

## *Cyprideis torosa* (Jones, 1850) in mainland Portugal: what do we know?

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**Abstract:** The distribution of Recent and Holocene *Cyprideis torosa* (Jones, 1850) from brackish estuaries and lagoons of mainland Portugal is presented; older Cenozoic *C. torosa* are also briefly mentioned. Around 550 specimens were found alive, in Melides lagoon (456) and salt marshes from large estuaries (90). Thousands of empty valves and carapaces, with different ornamentation, were found in the lagoon, the estuaries and in Holocene samples from boreholes, in the latter with higher concentration in sediments deposited in lagoons. The modern *C. torosa* was found living mainly in Melides lagoon, associated with brackish and freshwater ostracod species, in soft mud or muddy sand sediments from quiet zones, with salinities from 4.1 to 15.1; it is also found in soft mud to muddy sand sediments whose interstitial waters have salinities from 19.0 to 34.1, on salt marshes (tidal flat and low marsh) of large estuaries, similar to lagoons, in low hydrodynamic areas, together with other brackish ostracods. The main parameters controlling the distribution of *C. torosa* appear to be the substrate, water dynamics and emersion time, whereas water chemistry is more related to the morphology of valves. In general, *C. torosa* presents the same ecological characteristics in the Holocene and in modern times.

**Keywords:** Ostracods, salt marshes, estuaries, lagoons, Cenozoic, Portugal

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*Cyprideis torosa* (Jones, 1850) is a widespread brackish-water ostracod species, highly euryhaline, found from almost freshwater to fully marine, even hypersaline (over 60‰) water, in marginal-marine environments (lagoons, estuaries, deltas, salt marshes, coastal ponds, fjords, etc.) down to a depth of around 30 m (Athersuch *et al.* 1989; Meisch 2000). Its presence in inland waters is known only in slightly brackish lakes (Meisch 2000). It also tolerates a wide range of temperature and oxygen conditions; it prefers soft sediments (muddy or sandy mud substrate) where large amounts of organic detritus are present (Heip 1976), but also lives in pure sand and on algae (Athersuch *et al.* 1989). Heip (1976) refers to its exceptional concentration in some types of sediments, where it can even be the main component. It is known from the Miocene until Recent (Meisch 2000).

In Portugal, *C. torosa* is common in Recent and Holocene brackish-water coastal environments, both alive and dead, although much more frequently represented by empty valves in lagoons and estuaries. This species is referred to in several papers concerning brackish Holocene and Recent Portuguese ostracods (mixed with marine and also freshwater forms), especially those published after 1999: Paulo & Moutinho (1983), Hindson & Andrade (1999), Hindson *et al.* (1999), Cearreta *et al.* (2003), Cabral *et al.* (2006, 2011), Hilbich *et al.* (2008), Lord *et al.* (2011), Cabral & Loureiro (2013), Trog *et al.* (2013, 2015). In Martins *et al.*'s (2010) overview about the ostracods living in freshwater Portuguese habitats there is no reference to *C. torosa*.

In this work we present the current distribution of Recent and Holocene *C. torosa* in mainland Portugal and we examine the biological response of the species to differences in physical and chemical parameters within several estuarine salt marshes and the Melides lagoon. We also compare the modern *C. torosa* assemblages of the Melides lagoon (part of an ongoing work with the aim of characterizing the seasonality signal of modern ostracod faunas and the role of the sandy barrier in the environmental

evolution of the lagoon through time) and of the estuarine salt marshes with those found in the Holocene sedimentary records.

The material presented here comes from:

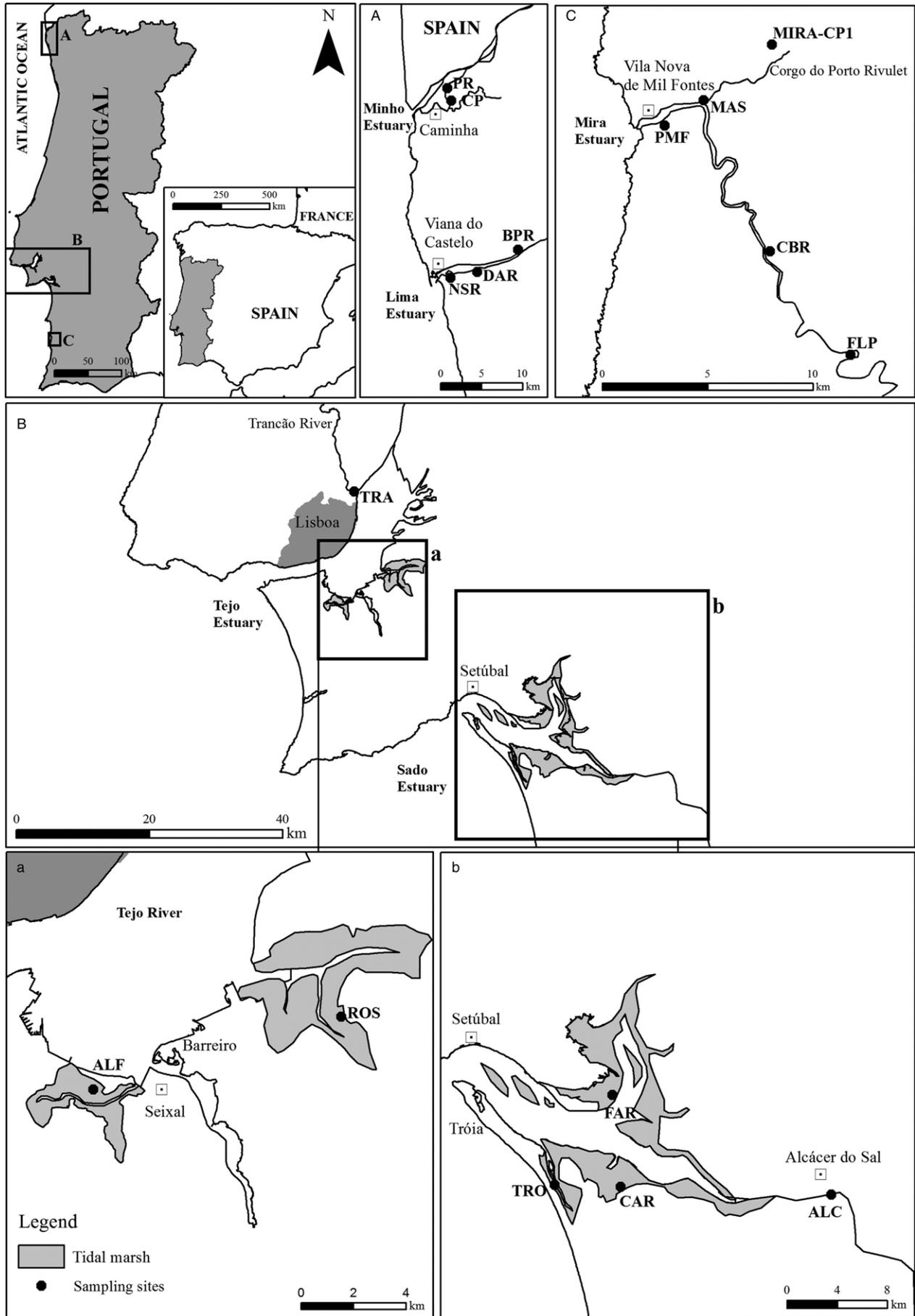
- (a) observations of one of the authors (MCC) on Recent ostracods in sediments from different estuaries and lagoons of western Portugal and on Holocene ostracods from long boreholes (several projects led by MCF, FF, CA, some completed, others ongoing, all having as one of their objectives the determination of the ostracod assemblages and their distribution in mainland Portugal);
- (b) information from unpublished notes (MCC);
- (c) reports of several research projects (MCC);
- (d) Master degree theses (all supervised by MCC in the Department of Geology, Faculty of Sciences, University of Lisbon); and
- (e) published papers.

*Cyprideis torosa* is a very ecologically tolerant species, colonizing highly fluctuating and stressed habitats; it was often found in both Recent and Holocene sediments from Portuguese estuaries and lagoons, showing different morphological aspects and in contrasting abundances and associations. This motivated us to compile and discuss the data and try to understand the most important environmental parameters limiting the occurrence and distribution of this species, hoping that this may be useful for researchers working on the same subject.

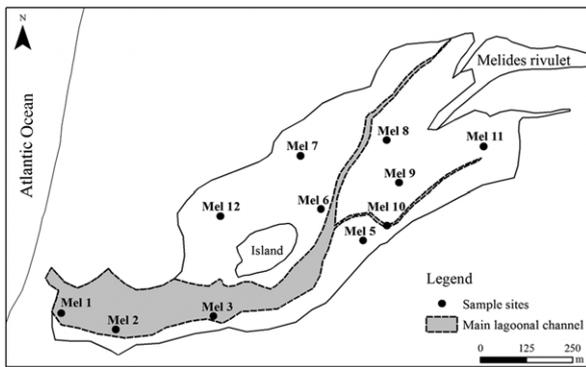
### Study areas

The studied areas are the same as those reported in Cabral & Loureiro (2013), except the continental shelf and slope of western Algarve; here we add eleven new samples from the surface sediment layer of Melides lagoon and one borehole taken in Mira river.

Recent material comes from several estuaries of the western Portuguese coast (Fig. 1) and Melides lagoon (Fig. 2):



**Fig. 1.** Location map of the studied transects in the Portuguese estuaries: (A) Minho estuary (CP and PR) and Lima estuary (NSR, DAR, BPR). (B) Tejo and Sado estuaries, with TRA transect indicated in Tejo estuary – (a) Tejo estuary (ALF, ROS), (b) Sado estuary (ALC, CAR, FAR and TRO). (C) Mira estuary (PMF, MAS, CBR and FLP); MIRA-CP1 is a Holocene borehole in Corgo do Porto rivulet.



**Fig. 2.** Location map of the studied sites (surface samples) and of the main channel on Melides lagoon.

- Minho River and Coura tributary – 2 transects, 1 in the Coura confluence with the Minho River (CP), 1 in the lower Minho estuary (PR).
- Lima River – 1 transect in the lower estuary (NSR), 2 transects in the mid estuary (DAR and BPR).
- Tejo River and Trancão tributary – 2 transects in the lower Tejo estuary (ALF and ROS), 1 transect in the lower Trancão estuary (TRA), 100 m upstream the confluence with the mid Tejo estuary.
- Sado River – 3 transects in the lower estuary (FAR, CAR, TRO), 1 transect in the mid estuary (ALC).
- Mira River – 2 transects in the lower estuary (PMF and MAS), 2 transects in the mid estuary (CBR and FLP).

Each transect covered the tidal flat, low marsh (*c. Spartina*) and high marsh (*c. 'Salicornia' and Halimione*).

- Melides lagoon (Figs 2 and 3) – 11 sites inside the lagoon, among which 5 sites (1, 2, 3, 5 and 10) are located along the southern margin, where the currents are stronger; 3 sites (7, 8, 12) located on the northern margin, in a sheltered zone; 3 sites (6, 9 and 11) located in the central-eastern part of the lagoon, also in sheltered conditions, specially site 6 located near a lagoonal island.
- Holocene material comes from several boreholes taken from coastal lagoons and estuaries (Fig. 3). From north to south:
- Pederneira estuary/lagoon, west Portugal – 3 long boreholes in the Recent alluvial plain of Alcoa River, 2 in the inner infilled lagoon (S1 and S2), another in the middle infilled lagoon (S3).
- Sizandro estuary/lagoon, west Portugal – 1 long borehole in the alluvial plain of Sizandro River, around 10 km from the coast (RS06\_1).
- Tejo estuary – 1 long borehole in Lisboa downtown (esteiro da Baixa infilled rivulet), Praça do Comércio (PC).
- Melides lagoon, SW Portugal – 2 long boreholes, one in the alluvial plain of the modern lagoon (MIGM), another in the sand barrier (MB).
- Santo André lagoon, SW Portugal – 1 long borehole in the alluvial plain bordering the modern lagoon (LSA).
- Mira estuary, SW Portugal (Fig. 1) – 1 long borehole in the alluvial plain of Corgo do Porto tributary (MIRA-CP1).

## Material and methods

The forms found in salt marshes were generally collected in muddy sediment or in fine sand or silty sand substrates; the forms from Melides lagoon were collected in sediments varying from sand to mud; at each sampling point in marshes and Melides lagoon, one

sample was collected to study the sediment grain size (% of sand and mud = silt + clay). Sampling of marshes was undertaken in two different seasons, generally in autumn and spring, in December 2005 and May 2006; exceptions were the Minho estuary sampled in April and October 2011 and the Alfeite salt marsh (Tejo estuary) sampled in the early winter and summer (January and July 2011); Melides lagoon samples were collected during winter (February 2015). In the salt marshes the samples were collected with a cut-off syringe; sediment from Melides lagoon was retrieved using a van Veen grab operated from a boat and, once aboard, the sample was collected as in the salt marshes. Temperature, salinity, dissolved oxygen and pH were measured using direct-reading probes for estuarine waters, and also in marsh sediment interstitial waters (when enough water was accumulated inside a 40 cm-deep perforated hole, close to each sampling point). In Melides lagoon those parameters were measured at the water surface and bottom at each sampling point; the depth of each sampling point was also noted (Table 1).

Brackish waters were classified using the Venice system.

The samples (30 cm<sup>3</sup> each, from three 10 cm<sup>3</sup> aliquots of the topmost 1 cm surface sediment layer, immediately preserved in 70% alcohol after collection) were washed through a 0.063 mm sieve, immersed for at least 1 h in a [1 g l<sup>-1</sup>] Rose Bengal solution to facilitate the recognition of the live forms and rewashed to eliminate excess stain; they were then dried in an oven below 50°C.

Forms were identified as alive when containing the soft parts (appendages) and pink staining due to the Rose Bengal.

The Holocene samples (10 cm<sup>3</sup> each) for ostracod analyses were taken only from boreholes (drilled between 1998 and 2009) at 30–50 cm intervals with higher resolution in clay units and near lithological boundaries. Further laboratory procedures were the same as described for Recent material, without application of Rose Bengal solution.

All the ostracods were picked, both valves and carapaces of juveniles and adults, dead or alive. We considered 1 individual (1 specimen) = 1 valve or 1 carapace, dead or alive.

The taxa were identified only on the basis of valves and carapaces without soft parts.

Identification of the species found in association with *C. torosa* were based primarily on Yassini (1969), Barbeito-González (1971), Bonaduce *et al.* (1976) and Athersuch *et al.* (1989). For a complete systematic list and ecological characteristics of the living species of the salt marshes, see Cabral & Loureiro (2013).

All the studied specimens are deposited in the Cabral Collection of the Department of Geology, Faculty of Sciences, University of Lisbon.

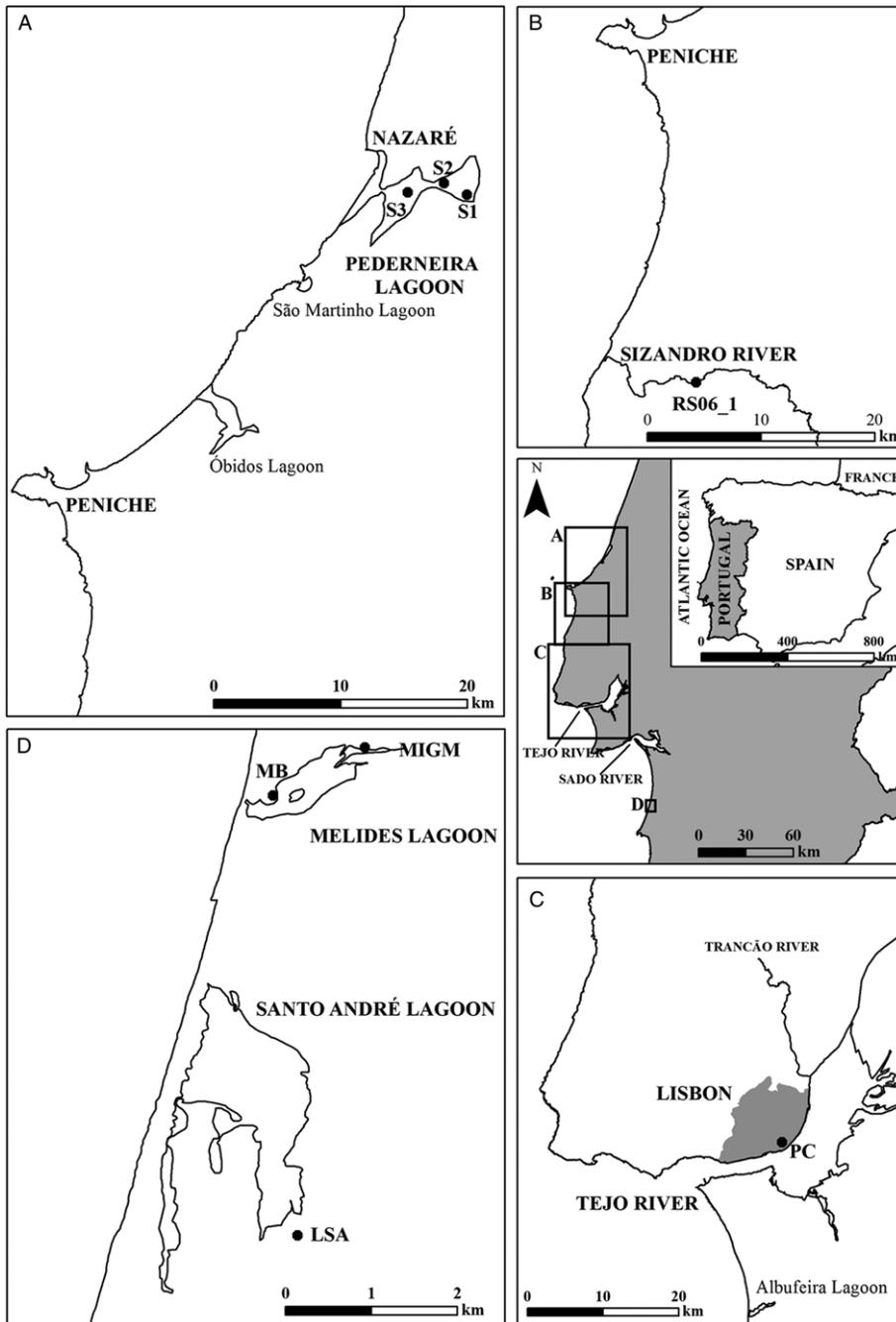
## Results and discussion

In the Recent sediments of mainland Portugal *Cyprideis torosa* was found in Lima, Tejo, Sado and Mira estuaries and in Melides lagoon, generally as empty valves. It was alive in some transects of Tejo and Sado estuaries and in six sites in Melides lagoon. In all of the studied Holocene boreholes (Lisboa – PC; Melides – MB and MIGM; Mira – MIRA-CP1; Pederneira – S1, S2 and S3; Santo André – LSA; Sizandro – RS06\_1) and most boreholes described in the literature (Hindson & Andrade 1999; Hindson *et al.* 1999; Hilbich *et al.* 2008; Trog *et al.* 2013, 2015), *C. torosa* was present.

### Ecology of Recent ostracod fauna

#### Estuaries

In all the Portuguese estuaries tides present a semi-diurnal high-mesotidal regime. The range varies between 2 m during neap waters and almost 4 m in spring tides but the astronomical tidal levels are often incremented by storm surges (Taborada & Dias 1991).



**Fig. 3.** Location map of the studied Holocene boreholes: (A) Pederneira lagoon (S1–S3); (B) Sizandro river (RS06\_1); (C) Tejo estuary (PC); (D) Melides lagoon (MB and MIGM) and Santo André lagoon (LSA).

In the studied salt marshes of the northwestern estuaries we can consider that *C. torosa* is not present. No specimens were found in Minho river and, in Lima river, only one dead adult valve, surely transported, was present in the lower estuary, NSR transect. The same pattern was seen in Mira river, SW Portugal (Loureiro *et al.* 2009), where only one juvenile, worn, dead valve was found in the lower estuary, PMF transect. These three rivers (Fig. 1), varying in length from 108 km (Lima river) to 300 km (Minho river) and in drainage area from 1600 km<sup>2</sup> (Mira river) to 17 080 km<sup>2</sup> (Minho river), have in common a relatively channelled and shallow estuary (maximum depth *c.* 10 m). The flux is relatively stable in the NW: *c.* 300 m<sup>3</sup> s<sup>-1</sup> in Minho river (Bettencourt *et al.* 2003), with an average annual precipitation higher than 1600 mm and which may reach more than 3500 mm (e.g. Fatela *et al.* 2014); *c.* 70 m<sup>3</sup> s<sup>-1</sup> in Lima river (Ramos *et al.* 2006), with an average annual precipitation of 1300 mm (Bettencourt *et al.* 2003); and highly variable in the SW, where the climate has typical Mediterranean characteristics with marked alternating seasons, with an annual precipitation around

645 mm (ICNB 2008) and a flux of 0–500 m<sup>3</sup> s<sup>-1</sup> in Mira river (ICNB 2008), where yearly average fluvial discharge is around 2.9 m<sup>3</sup> s<sup>-1</sup> (MARETEC 2015). The substrate is rich in sands in the NW estuaries, muddy in the Mira river.

The most important characteristic common to the three estuaries is the highly channelled morphology, without sheltered areas, promoting strong tidal currents over the salt marshes, which seems to prevent the presence of *C. torosa* in the estuary and associated salt marshes. It is clear that this species avoids active current waters.

The 325 km<sup>2</sup> Tejo estuary, located in the central-southwestern coast of Portugal (Fig. 1) is among western Europe's largest. Its hydrographical basin (81 310 km<sup>2</sup>) has 25 666 km<sup>2</sup> in Portugal and 55 644 km<sup>2</sup> in Spain (ARH Tejo 2011). The average annual precipitation in the Tejo basin is 700 mm (650 mm in the Spanish sector, 900 mm in the Portuguese right shore and 600 mm in its left shore; ARH Tejo 2011). The fluvial discharge average is around 300 m<sup>3</sup> s<sup>-1</sup>, but the annual average discharge ranges between 250 m<sup>3</sup> s<sup>-1</sup> and 5400 m<sup>3</sup> s<sup>-1</sup> under specially dry or wet conditions,

**Table 1.** Winter temperature, salinity, dissolved oxygen and pH values of Melides lagoon water, measured at surface, at 1 m depth and close to bottom sediment of each sampled site (in bold)

Site	Depth (m)	Temperature (°C)	Salinity (‰)	Dissolved oxygen (mg l <sup>-1</sup> )	pH
1	0.00	9.50	3.40	11.70	8.74
	1.00	9.40	3.40	11.50	8.65
	<b>1.80</b>	<b>9.50</b>	<b>3.40</b>	<b>11.70</b>	<b>8.63</b>
2	0.00	10.50	3.20	13.50	8.85
	1.00	10.50	3.20	12.70	8.82
	2.00	10.40	3.20	12.80	8.56
3	0.00	10.20	3.20	11.30	8.50
	1.00	10.20	3.20	11.19	8.44
	<b>1.60</b>	<b>10.20</b>	<b>3.20</b>	<b>11.00</b>	<b>8.41</b>
5	0.00	10.50	3.20	11.90	8.70
	1.00	10.40	3.20	11.70	8.57
	2.00	10.30	3.20	11.30	8.49
6	0.00	10.50	3.10	11.70	8.51
	1.00	10.50	3.10	11.70	8.53
	2.00	10.50	3.20	11.70	8.48
7	0.00	10.60	3.00	11.91	8.30
	1.00	10.40	3.10	11.10	8.38
	2.00	10.50	3.30	11.40	8.49
8	0.00	10.70	3.00	12.40	8.66
	1.00	10.70	3.00	12.10	8.63
	2.00	10.60	3.50	11.50	8.56
9	0.00	10.80	2.90	12.10	8.53
	1.00	10.80	2.90	12.06	8.54
	2.00	10.80	2.90	11.90	8.52
10	0.00	10.90	3.00	12.40	8.62
	1.00	10.90	3.00	12.10	8.57
	2.00	10.80	3.00	11.90	8.55
11	0.00	11.50	2.80	13.00	8.86
	1.00	11.50	2.80	12.80	8.73
	2.00	11.30	3.50	10.04	8.53
12	0.00	10.10	3.10	11.60	8.55
	1.00	10.10	3.10	11.40	8.50
	2.00	10.10	3.30	11.40	8.51
	<b>2.45</b>	<b>10.80</b>	<b>7.50</b>	<b>5.80</b>	<b>7.82</b>

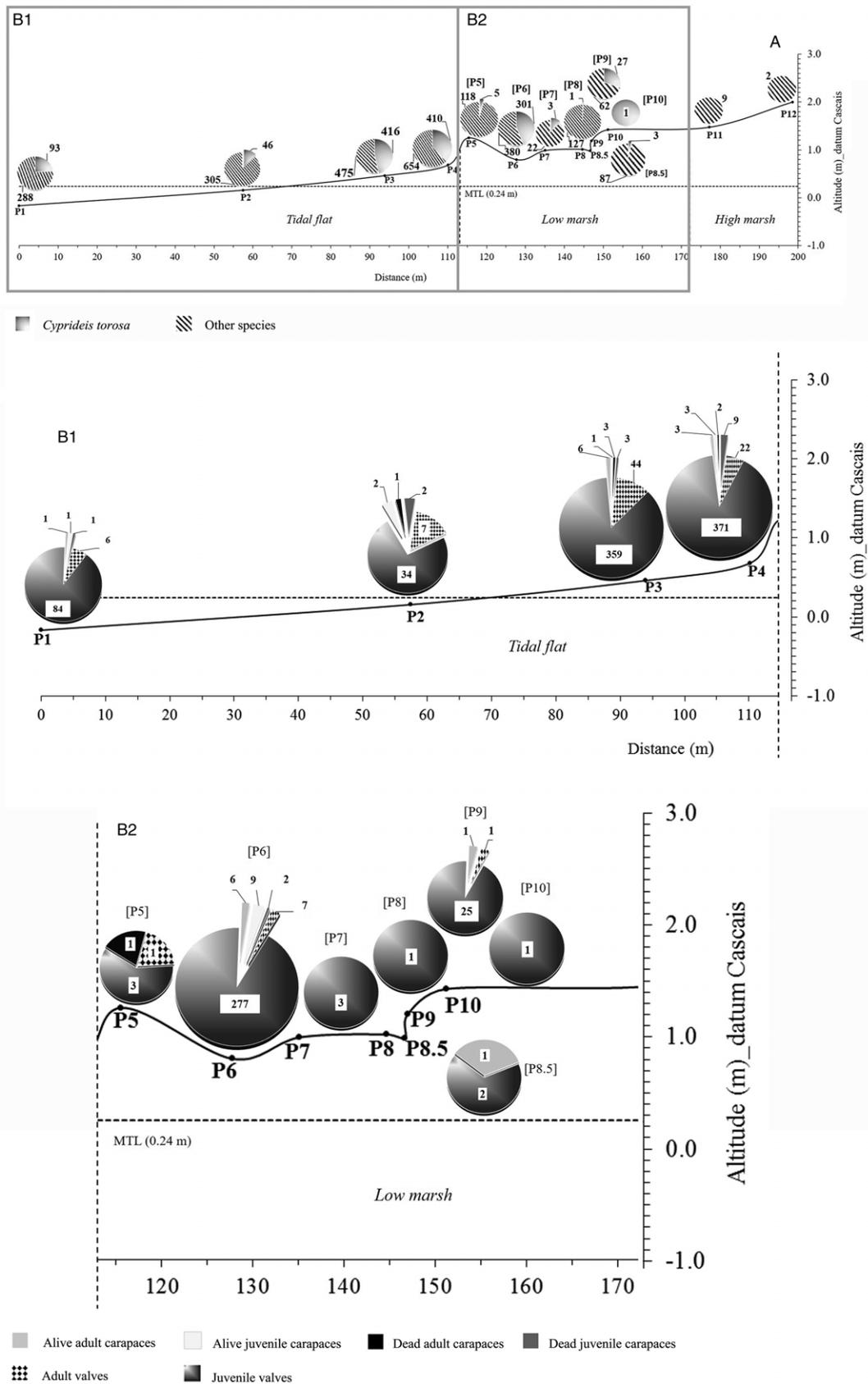
as recorded between 1973 and 1990 (ARH Tejo 2011; Bettencourt *et al.* 2003). For an average tide, the flux close to the Tejo mouth is around 40 000 m<sup>3</sup> s<sup>-1</sup> during flood and 50 000 m<sup>3</sup> s<sup>-1</sup> with ebb. The dynamic tidal effects are felt to a distance of 80 km upstream and the salt edges reach 50 km upstream with a flux of 300 m<sup>3</sup> s<sup>-1</sup>.

Tejo's salt marshes develop from the lower to the upper estuary, along 50 km, over an area of 18 760 000 m<sup>2</sup> (Bettencourt *et al.* 2003). They are very important in the left shore of the outer estuary, particularly in Seixal bay (Fig. 1) which forms a protected area, similar to an open lagoon and where the Alfeite transect (ALF) is located, the only one with an abundant ostracod population which comprises *C. torosa*.

In Tejo estuary, three salt marshes were studied (Fig. 1): Trancão (TRA), Rosário (ROS) and Alfeite (ALF), but *C. torosa* was found only in the Alfeite one. TRA salt marsh is relatively small, essentially muddy, located on the left bank of the lower Trancão estuary, which like the Minho, Lima and Mira estuaries is morphologically elongate, subjected to strong tidal currents, which does not allow the survival of *C. torosa*. ROS salt marsh is

characterized by a sandy/sandy-mud substrate and a high and rapidly variable morphology, with meandering channels and rapid formation/destruction of large zones of low marsh and tidal flat, which must prevent the permanent presence of *C. torosa*.

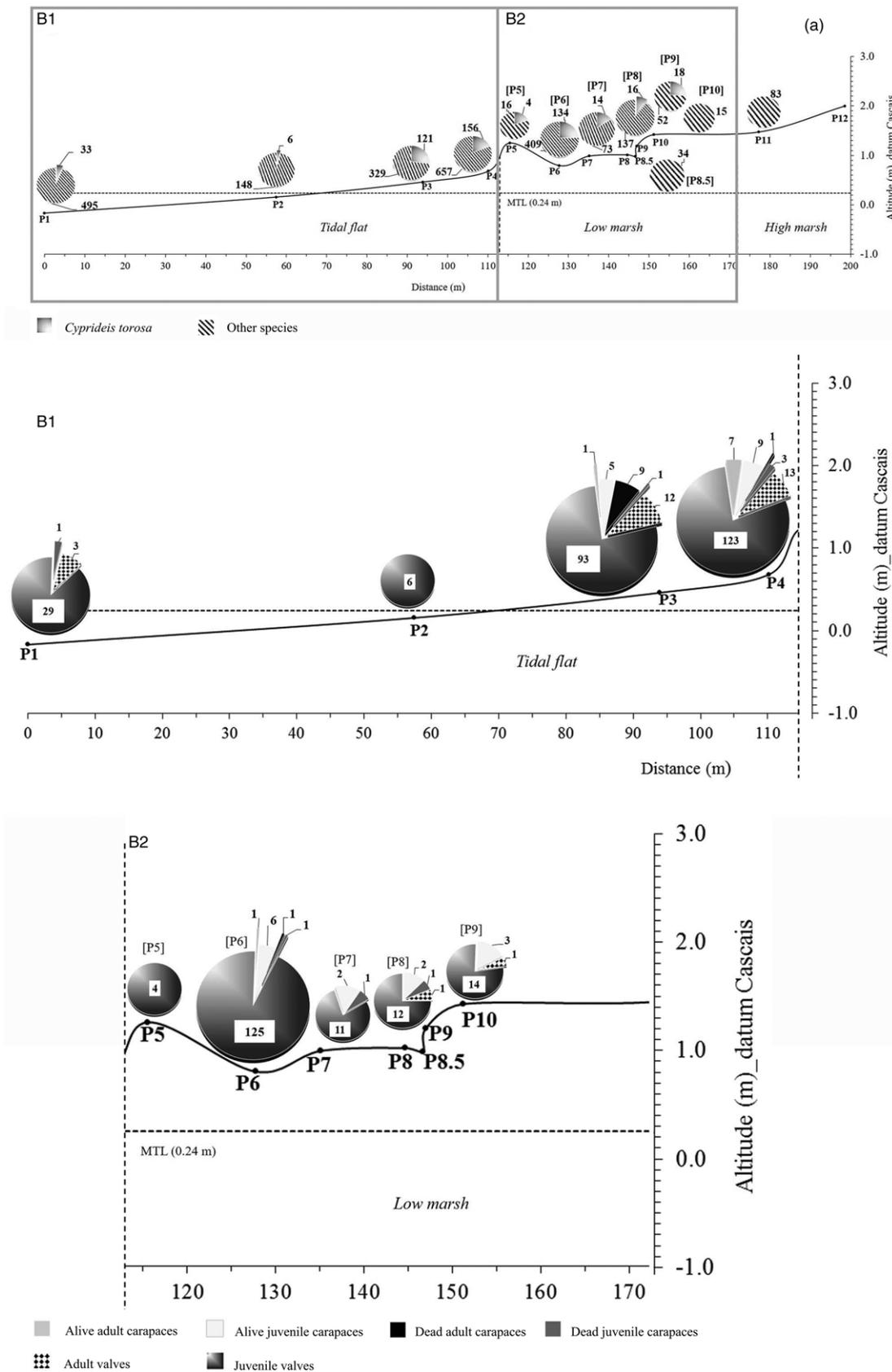
ALF salt marsh is extensive, gently dipping, with a long tidal flat, irregular low marsh and short high marsh (Figs 4 and 5); the sediment is mud in the tidal flat and lower part of the low marsh, sandy-mud upwards, particularly on the high marsh. The main physical parameters of the interstitial waters have a small variation range along the transect. For temperature and pH: the temperature remains between 14.1 and 16.6°C in winter and 20.4 and 21.7°C in summer and the pH between 6.44 and 8.02 in winter and 6.14 and 7.27 in summer. The salinity varies between 18.5 and 29.10 in winter and 29.7 and 35.3 in summer; the dissolved oxygen between 0.15 and 6.43 mg l<sup>-1</sup> in winter and 0.08 and 2.18 mg l<sup>-1</sup> in summer. In ALF transect (Figs 4 and 5) *C. torosa* is mainly represented by juvenile valves (>60% of *C. torosa* population in winter; >75% in summer) along the tidal flat and the low marsh; it is more abundant during winter (total of 1303 individuals, from which



**Fig. 4.** Tejo estuary marsh transect ALF. (A) Distribution (%) of *Cyprideis torosa* and other ostracod species along the transect in winter. (B1, B2) Distribution (%) of *Cyprideis torosa* (carapaces, valves, adults, juveniles, dead, alive) along the transect in winter: (B1) along the tidal flat; (B2) along the low marsh. MTL, mean tidal level. Pie charts show number of individuals. Small pie chart: <30 individuals; medium pie chart: 30 < individuals < 100; large pie chart: >100 individuals.

34 were alive, compared to 502 in summer, from which 32 were alive); the live specimens are more abundant in the tidal flat, in winter and in summer, with adults better represented in winter. In

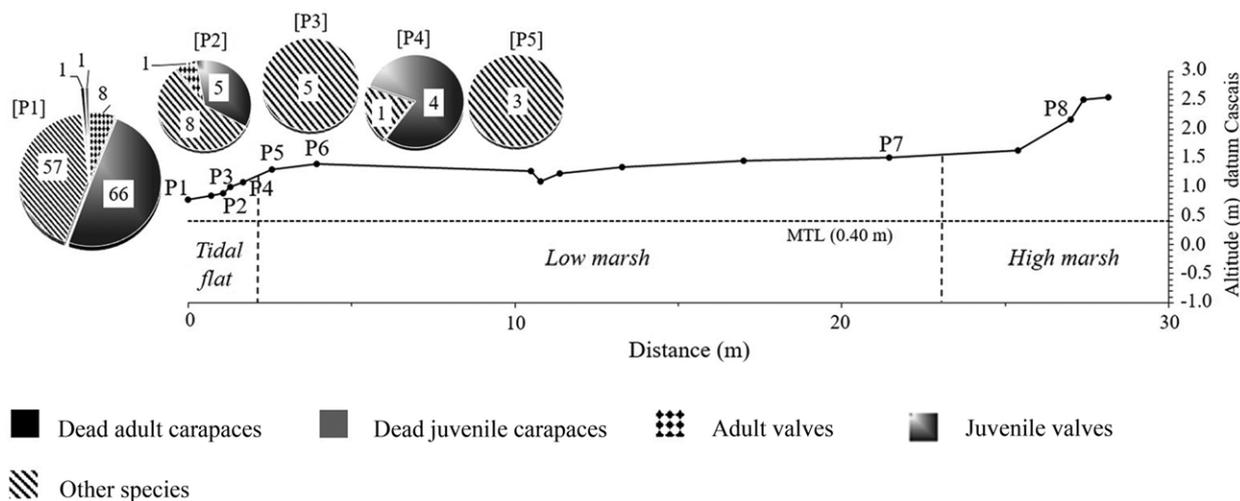
the high marsh *C. torosa* was not found, the only species present being *Terrestricythere* cf. *elisabethae* Horne et al. and *Tuberoxoxoconcha* cf. *atlantica* Horne, both in winter and



**Fig. 5.** Tejo estuary marsh transect ALF. **(A)** Distribution (%) of *Cyprideis torosa* and other ostracod species along the transect in summer. **(B1, B2)** Distribution (%) of *Cyprideis torosa* (carapaces, valves, adults, juveniles, dead, alive) in summer: (B1) along the tidal flat; (B2) along the low marsh. MTL, mean tidal level. Pie charts show number of individuals. Small pie chart: <30 individuals; medium pie chart: 30 < individuals < 100; large pie chart: >100 individuals.

summer. The diversity is low, with no more than 6 species per sample. Generally four brackish species, all of them autochthonous, with live individuals, are present in the tidal flat and the low marsh.

Ordered by abundance: *Loxoconcha elliptica* Brady, *C. torosa*, *Leptocythere porcellanea* (Brady) and *Leptocythere lacertosa* (Hirschmann), with *L. elliptica* largely dominant and mainly



**Fig. 6.** Sado estuary marsh transect CAR. Distribution (%) of *Cyprideis torosa* (carapaces, valves, adults, juveniles, dead, alive) and other ostracod species along the transect in autumn. MTL, mean tidal level. Pie charts show number of individuals. Small pie chart: <30 individuals; medium pie chart: 30 < individuals < 100; large pie chart: >100 individuals.

represented, as *C. torosa*, by juvenile valves. *Leptocythere porcellanea*, though less abundant, has many live specimens, especially in the low marsh where it is the most important species. *Leptocythere lacertosa* is almost only present in the tidal flat. *Cytherois fischeri* (Sars) is rarely present in the tidal flat and *Leptocythere ciliata* Hartmann in the low marsh.

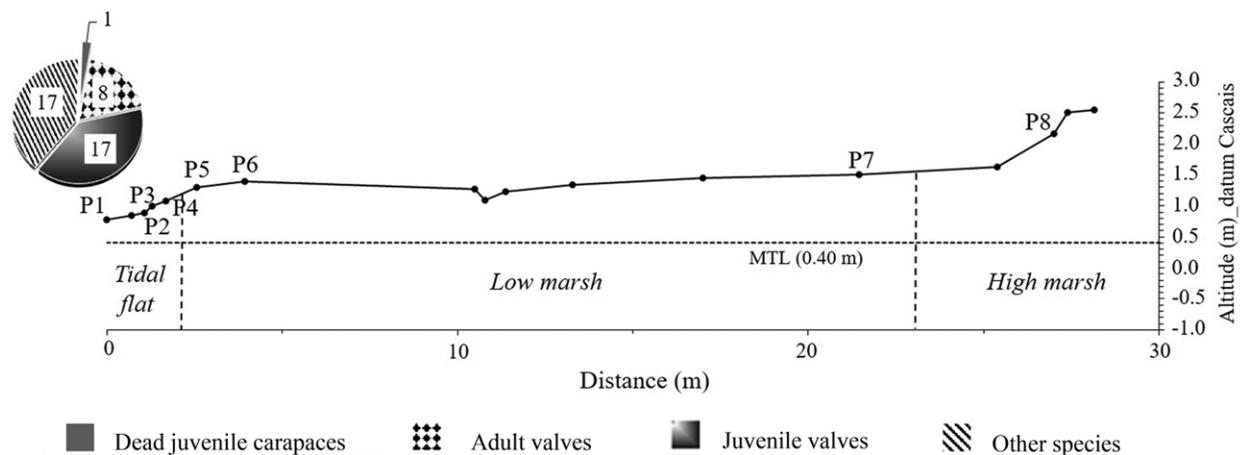
The Sado estuary is located on the SW coast of Portugal (Fig. 1). Its watershed defines an area of around 7670 km<sup>2</sup>. The average annual precipitation in the Sado basin is around 620–650 mm and its fluvial discharge varies from 1 m<sup>3</sup> s<sup>-1</sup> in the dry season to 50–80 m<sup>3</sup>/s under wet conditions, where peaks of 470 m<sup>3</sup> s<sup>-1</sup> may be recorded (Bettencourt et al. 2003). Sado’s yearly average natural fluvial discharge is around 40 m<sup>3</sup> s<sup>-1</sup>, very close to a Mediterranean type, but circulation inside the estuary is absolutely controlled by tides (Âmbar et al. 1980; Bettencourt et al. 2003). Considering a freshwater flux of 5 m<sup>3</sup> s<sup>-1</sup>, a salt wedge penetrates 8 km upstream from Alcácer do Sal (Fig. 1), whereas tidal influence may be felt up to 15 km upstream from this town, around 60 km from the Sado mouth (Bettencourt et al. 2003).

The Sado estuary may be divided into two zones, the Alcácer channel (1 transect –ALC) and a wide basin, between its end and the mouth of the river, which has the behaviour of a coastal lagoon (Bettencourt et al. 2003). Sado’s salt marshes are well developed

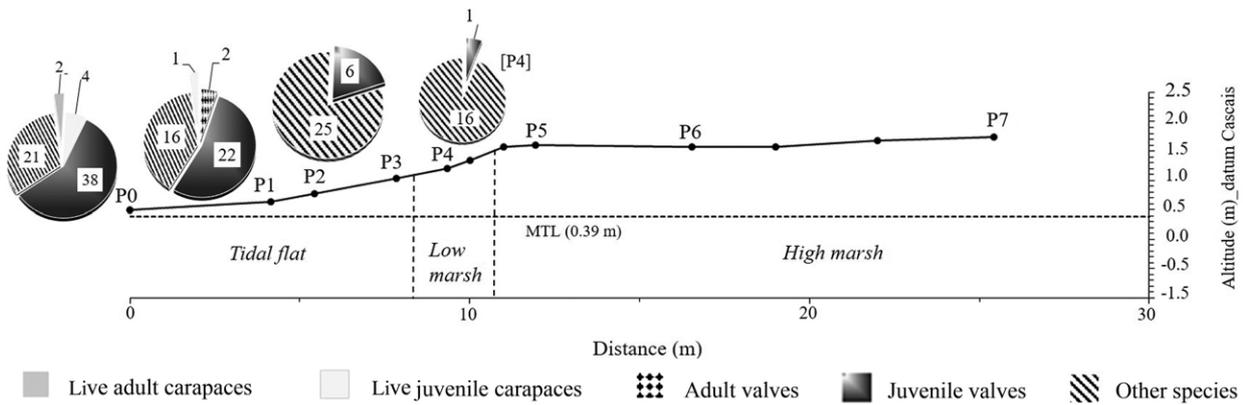
along the widest basin (3 transects – CAR, FAR and TRO) and in both terminal banks of the Alcácer channel. All the studied transects are narrow and ostracods are poorly represented.

*Cyprideis torosa* is absent from ALC transect (Fig. 1), where the river is relatively narrow, with a strong flow, low salinity (c. 2.9 in autumn high-tide; c. 0.3 in spring low-tide) and marshes almost absent, short, muddy and only vegetated by *Juncus*. In the salt marshes of the widest basin (lower estuary) *C. torosa* is generally represented by few live forms on the tidal flat and low marsh.

CAR salt marsh is located in the left shore of Sado estuary (Fig. 1); it is c. 28 m in length (Figs 6 and 7). The sediment is mud to sandy-mud (Moreira et al. 2009). The main physical parameters of the interstitial waters have a small variation range along the transect. For temperature and pH: the temperature stays between 13.4 and 14.4°C in autumn and 15.8 and 17.1°C in spring and the pH between 6.83 and 7.02 in autumn and 6.85 and 7.10 in spring. The salinity varies between 26.2 and 43.3 in autumn and 30.9 and 41.7 in spring; the dissolved oxygen between 0.24 and 5.53 mg l<sup>-1</sup> in autumn and 0.40 and 2.95 mg l<sup>-1</sup> in spring. In the CAR transect (Figs 6 and 7) *C. torosa* is always dead, in autumn and in spring, mainly represented by juvenile valves in the tidal flat. It is the dominant species (c. 65% of the population in autumn; c. 60% in spring), followed, in autumn, by *L. elliptica*, *L. porcellanea*,



**Fig. 7.** Sado estuary marsh transect CAR. Distribution (%) of *Cyprideis torosa* (carapaces, valves, adults, juveniles, dead, alive) and other ostracod species along the transect in spring. MTL, mean tidal level. Pie charts show number of individuals. Small pie chart: <30 individuals; medium pie chart: 30 < individuals < 100; large pie chart: >100 individuals.



**Fig. 8.** Sado estuary marsh transect FAR. Distribution (%) of *Cyprideis torosa* (carapaces, valves, adults, juveniles, dead, alive) and other ostracod species along the transect in autumn. MTL, mean tidal level. Pie charts show number of individuals. Small pie chart: <30 individuals; medium pie chart: 30 < individuals < 100; large pie chart: >100 individuals.

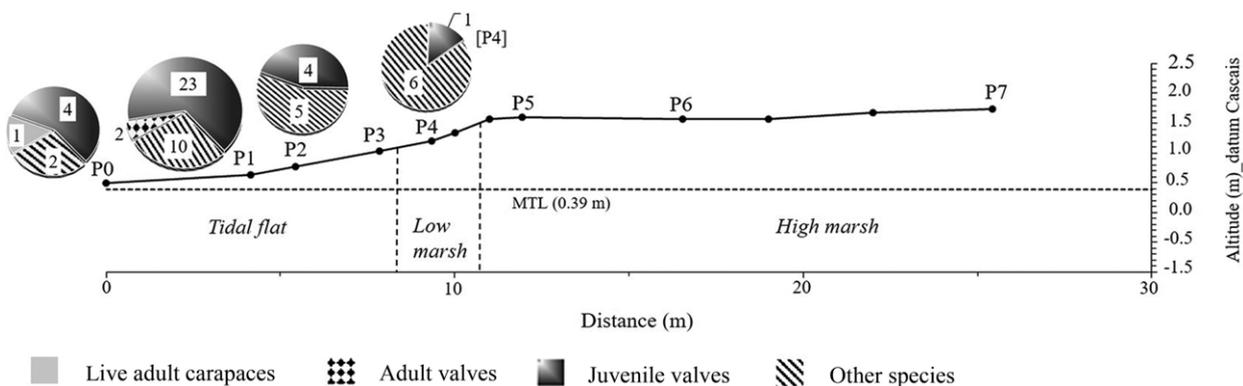
*L. lacertosa*, all with live and dead individuals and, finally, *L. ciliata* (1 live individual) and *Callistocythere murrayi* Whittaker (1 dead individual). In spring the ostracods were scarce, only represented in the lower part of the tidal flat (Fig. 7) by 3 species in addition to *C. torosa*: *L. lacertosa* (5 live, 4 dead individuals), *L. elliptica* (1 live, 1 dead individual) and *L. porcellanea* (1 dead individual). No ostracods were found on the high marsh, both in autumn and spring.

FAR salt marsh is located on the right shore of Sado estuary (Fig. 1); it is c. 25 m in length (Figs 8 and 9). The sediment is mud to muddy-sand (Moreira *et al.* 2009). The main physical parameters of the interstitial waters have a small variation range along the transect. For temperature and pH: the temperature remains between 12.1 and 13.3°C in autumn and 16.6 and 19.0°C in spring and the pH between 5.90 and 7.54 in autumn and 6.90 and 7.55 in spring. The salinity varies between 30.1 and 34.7 in autumn and 30.9 and 33.6 in spring; the dissolved oxygen between 0.28 and 6.12 mg l<sup>-1</sup> in autumn and 1.69 and 3.10 mg l<sup>-1</sup> in spring. In the FAR transect (Figs 8 and 9) *C. torosa* is present in the tidal flat, more abundantly in autumn (76 specimens) than in spring (35 specimens). It is represented almost only by juvenile valves and it is the dominant species in the lower part of the tidal flat, where live individuals were found: 7 in autumn and 1 in spring. In the low marsh one juvenile valve was found both in autumn and spring, together with a few specimens of *L. ciliata* (some alive in autumn and spring) and *L. porcellanea* (rarely alive in autumn); in the high marsh *C. torosa* is absent, as are other species.

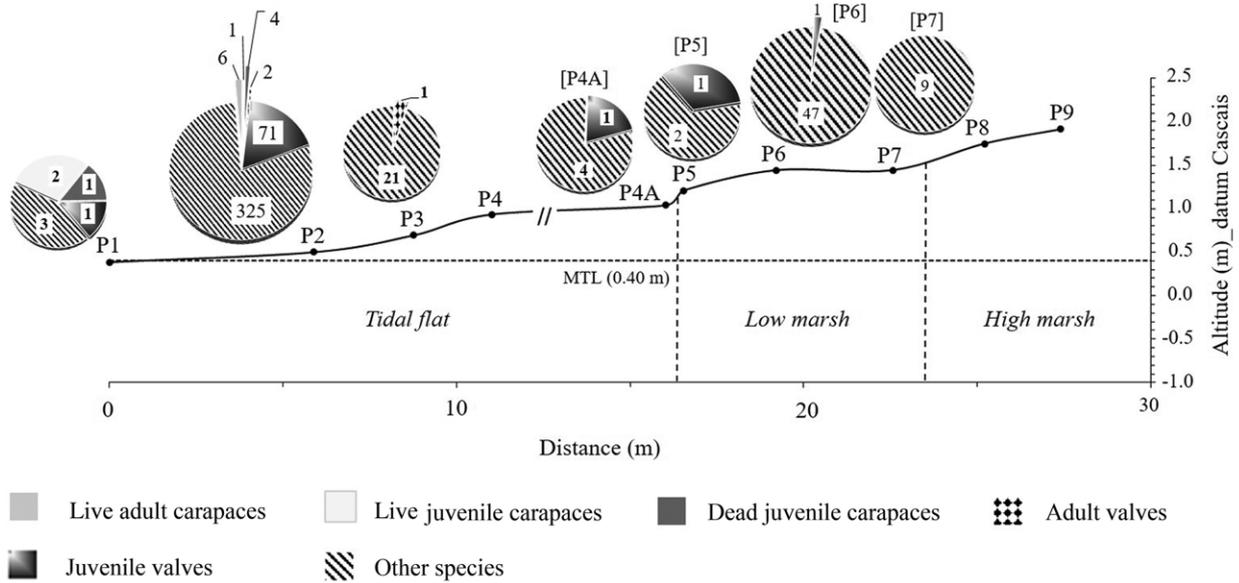
In the tidal flat the diversity is low: 6 different species in autumn, including *C. torosa*, 7 in spring, the most important ones being

*L. elliptica*, *L. ciliata* and *L. porcellanea* in autumn, with rare live individuals, and *Loxoconcha malcomsoni* Horne & Robinson, *Paradoxostoma sarniense* Brady, *L. porcellanea* and *L. ciliata* in spring, also with live individuals. It is important to stress the presence, in the tidal flat, of some worn valves belonging to sublittoral marine species, such as *Urocythereis britannica* Athersuch and *Paracytheridea depressa* G. W. Müller, which show the influence of tidal currents in this zone of the estuary.

TRO salt marsh is located in the left shore of the Sado estuary (Fig. 1), in a long south–north sand bar; it is c. 27 m in length (Figs 10 and 11). The sediment is mainly mud to muddy-sand in the tidal flat and low marsh, sand in the high marsh (Moreira *et al.* 2009). The main physical parameters of the interstitial waters have a small variation range along the transect. For temperature and pH: the temperature stays between 13.4 and 14.2°C in autumn and 15.9 and 20.5°C in spring and the pH between 6.39 and 7.15 in autumn and 6.29 and 7.53 in spring. The salinity varies between 16.2 and 32.2 in autumn and 17.1 and 34.1 in spring; the dissolved oxygen between 1.17 and 4.61 mg l<sup>-1</sup> in autumn and 0.36 and 2.74 mg l<sup>-1</sup> in spring. In TRO transect (Figs 10 and 11) *C. torosa* is mainly represented in the lower part of the tidal flat, in autumn and spring, by juvenile valves but also by live individuals (juveniles and adults): 9 in autumn, 7 in spring. In the lower part of the low marsh one juvenile valve was found in autumn, together with rare *L. ciliata* and *C. fischeri*; upwards, another juvenile valve was found in autumn, together with relatively abundant and live specimens of *L. ciliata* and *T. cf. elisabethae*; in the high marsh *C. torosa* is absent, as are other species. In the tidal flat the diversity is moderate: 9 different



**Fig. 9.** Sado estuary marsh transect FAR. Distribution (%) of *Cyprideis torosa* (carapaces, valves, adults, juveniles, dead, alive) and other ostracod species along the transect in spring. MTL, mean tidal level. Pie charts show number of individuals. Small pie chart: <30 individuals; medium pie chart: 30 < individuals < 100; large pie chart: >100 individuals.



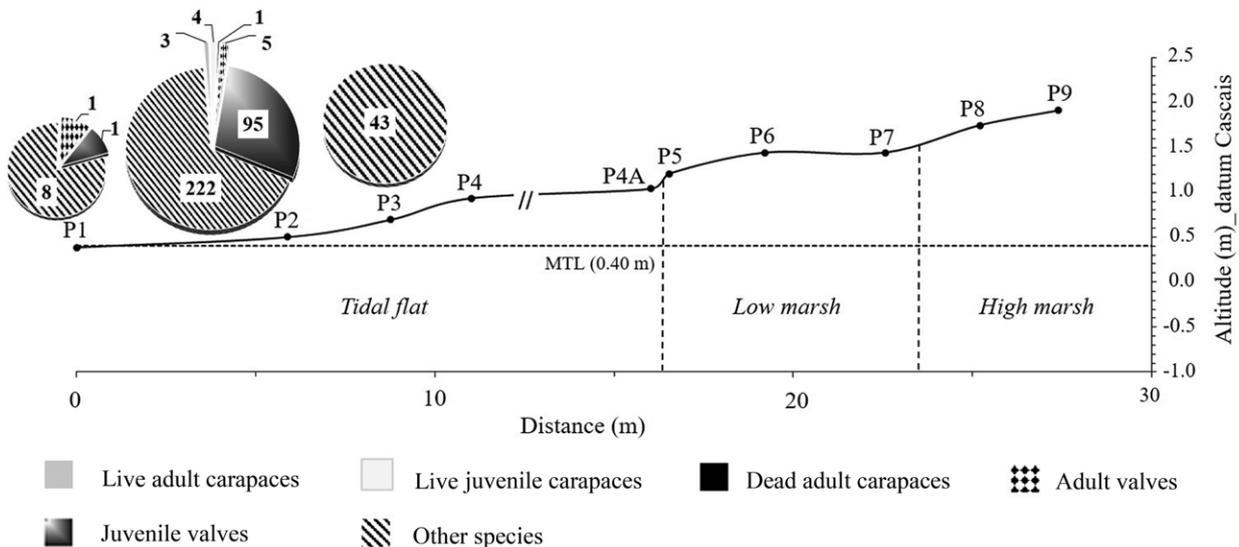
**Fig. 10.** Sado estuary marsh transect TRO. Distribution (%) of *Cyprideis torosa* (carapaces, valves, adults, juveniles, dead, alive) and other ostracod species along the transect in autumn. MTL, mean tidal level. Pie charts show number of individuals. Small pie chart: <30 individuals; medium pie chart: 30 < individuals < 100; large pie chart: >100 individuals.

species in autumn and spring, including *C. torosa*, the most important being *C. fischeri* (>100 individuals in each season, with c. 50% alive), *L. lacertosa* and *L. elliptica*; the other species are: *L. ciliata*, *L. porcellanea*, *Leptocythere* sp. B, *P. sarniense* and *L. malcomsoni* (only dead) in autumn, and *L. porcellanea*, *L. sp. B*, *P. sarniense*, *Paradoxostoma trieri* Horne & Whittaker and *Semicytherura tela* Horne & Whittaker in spring.

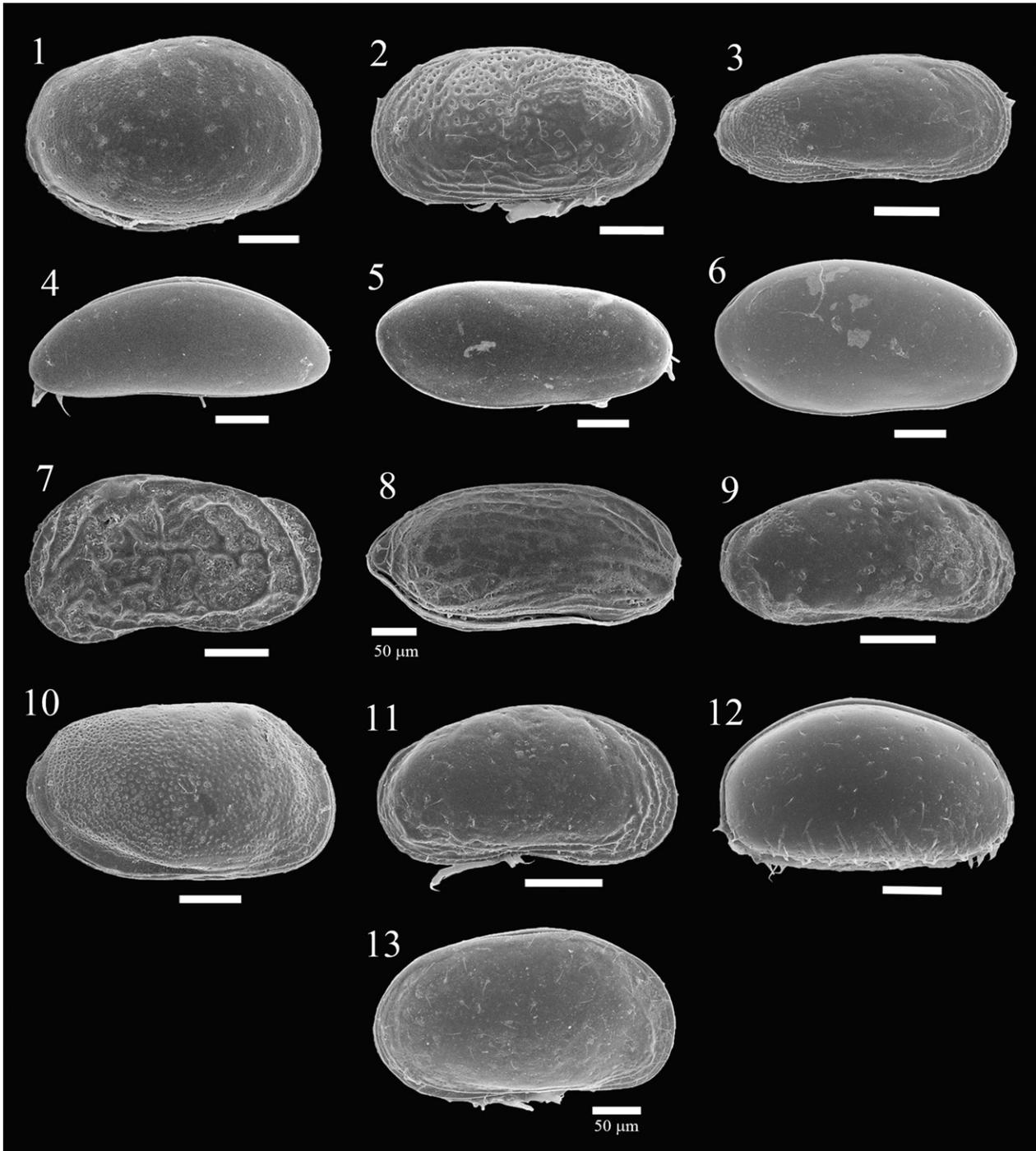
In the Portuguese estuaries *C. torosa* is relatively abundant, but occurs alive only in the tidal flat and low marshes of sheltered areas, with low dynamics, as in lagoons, allowing deposition of soft mud to sandy mud substrates; in sandy substrates *C. torosa* never appears alive (only empty valves), thus showing a clear preference for fine-grained sediments. In fact, in the studied transects *C. torosa* is much more abundant in ALF transect (Tejo estuary), which is the longest one, more sheltered, morphologically stable and muddy, located in a

very quiet area. The total absence of *C. torosa* from the high marsh and its higher abundance in the tidal flat shows that it cannot survive long emersion periods.

The interstitial waters of the sediments where *C. torosa* lives are polyhaline to euhaline (salinity range 19.0–34.1), slightly alkaline (pH range 7.06–8.02), with temperatures varying between 13.3 and 16.6°C in autumn/winter and 17.6 and 21.7°C in spring/summer and dissolved oxygen between 0.09–6.43 mg l<sup>-1</sup>. Along all the studied transects where *C. torosa* was found alive the maximum variation of these parameters was very close to the ones recorded for *C. torosa* in general (dead and alive). Major differences are related to pH, which reaches values lower than 7 in all transects, both in Tejo and Sado estuaries, in autumn/winter and spring/summer. It is possible that the pH could control the distribution of *C. torosa*, since in all the samples where it was lower *C. torosa* was not found alive.



**Fig. 11.** Sado estuary marsh transect TRO. Distribution (%) of *Cyprideis torosa* (carapaces, valves, adults, juveniles, dead, alive) and other ostracod species along the transect in spring. MTL, mean tidal level. Pie charts show number of individuals. Small pie chart: <30 individuals; medium pie chart: 30 < individuals < 100; large pie chart: >100 individuals.



**Fig. 12.** Ostracod species found in Portuguese estuaries together with *Cyprideis torosa*. **1.** *Loxococoncha elliptica* Brady, C, right view, f; Sado estuary, CAR-P1 aut.. **2.** *Leptocythere lacertosa* (Hirschmann), C, left view, f; Sado estuary, TRO-P2 aut.. **3.** *Leptocythere porcellanea* (Brady), C, right view, m; Sado estuary, TRO-P2 aut.. **4.** *Cytherois fischeri* (Sars), C, right view, f; Sado estuary, TRO-P2 aut.. **5.** *Paradoxostoma sarniense* Brady, C, right view, m?; Sado estuary, TRO-P2 aut.. **6.** *Paradoxostoma trieri* Horne & Whittaker, C, right view, f; Sado estuary, TRO-P2 spr.. **7.** *Callistocythere murrayi* Whittaker, C, left view, f; Sado estuary, CAR-P1 aut.. **8.** *Semicytherura tela* Horne & Whittaker, C, right view, m; Sado estuary, TRO-P2 spr.. **9.** *Leptocythere* sp. B, C, right view, f; Sado estuary, TRO-P2 aut.. **10.** *Loxococoncha malcomsoni* Horne & Robinson, C, right view, f; Sado estuary, TRO-P2 aut.. **11.** *Leptocythere ciliata* (Hartmann), C, right view, f; Sado estuary, TRO-P6 aut.. **12.** *Terrestriocythere* cf. *elisabethae* Horne, Smith, Whittaker & Murray, C, right view, Sado estuary, TRO-P6 aut.. **13.** *Tuberoloxococoncha* cf. *atlantica* Horne, C, right view, f?; Tejo estuary, ALF-P11 wint.. C, carapace; f, female; m, male; aut., autumn; spr., spring; wint., winter; scale bar 100 µm, except when indicated.

*Cyprideis torosa* tolerates hypoxic conditions, since it was found alive (though rarely) in sediments with interstitial water with a very low content of dissolved oxygen ( $0.09 \text{ mg l}^{-1}$ ).

*Cyprideis torosa* is more abundant, with a more complete population represented mainly by adults and the last instars, during autumn/winter. According to Heip (1976) and Home & Boomer (2000) *C. torosa* has a life-cycle of one generation per year, with the main period of growth,

maturation and reproduction in late spring and summer and the first adults appearing by autumn; the later-hatching individuals only mature in the following spring, leading to an overwintering population of larger juveniles and adults. The Portuguese population composition is in perfect accordance with these observations.

The ostracod assemblage, generally of low diversity, is composed of brackish species (Fig. 12), which vary in the tidal flat, low and

high marshes according to their tolerance to the fluctuating environmental parameters, particularly substrate, emersion time, salinity and temperature. The most common species in the tidal flat, where diversity and abundance are higher, are *C. torosa*, *L. elliptica*, *L. lacertosa*, *L. porcellanea* and *C. fischeri*; more rarely, *P. sarniense*, *P. trieri*, *L. malcomsoni* and *S. tela* are also found. In the low marsh the most important species are *L. ciliata*, *L. porcellanea*, *L. elliptica*, *C. torosa* and *T. cf. elisabethae* (very rare) and, in the high marsh, only *T. cf. elisabethae* and *T. cf. atlantica* were found. The highest diversity was found in the tidal flat of the TRO transect, the most sandy and closest to the Sado estuary mouth; the higher diversity may be related to the different substrate, richer in sands, and to the higher dissolved oxygen content of interstitial waters.

*Melides lagoon*

The Melides lagoon encompasses a 0.4 km<sup>2</sup> flooded area, its average depth and water storage capacity varying seasonally; the maximum depth does not exceed 5–6 m in the main channel where it abuts the southern bank (Fig. 2). The main lagoon body is separated from the open ocean by a closed sand barrier, consisting of a beach–foredune ridge and washover fans. The barrier is artificially breached at least once every year, generally in March/April, during spring tides, near site MEL 1; usually the inlet silts up naturally in less than one week. The physico-chemical parameters of the lagoon water mass are essentially controlled by the alternating opening/closure of the inlet. When the inlet is open, semi-diurnal tides propagate into the lagoon, renewing and homogenizing the water mass. When the inlet is closed (autumn and winter) the lagoon collects freshwater from the Melides rivulet and watershed, increasing its depth and generating a stratified water mass (Freitas et al. 2002).

The measured physico-chemical parameters in February 2015 are typical of a closed-inlet situation and the hydrosome below 2 m depth showed a clear increase in temperature and salinity and decrease in pH and dissolved oxygen (Table 1). In contrast with the homogeneity of the surface water, the characteristics of the near bottom water are variable in space.

In Melides lagoon *C. torosa* is extremely abundant, sometimes so abundant that its valves constitute a component of the bottom sediment; it is the most abundant and most frequently occurring ostracod species and it is the dominant species in all samples (Fig. 13).

From a total of 10 341 individuals, around 87% (8984 individuals) are *C. torosa*. In general it is more heavily represented (>800 individuals per sample) in the quiet north and central-eastern areas (sites 6, 8, 9, 11 and 12) than in the southern areas, where it may be absent (sites 1, 2 and 3) or vestigial (site 10); in site 5, though well represented, all the specimens were dead, including the other species. Site 7 is very particular since it is represented by a mono-specific population of *C. torosa*, with a high number of live individuals (93 in a total of 522), only exceeded in sample 11, but proportionally lower (195/2248).

*Cyprideis torosa* is particularly represented by valves, many in hyaline condition and belonging to all juvenile stages (generally >50% of the individuals in each sample); the adult valves, also mainly hyaline, represent <1/3 of the juvenile valves in each sample (Fig. 13); the number of dead and juvenile carapaces generally exceeds the number of live and adult ones; the live individuals are only present in the northern and central-eastern area of the lagoon (sites 6, 7, 8, 9, 11 and 12), suggesting the preference of the species for quiet zones, far from the main channel of the lagoon (Fig. 2), where deposition of fine sediments is promoted. In fact, the samples of these sites correspond to mud and muddy sand, containing more

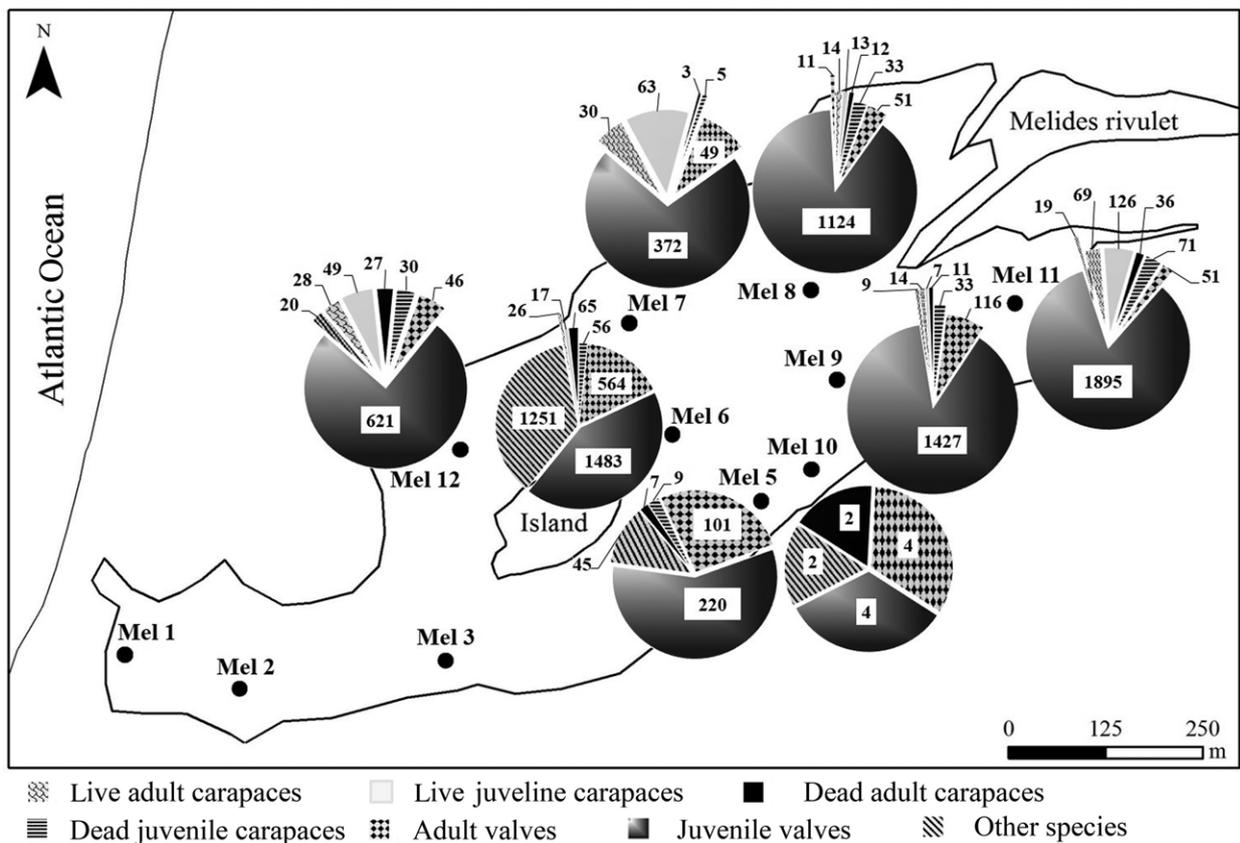


Fig. 13. Distribution (%) of *Cyprideis torosa* (carapaces, valves, adults, juveniles, dead, alive) and other ostracod species in Melides lagoon in winter. Pie charts show number of individuals.

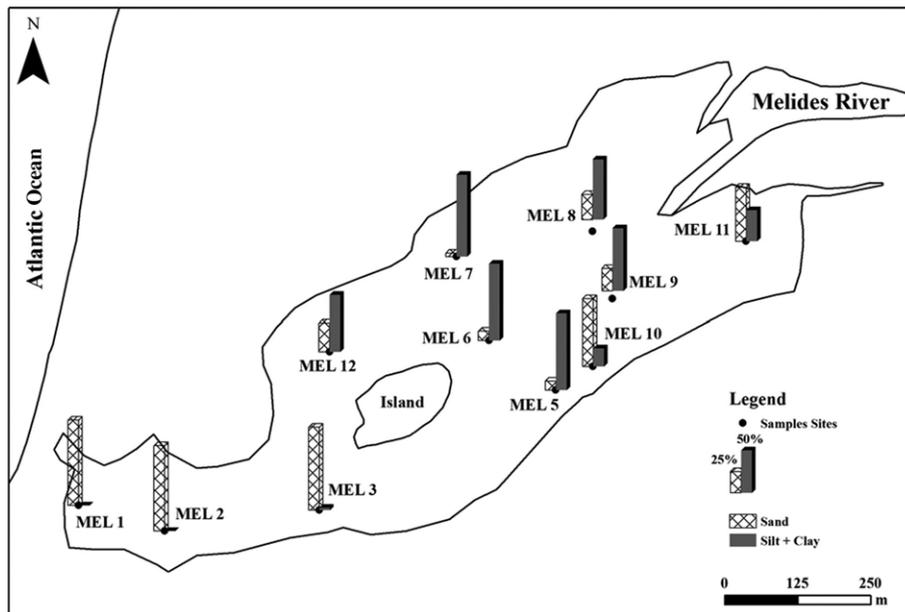


Fig. 14. Sand and silt + clay contents of the bottom sediments of Melides lagoon.

than 66% of silt + clay, except in site 11 (only 36.7% of silt + clay; Fig. 14); however, the latter site presents a high value of dissolved oxygen ( $7.8 \text{ mg l}^{-1}$ ; Table 1), which can possibly explain the abundance of live *C. torosa*; in site 7, where the live forms are also abundant, the sediment is muddy, with 96% of fine material.

The diversity is very low. *Cyprideis torosa* is always dominant and generally there are no more than 4 species per sample. The highest species diversity is found in sample 6, with at least 7 species, the most abundant being brackish forms (*C. torosa* and *Loxocochoa elliptica*); the remaining freshwater ones, all of them tolerating low salinities (Meisch 2000) are: *Cyprina* cf. *subsalsa* Redeke, *Heterocypris salina* (Brady), *Cypridopsis vidua* (O.F. Müller), *Sarscypridopsis aculeata* (Costa) and Ind. Gen. sp. (unidentified

juveniles) (Fig. 15). Most of the freshwater species are represented by allochthonous juvenile valves of Ind. Gen. sp., possibly transported from the nearby island (Fig. 13). The low salinity values in the bottom of the water mass, varying from 3.2 to 19.7 (with live ostracods being present only in sites with a salinity range between 4.1 and 15.1) explains the observed low ostracod diversity and the complete absence of marine species. *Cyprideis torosa* prefers oligo- to mesohaline waters, the living forms being more abundant in sites 7 and 11 (salinity = 8.5 and 4.1, respectively).

In summary, *C. torosa* is the main ostracod found in Melides lagoon and the only live species found during the winter season. Most of the population is autochthonous, but the presence of many worn or opaque valves in some sites, and the rare presence of some

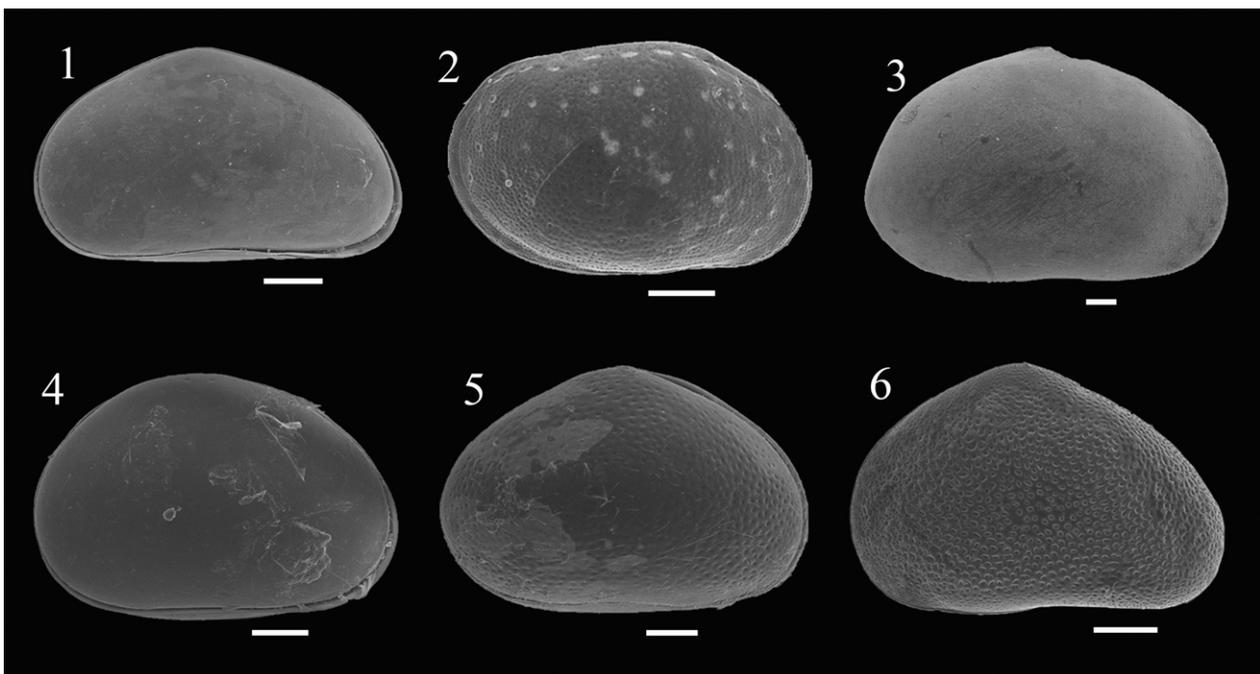


Fig. 15. Ostracod species found in Melides lagoon, together with *Cyprideis torosa*. 1. Ind. Gen. sp., C, left view, j; MEL6 wint.. 2. *Loxocochoa elliptica* Brady, RV, external, f; MEL12 wint.. 3. *Heterocypris salina* (Brady), RV, external; MEL6 wint.. 4. *Cyprina* cf. *subsalsa* Redeke, C, right view, MEL6 wint.. 5. *Cypridopsis vidua* (O.F. Müller), C, right view, f; MEL6 wint.. 6. *Sarscypridopsis aculeata* (Costa), LV, j; MEL6 wint.. C, carapace; LV, left valve; RV, right valve; f, female; j, juvenile; wint., winter; scale bar 100  $\mu\text{m}$ .

'freshwater' species in almost all samples, suggests remobilization inside the lagoon. *Cyprideis torosa* prefers to live in a soft mud to muddy sand substrate, in quiet oligo- to mesohaline waters, with a range of dissolved oxygen from 0.28 to 7.8 mg l<sup>-1</sup> and pH from 7.20 to 8.25. Due to its exceptional abundance in some of the Melides samples and in other Portuguese lagoons (Santo André and Albufeira, unpublished data) it is evident that the lagoonal environment is one of its preferred habitats.

## Palaeontology research

### Holocene

In the studied sedimentary columns from Holocene marginal-marine environments, all of them dated using AMS <sup>14</sup>C radiocarbon dating techniques on particulate carbon in sediment (dates undertaken by Beta Analytic Radiocarbon Dating Laboratory, Miami, USA), *C. torosa* is always present, its vertical (in time) distribution depending on the marine influence and river discharge. An evolutionary model for the Holocene of western Iberian marginal-marine environments has already been established; this model considers drowning of previously dissected landscapes by the Holocene transgression, followed by barrier encroachment contemporaneous with deceleration of sea-level rise in the middle Holocene. Early estuarine/ria environments were transformed into lagoons and barred estuaries, the former permanently or temporarily closed by sandy barriers (e.g. Santo André, Melides, Pederneira and Sizandro lowlands, Fig. 3; Cearreta *et al.* 2003; Freitas *et al.* 2003; Cabral *et al.* 2006, 2011; Lord *et al.* 2011). One paradigmatic example is illustrated in Figure 16, from Pederneira estuary/lagoon (borehole S2), near Nazaré.

In all lowlands several palaeoenvironmental stages may be recognized, with the earliest (Lateglacial to Early Holocene; Fig. 16, Zone I) and the latest (Late Holocene; Fig. 16, Zone V) being characterized by total or almost total absence of ostracods. In the first (oldest) stage this absence is interpreted as due to a high energy fluvial environment, contemporaneous with a sea level much lower than the present one. In the last (youngest) stage the absence of ostracods is interpreted as due to the terrestrialization of the former barred marginal-marine systems by progressive infilling with fluvial sediments; when ostracods are present, they are very rare, belonging to freshwater genera such as *Ilyocypris*, *Heterocypris* and *Limnocythere*, all of them with species tolerating slightly salty inland and coastal waters (Meisch 2000). In between these two stages, two to five more can occur (some including sub-stages), their number depending on the physical characteristics of the marginal-marine system and on the location of the borehole (alluvial plain, barrier, medium estuary, lagoon, etc.).

The second stage (Early Holocene; Fig. 16, Zone II) records the first occurrence of ostracods, initially represented by brackish forms, generally *C. torosa* and *Loxoconcha elliptica*, both scarce and mixed with a few littoral marine forms also in low abundance; *C. torosa* is usually represented by empty valves, some hyaline, some opaque, some worn. This stage corresponds to a progressive development of a brackish estuarine environment, due to the rapid sea-level rise during the Holocene transgression.

In the third stage (Middle Holocene; Fig. 16, sub-zones IIIA and IIIB) *C. torosa* (and *L. elliptica*) are usually (but not always) present, varying in number; *C. torosa* is represented by adult and juvenile carapaces and valves, both hyaline and opaque, sometimes worn, with a mixture of autochthonous and allochthonous faunas. However, the littoral and sub-littoral marine species are the most diverse and abundant forms and progressively increase upstage, generally reaching their maximum (c. 10–60 different species) at the top; in some cases, deep-water marine species are also found. This stage developed in consequence of rapid sea-level rise promoting the progressive

change of the former incipient estuarine environment into a deeper, fully or almost fully marine one, with salinity near 30–35.

Finally, in the fourth stage (Middle and Late Holocene; Fig. 16, Zone IV) almost only brackish species are present; *C. torosa* is, in general, abundantly represented, frequently by hundreds of valves and carapaces, most of them hyaline and well preserved, forming mono- to oligo-specific autochthonous assemblages; in the latter case, *C. torosa* is accompanied by *L. elliptica*, which varies significantly in abundance. The existence of nearby salt marshes is indicated by scarce *Cytherois fischeri* and species of the genus *Leptocythere*, among which *L. porcellanea* and *L. lacertosa* are the most important. In addition, rare freshwater species, represented only by one or two specimens have also been found. This stage is contemporaneous with a pronounced decrease in the rate of sea-level rise followed by stabilization of mean sea level close to the present-day level; in most cases it corresponds to the development of a restricted lagoonal environment, separated from the sea by a very effective sandy barrier.

The similarity in abundance, dominance, population composition and preservation of *C. torosa* found in present-day lagoons, such as Melides, and in the Holocene sedimentary record, demonstrates the utility of this ostracod species as a marker to interpret lagoonal environments developed during the Holocene.

In cases where marginal-marine environments remained throughout the Holocene as open estuaries with intense flow, *C. torosa* is poorly represented in sediment (e.g. Schriek *et al.* 2008, on the Tejo upper estuary). Results obtained by Almeida *et al.* (2009) from the PC core made in the Tejo estuary (Fig. 3) are congruent with this observation. Here, the hydrodynamic regime allowed *C. torosa* to be represented by only rare worn valves, in 2 samples out of 100 studied. These samples yielded high ostracod diversity, with autochthonous and allochthonous assemblages, *C. torosa* clearly being a transported form.

In the Mira estuary (Fig. 1), a 27 m-long borehole (MIRA-CP1) drilled in the alluvial plain of the Corgo do Porto tributary, located 3.5 km upstream from the mouth, was studied for foraminifera by Alday *et al.* (2006). *Cyprideis torosa* was only found in the upper section of the core (between 1.94 and 3.99 m below mean sea level), in muddy and sandy substrate, together with other brackish species generally found in salt marshes and/or in open estuarine environments, e.g. *C. fischeri*, *L. lacertosa*, *L. elliptica*, *L. malcomsoni*, *Leptocythere fabraeformis* (G.W. Müller), *Loxoconcha rhomboidea* (Fischer), *Xestoleberis labiata* Brady & Robertson; towards the base of this section of the core, littoral marine species were also well represented, such as *Carinocythereis whitei* (Baird), *Aurila convexa* (Baird), *U. britannica* (unpublished data, ongoing work). In terms of palaeoenvironmental reconstruction, these results are in agreement with those obtained from foraminifera (Alday *et al.* 2006); in fact, *C. torosa* occurs in foraminiferal zones dated to the Middle–Late Holocene that were interpreted by those authors as indicating the development of a progressively more restricted estuarine environment. This phase matches the time-window during which the lagoonal phase was established in the other studied Portuguese marginal-marine barred environments previously discussed. This suggests that *C. torosa* only occurred in the Mira estuary during a less energetic period, post-dating the stabilization of sea-level rise, and probably colonizing salt marshes.

Similar results were found by Hindson *et al.* (1999), Hilbich *et al.* (2008) and Trog *et al.* (2013, 2015) in several Holocene estuaries on the southern Portuguese coast. *Cyprideis torosa* occurs through the cores, usually associated with *L. elliptica* and other brackish and marginal-marine species. The assemblages vary according to the estuary (more open, more restricted), but for the time period characterized by progressive siltation related to the stabilization of sea-level rise, they are generally represented by the brackish species *C. torosa*, *L. elliptica*, *Leptocythere* spp. and *Cytherois fischeri*, together with a few littoral marine species. This is the case in Alcantarilha estuary (Trog *et al.* 2013), with *C. torosa*, *L. elliptica*,

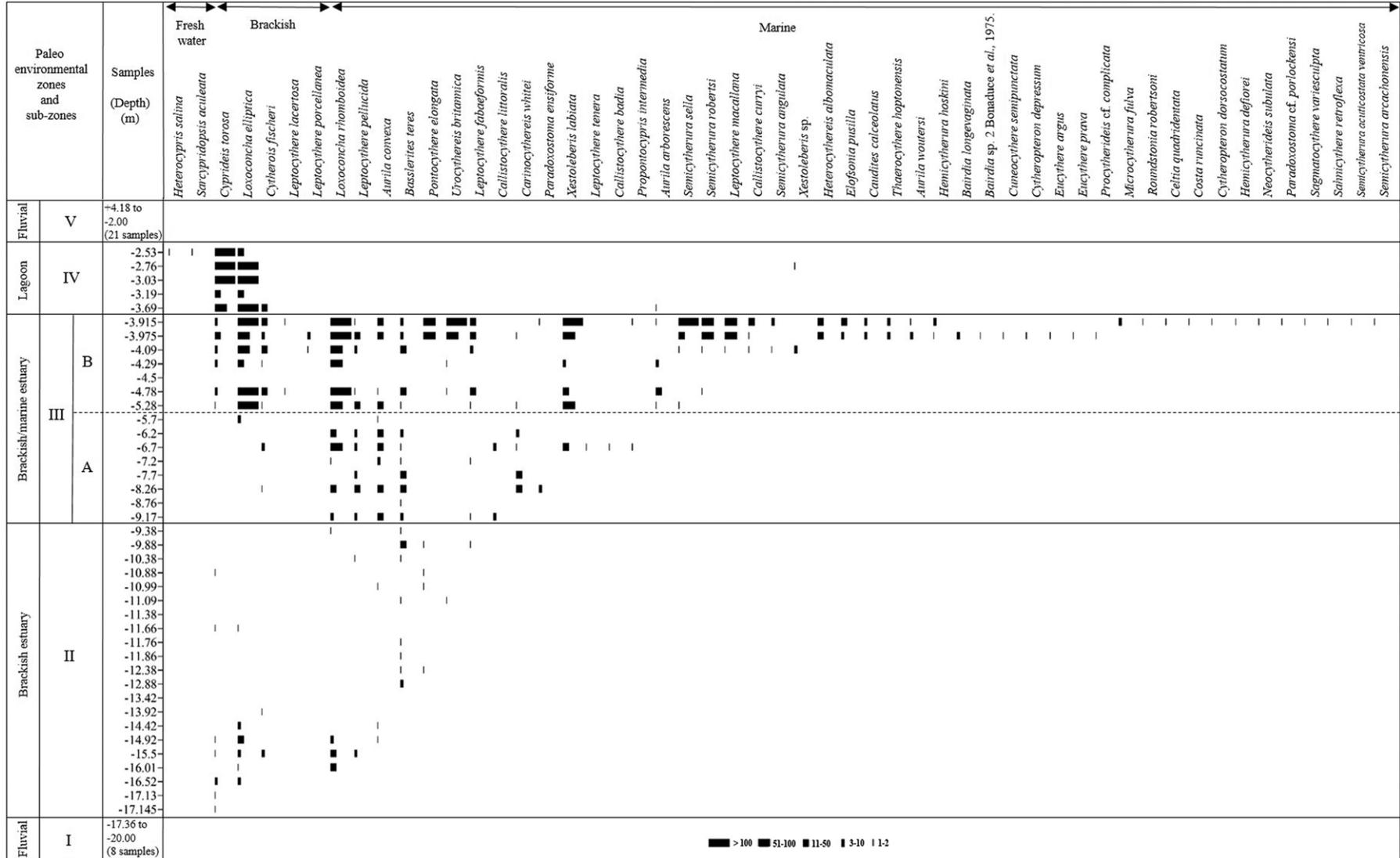


Fig. 16. Frequency distribution of the ostracod species in S2 borehole, Pedemeira estuary/lagoon, Nazaré, along the Holocene, with indication of the palaeoenvironmental ostracod zones, abundance, diversity and ecological groups. Systematics list in Cabral & Loureiro (2013).

*Leptocythere* spp. and the marine species *U. britannica* and *Cytheretta adriatica* Ruggieri.

We conclude that the behaviour of *C. torosa* during the Holocene and in modern times was very similar, in analogous environments, the species being more abundant in lagoons than in estuarine tidal flats and salt marshes, preferring brackish waters, oligo- to polyhaline, relatively quiet, with muddy and sandy-mud sedimentation. This highlights the influence of these three parameters (salinity, water dynamics, substrate) in controlling the distribution of the species. Water dynamics and substrate vary less than the salinity, suggesting that salinity plays a weaker role.

### Miocene, Pliocene and Pleistocene

There are few studies and publications about the brackish Miocene, Pliocene and Pleistocene Portuguese ostracods. Nascimento, who studied Miocene ostracod assemblages both in the Tagus Basin (Nascimento 1981) and in the Algarve (Antunes *et al.* 1981), never refers to the presence of *C. torosa*. Most of the ostracod species found were marine and very few were typical of freshwaters. In Nascimento (1993), dedicated to the *Cyprideis* group taxa occurring in the Tagus Basin, the species considered belong to the genera *Hemicyprideis*, *Miocyprideis* and *Neocyprideis*. For the Pliocene, ostracods have rarely been studied. Only Nascimento (1990) reported a Pliocene ostracod 'biozone' from an infralittoral environment, without *C. torosa*. Finally, in the Pleistocene, the published works concerning Portuguese ostracods, all focused in the Algarve region (Antunes *et al.* 1986; Cabral *et al.* 2004, 2005a, b), only reported freshwater to slightly brackish (oligohaline) species, not including *C. torosa*.

### Morphology of valves

#### Surface ornamentation – nodes, punctation, reticulation

It is well known that the surface of *C. torosa* valves show wide variation, from smooth to punctate, reticulate, with or without nodes. This variation in surface features has been studied in several works (e.g. Sandberg 1964; Kilenyi 1972; Carbonel 1980; Bodergat *et al.* 1991; Gliozzi & Mazzini 1998; Keyser 2005; Frenzel *et al.* 2012), and is usually related to the salinity range and water chemistry.

Nodes appear in low salinity (oligohaline) environments. Some authors quote a salinity critical level, but they give widely different values. Kilenyi (1972, p. 51) states that although noded specimen numbers increase with decreasing salinity, '... there is no linear or even simple nonlinear relationship between the two'. Keyser (2005) explains the appearance of nodes by pathological reactions during the moulting process, influenced by the total ion concentration and  $\text{Ca}^{2+}$  availability. Frenzel *et al.* (2012) conclude that there is a clear negative linear correlation between the proportion of noded individuals from the Baltic Sea coast and salinity, and that deficiency of  $\text{Ca}^{2+}$  causes heavier nodding in laboratory cultures, the critical level, depending also on stability of salinity conditions, varying from 8 to 14.

Salinity is also the parameter most invoked to explain differences in valve ornamentation. For Gliozzi & Mazzini (1998), more reticulated shells are common at low salinities, whereas at higher salinities (above 10‰) the shells become either punctate or smooth. Carbonel (1980) studied the reticulation of *C. torosa* populations from different climatic regions and environments and concluded that valve reticulation does not depend on water salinity but is related to the  $\text{Mg}^{2+}$  content, particularly the  $\text{Mg}^{2+}/\text{Ca}^{2+}$ ; when  $\text{Mg}^{2+}/\text{Ca}^{2+} > 3$ , valves became reticulate; for  $\text{Mg}^{2+}/\text{Ca}^{2+} < 3$  valves are finely punctate or even smooth; on the contrary, nodding seems directly related with salinity. Bodergat *et al.* (1991) relate the nodes, reticulation and heavy calcification of the carapaces to the presence of dissolved Si, Al, Fe, Mn and Ba ions in the water.

In all the studied Portuguese material the valves of *C. torosa*, adults and juveniles, are generally well calcified, always without nodes, and their surfaces are smooth or almost smooth (Fig. 17:12), punctate (Fig. 17:1, 17:6, 17:8) or reticulate (Fig. 17:3), the punctate being the most frequent. The punctation pattern varies from fine to coarse pits and the reticulated valves are the rarest ones.

In the modern estuaries of Tejo and Sado the valves are generally finely punctate, but all types of ornamentation were found. In ALF transect (Tejo), most valves are finely punctate to smooth, the latter being most frequent in juveniles; there are no reticulated valves and the coarsely punctate valves are relatively rare. In the three Sado transects (CAR, FAR and TRO) the valves are also punctate, but generally more coarsely and, in some cases, reticulated, particularly in the adults from the lowest part of the tidal flat; juvenile valves are mainly finely punctate to smooth. The differences in ornamentation found in these two estuaries cannot be explained by salinity differences. The salinity measured in interstitial waters in Tejo (ALF) and Sado (FAR, CAR, TRO) is high: Tejo (19.0–34.3); Sado (26.2–41.4) and this should promote punctate or smooth valves, according to Gliozzi & Mazzini (1998). This happens in Tejo estuary (ALF), but in Sado estuary (CAR, FAR and TRO), where the salinity is even higher, the valves are coarsely punctated, even reticulated (Fig. 17:1, 17:3, 17:6) in all transects. Following Carbonel (1980), the  $\text{Mg}^{2+}/\text{Ca}^{2+}$  content of the water should be the main control of the *C. torosa* valve ornamentation. Unfortunately, no Mg/Ca data are available to test this relationship in the areas addressed in this study.

In the modern material from Melides lagoon most valves are finely punctate, both juveniles and adults; several adult valves are nearly smooth and less frequently coarsely punctate, this last type being more abundant in males. However, two samples exhibit a variation in ornamentation: MEL 6, where most of the valves (juveniles, females and males) are slightly thinner, very finely punctate or almost smooth, the coarsely punctate being almost absent; MEL 11, with almost all the valves well calcified and punctate, the smooth ones absent. Curiously, these two samples correspond to the extreme values of salinity found in the lagoon (15.10 in MEL 6 and 4.10 in MEL 11), suggesting the existence of a relationship between ornamentation and salinity, ornamentation being more pronounced at low salinity, in agreement with Gliozzi & Mazzini (1998).

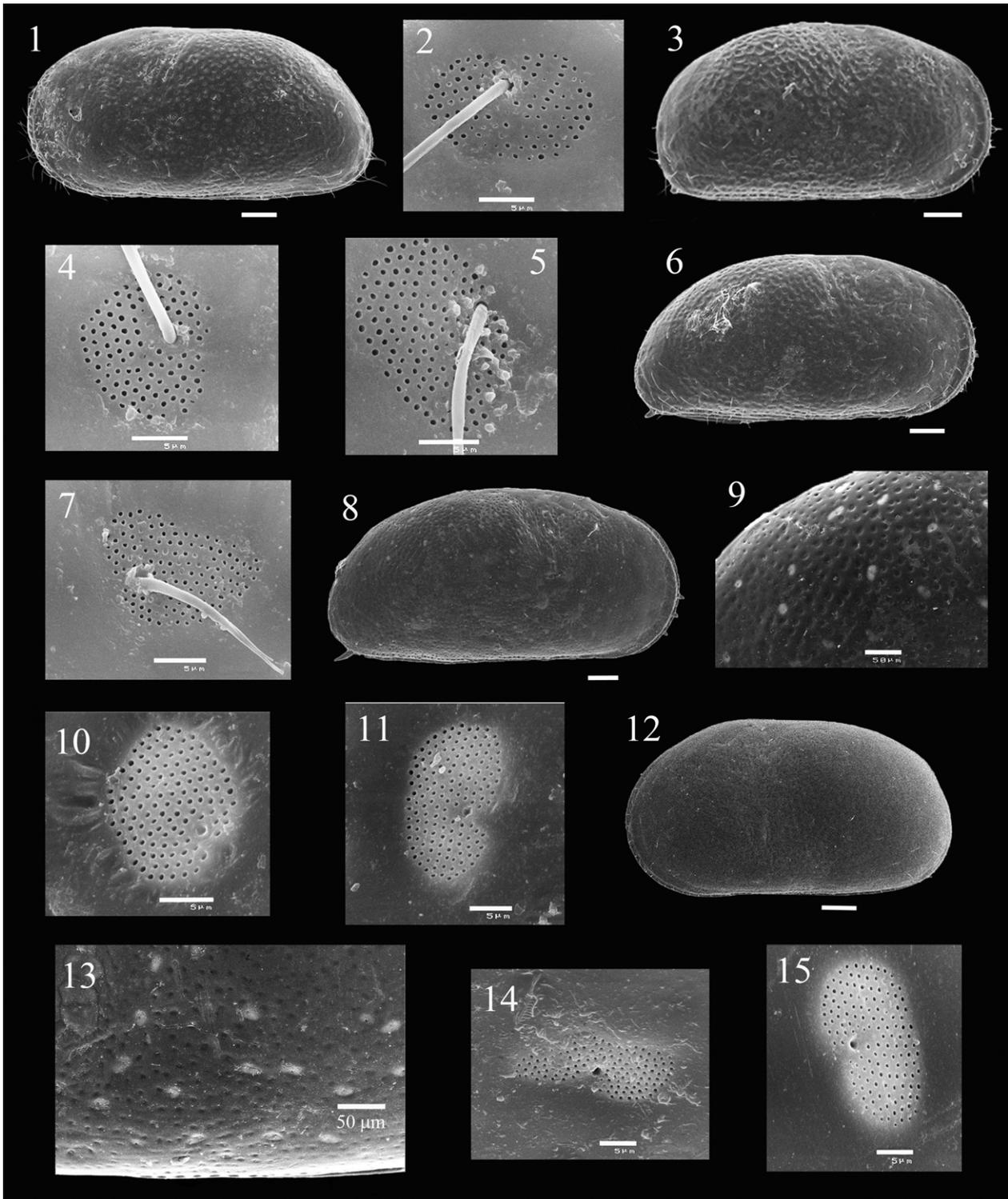
In the Holocene material all types of ornamentation were found (punctate, smooth, reticulate) in the same sample, except in Pederneira lagoon, core S2 (Cabral *et al.* 2011), where we clearly observed an evolution in the valves of *C. torosa* belonging to the lagoonal environment (Fig. 16, Zone IV). In the base of Zone IV the valves of *C. torosa* were less ornamented (smooth or punctate) and in the top of the same zone they were more strongly punctate or reticulate, suggesting an alteration in water chemistry, probably a decrease in salinity, in agreement with the proposed evolution model.

The only known Portuguese noded specimens of *C. torosa* were found by Trog *et al.* (2015), in Central Algarve, south Portugal, in Holocene sediments from Carcavaí estuary, together with no-node specimens of *C. torosa* and other brackish species, such as *L. elliptica* and *C. fischeri*.

From our observations in marginal-marine environments of mainland Portugal it was not possible to explain the variation in the ornamentation of *C. torosa* valves as a consequence of salinity variations, though in most cases the relationship between ornamentation and salinity seemed present. Carbonel (1980) suggests an alternative explanation, but confirming it would require measuring the  $\text{Mg}^{2+}$  and  $\text{Ca}^{2+}$  water contents.

#### Sieve-plates

The valves of *C. torosa* have also been studied concerning the form of their sieve pores. According to Rosenfeld & Vesper (1977) there is a relationship between salinity and the shape of the sieve pores,



**Fig. 17.** *Cyprideis torosa* (Jones, 1850) in Sado estuary (1–7) and Melides lagoon (8–15). **1, 2.** *Cyprideis torosa*, LV, external, m; punctated valve; Sado estuary, CAR-P1 spr.; (2) showing round sieve pore. **3–5.** *Cyprideis torosa*, RV, external, f; reticulated valve; Sado estuary, CAR-P1 spr.; (4, 5) showing round sieve pore. **6, 7.** *Cyprideis torosa*, RV, external, m; punctated valve; Sado estuary, CAR-P1 spr.; (7) showing irregular sieve pore. **8–10.** *Cyprideis torosa*, RV, external, m; punctated valve; Melides lagoon, MEL6 wint.; (9) sieve pores (in white) general view, postero-dorsal zone; (10) showing round sieve pore; (11) showing round to oblong sieve pore. **12–15.** *Cyprideis torosa*, LV, external, f; smooth valve; Melides lagoon, MEL6 wint.; (13) sieve-pores (in white) general view, ventral zone. (14) showing irregular sieve pore; (15) showing round to oblong sieve pore. C, carapace; LV, left valve; RV, right valve; f, female; m, male; spr., spring; wint., winter; scale bar 100 µm, except when indicated.

which varies from round, through oblong to irregular, with the proportion of rounded-shaped sieve pores decreasing when salinity increases. The authors provide diagrams allowing estimation of palaeosalinity from the proportions of rounded/oblong/irregular

sieve pores in fossil *C. torosa* valves, based on modern samples from water habitats with known salinities (marginal-marine and lakes from Germany, Denmark and Israel). This analysis needs very well-preserved and clean adult valves and is time-consuming with

the scanning electron microscope (SEM), whether we do complete (photo)cartography of the valves or if we only count the different sieve-pore types. Few studies until now have checked the method, probably because it is time-consuming (e.g. Gliozzi & Mazzini 1998; Keatings *et al.* 2007; Frenzel unpublished data, in Pint *et al.* 2012, p. 339). Gliozzi & Mazzini (1998) studied Early Pleistocene material from brackish marshes in Italy; Frenzel (2009, in Pint *et al.* 2012) studied Recent material from marginal-marine settings of the Baltic Sea coast; in both works the results seem to confirm Rosenfeld & Vesper's observations. In Keatings *et al.* (2007) the studied material comes from Lake Qarun, Egypt, with athalassic waters; the results were clearly unreasonable. As concluded by Keatings *et al.* (2007), Rosenfeld & Vesper's (1977) calibration is only useful if the water chemistry of the studied habitat is inside the range of site types used by these authors, which is the case of marginal-marine environments.

We tried to analyse several empty valves from Sado estuary, CAR transect (Fig. 17:1–17:7) and from Melides lagoon, MEL 6 (Fig. 17:8–17:15) without counting the total number of each type of sieve pore present in a valve, as it takes too much SEM time. The CAR valves come from the tidal flat, sample P1 spr., with salinity of the interstitial waters *c.* 30; in Melides lagoon the salinity at the bottom of the water mass in site 6 was *c.* 15. With this quick observation, we realized that in these adult valves, almost smooth, punctate or reticulate, the round pores were dominant in the central part of the valves, while in the periphery the oblong pores predominated (Fig. 17:9 and 17:13). However, distinguishing the different sieve-pore types was not always easy, especially the round from the oblong ones; so, to assess the proportions of the three types of sieve pores is a subjective task, which could be more accurate using machine image-analysis.

Recent studies of the shape, size and density of the sieve pores on the valves of a freshwater species from Turkey (Cabral *et al.* 2014) also show a slight dominance of oblong pores along the extreme periphery of the valve. For this Turkish species (*Gomphocythere besni* Kulköylüoğlu *et al.*), a map of the distribution of the sieve plates on a whole valve was made, using *c.* 72 SEM photos for a single valve, which allowed a grid-count of all the valve's sieve pores. This objective method applied to *C. torosa* would allow trustworthy distinction among the three types of sieve pores and comparison between the two species. This would be valuable for establishing the relationship between sieve-pore shape and salinity.

## Conclusions

In mainland Portugal *C. torosa* lives in marginal-marine zones, namely lagoons and estuaries: Melides lagoon, where it is very abundant and the dominant species; and the large Tejo and Sado estuaries, in their tidal flats and low marshes of sheltered areas with almost lagoonal dynamics, where it becomes frequent. It is never present in estuaries with pronounced channelled morphology, which promotes strong tidal currents.

*Cyprideis torosa* was never found alive in the high marsh zone reached by marine water only during high tide, indicating that it can endure only short emersion times. It is more abundant in sediments in autumn/winter than in spring/summer, which is in accordance with its life-cycle. In agreement with previous authors our data show that this species prefers soft mud to a sandy-mud substrate and is highly euryhaline and eurythermic; in Portuguese estuaries, it was found living in a salinity range of 19.0–34.1 and a temperature range of 13.3–21.7°C, in sediment interstitial water; in the Melides lagoon, the salinity range varies from 4.1 to 15.1 and the temperature from 10.8 to 14°C at the bottom of the water mass, near the sampling sites, during winter. It prefers slightly alkaline waters with pH > 7 and tolerates hypoxic conditions, supporting a concentration of dissolved oxygen as low as 0.09 mg l<sup>-1</sup>.

*Cyprideis torosa* occurs in different ostracod assemblages: in Melides lagoon associated with fresh- to slightly brackish-water species and rare brackish species; in the estuaries associated with typical brackish species.

It is clear that the distribution of *C. torosa* is controlled by the hydrodynamics of the water body, emersion time and substrate, more than by salinity, temperature or dissolved oxygen, all of which show large variation. This is evident in the studied estuaries, where large amounts of data were available; for modern lagoons, where data are less abundant (only one lagoon, in winter season, was studied), studies must continue in other seasons and locations to reinforce these conclusions. The effect of water chemistry is apparently more important in determining differences in both carapace ornamentation and shape of the sieve pores, but this would require further study, which is a possible new research line.

In the Holocene *C. torosa* is generally present through the borehole records, concentrated during the late Early to the early Late Holocene, particularly in sediments deposited in lagoonal environments, where it is very abundant and generally the dominant species, and in estuaries, with lower abundance. The associated species vary according to the environment, being similar to those found nowadays. Generally, *C. torosa* presents the same ecological preferences (substrate, lagoon v. estuary preference, similar assemblages) in the Holocene and in modern times.

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