



## Research paper

# Response of ostracods to abrupt climate changes in the Western Mediterranean (Gulf of Lions) during the last 30 kyr

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## ABSTRACT

Global climate changes attract the attention of researchers working with paleoceanographic proxies for reconstructing past ocean circulation changes and the physico-chemical parameters that control environmental conditions. Moreover, recent studies highlight the importance of climate change on deep sea benthic biodiversity.

Deep sea benthic fauna are not isolated from atmospheric processes and climate changes controlling surface ocean biota, for benthic assemblages respond to changing climatic conditions as well. Substrate and physico-chemical characteristics of bottom waters have particularly strong influence on ostracod species distribution in all marine settings, making them excellent environmental indicators.

This paper focuses on changes in ostracod assemblages at MD99-2348 site, located on the continental slope of the Gulf of Lions to determine the relationship between climatic-driven oceanographic changes and ostracod diversity and abundance. High abundances of *Henryhowella asperrima* and *Echinocythereis echinata* during Heinrich events (HE1 and HE2) may result from increased oxygenation of the bottom water and a more pulsed supply of nutrients (organic matter). Formation of surface cold water that increases the oxygen content in deep layers in the water column is linked to the intensification of northerly wind (Tramontane and Mistral) in northwestern Mediterranean during the acme of HEs, when high latitudes bodies of cold air (Mobile Polar Highs) reach the Mediterranean area. Moreover, the concomitant high abundance of *Krithe pernoidea*, which proved to be very sensitive to variable oxygen levels, probably records even shorter (millennial to centennial scale) climate oscillations.

Changes in environmental conditions are illustrated by the shift of *C. testudo*–*Loxoconcha* spp. vs. *Pseudocythere* sp.–*Macrocypris* sp. that indicates detrital input, primary productivity and the possible impact of sea level oscillation on benthic assemblages since the LGM.

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## 1. Introduction

Ostracods are small crustaceans with a bivalved calcareous carapace that live in a wide range of terrestrial and marine aquatic environments. Deep sea benthic ostracods are distributed worldwide within the first mm of the bottom sediment (approximately the same environments as foraminifera). A number of important ecological factors, including salinity and dissolved oxygen content, in bottom-water control ostracod fauna and diversity (Brouwers, 1988).

Recently, numerous studies of ostracod fauna, and its applications in paleoceanography, have been carried out in conjunction with studies of other faunal groups (e.g., foraminifers). The interest of using ostracod assemblages in paleoclimatic and paleoenvironmental

reconstructions mainly lies in their well known immediate response to variations in environmental parameters (salinity, temperature, and dissolved oxygen). Recent advances in the understanding of (paleo) diversity and evolution of ostracods lead researchers to conduct a large number of paleoclimatic reconstructions at all latitudes using ostracod assemblages (Alvarez Zarikian et al., 2009; Corregge, 1993; Cronin et al., 1999; Cronin and Raymo, 1997; Didié and Bauch, 2000; Dingle and Lord, 1990; Dingle et al., 1989; Ducassou et al., 2004; Gasse et al., 1987; Jones et al., 1999; Passlow, 1997; Yamada et al., 2005; Yasuhara et al., 2008).

For this study, we focused our attention on the abundance of certain species in relation to oxygen and nutrient content in bottom waters (Ayress et al., 1997; Caralp et al., 1993; Cronin et al., 1999; Dingle and Lord, 1990; Dingle et al., 1989; Gooday, 1988; Loubere, 1991; Smart et al., 1994). We analyzed the relationship between ostracod internal structure, surface water circulation, ventilation and the oxygen content of the sediment/water interface (Corbari et al.,

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2004; McKenzie et al., 1989; Peyrouquet, 1977, 1979; Zhou and Ikeya, 1992).

Ostracod abundance and diversity are related to oceanic circulation, which is linked to climate-forced changes. If ostracods are reliable proxies of water circulation changes and their response is immediate, then they record climate variations not only at glacial-interglacial time scale, but also at short-term environmental changes as described by Didié and Bauch (2000).

In this work, we analyse ostracod fauna from core MD99-2348, located on the continental slope in the Gulf of Lions (GoL).

The GoL belongs to the Western sector of the Mediterranean Sea, which has been intensively studied during recent years with respect to Quaternary paleoceanographic conditions (Cacho et al., 2002; Frigola et al., 2008; Moreno et al., 2005; Pérez-Folgado et al., 2003). Our objective is to focus on ostracod response to variations in oceanographic conditions within the last 30 kyr, which are characterized by a series of cooling (Stadials) and warming episodes (Interstadials) (Johnsen et al., 1992) known as Dansgaard-Oeschger (D-O) events (Bond et al., 1993; Dansgaard et al., 1993). Additional abrupt cooling episodes, the Heinrich events (Heinrich, 1988), occurring at the end of each “Bond cycle” resulted in massive ice discharges accompanied by deposition of ice rafted debris (IRD) in the North Atlantic (Heinrich, 1988; Hemming, 2004).

The GoL continental shelf is distant from the former ice sheet and therefore disconnected from the direct effect of the expansion/retreat North Atlantic ice fronts during Late Quaternary stadial/interstadial oscillations. However, abrupt and short time scale climate changes play a major role in western Mediterranean circulation. In particular, the GoL registered an increase of Western Mediterranean Deep Water (WMDW) ventilation associated with strengthening of northwesterly winds (Cacho et al., 2000; Frigola et al., 2008; Sierro et al., 2005), during the Stadials. In addition, deep water temperatures in the Alboran Sea have been recently reconstructed by Cacho et al. (2006) for the last 50 kyr based on Mg/Ca ratios in benthic foraminifera (core MD95-2043). This record shows significant temperature oscillations (1–4 °C) in relation to the D-O cycles, with cold temperatures associated with stadial intervals.

Of course, climate variability involves not only oceans, but also atmosphere and continents. The western Mediterranean is known to be highly sensitive to intense outbursts of cold air over the basin during times of southward expansion of polar air masses (i.e. Heinrich events) with direct effects on SST and primary productivity (Cacho et al., 2000, 2006; Moreno et al., 2005; Rohling et al., 1998).

Recent research on present day climatic variability has highlighted the role of Mobile Polar Highs (MPHs) as control mechanisms of climatic conditions at high and mid-latitudes, and it was also proposed that they controlled climatic changes in the past (Leroux, 1993, 1996).

The MPHs are defined as large mobile lenticular bodies of dense cold air in the lower levels of the troposphere, between polar and temperate latitudes (Leroux 1993, 1996). MPHs are responsible for variations in air pressure, wind velocity and direction, temperature and precipitation in the extra-tropical regions.

During long cold intervals, cold and dry winds blowing over Scandinavia's MPH can reach the Mediterranean area, causing local intensification of north winds (i.e., in the Gulf of Lions) and, consequently, enhancing dry and cold climate conditions.

The mechanism of sinking of the surface water under the influence of a long period of north winds (winter during the Interstadial) develops as follows: during winter, the strengthening of the cold and dry northerly winds increases surface water density that sinks to the bottom inducing an effective mix in the water column and increasing the oxygenation in the bottom water/sediment interface.

Water ventilation and surface productivity control food and oxygen supply to the deep sea, which are major factors for benthic organisms (Gooday, 1988; Smart et al., 1994). Our results provide new

clues for understanding the response of benthic ostracod fauna to such climate-induced changes.

This work will contribute to understand the link between marine and atmospheric processes oscillating on a millennial time scale and their effects on western Mediterranean ocean circulation.

## 2. Site and core material

The GoL is a passive, prograding and subsiding margin located in the north-western sector of the Mediterranean Sea (Fig. 1), bounded to the west and to the east by Pyrenean and Alpine orogenic belts, respectively (Berné and Gorini, 2005). It formed in response to Late Eocene–Oligocene rifting of Corsica and Sardinia. During the Messinian, a major erosional surface formed as a consequence a dramatic sea-level drop that followed the Messinian Salinity Crisis (Ryan and Cita, 1978). Post-Messinian deposits are characterized by increasing sediment supply due to the amplification of glacial/interglacial cycles, leading to the development of large Pliocene/Pleistocene prograding bodies (Lofi et al., 2003).

The present day sea floor morphology is characterized by (1) an inner shelf mainly made of transgressive and modern prodeltaic muds (Berné et al., 2007), (2) a sandy outer shelf (between –80 and –120 m) formed by forced regression of shoreface sands between MIS3 and MIS2 (Bassetti et al., 2008; Jouet et al., 2006a), and (3) a muddy shelf edge/upper slope represented by prodeltaic/hemipelagic muds deposited around MIS2/MIS3, when deltas were situated in the vicinity of the shelf edge, providing a large amount of detrital material (Fig. 1).

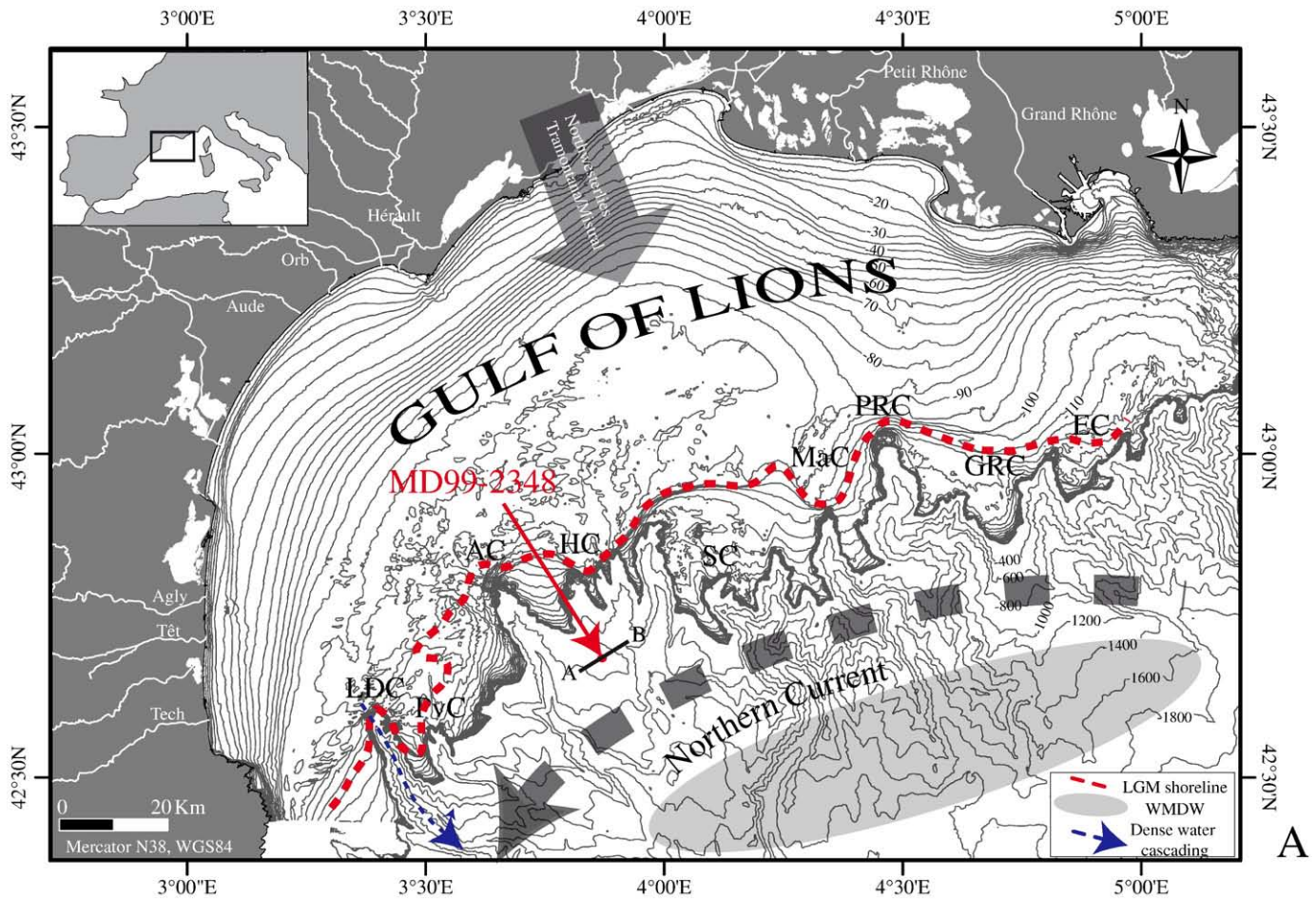
On seismic profiles, the upper Quaternary sequence is characterized by the stacking of several prograding wedges bounded by discontinuities (Rabineau et al., 2005) that extend seaward to correlative conformities, in correspondence of the continental slope which is incised by numerous canyons descending down to the abyssal area of the Algero-Balearic Basin.

The continental shelf was exposed during the Last Glacial Maximum (see position of LGM shoreline in Fig. 1) but, because of high sediment supply (mainly from the Alps through the Rhône River) and very limited tectonic activity, the area beyond the shelf edge was never subject to sub-aerial erosion and represents a favorable environment for obtaining a high resolution, continuous and undisturbed sedimentary archive. In addition, the imprint of sea-level changes in continental slope sediment record has been recently identified and synchronized with Greenland ice core, enabling to recognize the precise time at which major floods occurred at the GoL continental shelf over the past 270 kyr (Sierro et al., 2009).

Core MD99-2348 was retrieved during the IMAGES 5 cruise of the *Marion Dufresne* at 300 m water depth from the upper slope of the GoL. The coring site is situated on the interfluvial of the Bourcart (Aude) and Hérault canyons, in a zone that was not affected by mass wasting as seen by the fairly parallel and continuous seismic reflections at the position of the core (Figs. 1 and 2). The core material consists of 22.6 m of mostly fine-grained sediment (gray silty mud) with a cm-thick sand layer at the top of the core.

The sedimentation rate varied from 0.2 to 0.26 cm/year between 25 and 21 kyr (Sierro et al., 2009). High sedimentation rate was registered between 21 and 20 kyr, which was related to the proximity of the Rhone deltaic system on the slope area because of the significant sea-level fall during MIS2. Afterwards, it gradually decreased reaching about 0.17 cm/year at 15 kyr. The youngest sediment layer in core MD99-2348 (50 cm) corresponds to the last 15 kyr (deglaciation) and it is characterized by extremely low sedimentation rate (see “Chronostratigraphy” for details).

Thus, an expanded and continuous sedimentation between 25 and 15 kyr provided good material for high resolution analysis of microfungal assemblages. The core was sampled in 10 cm intervals and a total of 227 samples (1-cm-thick) were collected. Ostracods



**Fig. 1.** Bathymetric map of the Gulf of Lions and location of the studied core MD99-2348. The arrow indicates the prevailing direction of winter winds and the shaded gray area points to the region influenced by Western Mediterranean Deep Water Formation. LDC, Lacaze-Duthiers Canyon; PVC, Pruvot Canyon; BC/AC, Bourcart or Aude Canyon; HC, Hérault Canyon; SC, Sète Canyon; MaC, Marti Canyon; PRC, Petit-Rhône Canyon; GRC, Grand-Rhône Canyon; and EC, Estocade canyon. A–B, seismic profile shown in Fig. 2.

were picked from all samples using standard micropaleontological techniques. The fraction  $>150\ \mu\text{m}$  was analyzed under binocular microscope and all specimens were handpicked, resulting in a diverse faunal assemblage and statistically reliable dataset.

### 3. Oceanographic setting

The general circulation in the GoL (Fig. 1) is mainly driven by the cyclonic Liguro-Provençal or Northern Current (Millot, 1987). The core of the Northern Current flows southwestward along the continental slope, but the trajectory can be temporally altered by northwesterly winds, when the superficial waters tend to penetrate onto the continental shelf (Durrieu de Madron et al., 1999).

The GoL is one of the main zones of formation of Western Mediterranean Deep Water (WMDW), mostly resulting from evaporation and cooling of sea surface water, especially during windy winters (Lacombe et al., 1985; Millot, 1999). The northerly winter winds that develop include:

- Mistral, a strong wind coming from the north or northwest which accelerates when it passes through the Rhone Valley. It brings cold and dry continental air over the warm western Mediterranean, generating intense air–sea heat exchanges (Flamant, 2003) and sea surface cooling (Millot, 1979),
- Tramontane, a cold northwesterly wind from the Pyrenees to the Mediterranean, similar to Mistral in its causes and effects but it

follows a different corridor (it passes between the Pyrenees and the Massif Central).

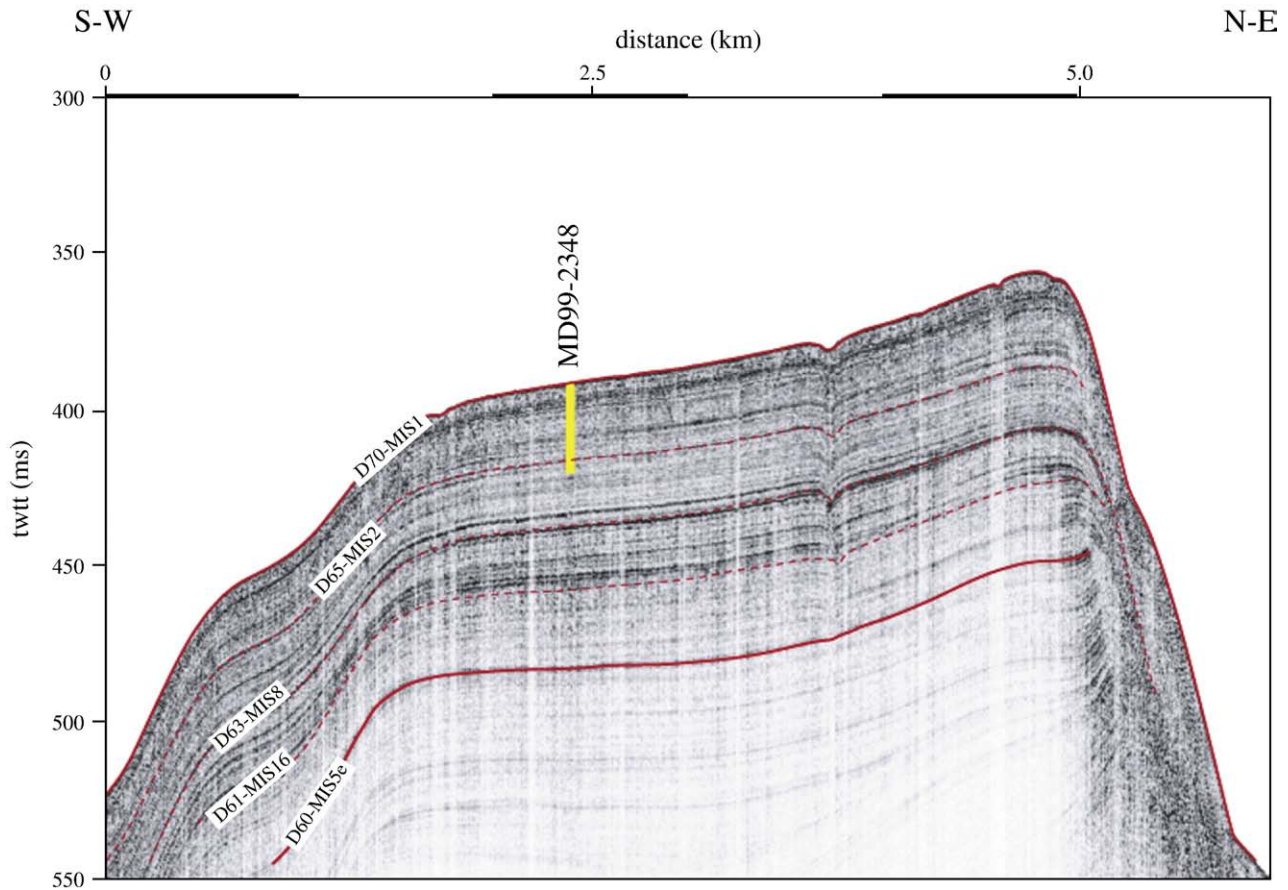
This mechanism of water circulation appears to be a general feature for the Mediterranean area.

Rigola et al. (2008) showed a temporary reduction in the WMDW formation during the HES, because of surface water freshening linked to the increased penetration of low-salinity waters in the Mediterranean. Freshened waters come from polar sources, mainly from the iceberg melting during the Heinrich events (Sierro et al., 2005).

Another process that drives sinking of large volumes of cold waters is related to episodic dense shelf-water cascading, as recently described by Canals et al. (2006). It seems that this process intensified during the last sea-level rise, possibly as a result of submersion of the continental shelf, where dense cold water forms (Melki et al., 2009).

### 4. Chronostratigraphy

The age model for the core MD99-2348 is mainly based on  $^{14}\text{C}$  dates. Thirteen dates have been obtained from biogenic carbonates (planktonic foraminifera) and span 15 kyr BP cal to 25 kyr BP cal. AMS  $^{14}\text{C}$  dates were performed by the Poznan Radiocarbon Laboratory of Adam Mickiewicz University (Poland). All dates reported here are given in calendar ages BP. Ages were calibrated by means of Calib 5.0.2 software (<http://calib.qub.ac.uk/calib/>), using the Marine04 calibration curve (Hughen et al., 2004; Reimer et al., 2004) with no deviation



**Fig. 2.** Seismic profile across the Bourcart (Aude)–Hérault canyon interfluvium at the position of core MD99-2348 on the upper continental slope (position in Fig. 1). Seismic surfaces are correlated at the regional scale and correspond to major interglacials and interstadials: D60: MIS5e; D61: MIS16, D63: MIS8, D65: MIS2, and D70: MIS1 (sea floor).

from the mean global reservoir correction ( $-400$  y). Calendar ages are given with 1 sigma standard error.

An accurate chronostratigraphy of the last glacial period in the GoL is also possible thanks to the deposition of several condensed layers (Sierro et al., 2009) rich in pelagic skeletal material and poor in detrital components that drape the transgressive littoral prisms and prodeltaic mud (Bassetti et al., 2006; Jouet et al., 2006b). The formation mechanism of such condensed layers (CL) was initially proposed for sediments in a similar physiographic situation in the Gulf of Cadiz (Sierro et al., 1999). Similarly, these CLs mark the rapid sea-level rise associated with several interstadials in the GoL over the last 270 kyr (Sierro et al., 2009). In core MD99-2348, the youngest CL corresponds to the last Greenland Interstadial (GIS-1 or Bølling-Allerød) and is situated within the uppermost 50 cm (14,500  $^{14}\text{C}$  BP calendar). It is rich in fine sand and planktic foraminifera and is easily distinguished from the underlying sediment represented by detrital, clay-rich hemipelagic mud with a low number of planktic foraminifera and a high sedimentation rate. GIS-2 was identified at 19 m below sea floor (mbsf, Fig. 3) in the core, but there is no CL at this level (Sierro et al., 2009). A sea-level rise of small amplitude during this lowstand period did not generate enough space on the shelf to form a CL on the slope.

Several peaks of the polar species *Neogloboquadrina pachyderma* (sin), in combination with  $^{14}\text{C}$  dates, allow us to identify the cooling events during the Heinrich events (Hemming, 2004) and other stadials (Sierro et al., 2009).

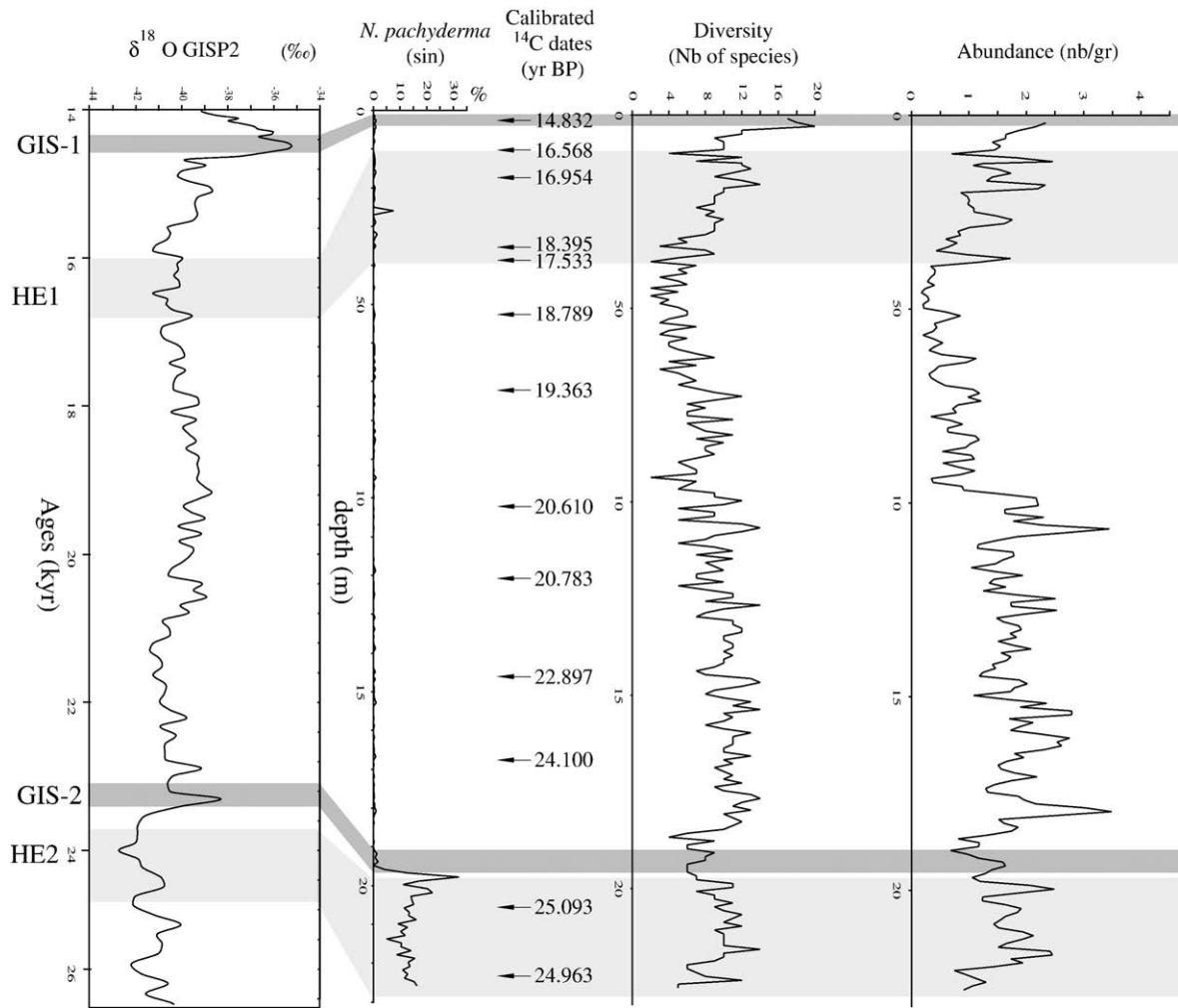
In core MD99-2348, HE1 and HE2 are distinguished by a marked increase in *N. pachyderma* (sin) abundance, at 3–4 and 20–23 mbsf respectively (Fig. 3).

In contrast to the high sedimentation rate that characterizes the 25–15 kyr interval, the deglacial–Holocene time is barely represented in this core, which is explained by rapid sea-level rise and the consequent increasing distance from the detrital source (sedimentation rate  $< 0.1$  cm/year).

## 5. Results: ostracod abundance and diversity

Well preserved ostracod valves and carapaces representing mainly a biocoenosis were found in all samples studied. Up to 20 species were found in a single sample, and the total abundance (valves per gram dry sediment) reached values up to 35 specimens/g. Lower abundance (1–2 specimens/g) and diversity were documented during periods of higher sedimentation rate (from 4 to 10 m in the core). Increased detrital input from the Rhone and other rivers is the main cause of dilution of benthic fauna. In GIS-1, the diversity and abundance are also high because of the presence of a CL that accumulated multiple generations of benthic ostracods. On the other hand, relatively low abundance (2 specimens/g on average) and diversity correspond to GIS-2 (Fig. 3), which was not affected by the formation of a CL.

The total number of specimens found in a sample ranges between 10 and 150 specimens, which are considered sufficient for marine ostracod studies (Cronin et al., 1999); however, the number of specimens was fewer than 10 in a few samples (less than 10% of the entire data set). None of the analyzed samples were barren of ostracods, and the samples with very low abundance are scattered throughout the sediment succession. Thus, the ostracod signal in the record is nearly continuous. In addition, all ostracods (juveniles and



**Fig. 3.** Vertical distribution of the cold species *N. pachyderma* (sin) in core MD99-2348 (Sierra et al., 2009), showing its high abundances during the Heinrich events and compared to abundance and diversity of ostracods in the same core. The absolute chronology is given in calibrated  $^{14}\text{C}$  dates. Abundance and diversity of ostracods are also correlated to the main climate events (Glacial Interstadials, and Heinrich events) established on the basis of ice core isotope chronology (GISP2, Meese et al., 1997).

adults) were generally well preserved with translucent valves, indicating that most of the samples were not affected by corrosion.

### 5.1. Relative abundances

Taxonomic identification at species level was possible for most of the taxa, since Mediterranean ostracods are fairly well studied (Bonaduce et al., 1975; Peypouquet and Nachite, 1984) and the observed assemblages represent typical Mediterranean association previously described for the Late Quaternary upper slope sediments of the Rhodanian margin (El Hmaidi et al., 1998, 1999). However, some of the congeneric species were grouped together to display trends in faunal composition.

Diverse marine ostracod assemblages are evenly distributed along the core (Fig. 4), such as two species belonging to the genus *Cytheropteron* (*C. alatum*, and *C. rotundatum*) with abundances up to 40%, together with species of the genus *Argilloecia* sp. and *Loxoconchidea minima*. Cosmopolitan species of the genera *Loxoconcha*, *Semicytherura*, *Paradoxostoma* and *Leptocythere* are also well represented through the core, comprising up to 70% of the assemblage.

Besides this main assemblage, three other assemblages defined by the presence of particular ostracod genera seem to be restricted to two time intervals between HE1 and HE2.

*Polycope* sp. appeared shortly after the end of GIS-2 (Fig. 5), and shows a maximum peak at about 17 m and a gradual upward decrease

until it almost disappears at ~10 m (20.6 kyr). *Polycope* has a high tolerance of oxygen-deficient conditions (Benson et al., 1983); hence, its high abundance might be related to diminished oxygen content, possibly because the sedimentation rate increased abruptly during that time (Sierra et al., 2009).

A similar trend is observed for the deep cold water species *Cytheropteron testudo* (*sensu* Bonaduce et al., 1975). Nonetheless, *C. testudo* shows its maximum between 14 and 16 m in the core (20–22 kyr), followed by a drastic reduction after 19 kyr and a relatively high abundance (10 and 20%) during HE1 and HE2. This species is considered to be a “northern guest” of the Mediterranean Plio-Pleistocene. It occurs through the Last Glacial, and its Last Occurrence (LO) is around the end of the Younger Dryas Event (Bonaduce and Sprovieri, 1984; Ciampo, 2004).

*Paracypris* sp., *Macrocypris* sp., and *Pseudocythere* sp. seem to have gradually replaced the above described assemblage (*Polycope*–*C. testudo*) in the interval between 20 and 19 kyr (above 10 m in the core, Fig. 5), as indicated by  $^{14}\text{C}$  dates.

*Polycope* anti-correlates with the adult Krithids (Fig. 7), but it appears during the HE2, when the adults of *Krithie pernoides* (small vestibule) decrease. *Polycope* spp. completely disappears after 19 kyr.

The assemblage that includes *Henryhowella* sp., *Echinocythereis echinata* and *Krithie* spp. (Fig. 6) shows a very interesting distribution pattern, in particular with respect to the cool episodes such as the Heinrich events. The two genera *Echinocythereis* and *Henryhowella*,

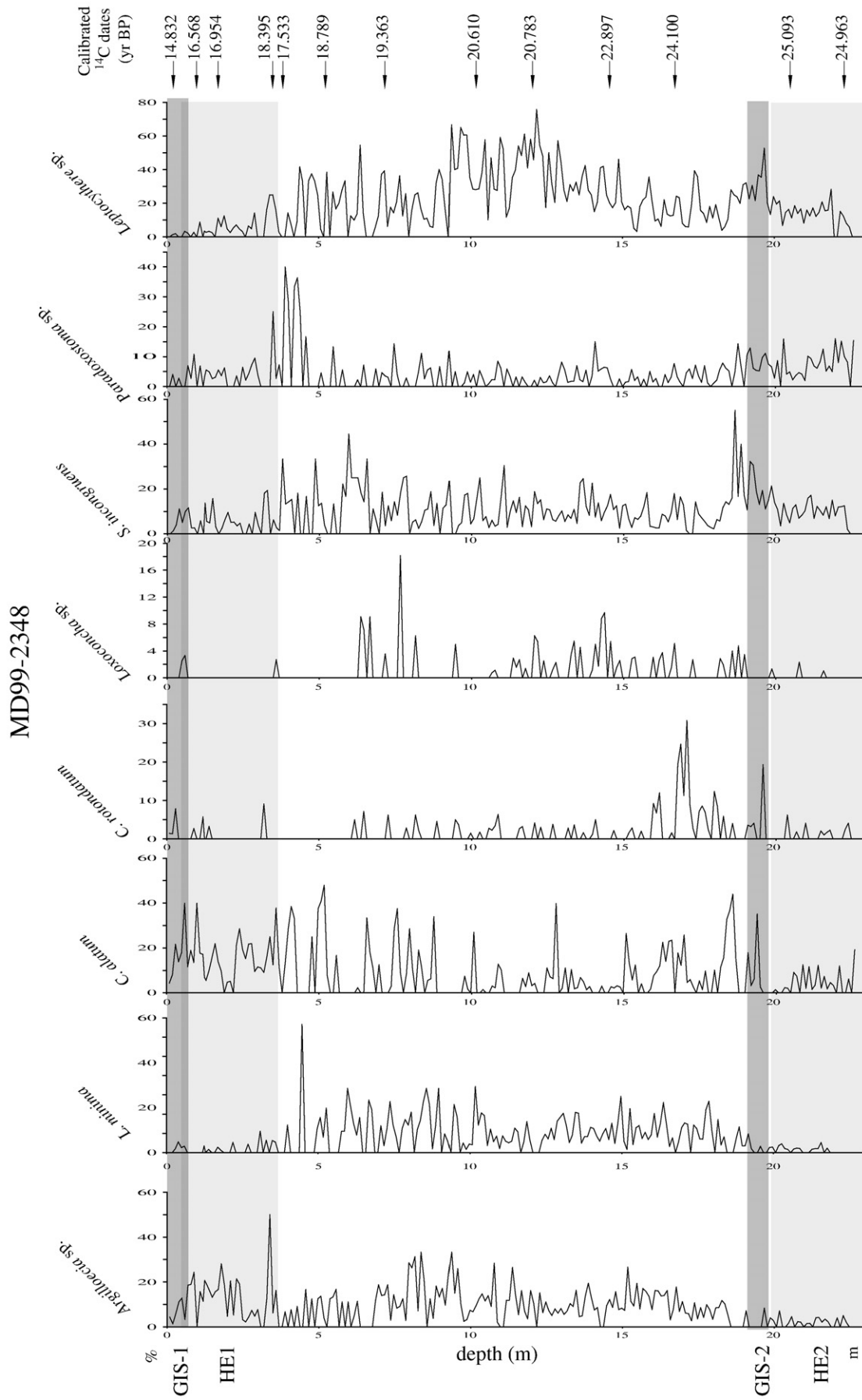


Fig. 4. Diverse marine species (*C. alatum*, *C. rotundatum*, *Argilloeca* sp., and *L. minima*) and cosmopolitan genera (*Loxoconcha* sp., *Semicytherura* sp., *Paradoxostoma* sp. and *Leptocythere* sp.) showing a global homogeneous distribution in MD99-2348 (mbsf).

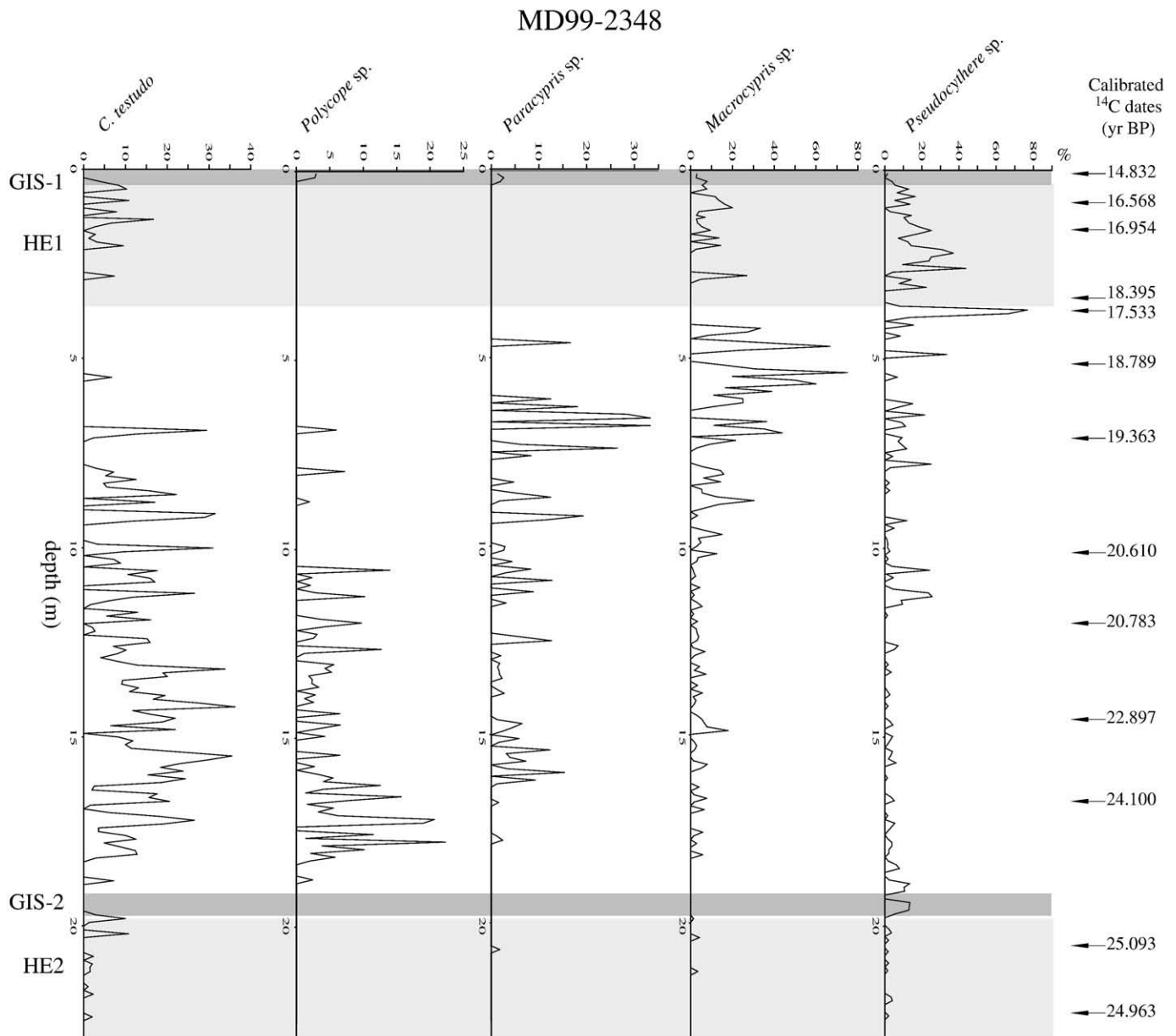


Fig. 5. Abundance pattern of *Polycope* sp. ( $O_2$ -deficiency tolerant species), *C. testudo* (Mediterranean cold guest), *Macrocypris* sp., *Paracypriis* and *Pseudocythere* sp. in MD99-2348 (mbsf).

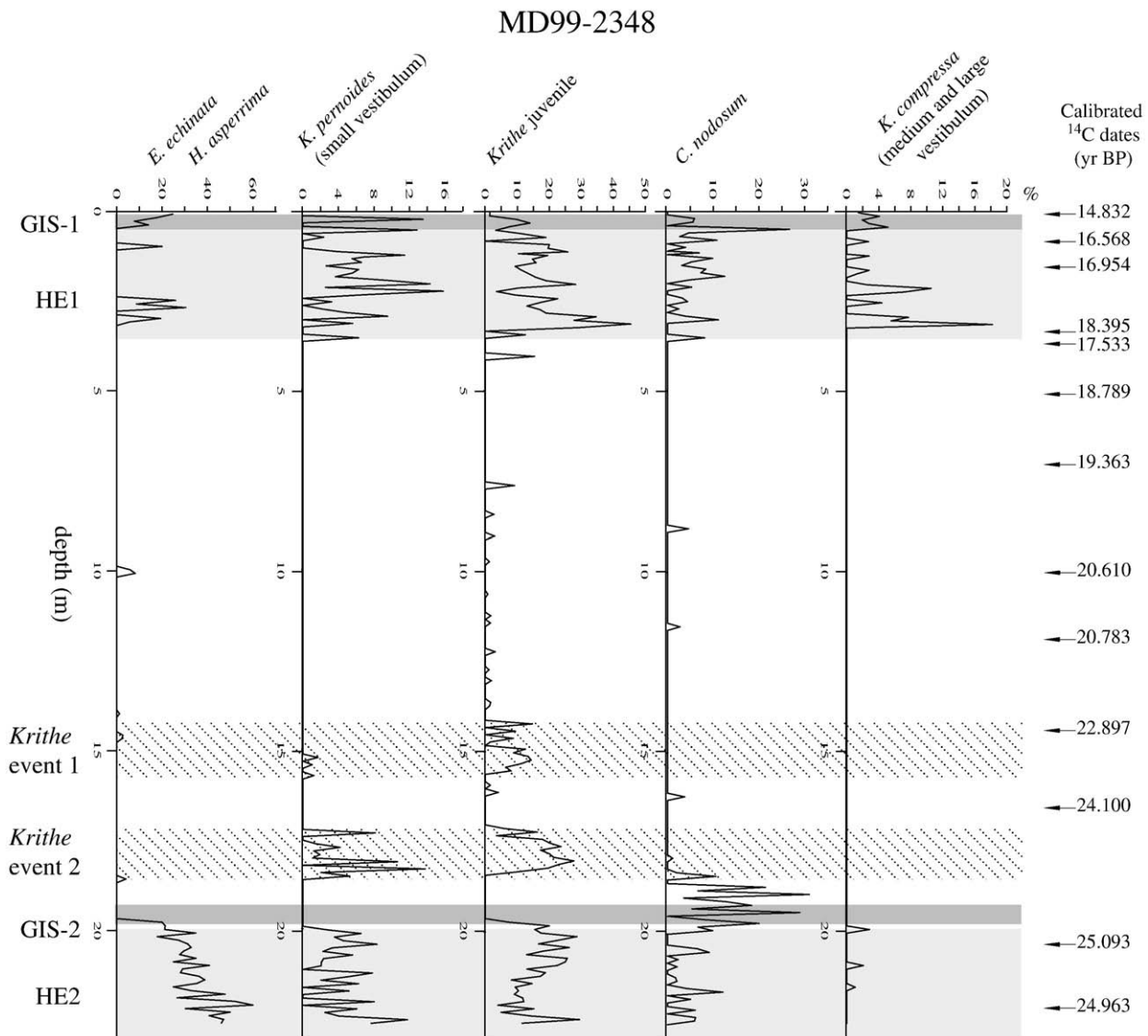
well known for inhabiting well oxygenated, nutrient-rich cold waters (Didié et al., 2002), are limited to the intervals corresponding to the onset of HE1 and HE2. The total abundance of species belonging to *Krithe* is also an interesting marker. According to Cronin et al. (1999), *Krithe*, which is a common element in deep waters, predominates in North Atlantic regions during glacial periods (Dingle and Lord, 1990). It is mainly associated with cold water masses (Ayress et al., 1997; Cronin et al., 1999).

In core MD99-2348, we observe important peaks in the total abundance of *Krithe* (commonly reaching the 50% of the total assemblage, Figs. 6 and 7) precisely in the intervals corresponding to HE1 and HE2, which are defined on the basis of  $^{14}C$  dates and on the occurrence of *N. pachyderma* (sin) (Fig. 8). Minor peaks are found around 15 and 17 m. *Krithe* is very rare in the rest of the record (Fig. 6). Many of the *Krithe* specimens in minor abundance peaks are juveniles that do not allow identification at species level.

Adult valves belong to two species: *K. pernoides* (= *Krithe* sp. A of Peypouquet (1977) and *Krithe compressa* (Abate et al., 1993), the latter appearing particularly abundant. Both species show significant variations in the dimension of their vestibule: from small to medium in *K. pernoides*, and generally large for *K. compressa*.

The abundance of *Cytheropteron nodosum* is comparable to that of the *Krithe*'s vertical distribution (Fig. 6) during the HE1. *C. nodosum* is a common species both at high latitudes and in Pleistocene sediments of northwestern Europe and Arctic shallow shelves (Cronin et al., 1991; Stepanova and Yu, 2006; Whatley and Masson, 1979). However, we find a high abundance of *C. nodosum* after the end of HE2 and during GIS-2. Thus, we think that the parameters that control its distribution are not exactly the same as for the *Krithe*s.

Several other ostracod genera show either very low abundance (<10%) or discontinuous occurrence (*Monoceratina mediterranea*, *Bythocythere* gr. *turgida*, *Cytheropteron monoceros*, *Sagmatocythere*



**Fig. 6.** Vertical distribution of *Henryhowella* sp.+ *Echinocythereis* sp. and the *Krithe* group (*K. pernoides*, *K. compressa*, juveniles). *C. nodosum* has a distribution similar to *Krithe* in MD99-2348 (mbsf).

*multifora*, and *Pterygocythereis jonesii*). For this reason, they were not considered to be significant in our interpretations.

## 6. Discussion

### 6.1. Ostracod faunal variations during climate oscillations

We focus now our attention on the groups that appear to have major environmental implications. In order to discuss paleoclimate interpretations of vertical faunal distributions, core depth (mbsf) was converted into calendar years (kyr) and the main environmental information inferred by ostracod assemblages are summarized in Table 1.

The *Henryhowella*–*Echinocythereis* group, here mainly represented by the genus *Echinocythereis*, indicates nutrient-rich conditions and well mixed water column with well oxygenated bottom waters (Table 1). This group shows an excellent correlation with the HE1 and HE2. Nonetheless, during the HE1, the abundance of the *Henryhowella*–*Echinocythereis* group is lower compared to HE2 (Fig. 7). Benthic foraminiferal  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  from the Alboran Sea (Cacho et al., 2006) show that a rapid depletion occurred during HE1, indicating

the onset of a drastic change in the benthic conditions towards a nutrient/oxygen-depleted environment, marked by the disappearance of the benthic foraminifer *Cibicides pachyderma* and the deposition of an organic-rich layer in the Alboran Sea (Cacho et al., 2002). Certainly, the *Henryhowella*–*Echinocythereis* group was not immune to the degradation of the bottom-water conditions that triggered a rapid decrease in their abundance.

The presence of *Krithe* group, mainly represented by *K. pernoides* specimens with small vestibule, is also noteworthy. By contrast, *K. compressa* is rare, has medium size vestibules, and appears sporadically during HE1 (Figs. 6 and 7, Table 1).

The distribution pattern of *K. pernoides* vs. *K. compressa*, and the fact that they almost never coexist, supports the hypothesis of Peypouquet (1979), who suggested that anterior vestibule size in *Krithe* is inversely correlated with dissolved oxygen content of the ambient seawater, such that a small vestibule indicates normally oxygenated seawater (5–7 ml/l dissolved  $\text{O}_2$ ), whereas a large vestibule indicates an oxygen-deficient environment (1–2 ml/l dissolved  $\text{O}_2$ ). This hypothesis proved to be consistent with the results from Atlantic Ocean bottom samples taken at different latitudes ranging from polar regions (Arctic) to equatorial areas (Peypouquet,



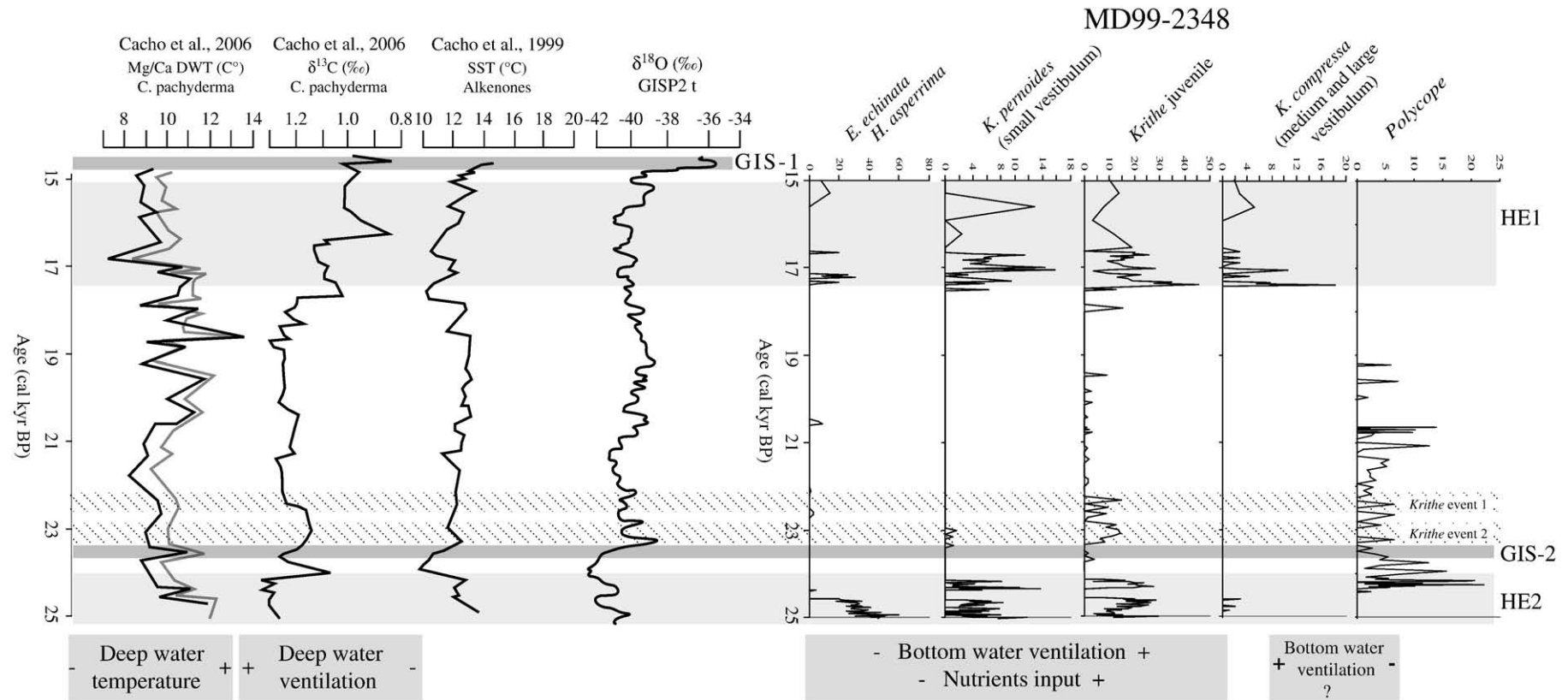
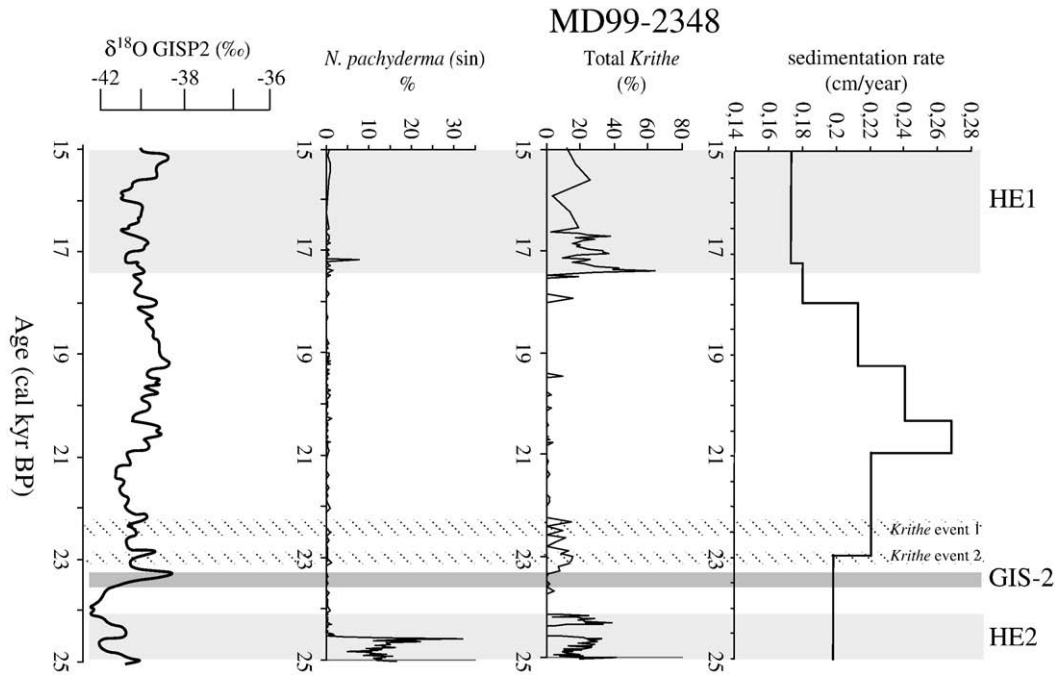


Fig. 7. Comparison between the abundances of *Henryhowella* sp + *Echinocythereis* sp. and the *Krithe* group (*K. pernoides*, *K. compressa*, juveniles) with Greenland ice core isotope record (Meese et al., 1997) and ventilation + deep water temperature parameters from Cacho et al. (2006). Core depth (mbsf) is converted into age (kyr) using the <sup>14</sup>C dates through Analyseries 2.0.4 by D. Paillard (<http://www.lsce.ipsl.fr/logiciels/index.php>).



**Fig. 8.** Correlation between the *N. pachyderma* (sin) abundance, the total *Krithe* and variation of sedimentation rate in core MD99-2348. The interpolation with the isotope chronology indicates a good match with the Heinrich events marked in the ice core isotope record (GISP2) and also the detection of two rapid supplementary episodes of possible climate degradation (*Krithe* event 1 and *Krithe* event 2).

1977) and also confirmed by additional tests on living ostracods carried out on material collected in the Gullmar Fjord (McKenzie et al., 1989). However, the hypothesis of a relationship between the size of the anterior vestibule in *Krithe* and the level of dissolved oxygen (Peypouquet, 1979) remains controversial. In fact, Zhao and Whatley (1997) and Whatley and Zhao (1993) critically discuss Peypouquet's hypothesis, suggesting that this relationship should be used with

caution because the influence of environmental parameters on *Krithe* morphology can be complex.

We certainly agree with the principle that this hypothesis cannot be applied without qualification, and that different factors might interfere in the *Krithe* physiological response (e.g., calcium balance, as suggested by McKenzie et al., 1989). Nonetheless, in MD99-2348 site, we have found a fairly good correspondence between small vestibule-

**Table 1**  
Ostracod assemblages and their association to environmental conditions at site MD99-2348.

Ostracod assemblages	Environmental conditions
Stadial assemblage (HE1 and HE2) <i>Echinocythereis echinata</i> Sars, 1865 <i>Henryhowella asperima</i> Reuss, 1850 <i>Krithe compressa</i> , Seguenza 1880 <i>Krithe pernoidea sinuosa</i> Ciampo, 1986 <i>Cytheropteron nodosum</i> Brady, 1868	Nutrient-rich conditions and well mixed water column with well oxygenated bottom waters. Peaks in <i>E. echinata</i> and <i>H. asperima</i> correlate well with high $\delta^{13}\text{C}$ in Cacho et al., 2006. <i>C. nodosum</i> is a common species both at high latitudes and in Pleistocene sediments of northwestern Europe and Arctic shallow shelves after Cronin et al., 1991; Stepanova and Yu, 2006; Whatley and Masson, 1979).
Glacial assemblage (Last Glacial Maximum) <i>Cytheropteron testudo sensu Bonaduce et al., 1975</i> , <i>Loxocochoa</i> Sars, 1866	<i>Loxocochoa</i> reflects the possible impact of sea-level changes since the LGM. Peaks correlate fairly well with the lower sea-level (see plot of global sea-level variations in Arz et al., 2007). <i>C. testudo</i> (sensu Bonaduce et al., 1975) is the "cold guest" (Bonaduce and Sprovieri, 1984; Ciampo, 2004).
Transitional assemblage <i>Macrocypris</i> Maddock, 1990 <i>Pseudocythere</i> sp. aff. <i>P. caudata</i> , Sars 1866 <i>Polycope</i> , Sars 1866	Epibathyal genera <i>Macrocypris</i> sp. prefers Mg-enriched waters, and easily incorporates Mg into its carapace. Its vertical distribution correlates with Mg/Ca oscillations (bottom water $T^{\circ}$ and surface productivity in Cacho et al., 2006). <i>Polycope</i> tolerates oxygen-impooverished substrate (low $\delta^{13}\text{C}$ in Cacho et al., 2006).
Cosmopolitan assemblage <i>Argilloecia</i> Sars, 1866 <i>Bythocythere turgida</i> , Sars 1866 <i>Cytheropteron alatum</i> Sars, 1866 <i>Cytheropteron monoceros</i> Bonaduce, Ciampo & Masoli, 1976 <i>Cytheropteron rotundatum</i> Müller, 1894 <i>Leptocythere</i> Sars, 1925 <i>Loxocochoidea minima</i> Bonaduce, Ciampo & Masoli, 1976 <i>Monoceratina mediterranea</i> , Sissingh 1971 <i>Paracypris</i> , Sars 1866 <i>Paradoxostoma</i> Fischer, 1855 <i>Pterygocythereis jonesii</i> , Baird, 1850 <i>Sagmatocythere multifora</i> , Norman, 1875 <i>Semicytherura incongruens</i> Müller, 1894 <i>Semicytherura</i> , Wagner, 1957	No major environmental implications at site MD99-2348.

*Krithe* and possible high oxygenated bottom waters, as mentioned above. Thus, we consider that the predicted values of dissolved oxygen in relation to different *Krithe* morphotypes should not be completely rejected, but instead should be used with caution.

In the time interval between the HE1 and HE2, adult *Krithe* specimens are rare, whereas juveniles are sometimes quite abundant. We observe two peaks in abundance of juvenile *Krithe*: around 23 and 22.5 kyr (*Krithe* event 1 and *Krithe* event 2, Figs. 6 and 7). In both cases, the juveniles are more abundant than adults. This indicates that the *Krithe* population has a quick response to variations in bottom-water conditions such as the high oxygen levels during cool event HE2 that allowed the growth of adult moult stage of *Krithe* specimens.

After the end of HE2, which denoted the most favorable environmental conditions for *Krithe*, a progressive decrease of the bottom ventilation prevented the development of a significant adult population of *Krithe*. Nonetheless, the two peaks in abundance of juvenile-*Krithe* that are estimated to have occurred around 22.5 kyr and 23 kyr (Fig. 7) indicate occasional re-establishing of favorable conditions for this species, but not good enough for reaching the adult stage.

Moreover, the *Krithe* abundance decreases upward starting from the HE2, until almost its complete disappearance after *Krithe* event 1. Sporadic return to fairly well oxygenated bottom waters (*Krithe* event 1 and *Krithe* event 2) is possibly related to periodic degradation of local climatic conditions and formation of deep water (Fig. 8). For now, this hypothesis remains speculative since we would need to obtain additional  $^{14}\text{C}$  dates in order to better calibrate the *Krithe* event 1 and *Krithe* event 2 chronologies.

The distribution of the ostracod assemblages at this site (MD99-2348) during cold stadials seems to be controlled by bottom-water properties that result from the interaction of atmospheric and oceanic processes.

In this respect, we believe that the mechanism of the surface water sinking under a long-term influence of north winds (winter during the Interstadial) depends on tropospheric circulation. Particularly important is the role of MPHs, which control basic climate parameters such as wind velocity, temperature and precipitation over the Mediterranean at all time scales, as shown in Leroux (1993). In addition, deep mixing in the water column accounts for the upwelling of nutrient-rich intermediate waters to the surface, triggering phytoplankton productivity. The resulting increased export production led to the proliferation of ostracod populations that grew in response to the higher phytodetritus flux to the bottom.

Our results show that the most sensitive genera (*Henryhowella*, *Echinocythereis*, and *Krithids*) respond immediately to millennial-scale disturbances in their habitat caused by climatic changes. Thus, they represent good biological indicators in climate-driven oceanographic processes.

The *Polycope* spp. assemblage is another useful component in paleoenvironmental reconstructions because of its tolerance to oxygen-deficient conditions (Benson et al., 1983), and/or sensitivity to increased surface productivity (Cronin et al., 1995). In MD99-2348, the anti-correlation between adults of small vestibule *K. pernoides* and *Polycope* spp. (Fig. 7) is coherent with the hypothesis relating the small vestibule *Krithids* to well oxygenated conditions (Table 1). On the other hand, *Polycope* increases when the adults of *Krithe* nearly disappear (see HE2 in Fig. 7) and the totality of *Krithe* assemblage is represented by juveniles.

These concomitances confirm the above discussion about the degradation *K. pernoides* life conditions. *Krithids* are unable to reach the adult stage and *Polycope* starts colonisation because it tolerates oxygen-impoverished substrate (see also  $\delta^{13}\text{C}$  and Mg/Ca values from Cacho et al., 2006 showed in Fig. 7) and is able to penetrate deep into the sediment in a much lower oxygenated microhabitat.

Epibathyal–sublittoral taxa, such as *Pseudocythere* sp. and *Macrocypris* sp. (Didié and Bauch, 2000; Didié et al., 2002; El Hmaidi et al.,

2010) are relatively abundant during the deglaciation (since 19 kyr ago, approximately). The sea-level rise (Arz et al., 2007) may explain the replacement of the *Loxoconcha* sp. group, (mostly consisting of shallow-water species that are obviously more abundant during the LGM low sea-level, Fig. 9, Table 1), by increases of *Pseudocythere* sp. and *Macrocypris* sp. assemblage.

Possible increasing surface productivity can be inferred by the oscillation of *Macrocypris* sp. abundance. This genus is known to prefer Mg-enriched waters, and easily incorporates Mg into its carapace (Cadot et al., 1972; Durazzi, 1977; Wansard, 1999). During the glacial time (before 19 kyr), the presence of *Macrocypris* sp. is still quite low (<20%), and it becomes particularly interesting during the deglaciation (Fig. 9, Table 1). After the end of the LGM, *Macrocypris* sp. abundances are >20% with several peaks, ranging from 30 to 70% between 17 and 19 kyr. This observation highlights the rapid change of ostracod assemblages at the end of the LGM coinciding with increasing surface productivity and/or changes in detrital input linked to the precipitation balance (increase of torrential rainstorms with increased runoff during dry climate episodes in the Mediterranean, as suggested by Jimenez-Espejo et al. (2008).

*Macrocypris* sp. is also inversely correlated with *C. testudo* (*sensu* Bonaduce et al., 1975), which we consider as a glacial marker (Fig. 9).

As for the interstadials, the number of species and their abundances do not display significant variations along the core, except for a small decrease during GIS-2 (Fig. 3). We might infer that environmental conditions are less suitable for the ostracod population during interstadials. In fact, bottom-water ventilation is more difficult during temperate climate conditions. However, the low sedimentation rate during the GIS does not allow precise consideration and additional data are necessary to confirm this hypothesis, ideally coming from a more expanded section.

## 7. Summary and conclusions

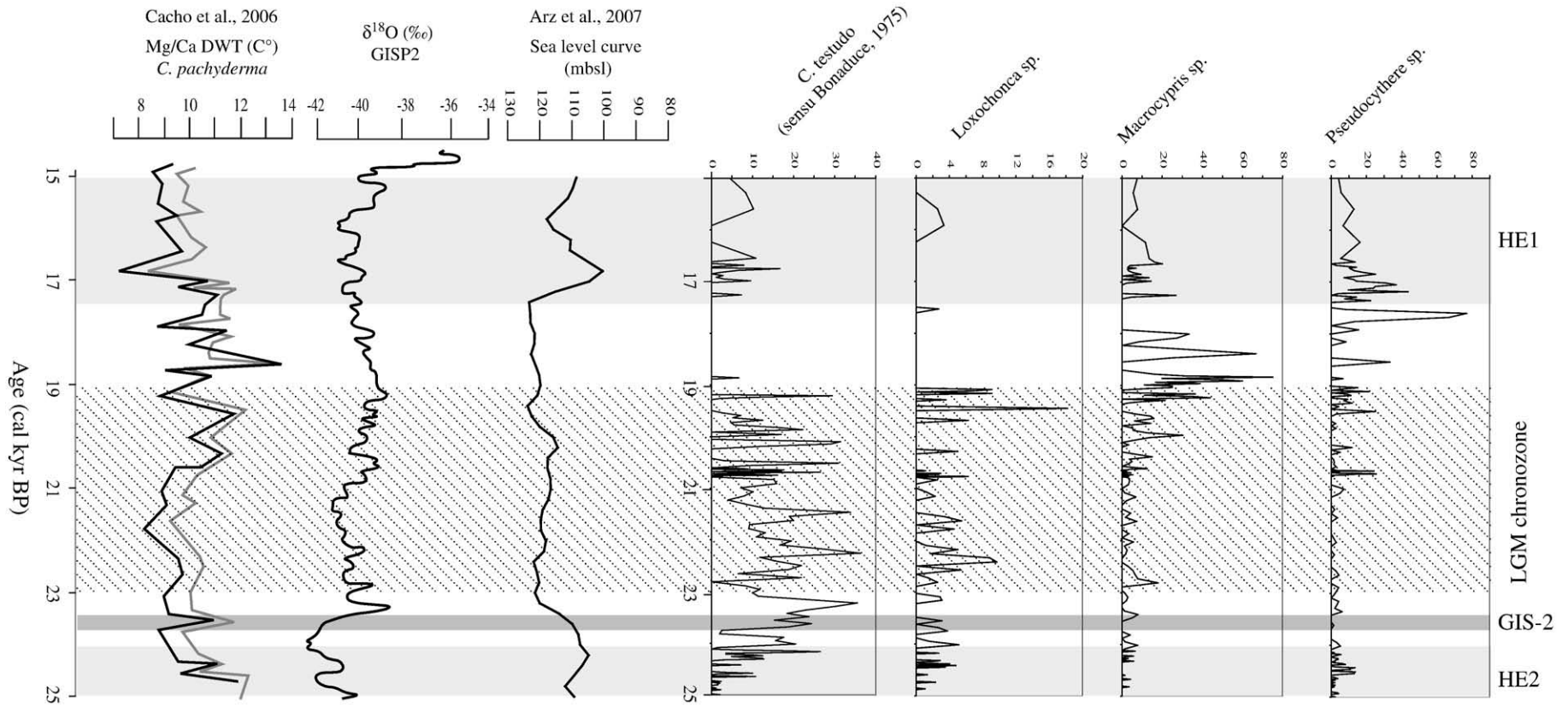
The core MD99-2348 from the GoL has been investigated in order to decode the response of deep sea benthic ostracods to distinct climate events over the last 30 kyr.

The “cold assemblage” dominated by *Henryhowella* and *Echinocythereis* shows the highest abundance during periods characterized by high bottom-water oxygenation. These episodes correlate with the highest abundance of *N. pachyderma* (sin), which marks the well known HEs in the western Mediterranean (Sierro et al., 2009).

Our results show that the presence of *Henryhowella* and *Echinocythereis* can be a useful indicator of the surface dense water sinking due to an intensification of NW winds (Tramontane and Mistral). Thus, cold, oxygen- and nutrient-rich dense waters sink down to the continental rise providing environmental conditions suitable for opportunistic benthic ostracods.

The high abundance of *Krithe* during these cold events may give an even more specific indication of bottom-water ventilation conditions. Based on our data, it appears that the dominance of *K. pernoides* (small vestibule and normal water oxygenation) during the HEs is consistent with the occurrence of *Henryhowella*–*Echinocythereis* group, which prefers oxygen- and nutrient-rich waters. Moreover, the increase of *Krithe* abundances during the events *Krithe* event 1 and *Krithe* event 2 at ~22.5 kyr and 23 kyr, respectively, correspond to two additional episodes of cooling. This sudden reappearance of *Krithe*, which often does not reach the adult moult stage strongly suggests that *Krithe* responds rapidly to abrupt changes of physico-chemical conditions of the bottom waters.

Major change in environmental conditions is clearly marked by the shift of two different groups (*C. testudo*–*Loxoconcha* spp. vs. *Pseudocythere* sp.–*Macrocypris* sp.) that reflect detrital input and productivity changes in the Mediterranean, as well as the possible impact of sea-level changes on benthic assemblages, since the LGM.



**Fig. 9.** Comparisons among (1) the abundances of *C. testudo*, *Loxoconcha* sp., *Macrocypris* sp., *Pseudocythere* sp. and the *Krithe* group (2) Greenland ice core isotope record (Meese et al., 1997), (3) ventilation + deep water temperature parameters from Cacho et al. (2006) and (4) sea-level curve obtained by Arz et al., 2007.

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## Appendix A. Taxonomic appendix: taxa cited in the text

<i>Argilloecia</i> Sars, 1866	<i>Loxoconcha</i> Sars, 1866
<i>Bythocythere turgida</i> , Sars 1866	<i>Loxoconchidea minima</i> Bonaduce,
<i>Cytheropteron alatum</i> Sars, 1866	Ciampo & Masoli, 1976
<i>Cytheropteron monoceros</i> Bonaduce,	<i>Macrocypris</i> Maddock, 1990
Ciampo & Masoli, 1976	<i>Monoceratina mediterranea</i> , Sissingh 1971
<i>Cytheropteron nodosum</i> Brady, 1868	<i>Paracypris</i> , Sars 1866
<i>Cytheropteron rotundatum</i> Müller, 1894	<i>Paradoxostoma</i> Fischer, 1855
<i>Cytheropteron testudo sensu</i>	<i>Polycopse</i> , Sars 1866
<b>Bonaduce et al., 1975</b>	<i>Pseudocythere</i> sp. aff. <i>P. caudata</i> , Sars 1866
<i>Echinocythereis echinata</i> Sars, 1865	<i>Pterygocythereis jonesii</i> , Baird, 1850
<i>Henryhowella asperrima</i> Reuss, 1850	<i>Sagmatocythere multifora</i> , Norman, 1875
<i>Krithe compressa</i> , Seguenza 1880	<i>Semicytherura incongruens</i> Müller, 1894
<i>Krithe pernoidea sinuosa</i> Ciampo, 1986	<i>Semicytherura</i> , Wagner, 1957
<i>Leptocythere</i> Sars, 1925	

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