). DBUA/OS 0057. R.V.; 15) *Cylindroleberis* sp. DBUA/OS 0180. R.V.

were found living together. The highest concentrations of living ostracods were found on the southern shores of São Miguel Island, at depths ranging from 1 to 15m. Comparisons of the total number of specimens (both live and dead) along a bathymetric sampling (between 0 at 20m depth) at all sites in São Miguel Island indicate that there is not a direct relationship between abundance and depth (Fig. 4A). Nevertheless, and excluding the sandy beach habitats, in both living and dead assemblages, the abundance of ostracods is higher in the first 20m depth (Fig. 4A, B).

Dead Ostracoda assemblages

The remains of ostracods (empty carapaces and disarticulated valves) are relatively diverse, comprising 8 families, 12 genera and 15 taxa, and are represented by different ontogenetic stages (instars). The dead assemblages are dominated by specimens belonging to Loxoconchidae (33%), Hemicytheridae (26%), Bairdiidae (25%), Xestoleberididae (7%) and Trachyleberididae (6%) (Table 3; Figs. 3; 5).

The sediments with higher ostracod abundance and diversity were collected at depths between 0 and 54m, where fine to medium sand predominate. The samples with higher ostracod concentration occurred at different depths and places: two samples between 3 and 23m in the East and the South coast of Terceira Island, respectively; four samples between 0 and 20m, all in the South coast of São Miguel Island (in this case, two of them were at the same area, around the sewage treatment system of Ponta Delgada); two samples between 10 and 30m in the
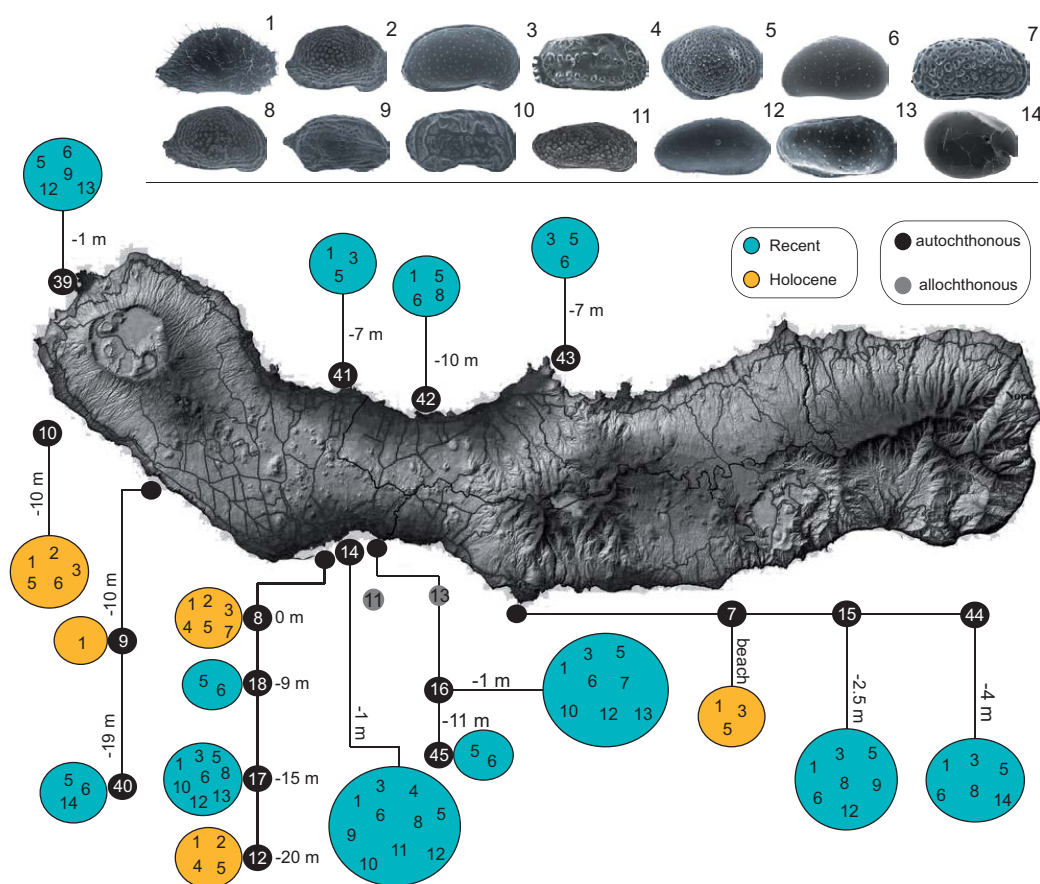
FIGURE 3. Geographical distribution of the Recent and Holocene marine ostracods from São Miguel Island. 1) *Neonesidea longisetosa*; 2) *Aurila woutersi*; 3) *Heterocythereis albomaculata*; 4) *Carinocythereis whitei*; 5) *Loxoconcha rhomboidea*; 6) *Xestoleberis rubens*; 7) *Urocythereis britannica*; 8) *Aurila convexa*; 9) *Semicytherura* sp.; 10) *Callistocythere* sp.; 11) *Leptocythere pellucida*; 12) *Lanceostoma* sp.; 13) *Loxoconcha malcomsoni*; 14) *Cylindroleberis* sp.

Southwest coast of Faial; and finally, two samples between 1 and 54m, both in the East end of Pico Island (Figs. 3; 5).

Statistical analysis of the factors affecting the ostracod assemblages

According to the DIC values (Table 4), the more informative Bayesian model (lowest DIC) incorporated the island effect, particularly due to a better adjustment to the possible differences in total abundance between islands. The island model also performed better that the null model for Shannon diversity and species richness. For the factors depth class, habitat type and sediment type, the respective models were better than the null model only for total abundance (Table 4).

The model based on depth only showed differences among depth classes for total abundance (total number of dead ostracods found), with the intermediate depth class (class 2: from 10 to 30m depth) showing the highest abundance (Fig. 6A). Regarding habitat type, the highest abundance was found for communities located at the

sublittoral (Fig. 6B) and the lowest number of species was found in the samples collected at beaches (Fig. 6C), where not a single specimen was found alive. The model based on orientation did not show any differences between different orientations (not shown), whereas the model including island effect (Fig. 7A-D) showed many differences among islands, particularly for total abundance (Fig. 7A) and species richness (Fig. 7B). Dead ostracods' total abundance was found to be higher in medium to coarse sands (Fig. 8A), whereas species richness was higher in sands ranging from fine-to-medium, to medium grain size (Fig. 8B).

The results of a discriminant analysis based on individual species abundance, species richness and total abundance (all log transformed), and also on the Shannon-Wiener and evenness diversity indices, showed a good discrimination between ostracod communities collected at different habitats, with a minor overlap between communities from beaches and the sublittoral (Fig. 9). The two canonical discriminant functions used in the analysis explain 85.3 and 14.7% of the detected variance, respectively.

Fine to medium sands are mostly located at depths lesser

TABLE 2. Total number of live and dead specimens of ostracods by sites and by species. Sites 5, 14, 15, 16, 17, 22, 34, 35, 36 and 38, contained living specimens; all other sites contained only dead specimens. For the complete list and geographical localization of the collecting sites, please consult Table 1. *L. rho: Loxoconcha rhomboidea; L. mal: Loxoconcha malcomsoni; N. lon: Neonesidea longisetosa; A. con: Aurila convexa; A. wou: Aurila woutersi; X. rub: Xestoleberis rubens; X.* cf. *dep: Xestoleberis* cf. *depressa; H. alb: Heterocythereis albomaculata; U. bri: Urocythereis britannica; L. pel: Leptocythere pellucida; C. whi: Carinocythereis whitei; Cal* sp.: *Callistocythere* sp.; *Sem* sp.: *Semicytherura* sp.; *Lan* sp.: *Lanceostoma* sp.; *Cyl* sp.: *Cylindroleberis* sp.

Sites	L. rho	L. mal	N. lon	A. com	A. wou	X. rub	X. cf. dep	H. alb	U. bri	L. pel	C. whi	Cal sp.	Sem sp.	Lan sp.	Cyl sp.
1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
4	14	12	6	0	0	28	1	0	0	0	1	1	0	1	0
5	7	0	0	0	0	4	0	0	0	0	0	0	0	3	0
6	11	5	6	0	0	14	3	0	0	0	0	0	0	0	0
7	16	0	15	3	0	0	0	7	3	0	0	0	0	0	0
8	19	0	36	8	0	1	0	20	17	6	96	0	0	0	0
9	5	0	10	1	0	0	0	0	1	0	0	0	0	0	0
10	137	14	76	8	0	9	0	10	4	0	0	0	0	0	0
11	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0
12	29	3	17	26	0	6	0	7	5	6	30	0	1	0	0
14	10	0	5	3	1	28	0	35	0	1	3	2	8	3	3
15	5	0	4	3	0	15	0	37	0	0	0	0	14	20	0
16	4	2	4	0	1	3	0	30	1	0	0	1	0	1	0
17	9	3	5	2	0	14	0	1	0	0	0	7	0	2	3
19	122	26	82	35	0	37	0	18	23	0	1	0	0	0	0
20	2	24	9	2	1	6	3	19	0	1	0	17	0	0	4
21	59	62	19	17	0	25	0	0	0	0	1	10	0	6	0
22	1	43	2	0	0	64	0	4	0	0	0	2	0	0	2
23	4	0	22	11	0	0	0	0	3	0	0	0	0	0	0
24	88	14	147	23	0	18	0	5	3	0	2	1	3	4	0
25	9	0	36	4	0	0	0	6	11	1	2	0	0	0	0
26	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
28	2	0	6	3	0	0	0	2	8	0	0	0	0	0	0
29	16	0	1	6	0	3	0	170	2	4	1	0	0	0	0
30	0	0	8	1	0	0	0	2	5	0	0	0	0	0	0
31	31	0	41	18	0	0	0	22	7	0	1	0	0	0	0
32	0	0	10	3	0	0	0	0	12	1	0	0	0	0	0
33	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
35	25	4	2	1	0	14	0	28	0	0	0	1	0	11	0
36	1	0	0	0	0	4	0	0	0	0	0	0	0	0	0
37	4	0	1	0	0	0	0	1	0	0	0	0	0	0	0
38	10	37	1	1	2	11	0	0	0	0	0	1	2	0	1
TOTAL	646	249	575	179	5	309	7	425	108	20	138	44	28	53	13

than 30m, in places where higher energy environments and turbulence tend to prevail (Fig. 10). At greater depths, in sites where coarse sands to gravel predominate, the faunal autochthonous association is typically composed by species of the genera *Loxoconcha*, *Heterocythereis*, *Neonesidea*, and *Urocythereis*. As regards to the maximum bathymetric range for species around the Azores insular shelf, *Aurila woutersi*, *Callistocythere* sp., *Lanceostoma* sp., *Carinocythereis whitei*, *Xestoleberis* cf. *depressa* and *Loxoconcha malcomsoni* are shallow-water species, occurring in waters less than 30m depth; *Aurila convexa*, *Xestoleberis rubens*, *Loxoconcha rhomboidea* and *Heterocythereis albomaculata* may occur between 30 and 55m depth; and *Neonesidea longisetosa* and *Urocythereis britannica* may occur as deep as ~90m depth. The genera

Aurila and *Xestoleberis* are represented by both littoral species (*Aurila woutersi* and *Xestoleberis* cf. *depressa*) as well as by species occurring at greater depths (*Aurila convexa* and *Xestoleberis* rubens) (Fig. 11).

Indic species revealed that *Xestoleberis rubens* (0.818, p=0.015) was associated to depth classes 1 (<10m) and 2 (10-30m). Regarding islands, *Xestoleberis* cf. *depressa* was associated to Formigas (IndVal=0.85, p=0.039), *Loxoconcha malcomsoni* was associated to Formigas, Terceira and Flores (IndVal=0.804, p=0.042), *Aurila convexa* was associated to São Miguel, Terceira, Pico and Faial, (IndVal=0.881, p=0.033), and *Neonesidea longisetosa* was associated to Formigas, São Miguel, Terceira, Pico, Faial and Flores (IndVal=0.951, p=0,016). Regarding habitat

TABLE 3. Total number and percentage of live and dead specimens of the different ostracod species collected in the Azores islands

Family	Species	Live	%	Dead	%
Loxoconchidae	*Loxoconcha rhomboidea*	72	12.3	574	25.9
Loxoconchidae	*Loxoconcha malcomsoni*	89	15.2	160	7.2
Bairdiidae	*Neonesidea schulzi*	23	3.9	552	24.9
Xestoleberididae	*Xestoleberis rubens*	161	27.5	148	6.7
Xestoleberididae	*Xestoleberis* cf. *depressa*	0	0	7	0.3
Hemicytheridae	*Aurila convexa*	10	1.7	169	7.6
Hemicytheridae	*Aurila woutersi*	4	0.7	1	0
Hemicytheridae	*Urocythereis britannica*	1	0.2	107	4.8
Hemicytheridae	*Heterocythereis albomaculata*	135	23	290	13.1
Trachyleberididae	*Carinocythereis whitei*	3	0.5	135	6.1
Leptocytheridae	*Callistocythere* sp.	14	2.4	30	1.4
Leptocytheridae	*Leptocythere pellucida*	1	0.2	19	0.9
Cytheruridae	*Semicytherura* sp.	24	4.1	4	0.2
Paradoxostomatidae	*Lanceostoma* sp.	40	6.8	13	0.6
Cylindroleberididae	*Cylindroleberis* sp.	9	1.5	4	0.2
	TOTAL	586	100	2213	100

type, *Neonesidea longisetosa* (IndVal=0.897, p=0.042) and *Urocythereis* brittanica (IndVal=0.754, p=0.032) were found to be associated to the sublittoral.

DISCUSSION

Taphonomic approach

The environmental depositional energy can be estimated using sediment grain size and water depth as proxies, and by plotting the samples onto a schematic representation that reflects the taphonomic fidelity of each deposit. These plots can be considered as taphonomically-controlled facies and can be used as predictive tools for estimating how much time-averaging is likely to affect a deposit (see Park *et al.*, 2003 for an overview) (Fig. 10). The Azores shores are considered as a high energy environment, with the exception of a few protected sites (Borges, 2003). In these oceanic islands, dynamic cells make long shore currents to be negligible in comparison with downwelling shore oblique currents, which transport the sediments, moving them from the exposed beach to the underwater beach (*cf.* Fig. 11) (Borges *et al.*, 2002; Meireles *et al.*, 2013). In these high energy environments, the abundance of ostracods is higher in the sublittoral, at depth ranges of 0-20m (Fig. 6A, B), and the diversity is higher in fine to medium- to medium-sandy substrates (Fig. 8B), with less turbulence and thus, with inferred lower energy (*cf.* Fig. 10).

Kontrovitz *et al.* (1998) made one equation to discriminate if some taphonomic processes were important in altering an assemblage of ostracods. They showed that such assemblages may be sampled and that the width, thickness, and MPS (maximum projection sphericity) of the carapaces could be determined as a function of each species. The amount of pressure required to crush each ostracod carapace could then be estimated by using the equation for that species. If within the assemblage the pressure that would be required to crush the samples varies greatly, then one could conclude that the assemblage is unlikely to have been altered by pressure. Otherwise, the weaker ostracod carapaces probably would have been crushed. If, however, the only ostracods present in the sample require large pressures to be crushed or all require about the same pressure, then one might suspect that the assemblage may have lost carapaces/species due to forces exerted by the overlying sediments. Under the latter conditions, the investigator could misinterpret palaeoenvironmental conditions, if wrongly assuming the presence of a nearly complete and useful assemblage for such a purpose (Kontrovitz *et al.*, 1998). Moreover, models that rely exclusively on death assemblages will be always less informative than those based upon live assemblages (Park *et al.*, 2003). Our samples include a mixture of fragile and resistant carapaces, the latter being predominant (*cf.* Fig. 2). As expected, fragile carapaces of shallow-water species (*e.g.* *Lanceostoma* sp.) are better represented in the shallow (and more recent) samples than in the deeper ones (which are also older and were subjected to transport). Thus, transport of sediment becomes an important item that must be taken into account when ostracods are used as proxy indicators for biodiversity and conservation practices in steep gradient coasts such as those around the Azores islands, and should be included in any model developed (*cf.* Fig. 10).
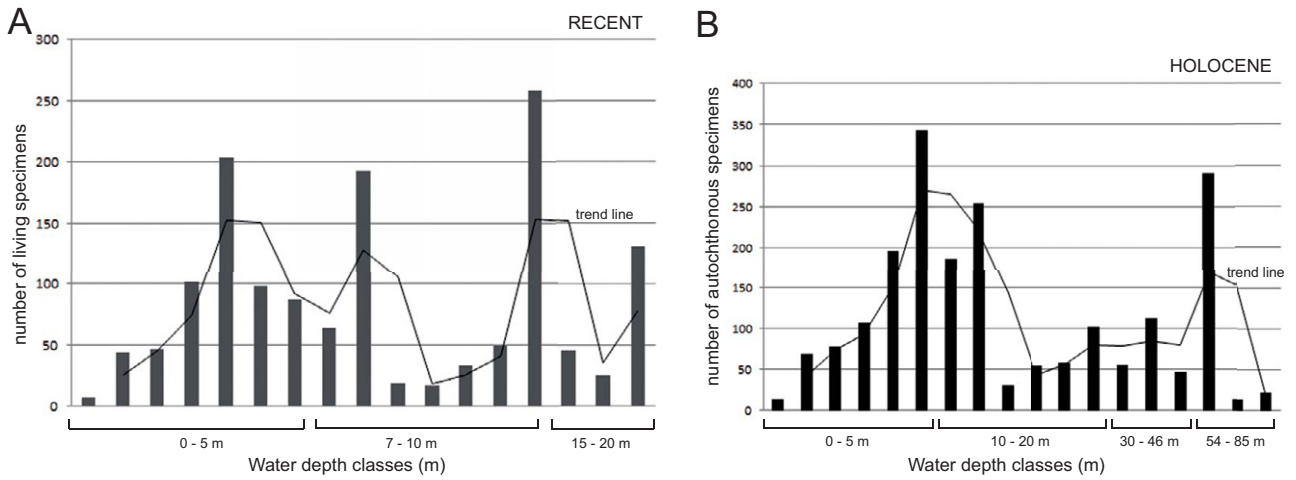
FIGURE 4. Total number of specimens for water depth classes. A) number of Recent (living) specimens, and B) number of autochthonous Holocene specimens.
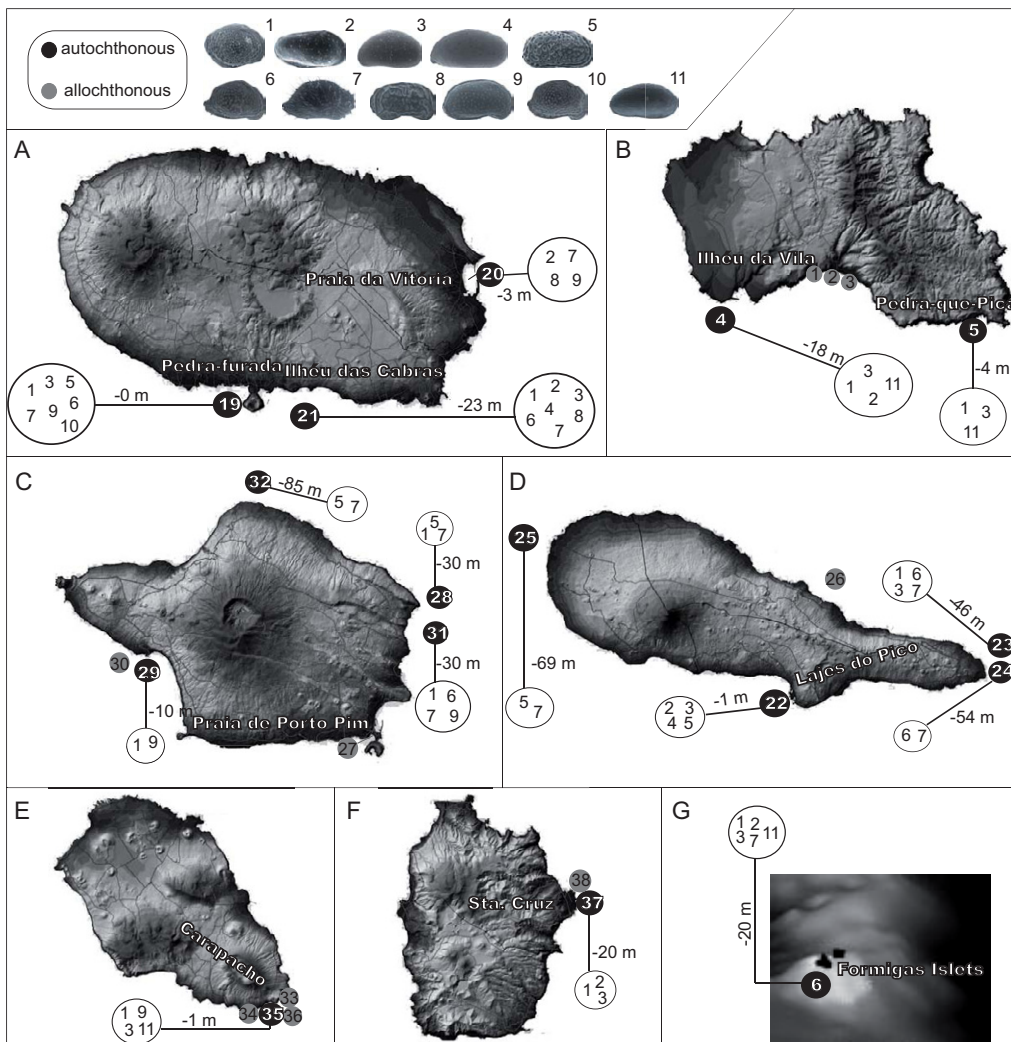

FIGURE 5. Geographical distribution of the Recent marine ostracods from the Azores archipelago. 1) *Loxoconcha rhomboidea*; 2) *Loxoconcha malcomsoni*; 3) *Xestoleberis rubens*; 4) *Xestoleberis* cf. *depressa*; 5) *Urocythereis britannica*; 6) *Aurila convexa*; 7) *Neonesidea longisetosa*; 8) *Callistocythere* sp.; 9) *Heterocythereis albomaculata*; 10) *Aurila woutersi*; 11) *Lanceostoma* sp.
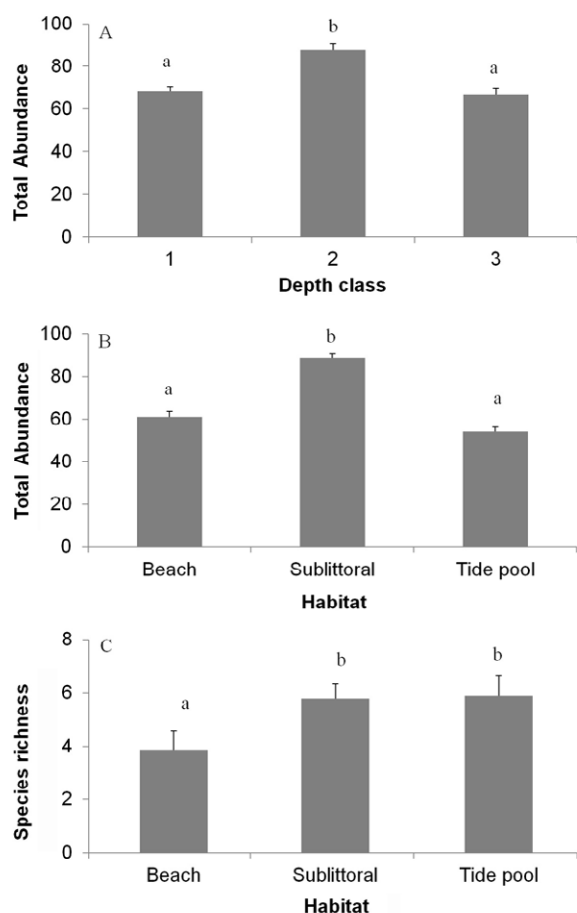
FIGURE 6. Effect of the environmental factors (bathymetry and habitat) on the abundance and diversity of the ostracod communities in the Azores Archipelago (35 samples). Evaluation of Bayesian models assessing the effect of: A) Depth class on total abundance (depth classes, 1: <10m; 2: 10-30m; 3: >30m); B) Habitat type on total abundance (beach; sublittoral; and tide pools); and C) Habitat type on species richness (beach; sublittoral, and tide pools). Bars represent mean+standard error. The posterior distributions of the parameters were obtained after convergence (100,000 model updates). Different letters indicate that the posterior distribution of the difference between the means does not include zero (based on the analysis of the 95% credibility interval).

Other important components that are present in the taphonomic studies are the synecology indices (*i.e.* describing associations in relation to environmental parameters), which are based on the quantitative analysis of the assemblages and that may shed light on the stability of the environment. Low diversity assemblages with few or single dominating species point to stressed, unstable conditions (Frenzel and Boomer, 2005). For instance, high sedimentation rates, recorded for areas of the Baltic Sea, showed low diversity and abundance (Rosenfeld, 1977). The number of autochthonous dead specimens decreases with depth, suggesting a shift from life-dominated assemblages in the shallower depths, to death assemblages (with autochthonous and allochthonous specimens) at greater depths (Fig. 4B). This trend is expected when

significant transport occurs and is in agreement with Park *et al.* (2003) and Machado *et al.* (2005).

The abundance of the Azorean ostracod species is related to depth (Figs. 4B; 6A), grain size (Fig. 8A),
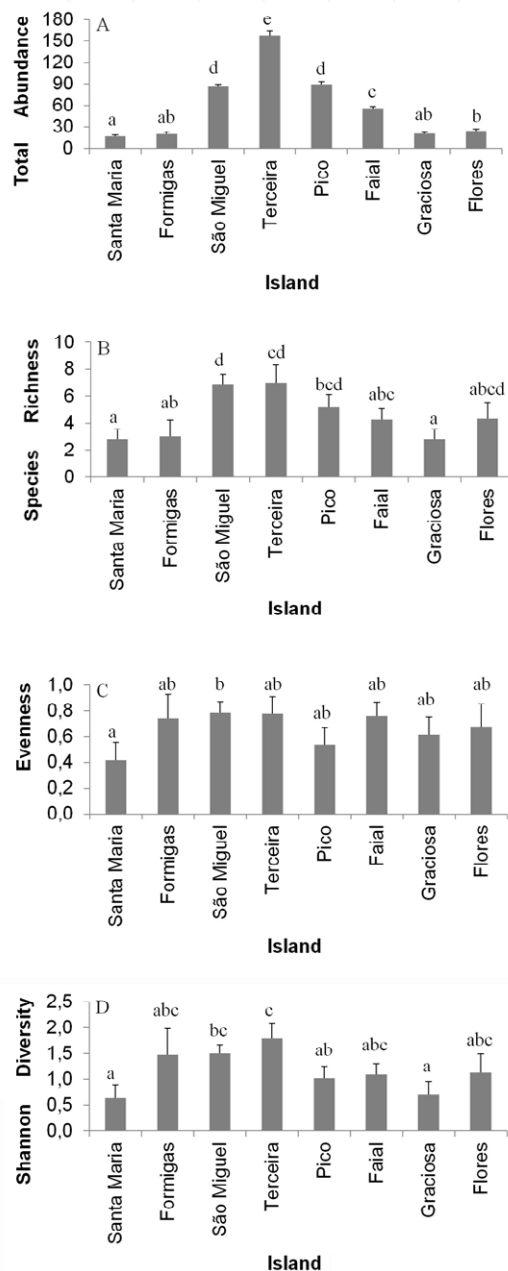
FIGURE 7. Effect of the environmental factors (island) on the abundance and diversity of the ostracod communities in the Azores Archipelago (35 samples). Evaluation of a Bayesian model assessing the effect of island (Santa Maria, Formigas, São Miguel, Terceira, Pico, Faial, Graciosa and Flores) on the diversity of recent Ostracod communities in eight Azorean islands. Posterior distributions obtained after convergence (100,000 model updates). The model determined the effect of the factor island on total abundance, species richness, Eveness and Shannon Diversity index. Different letters indicate that the posterior distribution of the difference between the means does not include zero (based on the analysis of the 95% credibility interval).
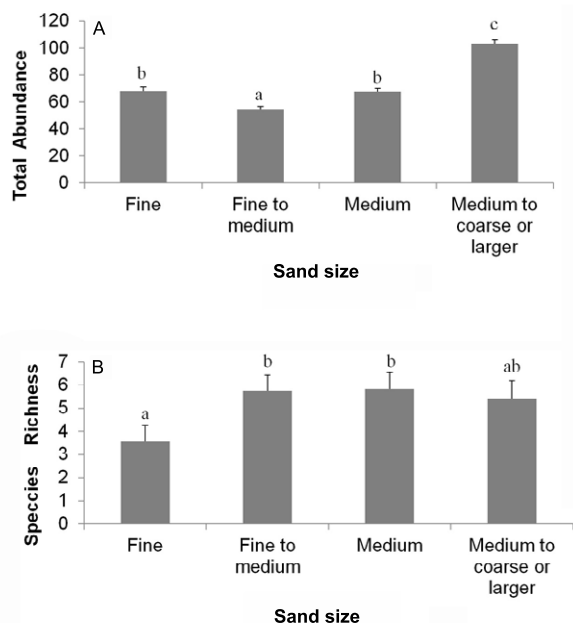
FIGURE 8. Effect of the environmental factors (sediment sand size) on the abundance and diversity of the ostracod communities in the Azores Archipelago (35 samples). Evaluation of a Bayesian model assessing the effect of sand size on: A) total abundance; B) species richness. The posterior distributions of the parameters were obtained after convergence (100,000 model updates). Different letters indicate that the posterior distribution of the difference between the means does not include zero (based on the analysis of the 95% credibility interval).

and geographical coast location (Fig. 7A). The higher abundance of ostracods in the southern and eastern shores is probably a result of a relatively higher stability of the bottom sediments during longer periods in these sites, as the mean wave height in the northern coasts exceeds up to 20% the value of the southern coasts (*cf.* Borges, 2003). We cannot, however, exclude that these deposits and their faunas have undergone transport, particularly in areas with higher-energy conditions, by downwelling shore oblique currents.

Comparison of live and dead assemblages from similar depths and substrates around the archipelago indicates that there are some distribution oddities. For example, all species presently known in the Azores occurred at Terceira Island, with the exception of *Lanceostoma* sp. However, this species also occurs at Graciosa Island, just 60km distance. Santa Maria Island and Formigas Islets (about 38km apart) have similar species composition, except for *Neonesidea longisetosa* that is not present at Santa Maria (*cf.* Fig. 5).

The standard of length classes' distribution present in one taphocoenosis can be used to describe how the death of the animals occurred (Shipman, 1981). Using this method plus the ontogenetic structure of the populations (after Whatley, 1988; *cf.* Electronic Appendix, available at www. geologica-acta.com), we identified two different types of death: i) non-selective death (*i.e.*, catastrophic, affecting in a similar manner both juveniles and adults); and ii) selective death (natural, thus with different mortality rates). Most of the samples present a selective death (natural) with the exception of samples 6, 7, 9, 25 and 32 (*cf.* Table 1) that present a non-selective death (catastrophic). In general, the samples collected in protected sites or on the South shores of the islands present a selective death (natural), probably with fast burial (*e.g.* assemblages nº 4, 12, 31; *cf.* Figs. 3; 5). These areas present a reduced hydrodynamism and thus, probable higher sedimentation rates. Based on these findings and the characteristics of the present-day taxa we were able to develop a model of how assemblages occur on these settings, relating these items with the bathymetric range of the ostracod species (Fig. 11). Considering the type of substrate, depth and marine environment (tide pools, beach and sublittoral), we were able to display the distribution of the autochthonous ostracods on the insular Azorean shelf (see complete list of the typical association of species in Supplementary Electronic Appendix).

Ecological setting

In terms of abundance (number of specimens/100g dry sediment), we found considerable variation between samples, a situation that is in agreement with previous studies (*cf.* Figs. 6; 7; 8). Allison and Holden (1971) described differences in abundance, depending on the

TABLE 4. Evaluation of four Bayesian models assessing the effect of five different factors (Location, Island, Depth, Habitat, Sediment) on the diversity (Eveness, Shannon Diversity, Total Abundance, Species Richness) of Holocene Ostracoda assemblages in the Azores Archipelago. DIC values obtained after convergence (75,000 model updates)

| Diversity measures	DIC					
	Null model	Geographical location	Island effect	Depth	Habitat	Sediment type
Eveness	13.7	17.0	16.4	16.6	16.8	17.4
Shannon diversity	63.0	65.5	59.6	65.8	65.0	64.5
Total abundance	3380.0	3396.2	2431.2	3354.3	3301.4	3238.5
Species richness	189.1	191.6	187.6	192.6	189.9	191.8
Total	3645.5	3670.4	2694.8	3629.3	3573.2	3512.2

depth, with relatively lower values closer to the surface. Hull (1997) reported that abundances differ over the years, and also along the year. In Brazil, species abundance was higher than the values reported for the Azores (50 to 150 individuals/100g dry sediment), with some samples with abundances over 1,000 specimens/20g dry sediment, and also showing the already noted variation between samples (Machado *et al.*, 2005). Cabral *et al.* (2006) reported abundances between 10 to 100 specimens/10cm^3 sediment, depending on the area, for the Melides lagoon (80km south of Lisbon, mainland Portugal). Athersuch (1979) found similar abundance values for the littoral of Cyprus, with some species with more than 100 specimens/sample. For the Basque shelf, abundances were also similar, ranging from 11 to 156 specimens/sample (Pascual *et al.*, 2008).

If we consider ostracods as a grain of sand, the zonation displayed on Figure 9 suites well with the coastal fragmentation into dynamic cells, limited in terms of longshore sediment movement by virtually impermeable lateral boundaries where the dynamics of the beaches are essentially transverse to the shore (*cf.* Borges *et al.*, 2002), and with a morphodynamic continuum between two extreme situations, the profile of high energy (storm or winter profile) and the profile of low energy (swell or summer profile), with the sandy sediments moving from the exposed beach to the underwater beach and vice-versa, respectively (see Short (1999) for an overview).
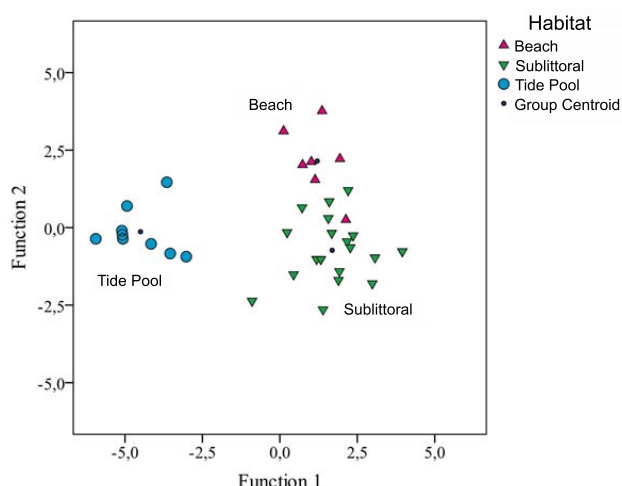

FIGURE 9. Discriminant analysis applied on the distribution of the ostracod communities in eight Azorean islands (35 samples), according to the type of habitat (beach, sublittoral, tide pools). Discriminant analysis is based on individual species abundance, species richness and total abundance (all three log transformed), and also on the Shannon and Eveness diversity indices.

Ostracod species richness assessments depend on the depth of collection, as the estimates are differently impacted by time-averaging. This is so, because transport of dead valve material occurs at higher percentages in the shallow depths and on the sublittoral. As a result of this, the biogenic material will accumulate at higher
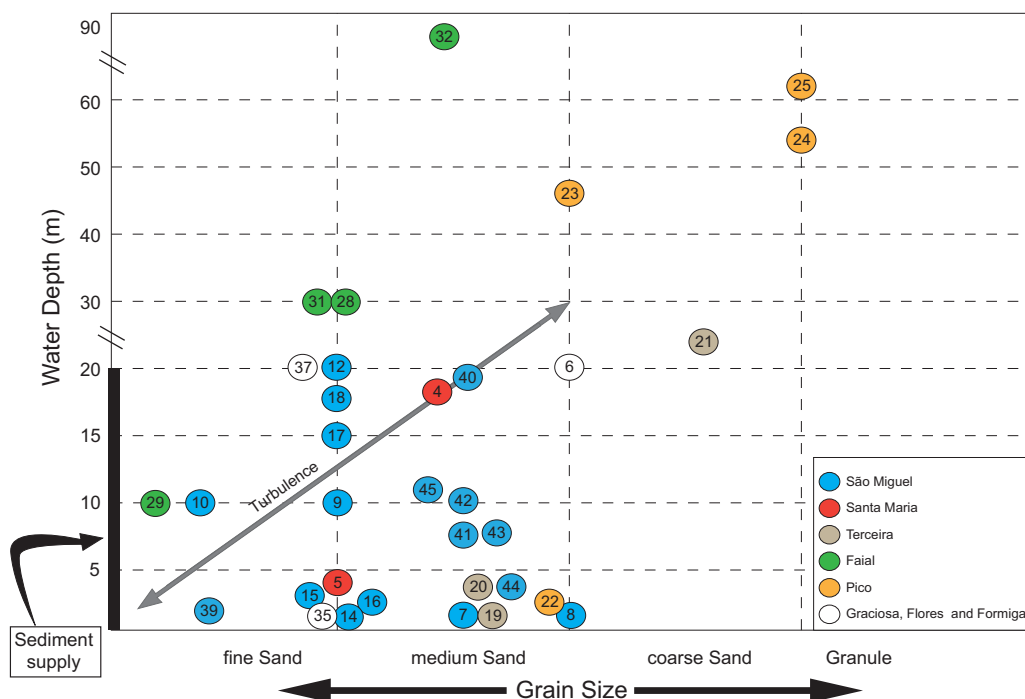
FIGURE 10. Distribution of ostracods as a function of depth, grain size and depositional environment. The sediment supply comes mainly from streams with an ephemeral torrential regime, or small permanent streams. Fine-sand: lower energy; medium sand: medium energy; coarse sand and gravel: higher energy (*cf.* Electronic Appendix).
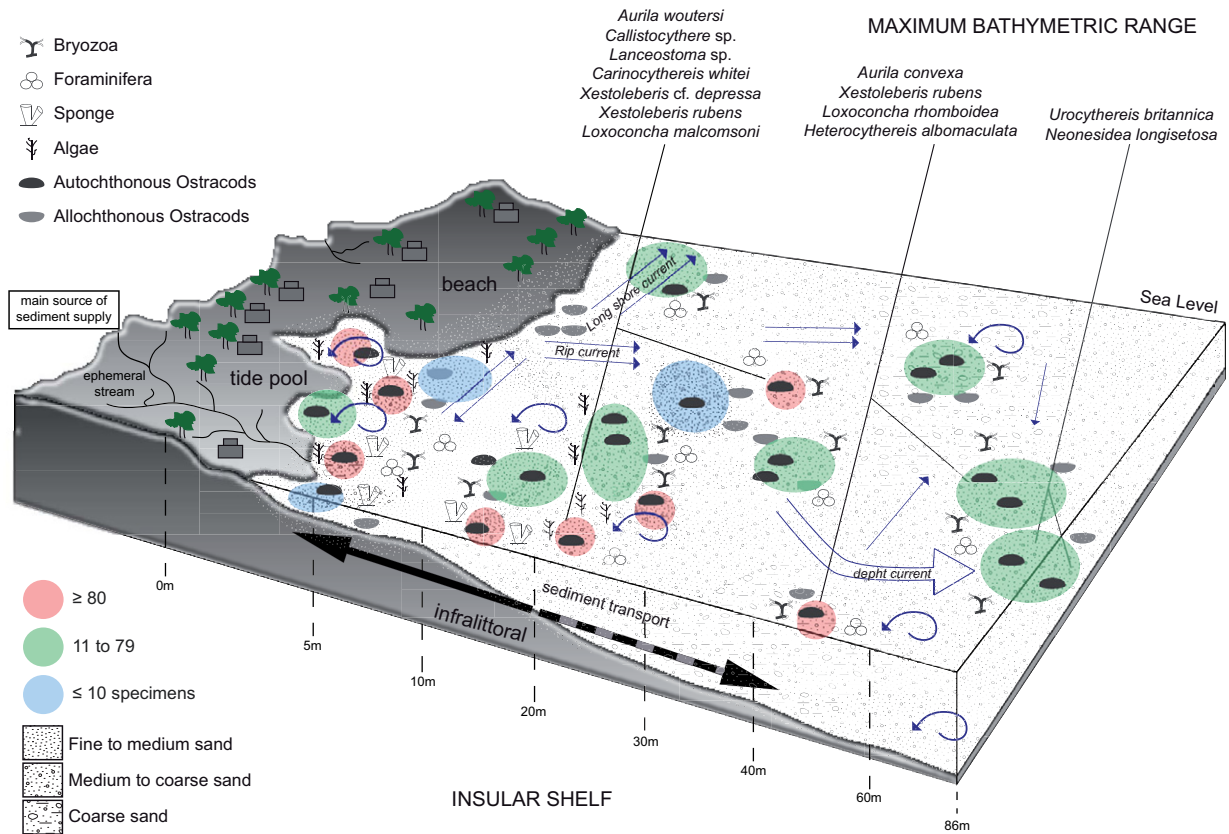
FIGURE 11. Cross-insular shelf profile with the maximum bathymetric range and distribution of the ostracods found in the Azores shallow marine environments, according to preferred bathymetry and type of sediment.

depths, suggesting that the well-preserved ostracod death assemblages in these areas will be a mirror of shallow and sublittoral life assemblages. However, caution must be taken, as below storm-wave base, both autochthonous and allochthonous species will be concentrated in the same area (Meireles *et al.*, 2013). The beach areas do not emulate the life assemblages, as all species are considered to be allochthonous, thus did not live there (moreover, following Whatley (1988), all samples also had fewer than 10 specimens/sample).

Several environmental factors affect the distribution and abundance of ostracods, in particular, the textural characteristics of the bottom substrate. Benson and Maddocks (1964), Puri (1966), Montenegro *et al.* (1998) and Coimbra *et al.* (1999) reported that grain size is one of the significant factors controlling the population structure, density and distribution of ostracod species, fine-grained sands with a high percentage of silt and clay being favoured (Machado *et al.*, 2005). High algal concentrations and seasonal changes can also influence the presence of ostracods (Hull, 1997). Furthermore, other factors like depth also affect ostracods richness. For instance, Ascoli (1964) found that the most favourable

environmental conditions for a high number of ostracod species was a depth between 50 and 250m, on a muddy and clayey bottom; towards either upper littoral or bathyal environments, the number of species decreased. Our observations showed more species at the sublittoral than at the beach faces (Fig. 9). However, tide pools seem to be an exception, deserving further studies. Besides sediment size and water depth, the morphology of the coast might also be important; for example, living ostracods in Kuwait Bay were abundant except in the tidal flat areas and the central channel (Al-Abdul-Razzaq *et al.* 1983).

With all these factors affecting ostracods occurrence, it is not surprising that considerable differences among islands have been found (Fig. 7), since all factors might interact differently at each Azorean island, as demonstrated by the more informative Bayesian model, the Island effect (*cf.* DIC values in Table 4). Also, habitat types, by differently combining several of the above mentioned factors (*e.g.* depth, size of the sediment, coastal morphology) were clearly discriminated in this study. Thus, in regards to the shaping of the Recent Azorean ostracod communities, we might be in the presence of large-scale (sea-surface currents, Holocene relative sea-level, storms)

and small-scale processes (geographical location, coastal fragmentation into dynamic cells with impermeable lateral boundaries, morphology of the coast, seafloor stability of the sediments).

CONCLUSIONS

This is the first palaeoecological study of the Recent ostracods from the Azores. So far, only two species had been reported: *Loxoconcha* rhomboidea and *Heterocythereis albomaculata* (Costa, 2010). This work increases the number of benthic shallow-water marine ostracods from this archipelago to 15 species, representing 8 families and 12 genera (*Loxoconcha*, *Neonesidea*, *Xestoleberis*, *Aurila*, *Urocythereis*, *Heterocythereis*, Carinocythereis, *Callistocythere*, Leptocythere, *Semicytherura*, *Lanceostoma* and *Cylindroleberis*; *cf.* Table 3; Fig. 2).

The living assemblages are dominated by specimens of the Loxoconchidae, Xestoleberidae and Hemicytheridae, whereas the dead assemblages are dominated by specimens of the Loxoconchidae, Hemicytheridae, Bairdiidae, Xestoleberidae and Trachyleberidae. The most abundant species, *Loxoconcha* rhomboidea, occurred in both living (0-20m depth) and dead assemblages, and together with *Neonesidea longisetosa* , *Xestoleberis rubens* and *Heterocythereis albomaculata* outlines an assemblage of species that are usually found together in the living assemblages. The shift from life-dominated assemblages in the shallower depths to death assemblages at greater depths is a consequence of significant transport downwards.

Interestingly, no living specimens were found in the samples collected at the beach faces, thus reinforcing the interpretations of Ávila *et al*. (2008) and Ávila (2013) who advocate that at a global scale, sandy beaches in oceanic islands located at temperate latitudes are almost or even completely devoid of life due to historical reasons related with the sea level changes: every time sea level drops below the insular shelf edge as a result of a glacial episode, sand grains slip along the steep insular slope and get lost to the abyssal depths. As expected, all shallow-water species associated to sandy environments are also lost (and thus these species are extirpated from the island). Moreover, this process has happened repeatedly during the several Pleistocene glacial episodes that impacted such oceanic islands, promoting successive events of local disappearances and thus explaining the reduced number (or even the non-existence) of endemic invertebrates associated to the shallow sandy environments of oceanic islands (Ávila, 2013; Ávila *et al*., 2008).

The new information herein provided by the marine ostracods of the Azores and the sustained development of this new research line, for which the present work is a first contribution, will most likely bring novel palaeoecological and taphonomic ideas to the global understanding of the Azorean shallow marine biota, both Recent and fossil.

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ELECTRONIC APPENDIX

Table I. Occurrences of autochthonous ostracods and associated fauna (including allochthonous ostracods) examined in this study. The classification of the environmental energy for each sample was estimated using two different methods: 1) the analysis of the instars (Population structure), based on Whatley (1988); and 2) the classification according to the direct sediment analysis of the grain-size (fine sand - lower energy; medium sand - medium energy; coarse sand and gravel – higher energy) (cf. Fig. 10). The Azores is considered to be a high environmental energy in all sampled sites

Sample	Autochthonous Ostracods	Associated Fauna	Environmental Energy (ostracod instars; Whatley, 1988)	Environmental Energy (sediment grain-size)
1	----	*Loxoconcha rhomboidea* (1 valve), *Carinocythereis whitei* (1 valve). Foraminifera and Bryozoa fragments).	High energy	----
2	----	*Urocythereis britannica* (1 valve). Bryozoa fragments.	High energy	----
3	----	?*Xestoleberis rubens* (1 carapace). Foraminifera.	High energy	----
4	*Loxoconcha rhomboidea*, *Loxoconcha malcomsoni*, *Xestoleberis rubens*, *Xestoleberis* cf. *depressa*.	*Neonesidea longisetosa* (1 carapace and 6 valves), *Semicytherura* sp. (1 valve), *Heterocythereis albomaculata* (1 valve), *Callistocythere* sp. (1 valve). Foraminifera and Bryozoa fragments (genus *Crisia* and *Scrupocellaria*).	Low energy	Medium energy
5	*Xestoleberis rubens*, *Loxoconcha rhomboidea*, *Lanceostoma* sp.	----	High energy	Medium energy
6	*Loxoconcha rhomboidea*, *Loxoconcha malcomsoni*, *Xestoleberis rubens*, *Lanceostoma* sp., *Neonesidea longisetosa*.	*Xestoleberis* cf. *depressa* (3 carapaces and 1 valve), *Aurila convexa* (4 valves), *Lanceostoma* sp. (2 valves), *Semicytherura* sp. (1 valve). Foraminifera, Echinoidea and Bryozoa fragments (genus: *Crisia*, *Scrupocellaria*, *Celleporina*, *Schizomavella*).	High energy	Higher energy
7	*Neonesidea longisetosa*, *Loxoconcha rhomboidea*, *Heterocythereis albomaculata*.	*Aurila woutersi* (1 carapace and 2 valves), *Urocythereis britannica* (3 carapaces). Foraminifera and Bryozoa fragments (genus *Crisia*, *Scrupocellaria*, *Disporella*).	Medium energy	Medium energy
8	*Carinocythereis whitei*, *Loxoconcha rhomboidea*, *Aurila woutersi*, *Neonesidea longisetosa*, *Heterocythereis albomaculata*, *Urocythereis britannica*.	Foraminifera and Bryozoa fragments (genus *Crisia*, *Scrupocellaria*).	Medium energy	Higher energy
9	*Neonesidea longisetosa*.	*Loxoconcha rhomboidea* (5 valves), *Aurila convexa* (2 carapaces), *Urocythereis britannica* (1 valve). Foraminifera and Bryozoa fragments (genus: *Crisia*, *Scrupocellaria*, family: Tubuliporidae).	Medium energy	Medium energy
10	*Neonesidea longisetosa*, *Loxoconcha rhomboidea*, *Xestoleberis rubens*, *Aurila woutersi*, *Heterocythereis albomaculata*.	*Urocythereis britannica* (4 valves), *Xestoleberis* cf. *depressa* (3 carapaces and 1 valve). Foraminifera and Bryozoa fragments (genus *Crisia* and *Scrupocellaria*).	Low energy	Lower energy
11	----	*Leptocythere pellucida* (2 valves), *Callistocythere* sp. (1 carapace). Foraminifera, Echinoidea and Bryozoa fragments.	High energy	----
12	*Carinocythereis whitei*, *Loxoconcha rhomboidea*, *Aurila woutersi*, *Neonesidea longisetosa*.	*Xestoleberis rubens* (6 valves), *Urocythereis britannica* (4 valves), *Leptocythere pellucida* (3 valves), *Heterocythereis albomaculata* (1 carapace and 6 valves), *Carinocythereis whitei* (1 valva). Foraminifera and Bryozoa fragments (genus *Crisia*, *Scrupocellaria*).	High energy	Medium energy
13	----	*Heterocythereis albomaculata* (1 carapace and 2 valves). *Loxoconcha rhomboidea* (1 valve), *Aurila woutersi* (1 valve). Bryozoa fragments (genus *Crisia*, and family: Tubuliporidae).	High energy	----
14	*Heterocythereis albomaculata*, *Xestoleberis rubens*, *Loxoconcha rhomboidea*, *Neonesidea longisetosa*, *Semicytherura* sp., *Lanceostoma* sp., *Aurila convexa*, *Callistocythere* sp., *Carinocythereis whitei*, *Leptocythere pellucida*.	----	Low energy	Medium energy
15	*Heterocythereis albomaculata*, *Lanceostoma* sp., *Loxoconcha rhomboidea*, *Xestoleberis rubens*, *Semicytherura* sp., *Neonesidea longisetosa*. *Aurila convexa*.	----	Low energy	Lower energy
16	*Heterocythereis albomaculata*, *Neonesidea longisetosa*, *Loxoconcha rhomboidea*, *Xestoleberis rubens*, *Loxoconcha malcomsoni*, *Urocythereis britannica*, *Lanceostoma* sp., *Callistocythere* sp.	----	Low energy	Medium energy
17	*Loxoconcha rhomboidea*, *Xestoleberis rubens*, *Callistocythere* sp., *Lanceostoma* sp., *Aurila convexa*, *Heterocythereis albomaculata*, *Neonesidea longisetosa*, *Loxoconcha malcomsoni*.	----	Medium energy	Medium energy