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Salt marsh ostracods on European Atlantic and North Sea coasts: aspects of macroecology, palaeoecology, biogeography, macroevolution and conservation

David J. Horne[1*], M. Cristina Cabral[2,3], Francisco Fatela[2,3] & Michaela Radl[4]

1. *School of Geography, Queen Mary University of London, Mile End Road, London E1 4NS, UK. Email: d.j.horne@qmul.ac.uk*
2. *Instituto Dom Luiz (IDL), Faculdade de Ciências, Universidade de Lisboa, Campo Grande, C1, 1749-016 Lisboa, Portugal. E-mail: mccabral@fc.ul.pt and ffatela@fc.ul.pt*
3. *Departamento de Geologia, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, C6, 1749-016 Lisboa, Portugal.*
4. *WMS WebMediaSolutions GmbH, Primoschgasse 3, 9020 Klagenfurt, Austria*

*Corresponding author

Abstract

Knowledge of European intertidal salt marsh ostracods is reviewed and synthesised, focusing on data from estuaries in Great Britain and the Iberian Peninsula, in order to establish a context for discussion of their taxonomy, biogeography, (macro)ecology, palaeoecology, (macro)evolution and conservation. The combined data support the emerging view that it is possible to recognise distinctive and ecologically significant salt marsh faunas with biogeographical continuity along the Atlantic and North Sea coasts of Europe, which have potential to be recognised in fossil assemblages. The study sites fall within the Temperate North Atlantic Biogeographic Realm, within which some salt marsh ostracod species can be assigned, tentatively, to either the Northern European Seas Province or the Lusitanian Province.

Keywords

Ostracoda, meiofauna, salt marsh, estuary, North Atlantic, faunal province

1. Introduction

Salt marshes are dynamic, intertidal ecosystems on sea and estuary coasts. They constitute a natural physical buffer against the coastal flooding and erosion that may be exacerbated by sea-level rise due to climate change. They provide valuable ecosystem services, functioning as nurseries for commercially important fisheries and feeding grounds for migratory birds. They are the focus of tensions between exploitation and conservation. Ostracods are recognised as abundant and significant components of salt marsh ecosystems, yet understanding of their role (e.g., in terms of biomass and the trophic structure of salt marsh communities) is limited and fundamental aspects such as their taxonomy are still under development. Our studies of intertidal salt marshes on the estuarine coasts of Portugal and Great Britain have documented ostracod assemblages that are taxonomically similar and include species that were hitherto regarded as rare (Horne & Boomer, 2000; Cabral & Loureiro, 2013; Cabral et al., 2017; Radl, 2017). The aim of this paper is to evaluate the emerging view that these ostracod species characterise a distinctive and ecologically significant salt marsh fauna with biogeographical continuity along the Atlantic and North Sea coasts of Europe, with potential to be recognised in fossil assemblages. We approach this task by attempting to synthesise the available information on salt marsh ostracod faunas, focusing particularly on previously unpublished data from our own study sites in Great Britain and Portugal, thus establishing a context in which questions of taxonomy, biogeography, (macro)ecology, palaeoecology, (macro)evolution and conservation are discussed.

2. Methods

Our dataset comprises ostracod species recorded from salt marshes in 12 estuaries: numbers 1–6 are in Great Britain, studied by Horne (1980, PhD thesis), Radl (2017, PhD thesis) and Horne (unpublished data); number 7 is in northern Spain, studied by Martínez-García et al. (2013); numbers 8–12 are in Portugal, studied by Loureiro et al. (2009), Monteiro, 2009 (MSc thesis), Cabral & Loureiro (2013), Cabral et al. (2017) and Cabral (unpublished data). Locations are shown in Figs 1, 2 and 5. Brief descriptions are given below, for further details including sampling methods see Supplementary Information. All ostracod species listed were considered to be alive at the time of collection, based primarily on presence of soft parts; staining with Rose Bengal (added to samples in the field) facilitated the picking of specimens from samples but was found unreliable as an indicator of “live” individuals because even empty shells (valves or carapaces) or dead specimens often contain sufficient organic material to be stained. In a few cases, ”live” presence was confirmed by microscopic observations of live ostracods within hours of collection.

Kyleakin
A small mesotidal estuarine inlet (An-t-Ob) fed by small streams, adjacent to the village of Kyleakin on the Isle of Skye, Scotland (Fig. 1C).

Blackwater Estuary
A small river estuary on the North Sea coast of southeast England; salt marsh surface, creeks and salt pans were sampled at Tollesbury (Fig. 1B1).

Thames Estuary
A mesotidal, major river estuary on the North Sea coast of southeast England; salt marsh was sampled at Two Tree Island (Fig. 1B1).

Gann Estuary
A meso-macrotidal small river estuary in southwest Wales opening into the Bristol Channel and thence the Atlantic Ocean (Fig. 1B3).

Severn Estuary
A macrotidal estuary on the Atlantic coast of southwest Britain. Salt marsh has been sampled at three sites on the southern (English) coast of the estuary (Fig. 1B4): Porlock Weir, a small, sheltered inlet close to the marine end of the outer estuary, Steart in mid-estuary and Severn House Farm in the inner estuary.

Western Yar Estuary
A mesotidal small river estuary on the Isle of Wight, southern England, draining northwards into the Solent and thence into the English Channel which connects the southern North Sea with the Atlantic. Salt marsh has been sampled at two sites (Fig. 1B2), one near the inner, upstream end of the estuary and the other near the mouth.

Tina Menor Estuary
A mesotidal small river estuary in northern Spain (Fig. 5); data are from Martínez-García et al. (2013)

Minho Estuary
A mesotidal river estuary in northern Portugal, opening into the Atlantic Ocean; salt marsh has been sampled on two transects (Fig. 2F), one in the Coura River tributary confluence with the Minho River (CP), the other in the lower Minho estuary (PR).

Lima Estuary
A mesotidal river estuary in northern Portugal, opening into the Atlantic Ocean; salt marsh has been sampled on one transect in the lower estuary (NSR) and two transects in the mid estuary (DAR and BPR) (Fig. 2E).

Tejo Estuary
A mesotidal, major river estuary (Tejo River and Trancão tributary) in southern Portugal, opening into the Atlantic Ocean; salt marsh has been sampled on two transects in the lower Tejo estuary (ALF and ROS) and one transect in the lower Trancão estuary (TRA) 100 m upstream of its confluence with the mid Tejo estuary (Fig. 2D).

Sado Estuary
A mesotidal river estuary in southern Portugal, opening into the Atlantic Ocean; salt marsh has been sampled on three transects in the lower estuary (FAR, CAR, TRO) and one transect in the mid estuary (ALC) (Fig. 2C).

Mira Estuary
A mesotidal river estuary in southern Portugal, opening into the Atlantic Ocean; salt marsh has been sampled on two transects in the lower estuary (PMF and MAS) and three transects in the mid estuary (CBR, MFP and OD) (Fig. 2B).

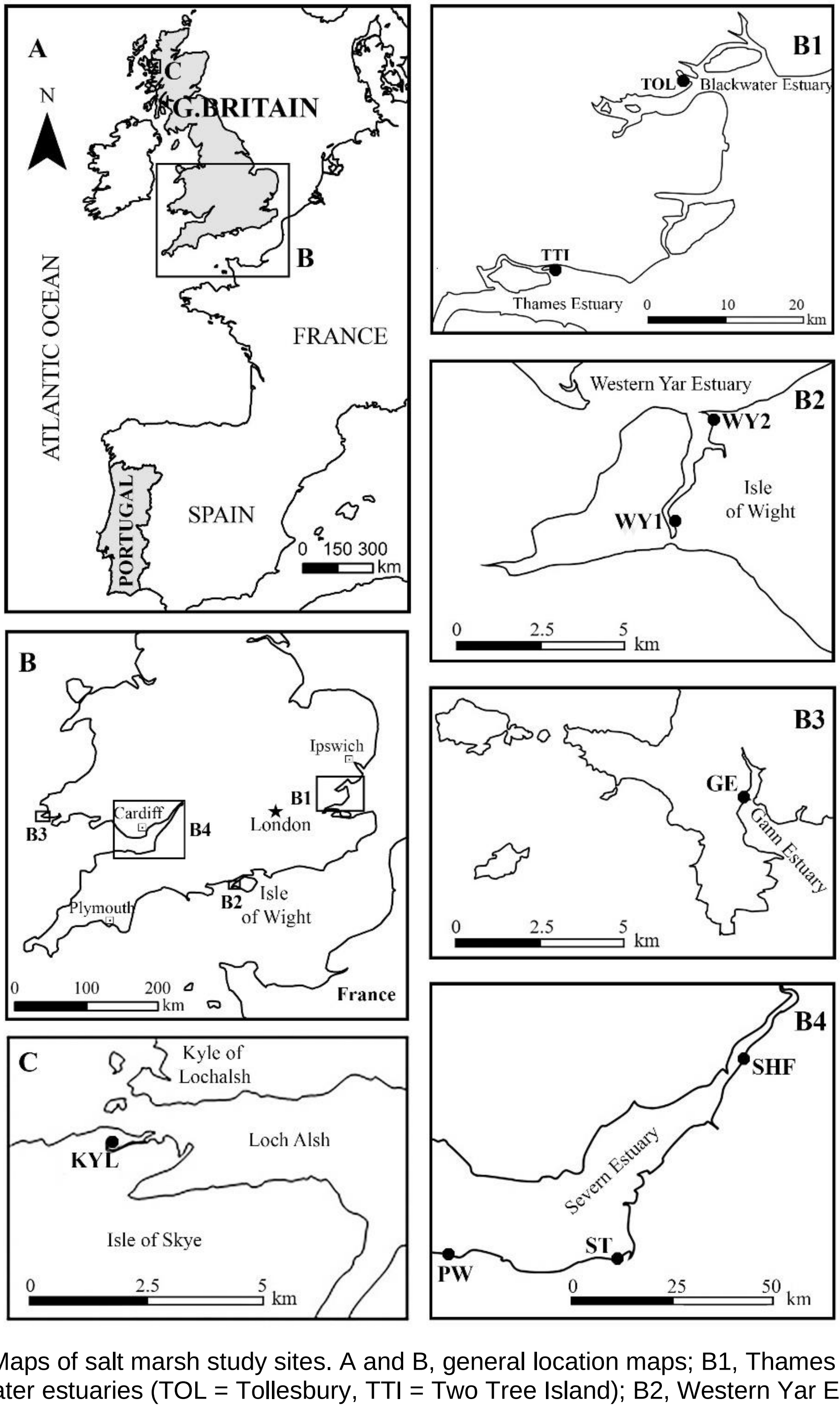

Fig. 1. Maps of salt marsh study sites. A and B, general location maps; B1, Thames and Blackwater estuaries (TOL = Tollesbury, TTI = Two Tree Island); B2, Western Yar Estuary (WY1 = outer estuary, WY2 = inner estuary); B3, Gann Estuary (GE = Gann Estuary); B4, Severn Estuary (PW = Porlock Weir, ST = Steart, SHF = Severn House Farm); C, Kyleakin (KYL= An-t-Ob estuarine inlet).

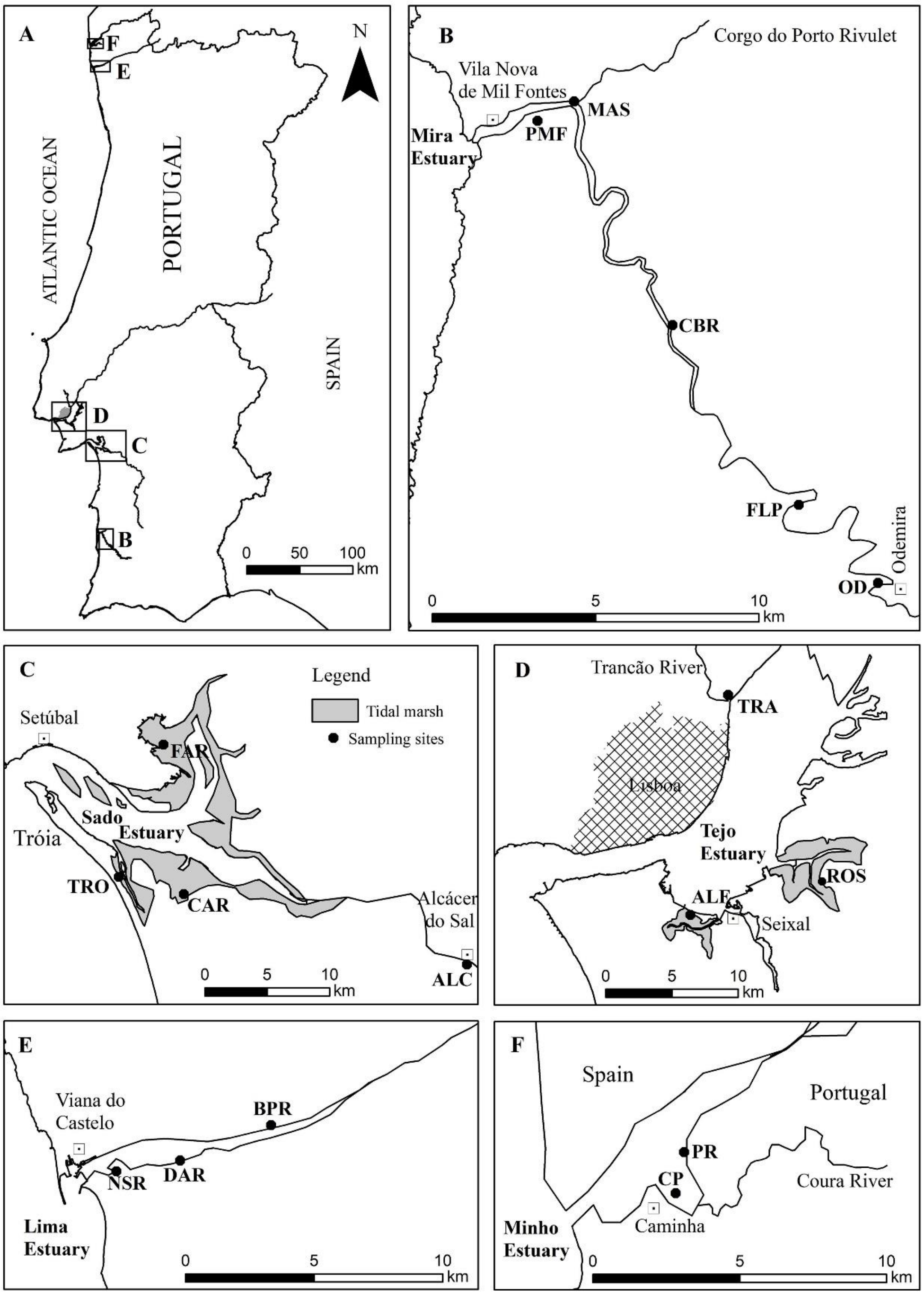

Fig. 2. Maps of salt marsh study sites. A, general location map of Portugal; B, Mira Estuary (PMF = Ponte de Mil Fontes, MAS = Moinho da Asneira, CBR = Casa Branca, FLP = Monte Flor do Pereiro, OD = Odemira); C, Sado Estuary (TRO = Tróia, CAR = Carrasqueira, FAR = Faralhão, ALC = Alcácer do Sal); D, Tejo Estuary (ALF = Alfeite, ROS = Rosário, TRA = Trancão); E, Lima Estuary (NSR = N. Sra. das Areias, DAR = Darque, BPR = Barco do Porto); F, Minho Estuary (CP = Comboios Portugueses, PR = Pedras Ruivas).

3. Results: systematics

A total of 29 ostracod species have been recorded from the salt marsh sites in our dataset, which comprises 11 British and Portuguese estuaries sampled by us and additionally the Tina Menor estuary in northern Spain (data from Martínez-García et al., 2013). Unfortunately our intention of verifying some of the identifications could not be fulfilled in time for the completion and submission of this work, due to restrictions arising from the coronavirus pandemic which prevented us from accessing our collections for several months; taxonomic uncertainties are therefore indicated herein by “cf.” in front of the species name.

Higher classification follows Horne et al. (2002) and Meisch (2000). Species are illustrated with SEM images in Figs 3 and 4. All the Portuguese studied specimens are deposited in the Cabral Collection of the Department of Geology, Faculty of Sciences, University of Lisbon. Specimens from the British studies are maintained in the collections of D.J. Horne and M. Radl at the School of Geography, Queen Mary University of London. Recorded occurrences are listed with reference to the 12 estuaries shown in Figs 1, 2 and 5.

Class OSTRACODA Latreille, 1806
Subclass PODOCOPA Sars, 1866
Order PODOCOPIDA Sars, 1866
Suborder CYTHEROCOPINA Gründel, 1967
Superfamily Cytheroidea Baird, 1850
Family Cytherideidae Sars, 1925
Genus ***Cyprideis*** Jones, 1857
Cyprideis torosa (Jones, 1850) – Fig. 3A; Kyleakin, Blackwater, Severn, Western Yar, Tejo, Sado, Mira.
Family Cytheruridae G. W. Müller, 1894
Genus ***Cytherura*** Sars, 1866
Cytherura gibba (O. F. Müller, 1785) – Fig. 3B; Kyleakin.
Genus ***Hemicytherura*** Elofson, 1941
Hemicytherura videns (G. W. Müller, 1894) – Fig. 3C; Mira.
Family Hemicytheridae Puri, 1953
Genus ***Hemicythere*** Sars, 1925
Hemicythere rubida (Brady, 1868) – Fig. 3D; Blackwater, Western Yar
Family Leptocytheridae Hanai, 1957
Genus ***Callistocythere*** Ruggieri, 1953
Callistocythere murrayi Whittaker, 1978 – Fig. 3E; Minho, Lima, Tejo, Mira.
Genus ***Leptocythere*** Sars, 1928
Leptocythere baltica Klie, 1929 – Fig. 3F; Blackwater, Gann, Minho, Lima.
Leptocythere castanea (Sars, 1866) – Fig. 3G; Kyleakin, Blackwater, Gann, Thames, Western Yar, Tina Menor.
Leptocythere ciliata Hartmann, 1957 – Fig. 3H; Blackwater, Gann, Thames, Severn, Western Yar, Minho, Lima, Tejo, Sado, Mira.
Leptocythere fabaeformis (G. W. Müller, 1894) – Fig. 3I; Western Yar, Mira.
Leptocythere lacertosa (Hirschmann, 1912) – Fig. 3J; Kyleakin, Blackwater, Gann, Thames, Severn, Western Yar, Tejo, Sado, Mira.
Leptocythere porcellanea (Brady, 1869) – Fig. 3K; Severn, Tina Menor, Minho, Lima, Tejo, Sado, Mira.
Leptocythere psammophila Guillaume, 1976 – Fig. 3L; Severn, Minho.
Leptocythere sp. A – Fig. 3M; Minho.
Leptocythere sp. B – Fig. 3N; Minho, Lima, Sado.
Family Loxoconchidae Sars, 1925
Genus ***Elofsonia*** Wagner, 1957
Elofsonia baltica (Hirschmann, 1909) – Fig. 3O; Blackwater, Gann.
Genus ***Hirschmannia*** Elofson, 1941
Hirschmannia viridis (O. F. Müller, 1785) – Fig. 3P; Western Yar.
Genus ***Loxoconcha*** Sars, 1866
Loxoconcha elliptica Brady, 1868 – Fig. 3Q; Blackwater, Gann, Thames, Severn, Tina Menor, Minho, Lima, Tejo, Sado, Mira.
Loxoconcha malcomsoni Horne & Robinson, 1985 – Fig. 3R; Blackwater, Western Yar, Sado, Mira.
Loxoconcha rhomboidea (Fischer, 1855) – Fig. 4A; Western Yar, Mira.
Genus ***Tuberoloxoconcha*** Hartmann, 1973
Tuberoloxoconcha cf. *atlantica* Horne, 1989 – Fig. 4B; Tejo, Mira.

Tuberoloxoconcha sp. 1 – Fig. 4C; Minho.
Family Paradoxostomatidae Brady & Norman, 1889
Genus ***Cytherois*** G. W. Müller, 1884
Cytherois fischeri (Sars, 1866) – Fig. 4D; Blackwater, Gann, Thames, Western Yar, Tina Menor, Minho, Tejo, Sado, Mira.
Cytherois cf. *stephanidesi* Klie, 1938 – Fig. 4E; Western Yar, Minho, Lima.
Genus ***Paradoxostoma*** Fischer, 1855
Paradoxostoma sarniense Brady, 1868 – Fig. 4F; Sado.
Paradoxostoma trieri Horne & Whittaker, 1985 – Fig. 4G; Thames, Western Yar, Sado, Mira.
Family Trachyleberididae Sylvester-Bradley, 1948
Genus ***Basslerites***, Teichert, 1937
Basslerites teres (Brady, 1869) – Fig. 4H; Mira.
Family Xestoleberididae Sars, 1928
Genus ***Xestoleberis*** Sars, 1866
Xestoleberis labiata Brady & Robertson, 1874 – Fig. 4I; Western Yar, Mira.
Superfamily Terrestricytheroidea Schornikov, 1969
Family Terrestricytheridae Schornikov, 1969
Genus ***Terrestricythere*** Schornikov, 1969
Terrestricythere cf. *elisabethae* Horne, Smith, Whittaker & Murray, 2004 – Figs 4J, K; Blackwater, Western Yar, Tejo, Sado, Mira.

Suborder CYPRIDOCOPINA Jones, 1901
Superfamily Cypridoidea Baird, 1845
Family Candonidae Kaufmann, 1900
Subfamily Cyclocypridinae Kaufmann, 1900
Genus ***Cypria*** Zenker, 1854
Cypria cf. *subsalsa* Redeke, 1936 – Fig. 4L; Mira.

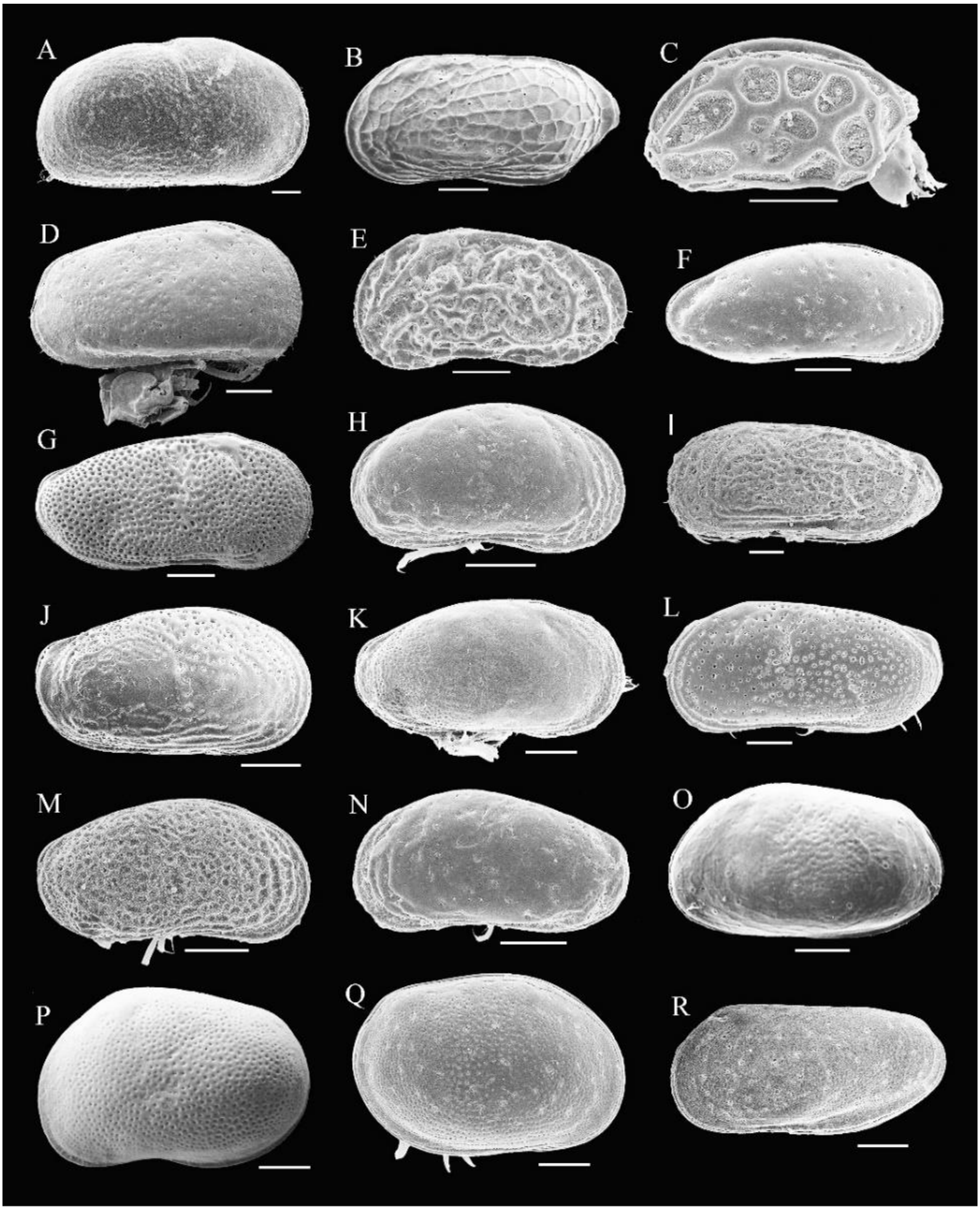

Figure 3. Scanning Electron Micrographs of valves and carapaces of salt marsh ostracod species from Great Britain and Portugal. A, *Cyprideis torosa,* female RV, Sado Estuary (TRO-P1 spr.), Portugal; B, *Cytherura gibba*, male LV, Seaton Delaval, Great Britain, BMNH 1985.171; C, *Hemicytherura videns*, male car. left side, Mira Estuary (PMF-P2 aut.), Portugal; D, *Hemicythere rubida*, male car. right side, Western Yar Estuary (WY1), Great Britain; E, *Callistocythere murrayi*, male LV, Tejo Estuary (ROS-P1 aut.), Portugal; F, *Leptocythere baltica,* male car. right side, Lima Estuary (NSR-P6 spr.), Portugal; G, *Leptocythere castanea*, male car. right side, Thames Estuary (TTI TCP 13), Great Britain; H, *Leptocythere ciliata,* female car. right side, Sado Estuary (TRO-P6 aut.), Portugal; I, *Leptocythere fabaeformis*, male car. left side, Mira Estuary (MAS-P1 aut.), Portugal; J, *Leptocythere lacertosa*, female car. right side, Mira Estuary (PMF-P1 spr.), Portugal; K, *Leptocythere porcellanea*, female car. right side, Sado Estuary (FAR-P2 spr.), Portugal; L, *Leptocythere psammophila,* male car. left side, Minho Estuary (PR-P3 aut.), Portugal; M,

Leptocythere sp. A, female car. right side, Minho Estuary (CP-P2 aut.), Portugal; N, *Leptocythere* sp. B, female car. left side, Minho Estuary (CP-P2 aut.), Portugal; O, *Elofsonia baltica*, male LV, The Fleet lagoon, Great Britain, BMNH 1982.175; P, *Hirschmannia viridis,* female LV, The Fleet lagoon, Great Britain, BMNH 1985.169; Q, *Loxoconcha elliptica*, female car. right side, Minho Estuary (CP-P2 aut.), Portugal; R, *Loxoconcha malcomsoni*, male car. left side, Mira Estuary (PMF-P4 aut.), Portugal. RV = right valve, LV = left valve, car. = carapace, spr. = spring, aut. = autumn; sample numbers or BMNH acquisition numbers are given in parentheses (the latter refer to a collection in The Natural History Museum, London, UK). Scale bars = 100 µm.

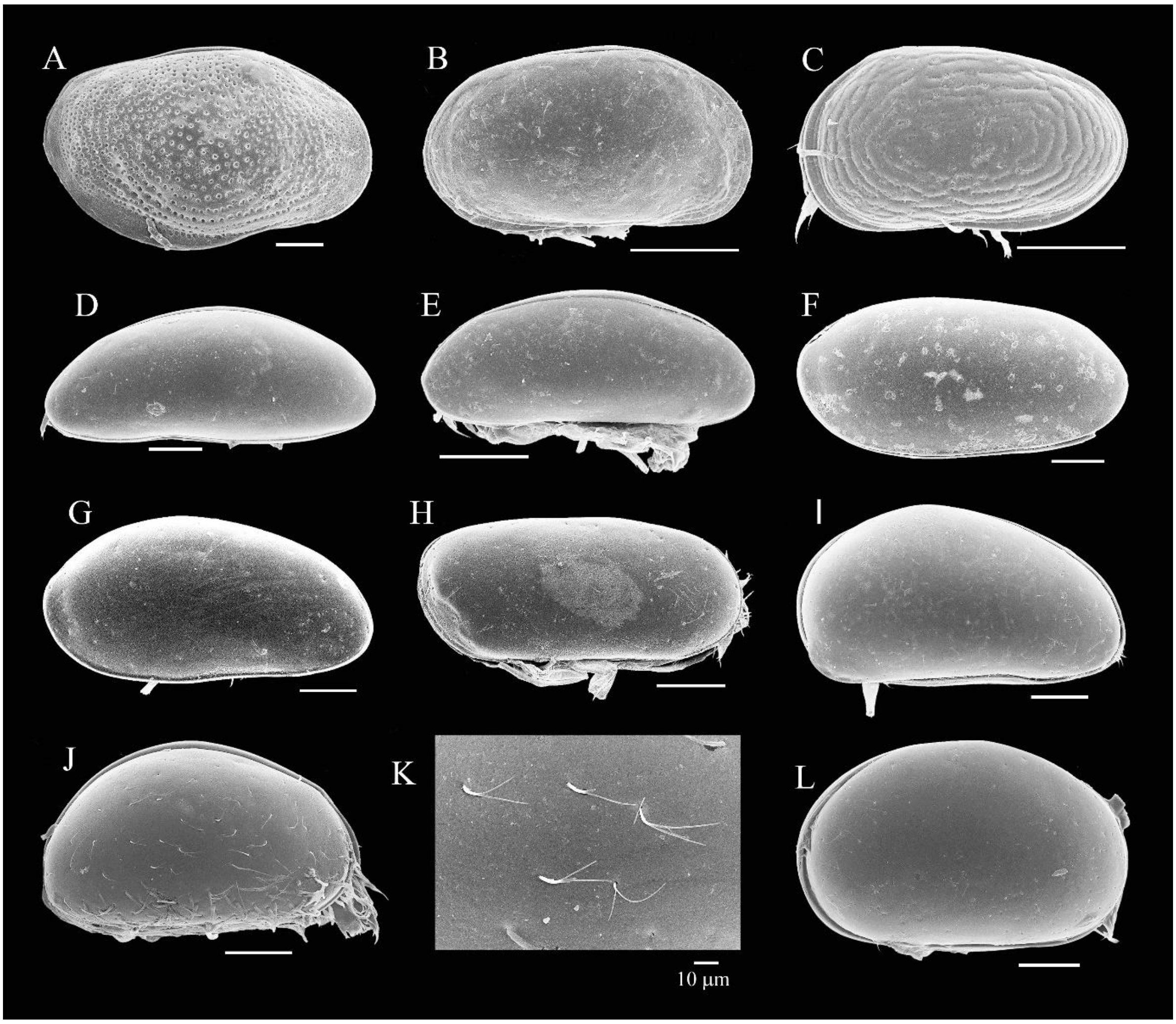

Figure 4. Scanning Electron Micrographs of valves and carapaces of salt marsh ostracod species from Great Britain and Portugal. A, *Loxoconcha rhomboidea*, male car. right side, Mira Estuary (PMF-P5' spr.), Portugal; B, *Tuberoloxoconcha* cf. *atlantica*, male? car. right side, Tejo Estuary (ALF-11 wint.), Portugal; C, *Tuberoloxoconcha* sp. 1, female car. left side, Minho Estuary (CP-P7A aut.), Portugal; D, *Cytherois fischeri*, female car. left side, Mira Estuary (MAS-P1 aut.), Portugal; E, *Cytherois* cf. *stephanidesi*, car. right side, Minho Estuary (PR-P5 aut.), Portugal; F, *Paradoxostoma sarniense*, female car. right side, Sado Estuary (TRO-P2 spr.), Portugal; G, *Paradoxostoma trieri*, female? car. right side, Mira Estuary (PMF-P2 spr.), Portugal; H, *Basslerites teres*, car. right side, Mira Estuary (MAS-P1 spr.), Portugal; I, *Xestoleberis labiata,* female car. right side, Mira Estuary (MAS-P1 aut.), Portugal; J, K, *Terrestricythere* cf. *elisabethae*, car. right side (J) and detail of normal pores with sensilla (K), Sado Estuary (TRO-P6 aut.), Portugal; L, *Cypria* cf. *subsalsa*, car. right side, Mira Estuary (FLP-P3 wint.), Portugal. RV = right valve, LV = left valve, car. = carapace, spr. = spring, aut. = autumn; sample numbers are given in parentheses. Scale bars = 100 µm except for K = 10 µm.

4. Results: synthesis

Our combined dataset comprises 29 species, of which 24 were recorded at Portuguese sites and 20 at British sites (Fig. 5). In their review of British salt marsh ostracods Horne & Boomer (2000) listed 17 species recorded in salt marsh environments. Our more recently acquired British dataset confirms 16 of these, the exception being *Callistocythere murrayi* which we have not found living at any of our sites (but which is included in our Portuguese dataset); it also adds *Leptocythere ciliata*, *Leptocythere fabaeformis*, *Terrestricythere* cf. *elisabethae* and *Xestoleberis labiata* to the list.

The combined ostracod species records from each estuary were visualised geographically (Fig. 5) in order to assess the extent to which a distinctive and ecologically significant salt marsh fauna, with biogeographical continuity, can be recognised on the Atlantic and North Sea coasts of Europe. Full species lists for sampling sites are given in Supplementary Information. All 12 of our sites are within the Temperate North Atlantic Biogeographic Realm of Spalding et al. (2007), with sites 1–6 situated in the Northern European Seas Province and sites 7–12 in the Lusitanian Province.

Three Salt Marsh Ostracod Faunas (SMOF) of potential biogeographical significance can be recognised (Fig. 5), as summarised below.

1. A Temperate North Atlantic SMOF comprises species that are distributed throughout the study region: *Cyprideis torosa, Cytherois fischeri, Leptocythere ciliata, Leptocythere lacertosa, Leptocythere porcellanea, Loxoconcha elliptica, Loxoconcha malcomsoni, Loxoconcha rhomboidea, Paradoxostoma trieri* and *Terrestricythere* cf. *elisabethae*.

2. A Northern European Seas SMOF comprises species distributed through the northern part of the study region: *Cytherura gibba, Elofsonia baltica, Hemicythere rubida, Hirschmannia viridis, Leptocythere baltica, Leptocythere castanea* and *Leptocythere psammophila.*

3. A Lusitanian SMOF comprises species distributed through the southern part of the study region: *Basslerites teres, Callistocythere murrayi, Cypria* cf. *subsalsa, Cytherois* cf. *stephanidesi, Hemicytherura videns, Leptocythere fabaeformis, Leptocythere* sp. A*, Leptocythere* sp. B*., Paradoxostoma sarniense, Tuberoloxoconcha* cf. *atlantica, Tuberoloxoconcha* sp. 1. and *Xestoleberis labiata.*

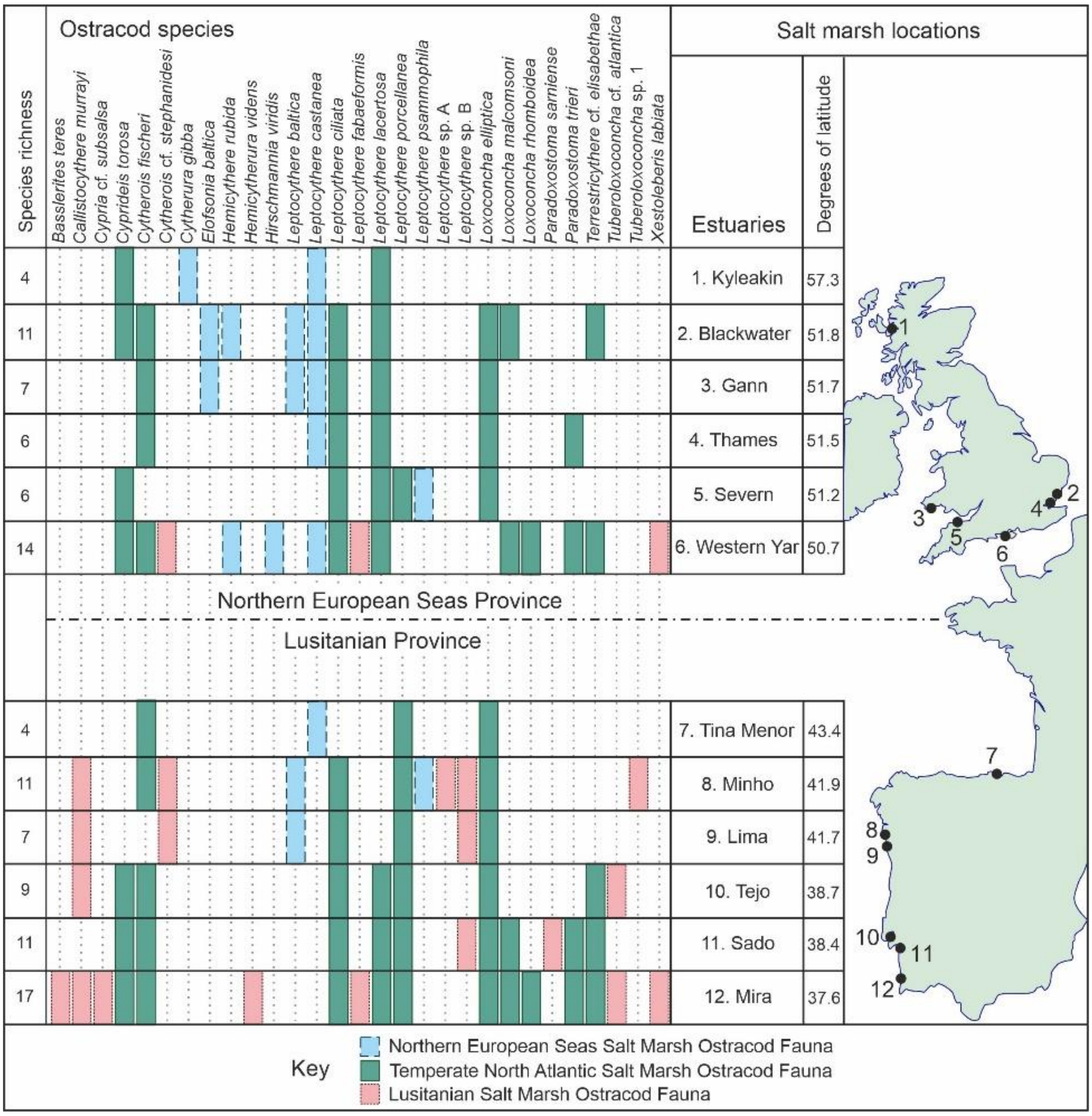

Figure 5. Biogeographical distributions of salt marsh ostracod species on the Iberian and British coasts. In addition to our own study sites from Great Britain (1–6) and Portugal (8–12) we have included one northern Spanish site (7) not shown in Figs 1 and 2, using data from Martínez-García et al. (2013). The vertical bars indicating species presence at sites are coloured according to the three salt marsh faunas described in the text. The grey vertical dotted lines are an aid to reading the figure and do not indicate presence of species at sites. A summary data table can be found in Supplementary Information.

The wide-ranging *Loxoconcha elliptica*, *Leptocythere ciliata* and *Leptocythere lacertosa* are perhaps the most characteristic species of the Temperate North Atlantic SMOF. The second and third SMOFs correspond approximately to the Northern European Seas (best characterised by *Leptocythere castanea*) and Lusitanian (characterised by at least one of *Callistocythere murrayi*, *Leptocythere fabaeformis* or *Leptocythere* sp. B) provinces respectively, but with considerable overlap that limits the utility of ostracod assemblages for locating the boundary between the two provinces. It must be noted, however, that while the above-mentioned species may be regarded as characteristic of salt marsh ostracod faunas, many of them can also be found living in other intertidal or shallow subtidal environments. Several species apparently restricted to one province as far as salt marshes are concerned have been recorded in the other province in other low intertidal or shallow subtidal habitats. For example, *Callistocythere murrayi* and *Cytherois stephanidesi,* apparently restricted to non-British sites in our salt marsh dataset, do occur in other habitats on southern British (English and Welsh) coasts (Athersuch et al., 1989). *Tuberoloxoconcha atlantica* was first described from a northwestern British locality in Scotland (Horne, 1989) although, as yet, its only salt marsh records are in Portugal. In the Severn Estuary, *Leptocythere castanea* was recorded abundantly and frequently in a high intertidal rock pool but not found in any salt marsh samples. Two species, *Hemicythere rubida* and *Loxoconcha malcomsoni*, show particular potential as salt marsh indicators because they are almost unknown in any other environment, but they have so far only been recorded in two and four, respectively, of the 12 estuaries in our dataset. *Leptocythere fabaeformis* can be regarded as a Lusitanian form that ranges as far north as the southern British coast (Western Yar Estuary), but in Portugal it has only been recorded alive in the lower Mira Estuary and then only in the adjacent tidal flat, not on the salt marsh itself. In SW France (Arcachon Basin), Yassini (1969) found this species living in sandy-muddy tidal flats (low "slikke") rich in plants (*Zostera* spp.), at depths of 0-10 m. On the basis of the occurrences shown in Fig. 5, *Leptocythere porcellanea* might be regarded as characteristic of the Lusitanian SMOF, since it was found in all of the Portuguese estuaries, from tidal flat to high marsh and in all salinity ranges, while British salt marsh records are restricted to the Severn Estuary. However, it has been found living in other estuarine habitats in Britain and as far North as the Baltic Sea (Athersuch et al., 1989); it is a senior synonym of *Leptocythere ilyophila* Hirschmann (first described from the Gulf of Finland), under which name it was commonly recorded prior to taxonomic revision by Horne & Whittaker (1985). Further study is needed to verify its distribution.

Taxonomic diversity in marine/estuarine biota is well-known to be influenced by salinity at local scales, such as within an estuary (e.g., Whitfield et al., 2012), while at wider, biogeographical scales it can vary in relation to latitude (e.g., Gray, 2001; Schoch et al., 2006). Our attempts to explore the extent to which such relationships can be recognised in salt marsh ostracod faunas are hindered by the patchiness of our combined dataset that is largely a consequence of the different research aims and designs of the British and Portuguese investigations from which it is derived. For example, useful salinity measurements are available for the Portuguese sites, which were the focus of ecological studies, but were not recorded for several of the British sites where contextual data collection focused primarily on salt marsh floral zonation and precise elevation, for the purpose of testing hypotheses of salt marsh response to sea-level change. Nevertheless, some potentially interesting preliminary results may be presented here.

Analyses of the influence of salinity is limited to the Portuguese sites as we lack adequate equivalent data for the British sites. Figure 6A and 6B compare species richness with maximum and minimum salinity respectively at the Portuguese study sites. For the same Portuguese sites as for the salinity plots, species richness is plotted against intertidal level (elevation) (Fig. 6C) and a similar plot (Fig. 6D) compares species richness with intertidal level (elevation) for three British sites (Blackwater, Thames and Gann estuaries). Note, however, that the British and Portuguese datasets are not directly comparable; the British data are for high, mid and low salt marsh, while the Portuguese data are for salt marsh (high and low) and tidal flat (upper).

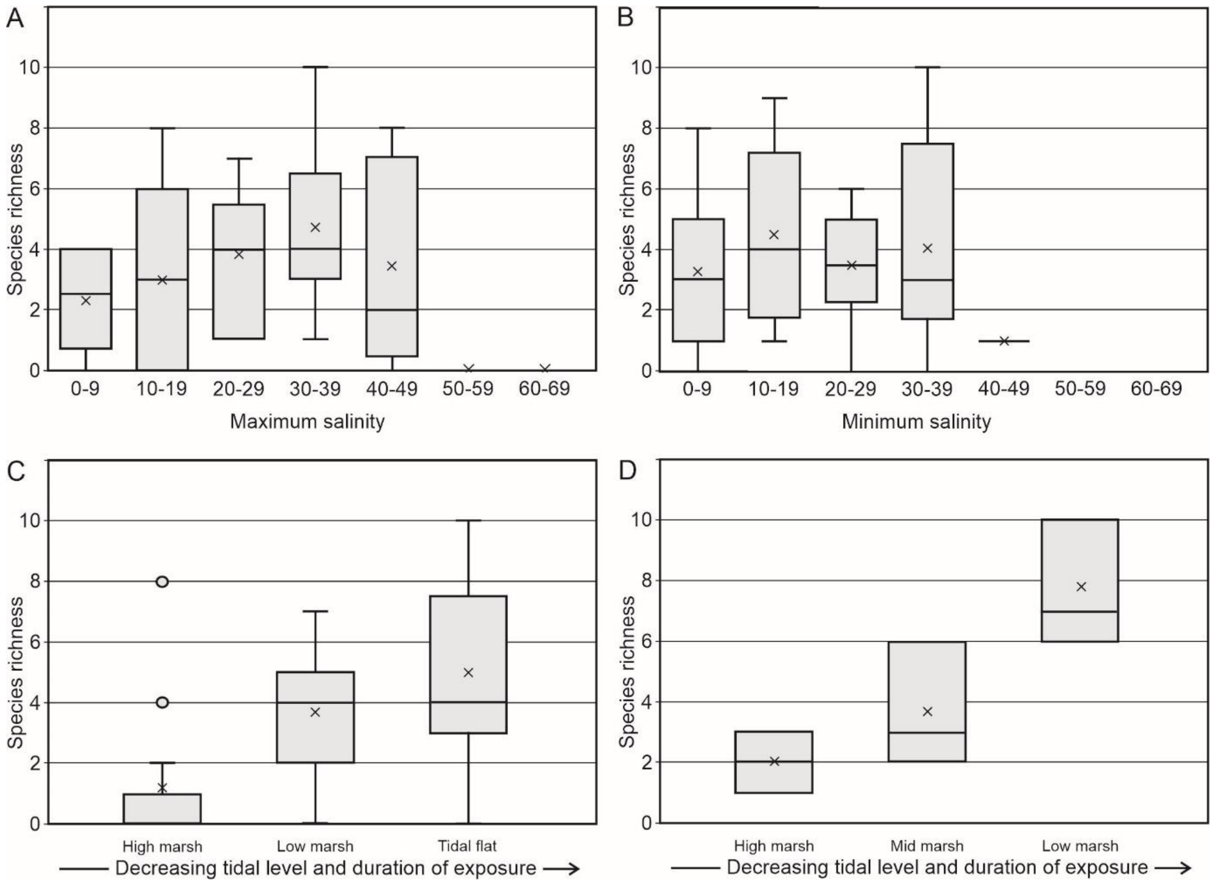

Figure 6. Box-plot comparisons of salt marsh ostracod species richness with: (A) maximum salinity: (B) minimum salinity; (C) elevation/intertidal level (tidal flat lowest, high marsh highest), note that two high marsh sites with anomalously high species richness (Mira Estuary, PMF: 8; Tejo Estuary, ALF: 4) are shown in as isolated dots; (D) elevation/intertidal level (high, mid and low marsh). A-C are based on combined data from five Portuguese estuaries (Lima, Minho, Mira, Sado and Tejo); D is based on combined data from three British estuaries (Blackwater, Gann and Thames). Salinity in practical salinity units (rounded to the nearest whole number). A summary data table can be found in Supplementary Information.

The complexity of the combined influences of tidal exposure (which varies with diurnal and lunar cycles and is subject to occasional perturbations by floods and storm surges) and salinity (which varies with tide cycles and also responds to seasonal variability in river discharge) renders meaningful analyses extremely difficult, requiring a more comprehensive dataset than we currently have at our disposal. Nevertheless, the crude analyses of our Portuguese data (Fig. 6A-C) show some indications that species richness increases with maximum salinity and decreases with elevation (i.e., increasing duration of exposure at low tide); the decline of species richness with increasing elevation/exposure is also shown by the British data (Fig. 6D). The reversal of the trend at the highest salinities (Fig. 6A, B: salinity 40 to 49) may be attributed to hypersalinity due high evaporation rates during low tide on exposed high salt marsh sites, resulting in extreme variations that can be tolerated by few species.

The different occurrences of the wide-ranging species are probably related to the physical and chemical characteristics of the salt marshes and estuaries, each species having its own particular requirements. Factors such as substrate, pH, salinity and duration of exposure during low tide are influenced by estuary morphology and hydrodynamics and are likely, in turn, to influence ostracod distribution. In the Mira Estuary in Portugal, clear differences were observed between inner to mid (less saline) and outer (more saline) estuary transects (Fig. 7). Here species richness (SR) strongly increased from the OD transect (SR = 3), where salinity values of interstitial waters are very low (from 0.0 to 3.8), to the PMF transect (SR = 14), with a salinity range of interstitial waters from 23.2 to 47.5.

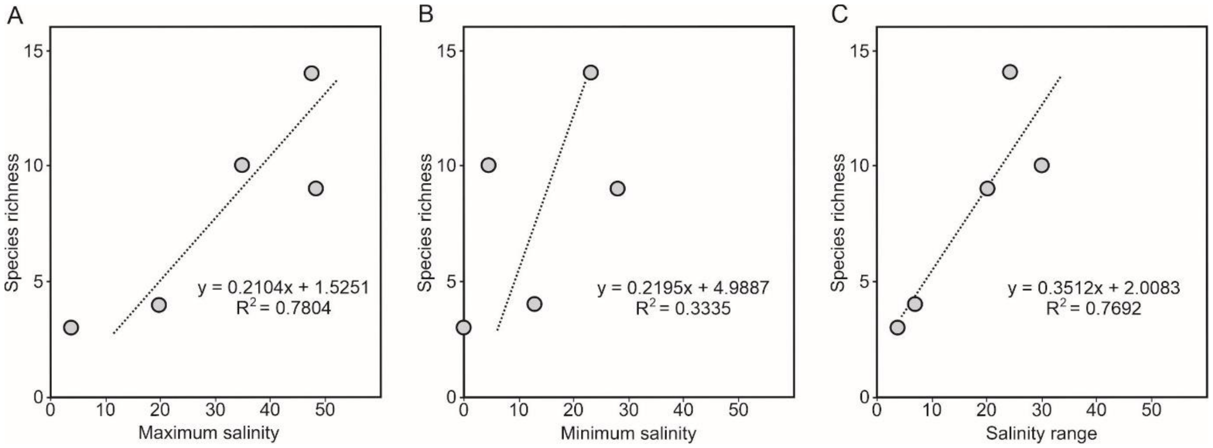

Fig. 7. Mira Estuary salt marsh ostracods; plots of species richness against (A) maximum salinity, (B) minimum salinity and (C) salinity range (in practical salinity units, rounded to the nearest whole number) of the combined values for each of five transects. Summary data can be found in Supplementary Information.

Both of the plots in Fig. 7 show species richness increasing with salinity, although the minimum salinity trend line has a low R^2 value (0.33) compared to those of the maximum salinity (0.78) and salinity range (0.77) trend lines. *Leptocythere porcellanea* and *Cytherois fischeri* are common to all five transects, with *L. porcellanea* present from the tidal flat to the high marsh, whereas *C. fischeri* was only found in tidal flat and low marsh, pointing to a higher tolerance of *L. porcellanea* to exposure. Surprisingly, *Loxoconcha elliptica*, a geographically wide-ranging species that is present in all the studied Portuguese estuaries (and frequently abundant) is absent from the lower estuary transects where species richness is higher; possibly it has a competitive disadvantage compared to other species.

On a wider, biogeographical scale, a plot of species richness against latitude (Fig. 8) for the 12 sites shown in Fig. 5 provides weak support for the hypothesis of a latitudinal gradient in taxonomic diversity (species richness declines towards higher latitudes).

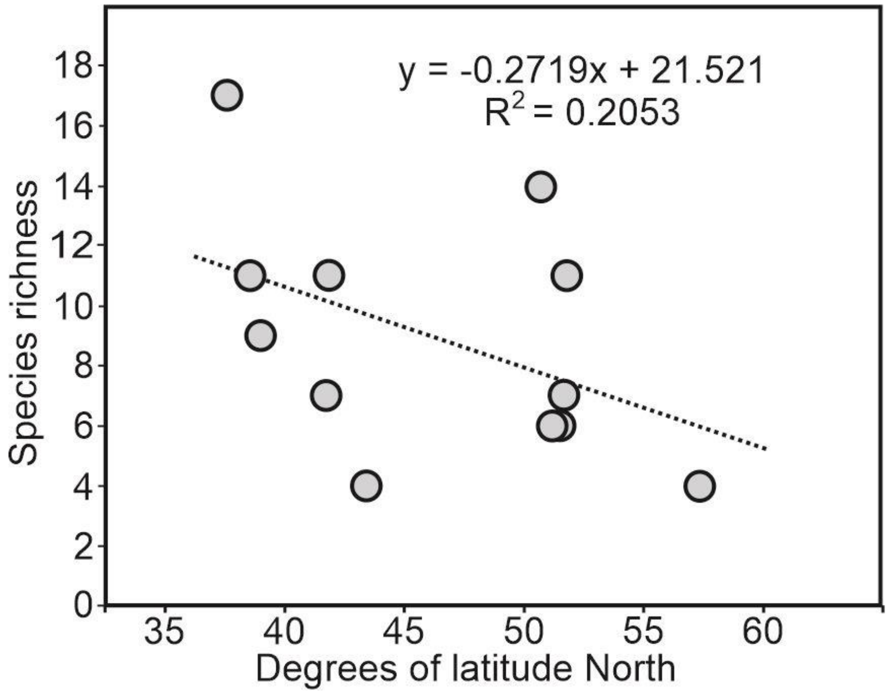

Fig. 8. Plot of species richness against latitude for the 12 sites shown in Fig. 5. A summary data table can be found in Supplementary Information.

5. Discussion

5.1 (Macro)ecology and palaeoecology

As already noted above, our SMOFs are not ecologically discrete but share taxa with other estuarine and coastal marine habitats, but they are nevertheless recognisable entities characterised by particular associations of species. The recognition of our SMOFs in fossil ostracod assemblages is therefore likely to be rendered difficult by (1) the fact that many of the component species also live in coastal marine/estuarine habitats other than salt marshes and (2) the transport and mixing of assemblages that is prevalent in macro- and meso-tidal settings. Such issues can be overcome, however, by careful consideration of the taphonomy and palaeoecology of the dominant taxa in fossil assemblages.

For example, channel-fill deposits east of Selsey Bill (0^o 47’ 18” W, 50^o 43’ 34” N) on the southern British coast have yielded diverse ostracod assemblages comprising predominantly marine and brackish water taxa (Whatley & Kaye, 1971), originally assigned to the Ipswichian (Eemian) interglacial (MIS5e) but now thought to represent an older (MIS7) interglacial (Whittaker & Horne, 2009). The lower part of the sequence was characterised by high diversity marine/brackish assemblages (c. 50 species) thought to have been deposited at the seaward end of a large estuary, but the upper part displayed low diversity brackish water assemblages (14 or fewer species) dominated by *Cyprideis torosa* and *Loxoconcha elliptica* (together comprising 60-70% of the assemblage in each sample) as well as other components of our Temperate North Atlantic SMOF (*Cytherois fischeri, Leptocythere lacertosa, Leptocythere porcellanea, Loxoconcha rhomboidea*), Northern European Seas SMOF (*Elofsonia baltica, Hirschmannia viridis, Leptocythere castanea*), with *Basslerites teres* of the Lusitanian SMOF as a very minor component of the lowest of the three samples. Note that some taxonomic names used by Whatley & Kaye (1971) have been corrected with reference to their appended taxonomic notes and synonymies provided by Athersuch et al. (1989). Moreover, the high abundance of specimens allowed Whatley & Kaye to demonstrate that the predominant species in these upper three assemblages all display population age structures with adults and juveniles, indicative of *in situ* or “indigenous” populations. Our present knowledge therefore confirms the conclusion of Whatley & Kaye (1971) that the upper part of the sequence represents deposition in a muddy salt marsh environment with reduced salinity. We may suggest, additionally, that the climate of the upper part of the sequence was not significantly warmer than that of today (Lusitanian SMOF taxa being absent except for the minimal presence of one species in the lowest of the three assemblages). Interestingly, the underlying outer estuary assemblages include not only the Lusitanian species *Semicytherura arcachonensis* and *Basslerites teres* but also *Hemicythere rubida*, a component of our Northern European Seas SMOF.

Another channel fill at Earnley, west of Selsey Bill, has yielded diverse marine and brackish water ostracod assemblages. The age of this channel fill is a matter for debate; at one time it was thought to be of similar age to the channel deposits on the east side of Selsey Bill (i.e., Ipswichian, MIS5e; Horne & Robinson, 1982) but was later considered by West et al. (1984), on the basis of pollen assemblages, to be of Hoxnian interglacial (MIS11) age or older, and subsequently assigned to the MIS9 interglacial (Whittaker & Horne, 2009). Of particular interest in the Earnley assemblages is the occurrence of two species previously regarded as "rare" but now recognised as important components of European Atlantic and North Sea coast salt marsh fauna: *Hemicythere rubida* (listed and illustrated as "*Cythere*" *rubida*) and *Loxoconcha malcomsoni* (listed as *Loxoconcha cuneiformis*, a preoccupied name later replaced with *L. malcomsoni* (Horne & Robinson, 1982, 1985)). Although salt marsh species are abundant (e.g., *Cyprideis torosa*, *Loxoconcha elliptica* and *Leptocythere castanea*) the assemblages also contain taxa more typical of lower intertidal sedimentary and phytal associations such as *Pontocythere elongata*, *Hemicythere villosa* and *Heterocythereis albomaculata*, so they have been interpreted as representing a coastal zone more seaward than the salt marsh (West et al., 1984). The more seaward zone could be the tidal flat adjacent to the salt marsh; in the Lima Estuary (NSR transect, the one closer to the mouth of the river) we found a very similar allochthonous assemblage (valves, frequently juveniles) with *Aurila convexa, A. woutersi, Cytheropteron dorsocostatum, Hemicythere villosa, Hemicytherura cellulosa, H. hoskini, Heterocythereis albomaculata, Palmoconcha laevata, Roundstonia robertsoni*, and others, together with the typical salt marsh assemblage (*Leptocythere baltica*, *L. ciliata*, *L. porcellanea*, *Loxoconcha elliptica*) in the tidal flat. Similarly, in the Mira Estuary (PMF and MAS transects, the two lower estuary ones) the observed ostracod assemblages were very diverse in the tidal flats, with abundant allochthonous (marine) ostracods, generally represented by rare (and often worn) valves of each species. In the PMF and MAS transects, both in autumn and spring, at least 50 marine species were identified. Loureiro et al. (2009) demonstrated clear differences between the allochthonous and autochthonous species assemblages in the Mira Estuary PMF (lower estuary) and CBR (mid estuary) transects.

5.2 Biogeography

The distributions illustrated in Fig. 5 demonstrate that there is not only a characteristic SMOF that can be recognised from southern Portugal to northern Britain, but that it can also be subdivided into two more geographically restricted SMOFs corresponding respectively (though not precisely) to the Temperate North Atlantic Biogeographic Realm, Lusitanian Province and Northern European Seas Province of Spalding et al. (2007). On geological time scales salt marshes are ephemeral environments subject to continuous recycling through rapid growth and destruction in dynamic coastal settings (Fagherazzi, 2013). Present-day salt marshes are young features and although their distribution and development within each estuary must have varied considerably, especially in historical times as the influence of human activity increased, none can have existed, even near these sites, much before the early Holocene when post-glacial sea-level rise began to approach its present elevation c. 10,000 years ago (Leorri et al., 2013; Behre, 2007). Salt marshes are also patchy, discontinuous environments separated by significant gaps, so maintaining continuity of fauna between them must present similar challenges to those seen in lake and island communities. These considerations may go some way to explaining why most components of SMOFs are also found in other marine and brackish water coastal environments and there are few, if any, that are unique to salt marshes. European salt marsh ostracods presumably survived the last glacial period in more southerly refugia before dispersing northwards again as climate warmed in the Late-glacial and Holocene. Differential rates and success of dispersal and colonisation would account for the different, overlapping ranges of the various species, suggesting a Gleasonian response (range adjustments by individual species) to climate change; on the other hand the continuity of certain associations that is apparent in assemblages of past interglacials, as discussed above, might be regarded as supporting evidence for a Clementsian response (i.e., range adjustment of a community) (Eliot, 2011; Hortal et al., 2012). Our combined dataset is too inconsistent and incomplete to support rigorous testing of such ideas, but it is to be hoped that future improvements may facilitate detailed analyses of metacommunity structures in terms of Clementsian and Gleasonian distributions, such as those carried out on river and riparian invertebrates by Tonkin et al. (2016) and by Heino et al. (2015) for a range of freshwater biota.

Why are some species recorded in both British and southernmost Portuguese localities, but apparently absent from more northerly estuaries of the Iberian Peninsula? In the Tina Menor estuary, out of a total of more than 1800 living specimens from 16 samples, only a single live specimen of *Cyprideis torosa* was recorded (from intertidal silty sand in the middle estuary) (Martínez-García et al., 2013). While this result may be to some extent influenced by limited sampling of salt pans and creek bottoms, we consider it to be most likely related to the dynamics of the estuary and the substrate, observing that the species has a preference for muddy or muddy sand sediments (Cabral et al., 2017). Indeed, although salt pans were never sampled in any Portuguese estuary, living *C. torosa*, was found to be relatively abundant and alive in Tagus and Sado estuaries, while in the Minho and Lima estuaries (both with sandy tidal flat and low marsh) only one or two transported valves were recovered; in the Mira estuary it was only found in sporadic sampling in March 2014, mainly on silty or silty sand substrates (Loureiro et al., 2009).

5.3 (Macro)evolution

Ostracods have the best fossil record of any arthropod group, encompassing 485 million years from Ordovician to Recent. How can we explain the paradox that the genus *Terrestricythere* is evidently a representative of an ancient lineage with Palaeozoic origins (Horne et al., 2004) yet has no recognised fossil record? Perhaps it is because the high intertidal environments that it inhabits have poor preservation potential. The other salt marsh species are all members of families (particularly the Leptocytheridae and Loxoconchidae) that diversified in the Cenozoic and have likely radiated into salt marsh environments over the past few tens of millions of years; *Terrestricythere,* on the other hand, may represent a lineage that has become super-adapted to the high intertidal environment over hundreds of millions of years (Horne, 2003; Horne et al., 2004). Further study of this enigmatic genus has significant potential to shed light on the evolutionary history of the Ostracoda.

5.4 Rare species and conservation

A number of previously little-known species have turned out to be relatively abundant and widespread on salt marshes, suggesting that their apparent rarity was a consequence of a lack of sampling of their preferred environments.

Loxoconcha malcomsoni was originally described on the basis of a single specimen by Malcomson (1886) as *L. cuneiformis*; since this was a preoccupied name, Horne & Robinson (1985) renamed the species after Malcomson, regarding it as an extinct Pleistocene form. Living populations were first discovered at two British localities, on the lower edges of salt marshes in the Western Yar Estuary (Isle of Wight) and Stiffkey (Norfolk) (Horne & Boomer, 2000). Subsequently it has been recorded living on salt marsh in the British Blackwater Estuary (Radl, 2017; and herein) and in the Portuguese Sado and Mira estuaries (Loureiro et al., 2009; Cabral & Loureiro, 2013; Cabral et al., 2017; and herein). It has also been recorded in the Azores archipelago in the mid-North Atlantic, living in intertidal pools with sandy sediments (Meireles et al., 2014a, b).

Hemicythere rubida was known only from sporadic occurrences in western Scotland, southern England and Ireland, although there were suggestions that it had been under-reported due to confusion with another brackish-water ostracod, *Cytheromorpha fuscata* (Athersuch et al., 1989). Subsequently, however, living populations were found in the Western Yar Estuary (Isle of Wight) (Horne & Boomer, 2000; and herein); in the Blackwater Estuary at Tollesbury, Radl (2017) found only empty shells, but Horne (herein) found living specimens in September 2019.

Leptocythere ciliata, once considered rare and known only from the North Sea coast of Germany, where it was first described by Hartmann (1957) as a subspecies of *L. lacertosa,* and from Porlock Weir in SW Britain (Horne, 1980), has now been recorded in five British and five Portuguese estuaries thanks to particular attention to the sampling of salt marshes (Cabral and Loureiro, 2013; Cabral et al., 2017; and herein). To these we tentatively add a Moroccan record from Nachite et al. (2010) whose ostracod fauna from the Tahadart estuary includes a species they identified as *Leptocythere* cf. *lagunae*, but their figured specimen bears a close resemblance to *L. ciliata.*

Terrestricythere elisabethae was first described from the surface of high-intertidal reed beds with oak leaf litter on a tributary of the Hamble Estuary and additional populations were found in similar settings in the Beaulieu Estuary, both in southern England (Horne et al., 2004). The discovery of these first British records of a genus known mainly from the northwestern Pacific region raised questions about whether the British populations represented a native species previously overlooked because of its unusual habitat and mode of life (unusually, these ostracods are able to crawl in exposed, damp habitats, dragging their own small blob of water with them), or an introduced and potentially invasive species. The former explanation is supported by subsequent finds of living populations on the mid to high salt marsh in the Blackwater and Western Yar estuaries in Britain (Radl, 2017; and herein) and the Tejo, Sado and Mira estuaries in Portugal (Cabral & Loureiro, 2013; Cabral et al., 2017; and herein). However, there remains uncertainty as to whether all these populations belong to the same species, a question that will only be resolved by further study of dissected soft parts. There may be some ecological differences; in the Blackwater Estuary living specimens were found not only among salt marsh plant leaf litter but also crawling on the roots of *Aster tripolium* to several cm depth in the salt marsh sediment, while at the southern site (WY1) in the Western Yar Estuary it was collected from oak leaf litter among reeds, a setting very similar to that at the original site on the Hamble, as well as in the sediment; in Portugal living specimens were always found in strongly vegetated sediment. Future investigations might seek to supplement comparative morphology with molecular studies to evaluate the genetic similarity or divergence of the different populations of *Terrestricythere.*

How do you determine whether a rare species is a potentially endangered native, or introduced and potentially invasive? In any particular geographical region there is a risk that a species may become the focus of inappropriate conservation efforts simply because it is rare and not known anywhere else in the world. The cataloguing of global biodiversity is far from complete, particularly with regard to small meiofaunal crustaceans such as ostracods. It is possible that in some cases, by striving to protect a rare species, conservationists may inadvertently be helping an introduced organism to gain a foothold. Invasive species, whether introduced directly by human activity or as a result of range changes in response to climate change, can pose threats to indigenous taxa by predation, hybridisation or competitive replacement. Most discussions of invasive crustaceans focus on larger taxa (e.g., crayfish, crabs, amphipods) (e.g., Van der Velde et al., 2000; Jaźdźewski & Konopacka, 2000); ostracods are rarely considered, either due to perceived difficulties of studying and identifying them, or perhaps because (if not simply overlooked) they are thought to be too small to be threatening. Bohonak & Jenkins (2003), in their review of dispersal in freshwater invertebrates, define invasion as: “Colonization that impacts other species already inhabiting an area”. If there are no demonstrable or recognised impacts on other species, then even those species that can be shown to have arrived in an area relatively recently should perhaps be regarded only as colonisers, not invaders.

There is only one well-documented case of an ostracod invasion of British waters, that of the myodocopan *Eusarsiella zostericola* which was introduced with American oysters to the marine coastal waters of SE England during the last century (Kornicker, 1975; Bamber, 1987), but there are several podocopan ostracod species in the salt marsh fauna that have been regarded as rare, in the sense that they were known only from a very few locations. As noted above, when *Terrestricythere* was first found in Britain, it was thought possible that it might have been introduced to Britain by human activity. The subsequent recognition of several additional populations in Britain and Portugal does not rule out the possibility that it was introduced, perhaps some time in the last century and in more than one location, and has spread widely on British and Portuguese coasts, but it also lends support to the alternative view that it is native to Europe and has simply been overlooked in the past due to its unusual habitat and mode of life. Ostracods have the advantage of a fossil record, offering the potential for establishing how long a particular species has inhabited a region. In the case of *Loxoconcha malcomsoni* and *Hemicythere rubida*, for example, their fossil occurrences in British Pleistocene deposits argue that they could be regarded as native species. *Loxoconcha malcomsoni* has also been found in two Portuguese Holocene cores (Cabral & Loureiro, 2013; Cabral et al., 2016). *Terrestricythere*, as noted above, has no known fossil record.

6. Conclusions and recommendations for future research

We conclude that, as we suspected, distinctive, characteristic salt marsh ostracod faunas (SMOFs) can be recognised. This finding has potential utility in palaeoenvironmental and palaeoclimatic reconstruction, as with due care and caution it is possible to recognise these SMOFs in Pleistocene fossil assemblages of past interglacials. An *in situ* fossil SMOF assemblage may be regarded as a proxy for sea-level since it represents a high intertidal setting. However, identifying these faunas with confidence is complicated, not only by issues of ecology (close juxtaposition of salt marsh with other intertidal environments such as mud flats) and taphonomy (post-mortem transport and mixing), but also by inconsistencies of sampling. To improve data quality and confidence, future research should endeavour to ensure comprehensive sampling of salt marsh habitats (e.g., different vegetation zones, salt pans/pools, creeks) at different times of year, so as to optimise representation of the full species richness of the faunas. Such work needs to be analysed with as full a dataset as possible with regard to tidal and salinity regimes and weather/climate variability.

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CRediT author statement

David J. Horne: Conceptualization, Methodology, Writing – Original draft, review and editing, Artwork, Visualization; **M. Cristina Cabral**: Conceptualization, Investigation, Methodology, Writing – Original draft, review and editing, Artwork, Visualization; **Francisco Fatela**:

Investigation, Methodology, Writing – review and editing, Visualization; **Michaela Radl**: Investigation, Methodology, Writing – review and editing.

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SUPPLEMENTARY INFORMATION

British study sites and ostracod faunas

All ostracod species listed were alive or assumed to be alive (based on presence of soft parts) at the time of collection; in a few cases this was confirmed by direct microscopic observations of living, moving specimens within hours of collection. Salinity in practical salinity units.

Kyleakin

KYL*,* 57 ° 16’ 18” N, 5 ° 44’ 26” W.
A small, mesotidal, estuarine inlet (An-t-Ob) fed by small streams, adjacent to the village of Kyleakin on the Isle of Skye, Scotland (Fig. 1C). The saltmarsh, with salt pans and shallow creeks, terminates in a 30 cm cliff descending to tidal flat; maximum tidal range is *c.* 6 m. The higher marsh vegetation is dominated by *Elytrigia repens* and *Festuca rubra*, that of the lower marsh by *Puccinellia maritima*, *Aster tripolium* and *Plantago maritima*. *Glaux maritima* appears throughout the marsh. No pioneer zone vegetation was present. Salt pans (salt marsh pools) and immediately adjacent tidal flat were sampled by DJH on 1:4:1996 and 7:6:2004, and by DJH and MR on 30:7:2012. A total of four species were recorded, in a salinity range of 17–35.

Salt marsh pool (salt pan) (salinity 32–35):

Cyprideis torosa
Leptocythere castanea

Tidal flat adjacent to salt marsh (salinity 17–32):

Cyprideis torosa
Cytherura gibba
Leptocythere castanea
Leptocythere lacertosa

Blackwater Estuary

Tollesbury, **TOL**, 51° 76’ 44” N, 0° 50’ 34” E.
A small, mesotidal river estuary on the North Sea coast of southeast England (Fig. 1B1); salt marsh surface, creeks and salt pans were sampled at Tollesbury. Mean range of spring tides is 4.7 m. The plateau-like saltmarsh is mature and intersected with complex dendritic channels up to 2 m deep and is backed by a sea wall built in the 1700s to protect the lower hinterland from the tides. Dominant plant species are *Elytrigia atherica* (high marsh), *Puccinellia maritima* (mid marsh) and *Atriplex portulacoides* (bordering creeks) (Hughes et al., 2009). Pioneer zone (low marsh) species *Salicornia europaea* and *Suaeda maritima* are scarce, usually on creek edges and fallen eroded sediment blocks together with the filamentous green algae (*Enteromorpha*). The saltmarsh is not grazed by livestock. High, mid and low marsh including salt pans and adjacent tidal flat (creeks) were sampled repeatedly by MR from October 2011 to July 2013, and the high marsh surface, creeks and salt pans by DJH on 8:9:2019. Eleven ostracod species were recorded:

Cyprideis torosa
Cytherois fischeri
Elofsonia baltica
Hemicythere rubida

Leptocythere baltica
Leptocythere castanea
Leptocythere ciliata
Leptocythere lacertosa
Loxoconcha elliptica
Loxoconcha malcomsoni
Terrestricythere cf. *elisabethae*

Note: *Hemicythere rubida* was not found alive in any of the 2011-2013 samples although empty shells were observed, but a sample taken subsequently by DJH in 2019 confirmed the presence of living *H. rubida*.

Gann Estuary

GE, 51° 72’ 15” N, 5° 10’ 02” W.
A meso-macrotidal small river estuary in southwest Wales, opening into Milford Haven and thence the Bristol Channel and the Atlantic Ocean (Fig. 1B3). The salt marsh vegetation shows a clear zonation with *Elytrigia atherica* in the high marsh, *Puccinellia maritima* and *Atriplex portulacoides* dominating the mid marsh plateau, and *Salicornia europaea* on the low marsh. Inside the estuary the saltmarsh terminates in a low cliff but at the entrance it slopes gently to the sandflat with a small area of pioneer marsh dominated by *Salicornia*. This area has never been grazed. Maximum tidal range *c*. 7 m. Samples were taken on high, mid and low marsh on 11:09:2011 by Dr Rob Hughes. Seven ostracod species were recovered:

Cytherois fischeri
Elofsonia baltica
Leptocythere baltica
Leptocythere castanea
Leptocythere ciliata
Leptocythere lacertosa
Loxoconcha elliptica

Thames Estuary

A mesotidal, major river estuary on the North Sea coast of southeast England.
Two Tree Island, TTI, 51°31'57" N, 0°37'40" E, near the mouth of the Thames Estuary on its northern coast, south of Leigh-on-Sea in Essex (Fig. 1B1). The plant species are similar to those at Tollesbury and the marsh is not grazed by livestock. The saltmarsh has a plateau with a cliff up to 1.5 m high with slumping in places, fronting the intertidal sandflats. Maximum tidal range is *c.* 6 m. Samples were collected on 24:11:2011 from the high, mid and low marsh by MR and Dr Rob Hughes. Six ostracod species were recovered:

Cytherois fischeri
Leptocythere castanea
Leptocythere ciliata
Leptocythere lacertosa
Loxoconcha elliptica
Paradoxostoma trieri

Severn Estuary

A macrotidal estuary on the Atlantic coast of southwest Britain. Salt marsh ostracods have been recorded at three sites: Porlock Weir, Steart and Severn House Farm (Fig. 1B4).

Porlock Weir, **PW**, 51 ° 13’ 18” N, 3 ° 37’ 50” W. A small, sheltered, estuarine inlet fed by a small stream, situated on the southern (English) coast of the Severn Estuary. Maximum tidal range *c.* 10 m (Bassindale, 1943). Mud and green algae in a creek dissecting the *Puccinellia*-dominated salt marsh surface were sampled repeatedly by DJH in 1977, salinities in the range 11–31 being noted. Four ostracod species were recorded:

Cyprideis torosa
Leptocythere ciliata
Leptocythere porcellanea
Loxoconcha elliptica

Steart*,* **ST**, 51 ° 12’ 13” N, 3 ° 3’ 50” W. Maximum tidal range *c.* 13 m, salinity range *c.* 24–28 (Bassindale, 1943; Haderlie & Clarke, 1958). *Spartina* marsh sampled by DJH in April 1977; three ostracod species were recovered:

Leptocythere lacertosa
Leptocythere porcellanea
Leptocythere psammophila

Severn House Farm, **SHF,** 51 ° 40’ 57” N, 2 ° 31’ 8” W. Maximum tidal range *c*. 10 m, salinity range *c.* 0–15 (winter), *c.* 20–26 (summer) (Bassindale, 1943; Haderlie & Clarke, 1958). *Spartina* marsh sampled by DJH in March 1977, yielding a single ostracod species:

Leptocythere porcellanea

Western Yar Estuary

A mesotidal, small river estuary on the Isle of Wight, draining northwards into the Solent and thence into the English Channel which connects the southern North Sea with the Atlantic (Fig. 1B2); sampled at two sites, one close to it inner, low salinity end (WY1) and the other close to its near-marine mouth (WY2) sampled by DJH in October 1995 (site WY2), and again by MR and DJH on 18:04:2013 (WY2) and 19:02:2014 (WY1 and WY2).

WY1, 50° 41' 1" N, 1° 30' 22" W, was on the eastern side of the estuary *c.* 150 m downstream of The Causeway; here the relatively small marsh plateau, with a few creeks, had a low cliff (*c.* 15 cm) dropping down to the tidal flat. The high marsh, dominated by *Phragmites australis* indicating a freshwater influence, gradually merged with the terrestrial vegetation including oak trees. *Spartina anglica* dominated the pioneer zone, above which *Atriplex portulacoides* dominated the mid marsh along the creeks, and *Puccinellia maritima* intermixed with *Phragmites*. Leaf litter from the adjacent trees was observed on the marsh surface. Three ostracod species were recovered:

Cytherois cf*. stephanidesi*
Hemicythere rubida
Terrestricythere cf. *elisabethae*

WY2, 50° 42' 8" N, 1° 30' 2" W, close to the mouth of the estuary, was south of Yarmouth harbour, on the east side of the estuary. The salt marsh here was a plateau with a few creeks and salt pans, approximately 50 cm above the tidal flat; the most common plants were *Elytrigia atherica* on the high marsh, *Puccinellia maritima* and *Atriplex portulacoides* on the mid-marsh (with some dead *Spartina* on the seaward edges), and *Salicornia europaea* and *Spartina anglica* in the low pioneer zone. The maximum tidal range is *c.* 5 m. Thirteen ostracod species were recovered:
Cyprideis torosa
Cytherois fischeri
Cytherois cf*. stephanidesi*
Hemicythere rubida
Hirschmannia viridis

Leptocythere castanea
Leptocythere ciliata
Leptocythere fabaeformis
Leptocythere lacertosa
Loxoconcha malcomsoni
Loxoconcha rhomboidea
Paradoxostoma trieri
Xestoleberis labiata

Spanish site and ostracod fauna

Tina Menor Estuary

43° 22’ 37” N, 4° 28’ 43” W
A mesotidal small river estuary in northern Spain (Fig. 5); data are from Martínez-García et al. (2013) who recorded five ostracod species alive in salt marsh samples:

Cytherois fischeri
Cytherois sp.
Leptocythere castanea
Leptocythere porcellanea
Loxoconcha elliptica

Portuguese study sites and ostracod faunas

In Portugal sediment sampling was carried out in autumn/winter and spring/summer during 2005–2006, 2011 and 2014. Each sample of 30 cm^3 (from three 10 cm^3 aliquots of the topmost 1cm surface sediment layer) were collected with a cut-off syringe and immediately preserved in 70 % alcohol. In the laboratory samples were washed through a 0.063 mm sieve and immersed in a 1g/l Rose Bengal solution to stain soft parts and facilitate the recognition of live specimens. All the ostracods were picked from the dried residues. Salinity was measured using direct-reading probes (WTW 197i) for estuarine waters and interstitial waters in marsh sediment (the latter accumulated inside a 40 cm-deep perforated hole) near each sampling point.

Each transect continuously covered the unvegetated tidal flat (or in the Mira estuary PMF with patches of marine intertidal green algae) as well as the vegetated low marsh (with *Spartina* spp.) and high marsh (with "*Salicornia*" spp. and *Halimione portulacoides*, or *Juncus* spp and *Phragmites* spp under brackish conditions). The substrate of tidal flats and tidal marshes is sandy in the Minho and Lima estuaries, but essentially muddy in the Tejo, Sado and Mira estuaries. The tidal regime along the Portuguese coast is high-mesotidal, semi-diurnal, the range varying between 2 m (neap tides) and almost 4 m (spring tides), but the astronomical tidal levels are often supplemented by storm surges (Taborda & Dias, 1991).
All ostracod species listed were alive or assumed to be alive at the time of collection, based on presence of soft parts and staining by Rose Bengal added to samples in the field. Salinity in practical salinity units.

Minho Estuary

A mesotidal river estuary opening into the Atlantic Ocean (Fig. 2F). The Minho river, with a length of 300 km and drainage area of 17,080 km2, drains into the Atlantic Ocean. It is a relatively channelled and shallow estuary (maximum depth *c.*10 m). River discharge is relatively stable: *c.* 300 m^3/s (Bettencourt *et al*., 2003), with average annual precipitation higher than 1600 mm, sometimes up to 3500 mm (e.g*.,* Fatela *et al*., 2014).
Two transects, one in the Coura River tributary confluence with the Minho River (CP), one in the lower Minho estuary (PR). Eleven ostracod species were recovered.

Comboios Portugueses transect – CP, 41º 52' 31'' N, 8º 49' 49'' W
Sampled by FF, MCC and JM on 28:4:2011 and 15:10:2011

High marsh (salinity 28.04.2011: **10.1**; 15.10.2011: **22.1**)

Tuberoloxoconcha sp. 1

Low marsh (salinity 28.04.2011: **6.2-18.2**; 15.10.2011: **22.0-25.0**)

Callistocythere murrayi
Cytherois cf. *stephanidesi*
Leptocythere porcellanea
Loxoconcha elliptica
Tuberoloxoconcha sp. 1

Tidal flat adjacent to salt marsh (salinity 28.04.2011: **7.1-16.3**; 15.10.2011: **10.6-22.3**)

Cytherois fischeri
Leptocythere porcellanea
Leptocythere sp. A
Leptocythere sp. B

Loxoconcha elliptica
Pedras Ruivas transect – PR, 41º 53’ 18’’ N, 8º 49’ 31’’ W

Sampled by FF, MCC and JM on 29:4:2011 and 15:10:2011

High marsh (salinity 29.04.2011: n/m; 15.10.2011: n/m)
No ostracods

Low marsh (salinity 29.04.2011: **2.5-12.9**; 15.10.2011: **9.5-20.9**)

Cytherois fischeri
Cytherois cf. *stephanidesi*
Leptocythere ciliata
Leptocythere porcellanea
Leptocythere psammophila
Leptocythere sp. A
Loxoconcha elliptica

Tidal flat adjacent to salt marsh (salinity 28.04.2011: **10.3**; 15.10.2011: **1.1**)

Cytherois fischeri
Cytherois cf. *stephanidesi*
Leptocythere baltica
Leptocythere porcellanea
Leptocythere psammophila
Leptocythere sp. A
Leptocythere sp. B
Loxoconcha elliptica

Lima Estuary

A mesotidal river estuary opening into the Atlantic Ocean (Fig. 2E). The Lima river, with a length of 108 km and drainage areas of 2,480 km^2, drains into the Atlantic Ocean. It is a relatively channelled and shallow estuary (maximum depth *c.* 10 m) with relatively stable discharge of *c*. 70 m^3/s (Ramos *et al*., 2006) and annual precipitation of 1300 mm (Bettencourt *et al*., 2003). One transect in the lower estuary (NSR), two transects in the mid estuary (DAR and BPR). Seven ostracod species were recovered.

Barco do Porto transect – BPR, 41º 42’ 05’’ N, 8º 44’ 46’’ W
Sampled by FF and JM on 29.11.2005 and 20.05.2006

High marsh (salinity 29.11.2005: n/m; 20.05.2006: n/m)

No ostracods

Low marsh (salinity 29.11.2005: **21.0**; 20.05.2006: **5.9-10.3**)

Callistocythere murrayi
Cytherois cf. *stephanidesi*
Leptocythere ciliata
Leptocythere porcellanea
Leptocythere sp. B considerei liso como sp. B mesmo sendo robusto.
Loxoconcha elliptica

Tidal flat adjacent to salt marsh (salinity 29.11.2005: **3.1-11.6**; 20.05.2006: **8.0**)

Leptocythere porcellanea
Leptocythere sp. B considerei liso como sp. B mesmo sendo robusto. Há sp. B verdadeiro
Loxoconcha elliptica

Darque transect – DAR, 41º 41' 16'' N, 8º 47' 07'' W
Sampled by FF and JM on 01.12.2005 and 21.05.2006

High marsh (salinity 01.12.2005: ***(6.5)***; 21.05.2006: ***(6.5)***)

No ostracods

Low marsh (salinity 01.12.2005: ***(6.5)***; 21.05.2006: ***(6.5)***)

Leptocythere baltica
Leptocythere ciliata
Leptocythere porcellanea
Loxoconcha elliptica

Tidal flat adjacent to salt marsh (salinity 01.12.2005: ***(6.5)***; 21.05.2006: ***(6.5)***)

Callistocythere murrayi
Leptocythere ciliata
Leptocythere porcellanea
Leptocythere sp. B

N. Sra. das Areias transect – NSR, 41º 41' 10'' N, 8º 49' 15'' W
Sampled by FF and JM on 29.11.2005 and 20.05.2006

High marsh (salinity 29.11.2005: **4.2**; 20.05.2006: **3.4**)

Leptocythere baltica
Loxoconcha elliptica

Low marsh (salinity 29.11.2005: **15.3-20.5**; 20.05.2006: **12.0-14.4**)

Leptocythere baltica
Leptocythere ciliata
Leptocythere sp. B
Loxoconcha elliptica

Tidal flat adjacent to salt marsh (salinity 29.11.2005: **19.7-24.6**; 20.05.2006: **10.5-24.8**)

Leptocythere baltica
Leptocythere ciliata
Leptocythere porcellanea
Loxoconcha elliptica

Tejo Estuary

A mesotidal river estuary opening into the Atlantic Ocean (Fig. 2D). Tejo River and Trancão tributary – two transects in the lower Tejo estuary (ALF and ROS), one transect in the lower Trancão estuary (TRA), 100 m upstream of the confluence with the mid Tejo estuary. One of the largest estuaries in western Europe (325 km^2), its hydrographical basin of 81,310 km^2 (ARH Tejo, 2011) receives average annual precipitation of *c.* 700 mm. Average fluvial discharge is c. 300 m^3/s, but the annual average ranges from 250 m^3/s to 5,400 m^3/s under especially dry or wet conditions (ARH Tejo, 2011; Bettencourt *et al*., 2003). Nine ostracod species were recovered.

Trancão transect – TRA, 38º 47’ 49’’ N, 9º 05’ 34’’ W

Sampled by FF and MCC on 05.07.2011

High marsh (salinity 05.07.2011: **42.5**)

Leptocythere ciliata

Low marsh (salinity 05.07.2011: **33.7**)

Leptocythere ciliata
Leptocythere porcellanea
Loxoconcha elliptica

Tidal flat adjacent to salt marsh (salinity 05.07.2011: n/m)

Cytherois fischeri
Leptocythere porcellanea

Rosário transect – ROS, 38º 40’ 24’’ N, 9º 00’ 44’’ W
Sampled by FF and JM on 06.12.2005 and 11.05.2006

High marsh (salinity 06.12.2005: **23.6-52.9**; 11.05.2006: **40.4**)

Leptocythere ciliata

Low marsh (salinity 06.12.2005: **33.1**; 11.05.2006: **32.9**)

Leptocythere lacertosa
Leptocythere porcellanea
Loxoconcha elliptica

Tidal flat adjacent to salt marsh (salinity 06.12.2005: **31.6-33.2**; 11.05.2006: **28.0**)

Callistocythere murrayi
Cytherois fischeri
Loxoconcha elliptica

Alfeite transect – ALF, 38º 39’ 05’’ N, 9º 07’ 26’’ W
Sampled by FF and MCC on 06.01.2011 and 05.07.2011

High marsh (salinity 06.01.2011: **20.9-25.7**; 05.07.2011: **35.3**)

Leptocythere porcellanea
Loxoconcha elliptica
Terrestricythere cf. *elisabethae*
Tuberoloxoconcha cf. *atlantica*

Low marsh (salinity 06.01.2011: **27.9-29.1**; 05.07.2011: **29.7-31.2**)

Cyprideis torosa
Leptocythere ciliata
Leptocythere lacertosa
Leptocythere porcellanea
Loxoconcha elliptica

Tidal flat adjacent to salt marsh (salinity 06.01.2011: **19.0-22.9**; 05.07.2011: **34.3**)

Cyprideis torosa
Cytherois fischeri
Leptocythere lacertosa
Leptocythere porcellanea
Loxoconcha elliptica

Sado Estuary

A mesotidal river estuary opening into the Atlantic Ocean (Fig. 2C). The Sado river catchment occupies an area of around 7,670 km^2, receiving average annual precipitation of *c.* 620-650 mm. Its fluvial discharge varies from 1m^3/s (dry season) to 50-80 m^3/s under wet conditions where peaks of 470 m^3/s may be recorded (Bettencourt *et al*., 2003); annual average discharge is *c.* 40 m^3/s, very close to a Mediterranean type, but circulation inside the estuary is controlled primarily by tides (Bettencourt *et al*., 2003, Âmbar *et al*., 1980). Three transects in the lower estuary (FAR, CAR, TRO), one transect in the mid estuary (ALC). Eleven ostracod species were recovered.

Alcácer do Sal transect – ALC, 38º 22’ 10’’ N, 8º 30’ 46’’ W
Sampled by FF and JM on 03.12.2005 and 24.04.2006

High marsh (salinity 03.12.2005:.n/m; 24.04.2006: n/m)

No ostracods

Low marsh (salinity 03.12.2005: **11.1-12.3**; 24.04.2006: **8.3**)

No ostracods

Tidal flat adjacent to salt marsh (salinity 03.12.2005: n/m; 24.04.2006: n/m)

No live ostracods, only juvenile valves of *Loxoconcha elliptica* in 03.12.2005

Faralhão transect – FAR, 38º 31’ 06’’ N, 8º 47’ 02’’ W
Sampled by FF and JM on 03.12.2005 and 24.04.2006

High marsh (salinity 03.12.2005: **30.9-61.8**; 24.04.2006: n/m)

No ostracods

Low marsh (salinity 03.12.2005: **32.6**; 24.04.2006: **33.6**)

Leptocythere ciliata
Leptocythere porcellanea

Tidal flat adjacent to salt marsh (salinity 03.12.2005: **30.1-34.7**; 24.04.2006: **30.9-32.6**)

Cyprideis torosa
Cytherois fischeri
Leptocythere ciliata
Leptocythere porcellanea
Loxoconcha elliptica
Loxoconcha malcomsoni
Paradoxostoma sarniense

Carrasqueira transect – CAR, 38º 24’ 41’’ N, 8º 45’ 32’’ W
Sampled by FF and JM on 03.12.2005 and 25.04.2006

High marsh (salinity 03.12.2005: n/m; 25.04.2006: n/m)

No ostracods

Low marsh (salinity 03.12.2005: **41.4-43.3**; 25.04.2006: **37.6-41.7**)

Leptocythere ciliata
Loxoconcha malcomsoni

Tidal flat adjacent to salt marsh (salinity 03.12.2005: **26.2-30.1**; 25.04.2006: **30.9-31.9**)

Leptocythere lacertosa
Leptocythere porcellanea
Loxoconcha elliptica

Tróia transect – TRO, 38º 25’ 46’’ N, 8º 49’ 26’’ W
Sampled by FF and JM on 03.12.2005 and 25.04.2006

High marsh (salinity 03.12.2005: **2.9-16.3**; 25.04.2006: n/m)

No ostracods

Low marsh (salinity 03.12.2005: **23.7-29.7**; 25.04.2006: **26.6-27.9**)

Leptocythere ciliata
Terrestricythere cf. *elisabethae*

Tidal flat adjacent to salt marsh (salinity 03.12.2005: **27.6-32.2**; 25.04.2006: **17.1-34.1**)

Cyprideis torosa
Cytherois fischeri
Leptocythere ciliata
Leptocythere lacertosa
Leptocythere porcellanea

Leptocythere sp. B
Loxoconcha elliptica
Paradoxostoma trieri
Paradoxostoma sarniense

Mira Estuary

A mesotidal river estuary opening into the Atlantic Ocean (Fig. 2B). The Mira river catchment occupies an area of *c.* 7,670km^2. The weather has typical Mediterranean characteristics with marked seasonality and annual precipitation of *c.* 645 mm (ICNB, 2008). Fluvial discharge varies from 0 m^3/s to 500 m^3/s, with an annual average of 2.9 m^3/s (MARETEC, 2020).
Two transects in the lower estuary (PMF and MAS), three transects in the mid estuary (CBR, MFP and OD). Seventeen ostracod species were recovered.

Odemira transect – OD, 37º 35’ 53’’ N, 8º 38’ 53’’ W
Sampled by FF on 25.3.2014
and by FF and MCC on 1.11.2014

Low marsh (salinity 25.03.2014: **1.0-1.4**; 01.11.2014: **1.6-2.5**)

Leptocythere porcellanea

Tidal flat adjacent to salt marsh (salinity 25.03.2014: **0.0**; 01.11.2014: **3.8**)

Cytherois fischeri
Leptocythere porcellanea
Loxoconcha elliptica

Monte Flor do Pereiro transect – FLP, 37º 37’ 05’’ N, 8º 40’ 35’’ W
Sampled by FF on 25.3.2014
and by FF and MCC on 1.11.2014

High marsh (salinity 25.03.2014: **19.8**; 01.11.2014: **19.0**)

Leptocythere porcellanea

Low marsh (salinity 25.03.2014: **12.9**; 01.11.2014: **17.1**)

Cypria cf. *subsalsa*
Cytherois fischeri
Leptocythere porcellanea
Loxoconcha elliptica

Tidal flat adjacent to salt marsh (salinity 25.03.2014: n/m; 01.11.2014: n/m)

Cypria cf. *subsalsa*
Leptocytherec porcellanea
Loxoconcha elliptica

Casa Branca transect – CBR, 37º 40’ 03’’ N, 8º 43’ 14’’ W
Sampled by FF and JM on 5:12:2005

and by FF, MCC and JM on 26:4:2006

High marsh (salinity 05.12.2005: **28.3-48.2**; 26.04.2006: **32.9-46.0**)

No ostracods

Low marsh (salinity 05.12.2005: **38.0**; 26.04.2006: **28.0**)

Callistocythere murrayi
Cytherois fischeri
Hemicytherura videns
Leptocythere ciliata
Leptocythere porcellanea

Tidal flat adjacent to salt marsh (salinity 05.12.2005: n/m; 26.04.2006: n/m)

Basslerites teres
Callistocythere murrayi
Cytherois fischeri
Hemicytherura videns
Leptocythere lacertosa
Leptocythere porcellanea
Loxoconcha elliptica

Moinho da Asneira transect – MAS, 37º 43’ 46’’ N, 8º 45’ 17’’ W
Sampled by FF and JM on 5.12.2005
and by FF, MCC and JM on 27.4.2006

High marsh (salinity 05.12.2005: **4.5-20.3**; 27.04.2006: **22.3-28.8**)

Leptocythere porcellanea

Low marsh (salinity 05.12.2005: **31.0-34.6**; 27.04.2006: **31.0-33.7**)

Cytherois fischeri
Leptocythere lacertosa
Leptocythere porcellanea
Paradoxostoma trieri

Tidal flat adjacent to salt marsh (salinity 05.12.2005: **33.4**; 27.04.2006: **32.1**)

Basslerites teres
Cytherois fischeri
Hemicytherura videns
Leptocythere fabaeformis
Leptocythere lacertosa
Leptocythere porcellanea
Loxoconcha elliptica
Loxoconcha rhomboidea
Paradoxostoma trieri
Xestoleberis labiata

Ponte de Mil Fontes transect – PMF, 37 43’ 32’’ N, 8º 46’ 04’’ W
Sampled by FF and JM on 5.12.2005 and 25.3.2014
by FF, MCC and JM on 27.4.2006
and by FF and JM on 25.03.2014

High marsh (salinity 05.12.2005: **28.8-47.5**; 27.04.2006: **11.7-43.3**)

Cyprideis torosa (2014 only)
Leptocythere ciliata
Leptocythere lacertosa
Leptocythere porcellanea
Loxoconcha malcomsoni
Terrestricythere cf. *elisabethae* (2014 only)
Tuberoloxoconcha cf. *atlantica*
Xestoleberis labiata

Low marsh (salinity 05.12.2005: **35.9-42.0**; 27.04.2006: **23.2-37.0**)

Cytherois fischeri
Hemicytherura videns
Leptocythere ciliata
Leptocythere lacertosa
Leptocythere porcellanea
Loxoconcha malcomsoni

Tidal flat adjacent to salt marsh (salinity 05.12.2005: **33.7-33.8**; 27.04.2006: n/m)

Basslerites teres
Cytherois fischeri
Hemicytherura videns
Leptocythere fabaeformis
Leptocythere lacertosa
Leptocythere porcellanea
Loxoconcha rhomboidea
Paradoxostoma trieri
Xestoleberis labiata

Summary table of data plotted in Figs 5–8

Estuary number is cross-referenced to Fig. 5.
Estuary and transect shows name of estuary and (if necessary) initials of transect; refer to Figs 1 and 2 for locations and to Supplementary Information (above) for names of transects.
Intertidal level ranges from tidal flat (lowest/shortest duration of exposure at low tide) to high marsh (highest/longest duration of exposure at low tide).
Minimum salinity (where available) is the lowest salinity value recorded, rounded to the nearest whole number, in practical salinity units.
Maximum salinity (where available) is the highest salinity value recorded, rounded to the nearest whole number, in practical salinity units.
Species richness 1 is the number of species recorded from each transect or site within an estuary, combining all available records from different seasons.
Species richness 2 is the total number of species recorded in each estuary, combining records from all available samples (e.g., from different sites and in different seasons).
Degrees of latitude N is a representative value for each estuary.

Estuary number	Estuary and transect	Intertidal level	Salinity min	Salinity max	Salinity range	Species richness 1	Species richness 2	Degrees of latitude N
1	Kyleakin	marsh + tidal flat				4	4	57.3
2	Blackwater	high marsh				3	11	51.8
2	Blackwater	mid marsh				6	11	51.8
2	Blackwater	low marsh				10	11	51.8
3	Gann	high marsh				1	7	51.7
3	Gann	mid marsh				3	7	51.7
3	Gann	low marsh				7	7	51.7
4	Thames	high marsh				2	6	51.5
4	Thames	mid marsh				2	6	51.5
4	Thames	low marsh				6	6	51.5
5	Severn	marsh				6	6	51.2
6	Western Yar	marsh				14	14	50.7
7	Tina Menor	marsh				4	4	43.4
8	Minho CP	tidal flat	7	22		5	11	41.9
8	Minho CP	low marsh	6	25		5	11	41.9
8	Minho CP	high marsh	10	22		1	11	41.9
8	Minho PR	low marsh	3	21		7	11	41.9
8	Minho PR	tidal flat	1	10		8	11	41.9
9	Lima BPR	high marsh				0	7	41.7
9	Lima BPR	low marsh	6	21		6	7	41.7
9	Lima BPR	tidal flat	3	12		3	7	41.7
9	Lima DAR	low marsh	7	7		4	7	41.7
9	Lima DAR	tidal flat	7	7		4	7	41.7
9	Lima DAR	high marsh	7	7		0	7	41.7
9	Lima NSR	high marsh	3	4		2	7	41.7
9	Lima NSR	low marsh	12	21		4	7	41.7
9	Lima NSR	tidal flat	11	25		4	7	41.7
10	Tejo TRA	high marsh	43	43		1	9	38.7
10	Tejo TRA	low marsh	34	34		3	9	38.7
10	Tejo TRA	tidal flat				2	9	38.7

10	Tejo ROS	high marsh	24	53		1	9	38.7
10	Tejo ROS	low marsh	33	33		3	9	38.7
10	Tejo ROS	tidal flat	28	33		3	9	38.7
10	Tejo ALF	high marsh	21	35		4	9	38.7
10	Tejo ALF	low marsh	28	31		5	9	38.7
10	Tejo ALF	tidal flat	19	34		5	9	38.7
11	Sado ALC	high marsh				0	11	38.4
11	Sado ALC	low marsh	8	12		0	11	38.4
11	Sado ALC	tidal flat				0	11	38.4
11	Sado FAR	high marsh	31	62		0	11	38.4
11	Sado FAR	low marsh	33	34		2	11	38.4
11	Sado FAR	tidal flat	30	35		7	11	38.4
11	Sado CAR	high marsh				0	11	38.4
11	Sado CAR	low marsh	38	43		2	11	38.4
11	Sado CAR	tidal flat	26	32		3	11	38.4
11	Sado TRO	high marsh	3	16		0	11	38.4
11	Sado TRO	low marsh	24	30		2	11	38.4
11	Sado TRO	tidal flat	17	34		9	11	38.4
12	Mira OD	low marsh	1	3	2	1	17	37.6
12	Mira OD	tidal flat	0	4	4	3	17	37.6
12	Mira FLP	high marsh	19	20	1	1	17	37.6
12	Mira FLP	low marsh	13	17	4	4	17	37.6
12	Mira FLP	tidal flat				3	17	37.6
12	Mira CBR	high marsh	28	48	20	0	17	37.6
12	Mira CBR	low marsh	28	38	10	5	17	37.6
12	Mira CBR	tidal flat				7	17	37.6
12	Mira MAS	high marsh	5	29	24	1	17	37.6
12	Mira MAS	low marsh	31	35	4	4	17	37.6
12	Mira MAS	tidal flat	32	33	1	10	17	37.6
12	Mira PMF	high marsh	12	48	36	8	17	37.6
12	Mira PMF	low marsh	23	42	19	6	17	37.6
12	Mira PMF	tidal flat	34	34	0	9	17	37.6

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