Late Pleistocene boreal molluscs in the Gulf of Cadiz: Past and current oceanographic implications

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ABSTRACT

Remains of molluscs were collected from the seafloor on the north-eastern margin of the Gulf of Cadiz, between 300 and 1000 m water depth, using different sampling methods (e.g. dredging, trawling and box-coring), during several deep-sea expeditions. Samples contained a suite of species which nowadays mostly occur northwards of the English Channel, together with other widespread species. Species now locally extinct in the Gulf of Cadiz and restricted to northern latitudes, which unequivocally indicate a faunal shift, include the gastropods *Buccinum undatum*, *Colus gracilis*, *Liomesus ovum* and *Neptunea antiqua*, the bivalves *Arctica islandica*, *Chlamys islandica*, *Modiolus modiolus*, *Mya truncata* and *Nuculana pernula* and the scaphopod *Antalis entalis*. These species represent "Boreal Guests" of marked palae-oclimatic significance, some of which are reported for the first time in the Gulf of Cadiz. The boreal species collected were mostly large (>5 cm) whereas smaller boreal species were extremely scarce, probably winnowed away by strong bottom currents. The pteropod *Limacina retroversa*, at present restricted to water masses northwards of the Iberian Peninsula but widespread in Mediterranean sediments of the last glaciation, was also recorded. Accelerator mass spectrometry (AMS) ^{14}C dates obtained from nine specimens of molluscs ranged between 26.1 and 14.6 kyr B.P., thus confirming their attribution to a last glacial assemblage. The abundance of these molluscan remains in the present Mediterranean Outflow Water pathway could be explained if this outflow was reduced in intensity or more likely shifted to a deeper level, leaving the upper slope in contact with suitable Atlantic intermediate waters. The findings of Boreal Guests in the Gulf of Cadiz document the continuity of the faunal shift which is well-known in the Mediterranean basin. Species still living in the Gulf of Cadiz and the Alboran Sea never-theless account for 84.6% of specimens among the larger species.

1. Introduction

1.1. Quaternary climate and sea-level setting

The Pleistocene (2.6 Ma−11.7 kyr before present [B.P.]) is characterized by significant climatic oscillations on a time scale in the order of 100 kyr, with expansions of ice sheets and important sea level drops caused by cooling events during stadial periods, alternating with interstadial episodes with raised sea level (Siddall et al., 2006; Denton et al., 2010; Elderfield et al., 2012; Sierro et al., 2020). Glaciations and deglaciations greatly influenced the structure of ecosystems, leading to large scale shifts in latitudinal species distributional ranges, among other effects (Raffi, 1986; Taviani et al., 1991).

The last glacial period of the Pleistocene ends with the Marine Isotope Stage 2 (Railsback et al., 2015) that was marked by the Last Glacial Maximum (LGM, 26.5 to 19 kyr B.P., Clark et al., 2009; Martrat et al., 2014) when the Northern Hemisphere ice sheets reached their maximum volume. Global sea level then dropped to −134 m (Lambeck et al., 2014). Nevertheless the LGM was not the coldest episode in the Gulf of Cadiz (GoC); it was followed by a

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complex period of deglaciation (Termination 1), beginning with a colder interval (18−14.6 kyr B.P., Barker et al., 2009; Denton et al., 2010) during which meltwater and drifting ice was released from the Northern Hemisphere ice sheets. This interval, generally referred to as Heinrich Stadial 1 (HS1), comprises two phases which are registered in North Atlantic marine sediments but not in the Greenland ice cores (Rasmussen et al., 2006). The earliest phase involved discharge of meltwater from European ice sheets into the North Atlantic (reaching a maximum between 18.3 and 17 kyr B.P., Toucanne et al., 2009; Naughton et al., 2023a). The second episode lasted until 14.6 kyr B.P. (Barker et al., 2009; Denton et al., 2010; Naughton et al., 2023a) and staged a massive discharge of ice-rafted debris from the Laurentide ice sheet into the North Atlantic (the Heinrich Event 1 in a strict sense, Andrews and Voelker, 2018) with two peaks estimated (Hodell et al., 2017) at ca. 16.1 kyr and ca. 15 kyr B.P. In the temperate Northeast Atlantic near the Iberian Peninsula, a substantial drop in sea surface temperature preceded the peak of ice-rafting (Denton et al., 2010) and was accompanied by an abrupt expansion of the polar planktonic foraminifer *Neogloboquadrina pachyderma* starting around 18 kyr B.P. (Voelker and de Abreu, 2011; Ducassou et al., 2018).

This stadial episode was followed by an abrupt warming event, detected about 14.7 kyr B.P. from the Greenland ice cores (Rasmussen et al., 2006) and initiating the Bølling−Allerød warm interval (Naughton et al., 2023b). A rapid return to near-glacial conditions occurred during the Younger Dryas event ca. 12.8−11.5 kyr B.P. (Rasmussen et al., 2006; Barker et al., 2009; Naughton et al., 2023c) which was the last phase of the glacial period.

Several authors have suggested a link between these climatic changes and the global thermohaline circulation, where surface circulation and heat flow towards high latitudes is motioned by the sinking of surface water and formation of the southward flowing North Atlantic Deep Water (NADW). McManus et al. (2004) found that the Atlantic Meridional Overturning Circulation (AMOC) started weakening prior to Heinrich Events in the North Atlantic region, and remained low until the rapid accelerations concurrent with the two strongest regional warming events during deglaciation. The slowdown of the AMOC and the coincident rise in Antarctic temperature have been highlighted as a possible driving factor for strong subsurface warming in high latitudes of the North Atlantic, resulting in rapid melting of the Hudson Strait and Labrador ice shelves (Álvarez-Solas et al., 2011; Deschamps et al., 2012; Max et al., 2022).

1.2. Benthic molluscs as indicators of environmental conditions

The distribution of benthic species is controlled by a combination of major environmental drivers including seawater temperature, salinity and productivity, as well as other essential predictors such as substrate type, water depth, and bottom currents among others (Lalli and Parsons, 1997; Reiss et al., 2015). Molluscs are a main component of marine benthic macroinvertebrate assemblages, and provide an accurate archive of palaeoclimatic information. Belanger et al. (2012) found that bivalve distribution patterns can be predicted accurately by very few readily available oceanographic variables (temperature, salinity, productivity), with temperature alone predicting 53−99% of the present-day distribution along coastlines. Moreover, temperature is a crucial variable modulating the distribution of species, because it constrains the reproductive phases of adults and the survival of larval stages (Hall, 1964; Raffi, 1986). Therefore, molluscs have been successfully used for past climate reconstructions (Raffi, 1986; Taviani et al., 1991; Roy et al., 1995; Garilli, 2011; Aguirre et al., 2019; Melo et al., 2022 among others).

The arrival of species from boreal areas of the North East Atlantic to the Mediterranean through the Strait of Gibraltar was a consequence of the onset of a high-seasonality climatic regime associated with significantly colder winters, diagnosed by a pronounced drop in the abundance of the tropical planktonic foraminifer *Globigerinoides ruber* (d'Orbigny, 1839) in the Mediterranean (Raffi, 1986; Thunell et al., 1991). Such species were called "boreal guests" (hereafter BGs) or "northern guests", a term first used for molluscs (Suess, 1883−1888; re-definition by Ruggieri, 1977 and Malatesta and Zarlenga, 1986) and then extended to other taxa including benthic foraminifers and ostracods (Faranda and Gliozzi, 2011), bryozoans, serpulid polychaetes and calcareous algae (Sanfilippo, 1998; Di Geronimo et al., 2000) as well as cold-water corals (Wienberg et al., 2010). The southward migration of BGs (mostly molluscs) into the Mediterranean basin during the last glaciation is well documented by many authors from marine thanatocoenoses on the outer continental shelf in the Mediterranean Sea: Cap de Creus area, north-eastern Spain (Mars, 1958; Martinell and Julià, 1973; Domènech and Martinell, 1982), the Gulf of Lion (Froget et al., 1972), the Adriatic Sea (Colantoni et al., 1975; Taviani, 1978; Curzi et al., 1984) and elsewhere (Delibrias and Taviani, 1985), among others. The group of BGs found to occur at that time in the Mediterranean Sea includes, among other species, the gastropods *Puncturella noachina*, *Buccinum humphreysianum* and *Buccinum undatum*, and the bivalves *Modiolus modiolus*, *Pseudamussium peslutrae* (formerly *Pseudamussium septemradiatum*), *Chlamys islandica*, *Acesta excavata* and *Arctica islandica*. Previous migrations of BGs have occurred throughout the Pleistocene, with at least three successive pulses that correspond partly to the Santernian, Emilian and Sicilian substages of the Calabrian (Early Pleistocene, 1.8−0.77 Ma B.P.) (Ruggieri et al., 1984; Malatesta and Zarlenga, 1986; Raffi, 1986).

1.3. The lack of molluscan records in the GoC

The large amount of data related to the occurrence of BGs in the Mediterranean basin during the last glaciation contrasts with the limited information existing for the GoC, mostly in the vicinity of the Strait of Gibraltar (Taviani et al., 1991, based on material collected by the French expedition BALGIM in 1984). Yet, the GoC had to be colonized as a premise for crossing the Strait of Gibraltar (Bouchet and Taviani, 1989 and references therein). Reports of cold-water species in this part of the North East Atlantic during the late Quaternary mostly focused on corals, with fossil reef-forming scleractinians widely distributed within the GoC and mainly associated with mud volcanoes, diapiric ridges, steep fault escarpments and coral mounds (Taviani et al., 1991; Wienberg et al., 2009, 2010), and to a lesser extent on molluscs (Taviani et al., 1991). Several gastropods and bivalves, some of which belonging to species still living in the area, were recorded in cores from IODP Expedition 339 in the GoC (sites U1386 to U1390, Stow et al., 2013). However these records are much older (50−800 kyr B.P.) than the time frame considered in this work, and none of them can be suspected as a BG.

1.4. Aim of this paper

The purpose of the present study is (1) to document extensive new records of mollusc BGs on the Spanish margin of the GoC, with the first record for some of them in the area, and (2) to discuss their relationships with the late Pleistocene palaeoceanographic conditions of the GoC, a key area connecting the Mediterranean with the rest of the NE Atlantic ocean.

2. Regional setting

2.1. Situation

The GoC is located in the North East Atlantic Ocean, and is connected with the Mediterranean Sea through the Strait of Gibraltar (Fig. 1). The shallowest part of the connection is situated at Camarinal sill, in the western sector of the Strait, with 284 m water depth (mwd) in its shallowest threshold (Luján et al., 2011). It is bordered by the south-western margin of the Iberian Peninsula (continental shelf ranging from 15 to 50 km width) and the north-western Moroccan margin (continental shelf of ca. 60 km width), with depths down to 4000 mwd in the abyssal plain to the west (Fig. 1).

2.2. Geological setting

Regarding the geological context, the GoC is largely affected by tectonics and diapiric processes related to a complex geodynamic evolution of the continental margin (Medialdea et al., 2009), with olistostrome/accretionary complex units that were emplaced in the Late Miocene in response to the NW-directed convergence between the African and Eurasian plates (Somoza et al., 2003). An extensive occurrence of diapiric ridges, mud volcanoes (hereafter MVs) and diapir/MV complexes (hereafter DMVs) together with other related fluid venting submarine structures have been observed throughout the Spanish−Portuguese margin of the GoC (Somoza et al., 2003; Fernández-Puga et al., 2007; Díaz del Río et al., 2014; Palomino et al., 2016; Lozano et al., 2020), as well as on the Moroccan margin (Gardner, 2001; Van Rensbergen et al., 2005). Moreover, seepage-related morphologies commonly associated with mud volcanism and mud diapirism are also abundant in the GoC, including collapse depressions, pockmarks, mud flows, carbonate mounds and slides (Pinheiro et al., 2003; Somoza et al., 2003; Fernández-Puga et al., 2007; León et al., 2010; Díaz del Río et al., 2014; Palomino et al., 2016; Lozano et al., 2020). Topographic features in the GoC also include a large field of hundreds of small (20−30 m in height) buried and exposed mounds situated among MVs and on top of diapiric ridges along the Moroccan margin, which are covered by fossil corals, and with an origin related to glacial periods since the Early-Middle Pleistocene Transition (Foubert et al., 2008; Wienberg et al., 2009; Vandorpe et al., 2017).
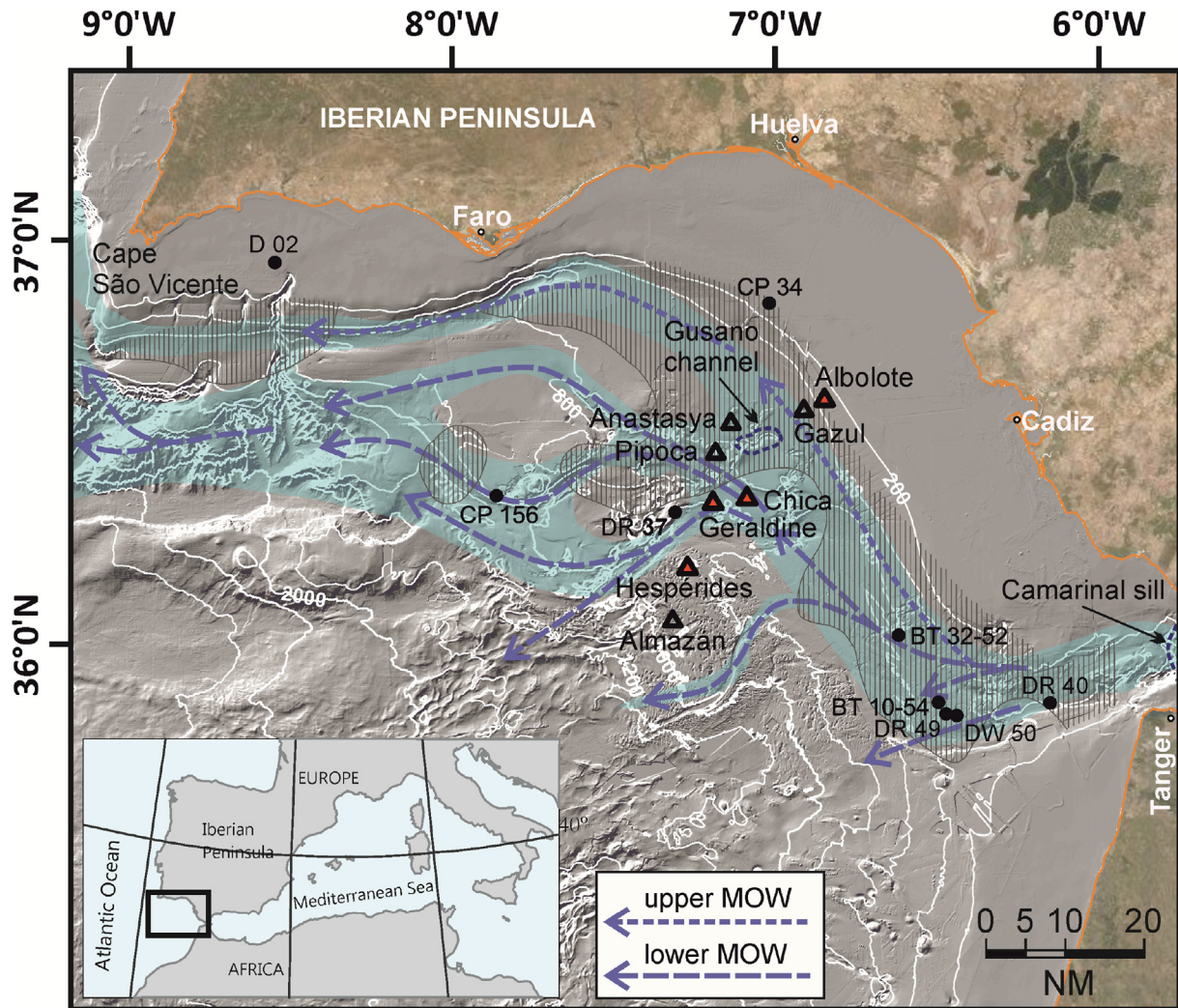
Fig. 1. Map of the Gulf of Cadiz showing the location of the mud volcanoes (empty triangles), diapir/mud volcano complexes (red-filled triangles) and other sampling stations (circles: TALISMAN, BALGIM, CIRCASUR) mentioned in the text, as well as the pathway of the Mediterranean Outflow Water (MOW; blue tone and dashed arrows, redrawn from Hernández-Molina et al., 2003). The vertically hatched areas are those for which Gasser et al., (2017: Fig. 19) reported the presence of the MOW in contact with the seafloor or less than 25 m from it.

All those elements contribute to shaping the benthic habitats (Lozano et al., 2020) as well as to directing the pathway of the water mass in contact with the bottom (Gasser et al., 2017; Sánchez-Leal et al., 2017).

2.3. Modern oceanographical pattern

The GoC has been the focus of attention of many studies dealing with deep-water circulation, mainly in the northern sector which is characterized by the exchange of water masses through the Strait of Gibraltar (Hernández-Molina et al., 2014; Gasser et al., 2017 and references therein; Sánchez-Leal et al., 2017). Relatively warm (16.6 °C–22.6 °C) and less saline (36.5) surficial North Atlantic Central Water (NACW) flows eastwards along the south-western Iberian margin and partly enters the Mediterranean Sea, whereas cool (12.9 °C) and highly saline (38.45) Mediterranean Outflow Water (MOW) flows westwards through the Strait of Gibraltar below the NACW and in some areas in close contact with the sea-floor (Ochoa and Bray, 1991; Gasser et al., 2017). After crossing the Strait, the MOW spreads westwards in the GoC and progressively sinks north-westwards, descending along the continental slope while its temperature, salinity and velocity decrease through mixing with the overlying fresher NACW (Iorga and Lozier, 1999). West of the 7°W, and partly due to topographical constraints, the MOW splits into two main branches. The upper branch flows at depths between 500 and 800 mwd along the upper slope until Cape São Vicente, remaining at most places in contact with the continental slope. The lower branches are located further south at depths between 800 and 1200 mwd, and detach from the seafloor in the western GoC, constituting the main path for MOW transport into the open ocean that can be traced westwards and northwards along the Iberian margin (Iorga and Lozier, 1999; Gasser et al., 2017). The MOW outflow entrains NACW as it plunges into the GoC, the subsequent mixing reducing the contrast in salinity and temperature between the outflow and surrounding waters (García-Lafuente et al., 2011).

The Atlantic intermediate water masses (summarized by Voelker et al., 2015 and Roque et al., 2019) comprise the eastern NACW, formed by strong evaporation first and further winter cooling later along the Azores Front (NACW sensu stricto, of sub-tropical origin). This NACW penetrates the GoC in the 100–700 mwd range, overlying the MOW with a sharp transition at the western approaches of the Strait of Gibraltar and only interacting with the upper core of the MOW further west. The Subarctic Intermediate Water (SAIW, sometimes treated as subpolar NACW) has a different origin north of the Bay of Biscay, flows southwards along the western Iberian margin and enters the GoC in the 400–900 mwd interval, therefore overlying the lower branch of the MOW. Finally, the Antarctic Intermediate Water (AAIW) flows along the African coast from the south, hardly reaches the GoC in the 600–1000 mwd interval below the NACW layers.

Surface circulation involves the Surface Atlantic Water (SAW) with the Azores current meandering eastwards towards the GoC and taking part (together with subtropical NACW) in the inflow of Atlantic water into the Mediterranean.

2.4. Palaeocirculation patterns

The MOW palaeocirculation in the GoC during the last 50 kyr has been the subject of divergent studies and hypotheses, mostly based on the sedimentological record in deep-sea cores. Huang and Stanley (1972), based on the analysis of Alboran Sea cores, formulated the unconventional hypothesis that before 10 kyr B.P. less dense Mediterranean water outflowed above denser Atlantic water entering the Strait of Gibraltar and then flowing into the Alboran Sea. In their view, the presence in the Alboran Basin of a layer of coarse terrigenous material derived mainly from the Strait of Gibraltar and the Spanish coast was best explained by the action of relatively powerful east-flowing bottom currents. However, this inversion could only be possible if Atlantic incoming water were colder (possibly due to a southward shift of the Polar Front) and/or the Mediterranean deep water less saline (due to increased rainfall and river runoff in the basin), a view which was rebutted by Diester-Haass (1973) and was not supported by Bethoux (1979).

It was also hypothesised (Cacho et al., 1999, 2000, 2001, based on planktonic foraminiferal record and geochemical proxies) that during the LGM, sea surface temperatures in the Alboran Sea were in the order of 10–12 °C and the stratification was not as sharp as today, resulting in an enhanced Mediterranean thermohaline circulation in comparison to the current warm interval. This better ventilation of the deep Mediterranean Sea may have been linked to an increased contribution of the Western Mediterranean Deep Water (WMDW) to the MOW (Voelker et al., 2006), and should result in the reinforcement of the denser MOW towards the Atlantic Ocean. However, as Cacho et al. (2000) admitted, MOW volume was also spatially constrained by the glacial sea level drop where Camarinal sill would be hardly more than 100 mwd, with a section reduced to 1/8 of its current one according to Bethoux (1979).

According to Sierro et al. (2020), the freshwater discharge during the Bølling warming caused a cascade effect which finally decreased the vertical density gradient to the west of the Strait of Gibraltar, resulting in a deepening of the higher density MOW, which in turn led to the intrusion of warm and salty water at deeper depths in the NE Atlantic. When melt-water input started to decrease, densities of mid-depth Atlantic waters rose and the MOW experienced a progressive shoaling that raised its velocity, as suggested by Voelker et al. (2006) and Sierro et al. (2020), generating a rapid warm and highly saline deep-water current that swept the seabed on which it was moving.

The MOW acts as a strong bottom current inducing the formation of channels, contourites and sediment drift bodies along the middle slope, generating the GoC contourite depositional system (Faugères et al., 1986; Sierro et al., 1999; Hernández-Molina et al., 2003, 2014; García et al., 2009). Several studies have addressed the evolution of the MOW through the analysis of deep-sea cores in the GoC contourite depositional system, and unanimously demonstrate the influence of the North Atlantic climate oscillations during the Heinrich Stadials and the Younger Dryas on the MOW circulation pattern in the GoC. Several peaks of the coarse fraction content in the sediment, interpreted as the result of higher intensity of the MOW, are recognized in cores throughout the GoC, but their position concerning the stadial intervals varies. Sierro et al. (1999) found two prominent sandy contourites on the upper continental slope (400–700 mwd) of the GoC, one at the base of the Bølling–Allerød time, the other after the Younger Dryas, reaching maximum grain-size values towards the late Holocene. Those coarser layers were interpreted as resulting from the balance between the intensity of the MOW (increasing during deglaciation events because the higher sea level allowed more flux through the Strait) and sediment input (trapped on the shelf during highstands and shifted seawards during lowstands). Llave et al. (2006) found a peak of sand content just after the LGM in a core situated at 582 mwd in the main pathway of the modern MOW. Conversely, in a much deeper part of the GoC (969–1515 mwd), Rogerson et al. (2005) found maximum sand content ca. 17 kyr B.P. during Heinrich Stadial 1 (HS1) whereas the Holocene part is essentially muddy; and Voelker et al. (2006) found similarly a peak of grain size within HS1 in another core situated at 1170 mwd. Thus, the influence of the lower branches of the MOW is assumed to be stronger under glacial conditions than nowadays (Llave et al., 2006;

Table 1
Location and details of sampling stations on the oceanographic expeditions TALISMAN 1883, BALGIM 1984, ANASTASYA 09/99, INDEMARES 0610, 0211, 0412 and CIRCASUR 2020 on the mud volcano field in the Spanish waters of the Gulf of Cadiz. BT, beam-trawl; DA, benthic dredge; BC, box-corer; MV, mud volcano; MD, mud diapir; DMV, diapir/mud volcano complex; SoG, Strait of Gibraltar.

Expedition	Sampling method	Sample code	Latitude start	Longitude start	Depth start (mwd)	Latitude end	Longitude end	Depth end (mwd)	Area
TALISMAN	Trawl	D02	36.88°N	−8.53°W	99				Portimão canyon
BALGIM	Benthic dredge	DR23	36.650°N	−7.317°W	556				Off Huelva
1984	Epibenthic sled	DW24	36.683°N	−7.317°W	545				Off Huelva
	Beam trawl	CP25	36.683°N	−7.317°W	544				Off Huelva
	Benthic dredge	DW28	36.767°N	−7.133°W	398				Off Huelva
	Beam trawl	CP34	36.816°N	−7.083°W	180				Off Huelva
	Benthic dredge	DR37	36.300°N	−7.250°W	864				Off Huelva
		DR40	35.833°N	−6.150°W	362				W Gibraltar
		DR42	35.900°N	−6.386°W	135				W Gibraltar
		DR45	35.733°N	−6.283°W	293				W Gibraltar
		DR49	35.883°N	−6.550°W	521				W Gibraltar
	Epibenthic sled	DW50	35.883°N	−6.533°W	523				W Gibraltar
	Beam trawl	CP54	35.683°N	−6.500°W	356				W Gibraltar
	Epibenthic sled	DW57	35.700°N	−6.583°W	548				W Gibraltar
	Beam-trawl	CP108	36.183°N	−8.100°W	1527				Off Huelva
		CP155	36.333°N	−7.683°W	903				Off Huelva
		CP156	36.333 N	−7.883 W	1135				Off Huelva
		CP157	36.350°N	−7.933°W	1108				Off Huelva
		CP160	36.250°N	−8.000°W	1350				Off Huelva
ANASTASYA 09/99	Benthic dredge	DA06/5	36.187°N	−7.324°W	721	36.191°N	−7.309°W	739	Hespérides DMV
INDEMARES 0610	Benthic dredge	DA04	36.575°N	−6.881°W	388	36.576°N	−6.879°W	375	Albolote DMV
		DA07	36.564°N	−6.943°W	495	36.562°N	−6.942°W	491	Gazul MV
		DA11	36.562°N	−6.939°W	461	36.564°N	−6.939°W	462	Gazul MV
	Beam-trawl	BT09	36.575°N	−6.880°W	380	36.577°N	−6.870°W	337	Albolote DMV
	Shipek grab	SK1.3	36.562°N	−6.939°W	461				Gazul MV
INDEMARES 0211	Benthic dredge	DA01	36.573°N	−6.878°W	335	36.575°N	−6.875°W	339	Albolote DMV
		DA17	36.457°N	−7.204°W	532	36.455°N	−7.206°W	585	Pipoca MV
		DA18	36.457°N	−7.207°W	554	36.457°N	−7.207°W	554	Pipoca MV
		DA19	36.463°N	−7.201°W	547	36.463°N	−7.205°W	545	Pipoca MV
		DA20	36.372°N	−7.123°W	756	36.375°N	−7.123°W	725	Chica DMV
		DA21	36.377°N	−7.121°W	727	36.379°N	−7.119°W	694	Chica DMV
		DA23	36.459°N	−7.228°W	752	36.459°N	−7.231°W	746	Pipoca MV
		DA24	36.476°N	−7.223°W	724	36.474°N	−7.220°W	723	Pipoca MV
		DA26	36.565°N	−6.932°W	443	36.564°N	−6.934°W	453	Gazul MV
		DA27	36.557°N	−6.946°W	461	36.559°N	−6.948°W	463	Gazul MV
		DA30	36.371°N	−7.117°W	653	36.370°N	−7.113°W	669	Chica DMV
		DA31	36.300°N	−7.199°W	742	36.301°N	−7.202°W	771	Geraldine DMV
		DA32	36.304°N	−7.234°W	945	36.307°N	−7.236°W	883	Geraldine DMV
		DA35	36.189°N	−7.304°W	740	36.192°N	−7.304°W	738	Hespérides DMV
		DA36	36.184°N	−7.309°W	696	36.186°N	−7.307°W	711	Hespérides DMV
		DA37	36.182°N	−7.308°W	678	36.179°N	−7.308°W	694	Hespérides DMV
		DA40	36.164°N	−7.299°W	892	36.164°N	−7.295°W	865	Hespérides DMV
		DA41	36.168°N	−7.328°W	950	36.169°N	−7.332°W	912	Hespérides DMV
		DA42	36.058°N	−7.329°W	903	36.061°N	−7.325°W	908	Almazán MV
		DA46	36.048°N	−7.346°W	934	36.046°N	−7.348°W	929	Almazán MV
		DA47	36.060°N	−7.331°W	902	36.059°N	−7.328°W	914	Almazán MV
	Beam-trawl	BT08	36.523°N	−7.154°W	478	36.526°N	−7.143°W	550	Anastasya MV
		BT20	36.453°N	−7.185°W	625	36.459°N	−7.193°W	616	Pipoca MV
		BT22	36.187°N	−7.292°W	758	36.179°N	−7.291°W	801	Hespérides DMV
		BT24	36.186°N	−7.307°W	704	36.180°N	−7.299°W	734	Hespérides DMV
		BT25	36.055°N	−7.329°W	894	36.060°N	−7.320°W	896	Almazán MV
		BT29	36.053°N	−7.339°W	860	36.048°N	−7.348°W	928	Almazán MV
		BT30	36.061°N	−7.336°W	912	36.059°N	−7.326°W	904	Almazán MV
INDEMARES 0412	Box-corer	BC07	36.588°N	−7.084°W	470				La Pepa MD
		BC11	36.465°N	−7.069°W	558				Gusano channel
CIRCASUR 2020	Beam-trawl	BT10-54	35.893°N	−6.554°W	534	35.901°N	−6.558°W	526	W SoG
		BT32-52	36.081°N	−6.700°W	625	36.078°N	−6.690°W	617	W SoG
		BT17-26	36.384°N	−7.046°W	567	36.391°N	−7.049°W	570	Chica DMV

Fig. 5) and also the glacial MOW settled deeper, leaving the bottom in ca. 2000 mwd instead of current ca. 1200 mwd, a depth now occupied by North Atlantic Deep Water (NADW) (Rogerson et al., 2005).

During the LGM, surface temperatures along the western Iberian Peninsula dropped by 2−4 °C in summer (also in winter south of 40°N) but the polar front remained further north (Eynaud et al., 2009; Voelker et al., 2009) and the general setting was not drastically different from present. Conversely, during HS1, peaks of the cold-water foraminifer *Neogloboquadrina pachyderma* were recorded in the GoC between 17.9 and 15.4 kyr B.P. (Voelker and de Abreu, 2011; Ducassou et al., 2018). This reflects a southward displacement of the Polar Front towards the West of the Iberian Peninsula (Eynaud et al., 2009; Barker et al., 2015; Sierro et al., 2020) with intrusion of subpolar waters into the GoC and, from there, into the Mediterranean.

Table 2
Occurrence and abundance of molluscs found in the thanatocoenosis dredged during the INDEMARES/CHICA programme on mud volcanoes, mud diapirs and diapir/MV complexes in the Spanish waters of the Gulf of Cadiz (GoC), with indication of the fluid venting submarine structures. Previous records for the GoC: (1) Locard (1897−1898); (2) Taviani et al. (1991); (3) Wienberg et al. (2009); (4) Salas (1996); (5) Bouchet and Warén (1985, 1993); (6) López-Correa et al. (2005); (7) Ducassou et al. (2018); (8) Utrilla et al. (2020). See Table 1 for the detail of sample locations. Rows 1−22 are the larger species (generally >5 cm). P: la Pepa; CG: Gusano channel; ANAS: Anastasya; GER: Geraldine; other site names in full.

		ALBOLOTE			GAZUL					P	CG	ANAS	PIPOCA			
		BT09 337-380	DA01 335-339	DA04 375-388	SK1.3 461	DA07 491-495	DA11 461-462	DA26 443-453	DA27 461-463	BC07 470	BC11 558	BT08 478-550	DA17 532-585	DA18 554	DA19 545-547	BT20 616-625
Species still living in the GoC	*Acesta excavata* (Fabricius, 1779)															
	Ampulla priamus (Gmelin, 1791)															
	Buccinum humphreysianum Bennett, 1824												2			1
	Buccinum oblitum Sykes, 1911															
	Colus islandicus (Mohr, 1786)											1				
	Colus jeffreysianus (P. Fischer, 1868)							1						1	2	
	Galeodea rugosa (Linnaeus, 1771)		4									6	6		2	1
	Glossus humanus (Linnaeus, 1758)						1									
	Lutraria lutraria (Linnaeus, 1758)						2									
	Neptunea contraria (Linnaeus, 1771)								2	7		2	5	4	1	
	Pseudamussium peslutrae (Linnaeus, 1771)		1	17		20						34	131	1		
	Ranella olearium (Linnaeus, 1758)		1		4				1			3			2	
	Troschelia berniciensis (W. King, 1846)												3			1
	Turrisipho fenestratus (W. Turton, 1834)														1	
Species locally extinct in the GoC	*Arctica islandica* (Linnaeus, 1767)	3			1											
	Buccinum undatum Linnaeus, 1758															
	Chlamys islandica (O.F. Müller, 1776)				1											
	Colus gracilis (da Costa, 1778)												2	2	3	
	Liomesus ovum (W. Turton, 1825)															
	Modiolus modiolus (Linnaeus, 1758)						1									
	Mya truncata Linnaeus, 1758						1									
	Neptunea antiqua (Linnaeus, 1758)												5			
	Antalis entalis (Linnaeus, 1758)															
	Curtitoma trevelliana (W. Turton, 1834)															
	Limacina retroversa (J. Fleming, 1823)					1							1			
	Nuculana pernula (O.F. Müller, 1779)					1										
	Propebela turricula (Montagu, 1803)										1					
	Puncturella noachina (Linnaeus, 1771)															
	Veleropilina reticulata (Seguenza, 1876)			1												

3. Material and methods

The material analyzed in the present study was collected mainly during the European LIFE + INDEMARES project, which aimed to provide the necessary scientific information for establishing a network of deep-sea areas of biological interest for Spanish waters to be incorporated in the EU Natura 2000 network. The samples were collected during multidisciplinary expeditions INDEMARES/CHICA 0610, 0211 and 0412 on board R/V *Emma Bardán*, R/V *Cornide de Saavedra* and R/V *Ramón Margalef* respectively, exploring a MV field located on the upper and middle slope of the north-eastern GoC continental margin (300−1200 mwd) (Fig. 1). Some material was obtained during ANASTASYA 09/99 expedition on board R/V *Cornide de Saavedra*, one of the first expeditions dedicated to a general investigation of sedimentary dynamics in the GoC, and during the CIRCASUR 2020 expedition on board R/V *Ramón Margalef*, aimed to an evaluation of the environmental status of the benthic habitats of the GoC between 30 and 1000 mwd within the monitoring programs of the EU Marine Strategy Framework Directive 2008/56/EEC. In addition, material coming from historical expeditions that sampled the GoC was incorporated into this study including that from BALGIM expedition (1984), carried out on board R/V *Cryos* (see Salas, 1996), and from TALISMAN 1883 expedition on board the steamer *Talisman*, one of the earliest French oceanographic expeditions dedicated to investigate the deep-sea (Filhol, 1884; Locard, 1897−1898; Dolan, 2020).

Sampling was carried out using small Shipek grab (SK, 0.04 m^2 of sampling area), a large box-corer (BC, generally ca. 0.09 m^2 of sampling area), a benthic dredge (DA, sampled area ca. 300 m^2), and a beam-trawl (BT, sampled area ca. 2000 m^2) (Table 1). Sediments collected with the BC (generally between 0.10 and 0.20 m below seafloor) were sectioned at 5 cm intervals and sieved on a 0.5 mm mesh. The material collected with the DA and BT was sieved through a sieve column of 10, 5, 1 and 0.5 mm mesh sizes. Large specimens were sorted on board and bulk samples of the finer fractions were preserved in 70% ethanol for further study. The fine fractions of the sediment (<5 mm) were available from the BC and most of the DA, whereas they were mostly lost in trawl (i.e., BT) samples.

Larger (>5 cm) molluscs were sorted to species on board and identified, with live-taken specimens and empty shells quantified separately. For bivalves, each valve was counted as representing one individual except in the rare cases where the complete shell was found with both valves in connection. In addition, the finer fraction (1−5 mm) was sorted under the stereo-microscope for selected dredge hauls and box-cores in which larger BGs were found. By "thanatocoenosis" in a broad sense, we designate the assemblage of dead shells found in the superficial layer of unconsolidated sediment on the sea bottom, collected with the dredge or box core. This thanatocoenosis can accumulate shells from different origins in space and time, therefore mixing shells of the modern benthic community with those of locally extinct species (Kidwell,

PIPOCA		CHICA			HESPERIDES								GER		ALMAZAN						
DA23 746-752	DA24 723-724	DA20 725-756	DA21 694-727	DA30 653-669	AN-DA06/5 721	BT22 758-801	BT24 704-734	DA35 738-740	DA36 696-711	DA37 678-694	DA40 865-892	DA41 912-950	DA31 742-771	DA32 883-945	BT25 894-896	BT29 860-928	BT30 904-912	DA42 903-908	DA46 929-934	DA47 902-914	previous records
												1									(6)
			1																		(1, 5)
		20	1																		(1, 2, 5)
			1		1										3	1					(2, 5)
			1		1							1		1	8		2	3		5	(1, 5)
	2	1	2		2																(1, 5)
																					(1, 4)
1	1	1	1		2	1	4	2	1	1	2	3	2		5			1	1		(1, 5)
		9																			(1, 2, 4)
			3	4								2									(1, 5)
		1			1	1									1		1			3	(1, 5)
		1																			(1, 4)
													1								(2)
																					(2)
					1									1		1		7			New
														2							New
																		2			(2)
					10																(1)
													1								New
													1								New
																					New
																		65			(7)
																					New
																					New
																					New
		3											1					1			(8)

2013), e.g. the BGs. In the context of the current-swept contourite system of the GoC, shells of BGs would occur on the seafloor either because no substantial sedimentation occurred since their deposition, or because erosion has removed the sediment which once covered them. There is no taphonomic clue to differentiate which are BGs remaining from times of the last glaciation and which are recently dead specimens from the modern assemblage (or from any intermediate age).

Species retained as possible BGs include, in addition to the dated ones, (1) species present in the thanatocoenosis and known to be locally extinct in the area, (2) species still living in the area but currently found in a bathymetric range which does not match the position of the sample, and (3) species represented by a large number of shells without any live-taken specimen. Information on the current distributions and bathymetric ranges of the molluscan species found in the thanatocoenosis was mostly obtained from sources stated in the "Distribution" tab of the species in the World Register of Marine Species (WoRMS Editorial Board, 2023) and are not repeated here. Main sources for distributions of some species in Mediterranean thanatocoenoses included Malatesta and Zarlenga (1986), Martinell et al. (1986) and Giribet and Peñas (1997). Information regarding current biological communities inhabiting the MV field of the north-eastern GoC was provided by Rueda et al. (2012, 2016), Díaz del Río et al. (2014), González-García et al. (2020), Lozano et al. (2020), Ramalho et al. (2020) (Bryozoans), Utrilla et al. (2020) (Mollusca), and Urra et al. (2021).

A total of ten age determinations were conducted on nine shells (one shell was dated twice independently for quality control) to obtain a time frame for the past occurrence of potential BG molluscs in the GoC. For this purpose, we selected well preserved shells, not showing marks of weathering, recrystallization, or any other degradation which would bias the radiocarbon dating (Rick et al., 2005). Samples were extracted from the thickest part of the shells (i.e., the columella in gastropods and the area near the umbo in bivalves) of two specimens of the bivalve *Arctica islandica*, two specimens of the gastropod *Neptunea contraria* and four specimens of *Neptunea antiqua*. These were dated by accelerator mass spectrometry (AMS) with a NEC 1.5SDH-1 Pelletron accelerator performed at the Direct AMS radiocarbon dating laboratory (https://www.directams.com/), and referred to as before present (BP, with P = 1950 CE).

Radiocarbon ages (AMS ^{14}C ages) were calibrated to calendar ages (cal. yr B.P.) with the CALIB 8.2 program (Stuiver et al., 2021) and the Marine20 calibration data set (Heaton et al., 2020). A conservative local reservoir effect (ΔR) of 100 (±100) ^{14}C yr was adopted to correct for regional differences in reservoir age in the GoC, according to Monge Soares and Matos Martins (2010). All ^{14}C analyses followed standard procedures.

4. Results

The thanatocoenosis analyzed in the coarse fraction of samples collected in the MV field of the north-eastern GoC comprised 748 shell remains belonging to a total of 22 larger (>5 cm) mollusc

Table 3
Occurrence and abundance of molluscs found in the thanatocoenosis dredged off Huelva (BALGIM, 1984 expedition), off S. Portugal (TALISMAN, 1883 expedition) and at the western approaches of the Strait of Gibraltar (BALGIM, 1984 and CIRCASUR, 2020 expeditions). Previous records for the GoC, references as in Table 2. See Table 1 for the detail of sample locations. * denotes the live-taken specimen of *Colus islandicus*. Rows 1—22 are the larger species (generally >5 cm).

		BALGIM off Huelva								
		DR23 556	DW24 545	CP25 544	DW28 398	CP34 180	DR37 864	CP155 903	CP156 1135	CP157 1108
Species still living in the GoC	*Acesta excavata* (Fabricius, 1779)									
	Ampulla priamus (Gmelin, 1791)					2				
	Buccinum humphreysianum Bennett, 1824									
	Buccinum oblitum Sykes, 1911						1			
	Colus islandicus (Mohr, 1786)						4		1*	6
	Colus jeffreysianus (P. Fischer, 1868)	1					7	1		3
	Galeodea rugosa (Linnaeus, 1771)									
	Glossus humanus (Linnaeus, 1758)					1				
	Lutraria lutraria (Linnaeus, 1758)									
	Neptunea contraria (Linnaeus, 1771)						2			
	Pseudamussium peslutrae (Linnaeus, 1771)	6	7	43	2					
	Ranella olearium (Linnaeus, 1758)						1			
	Troschelia berniciensis (W. King, 1846)									
	Turrisipho fenestratus (W. Turton, 1834)									
Species locally extinct in the GoC	*Arctica islandica* (Linnaeus, 1767)					1				
	Buccinum undatum Linnaeus, 1758						1			
	Chlamys islandica (O.F. Müller, 1776)									
	Colus gracilis (da Costa, 1778)									1
	Liomesus ovum (W. Turton, 1825)									
	Modiolus modiolus (Linnaeus, 1758)									
	Mya truncata Linnaeus, 1758									
	Neptunea antiqua (Linnaeus, 1758)									
	Antalis entalis (Linnaeus, 1758)									
	Curtitoma trevelliana (W. Turton, 1834)									
	Limacina retroversa (J. Fleming, 1823)									
	Nuculana pernula (O.F. Müller, 1779)									
	Propebela turricula (Montagu, 1803)									
	Puncturella noachina (Linnaeus, 1771)					2				
	Veleropilina reticulata (Seguenza, 1876)									

species, among which several are locally extinct and denote cold-water affinity. It also contained several cold-water corals, mainly *Desmophyllum pertusum* (Linnaeus, 1758) (also known as *Lophelia pertusa*), and *Madrepora oculata* Linnaeus, 1758, but also *Dendrophyllia alternata* Pourtalès, 1880. The detailed list of molluscan species with a quantification of their abundance is given in Tables 2 and 3, and a selection of species is illustrated in Figs. 2—4. This list comprises shells of species still living in the area along with others (BGs) constrained today to more northern areas, with no taphonomic clues allowing to distinguish them.

The locally extinct molluscan species which definitely qualify as BGs were found, following a bathymetric gradient from shallowest to deepest, at Albolote DMV, Gazul MV, Pipoca MV, Chica DMV, Hespérides DMV, Geraldine DMV, Almazán MV, as well as in the western approaches of the Strait of Gibraltar. Fine fractions (1—5 mm) in the dredge hauls yielded seven additional species (84 shell remains) suspected to be BGs (Table 2, Figs. 1—2); however, these were rare (low abundance and frequency of occurrence) and the bulk of the thanatocoenoses in that fraction comprises species currently living in the area.

Unquestionable BGs were represented by 115 individuals (indiv.) of the larger species, with the mytild *Modiolus modiolus*, the colid *Colus gracilis*, the buccinid *Neptunea antiqua* and the pectinid *Chlamys islandica* as the most abundant species (Tables 2 and 3). Regarding frequency of occurrence (%F), *Colus gracilis* (13.7%F), *Buccinum undatum* (10.3%F), *Modiolus modiolus* (8.6%F) and *Chlamys islandica* (6.9%F) were the most frequently collected truly BGs. Minoritarian truly BGs included the arcticid *Arctica islandica*,

the buccinid *Liomesus ovum* and the myid *Mya truncata* which were represented by four or fewer individuals (Tables 2 and 3). The western approaches of the Strait of Gibraltar were the area where a larger amount of truly BGs was collected (65 indiv.), followed by Pipoca MV (12 indiv.), Hespérides DMV (11 indiv.) and Almazán MV (10 indiv.), whereas the larger amount of species was collected at Gazul MV and at the western approaches of the Strait of Gibraltar (4 spp. in each). *Arctica islandica* and *M. truncata* was collected at the shallower sites, both of them off S. Portugal (99 mwd) and Gazul MV (443—462 mwd), *A. islandica* also at Albolote DMV (337—380 mwd) and off Huelva (180 mwd), whereas the rest of the species were collected mostly below 500 mwd.

Radiocarbon ages determined on nine mollusc specimens range between 26.1 and 14.6 kyr B.P. (Table 4), spanning the Marine Isotope Stage (MIS) 2 which includes the Last Glacial Maximum (LGM) and Heinrich Stadials 1 and 2. Ages of *N. contraria* cluster in the LGM (21.4 and 26.1 kyr B.P.). The ages of *A. islandica* are very similar (16.8 and 17.0 kyr B.P.) within Heinrich Stadial 1. Finally, *N. antiqua* specimens show the widest age range, with the oldest age of 21.9 kyr B.P. (LGM) and the youngest age of 14.6 kyr B.P. corresponding to the very beginning of the Bølling interstadial (14.7—12.9 kyr B.P.).

5. Discussion

5.1. Locally extinct and extant boreal molluscs in the Gulf of Cadiz

The main outcome of this study on bathyal thanatocoenoses of

BALGIM off Huelva		TAL. D02 99	CIRCASUR			BALGIM W of Gibraltar							previous records
CP160 1350	CP108 1527		BT10-54 526	BT17-26 567	BT32-52 617	DR40 362	DR42 135	DR45 293	DR49 521	DW50 523	CP54 356	DW57 548	
													(6)
							1				2		(1, 5)
					2	17			7	3			(1, 2, 5)
						14			13	6			(2, 5)
													(1, 5)
8								1				2	(1, 5)
				1									(1, 4)
			1		2								(1, 5)
			44			3			17	6			(1, 2, 4)
						7							(1, 5)
	4				2								(1, 5)
		1											(1, 4)
					1				1				(2)
			11		2					29	2		(2)
					1								New
													New
			13		3		2						(2)
		1											(1)
													New
													New
													New
													(7)
													New
													New
										1	3		New
													(8)

sedimentary areas of the GoC is that a nearly full complement of the BGs reported from the last glacial deposits in the Mediterranean Sea are also present in the GoC. Eight molluscan species found in these thanatocoenoses and currently restricted to higher latitudes (Table 5; Fig. 5, upper row) are the gastropods *Buccinum undatum*, *Colus gracilis*, *Liomesus ovum* and *Neptunea antiqua*, and the bivalves *Arctica islandica*, *Chlamys islandica*, *Modiolus modiolus* and *Mya truncata*, representing 15.4% of the larger species in the studied thanatocoenoses. Of these, *C. gracilis*, *N. antiqua* and *L. ovum* are reported for the first time in the GoC and these species were never reported from Mediterranean fossil deposits. A notable absence is that of the bivalve *Panomya norvegica* (Spengler, 1793), which was found in the platform of the Alboran Island (Alboran Sea) (Gofas et al., 2014) and elsewhere in the Mediterranean Sea but did not appear in our material. These findings of BGs in the GoC document the continuity of the faunal shift which so far lacked definite records in this intermediate region, filling the gap with the wealth of information available for the Mediterranean basin (Mars, 1958; Froget et al., 1972; Martinell and Julià, 1973; Colantoni et al., 1975; Taviani, 1978; Domènech and Martinell, 1982; Curzi et al., 1984; Delibrias and Taviani, 1985). As previously reported inside the Mediterranean, BGs remain a minority within the assemblages studied in the GoC, in which the bulk of the species is constituted by those that still live in the area.

Arctica islandica and *Mya truncata* were collected as early as 1883 from off Southern Portugal in 99 mwd, but the significance of those findings was not known at the time of Locard (1897). Considering the depth, those shells are likely to belong to a beach deposit of the last glacial, and were certainly outside the MOW at any time. Those species are also found on Albolote DMV and Gazul MV in the shallowest areas of the Shallow Field of Fluid Expulsion (SFFE). Conversely, *N. antiqua*, *L. ovum*, *C. gracilis* and *B. undatum* were found on MVs and DMVs of the deep sectors of the SFFE and in the Deep Field of Fluid Expulsion (DFFE), which are situated in an area which has today a high influence of the MOW.

The remainder of the larger species are still living in the studied area (Table 5; Fig. 5, lower row) or at least in specific sectors of the GoC and account for 84.6% (633 indiv.). These include *Colus jeffreysianus*, *Buccinum humphreysianum*, *Galeodea rugosa*, *Ranella olearium* and *Pseudamussium peslutrae* which also enter the Mediterranean and are present in the Alboran Sea (Bouchet and Warén, 1985, 1993 and our own observations). Most of these species are currently common and frequent components of molluscan assemblages from bathyal sedimentary bottoms of the GoC and the Alboran Sea (Ciércoles et al., 2018; González-García et al., 2020). Whether shells belonging to this group are contemporaneous with the BGs or originated in a more recent or modern assemblage can be proved only by dating (the case of *Neptunea contraria*), since the shells are found on the sea bottom in a time-condensed deposit and not in distinct strata.

The significance of *P. peslutrae* (formerly better known as *Pseudamussium septemradiatum*) was discussed by Taviani et al. (1991). This species is often thriving in huge numbers in Pleistocene glacial assemblages of the Mediterranean, intimately associated with BGs assemblages, and valves from the Southern Adriatic Sea have been dated in the range of 19—15.3 kyr B.P. by Colantoni et al. (1975). As a consequence, it has always been considered a genuine BG by different authors (Malatesta and Zarlenga, 1986, and references
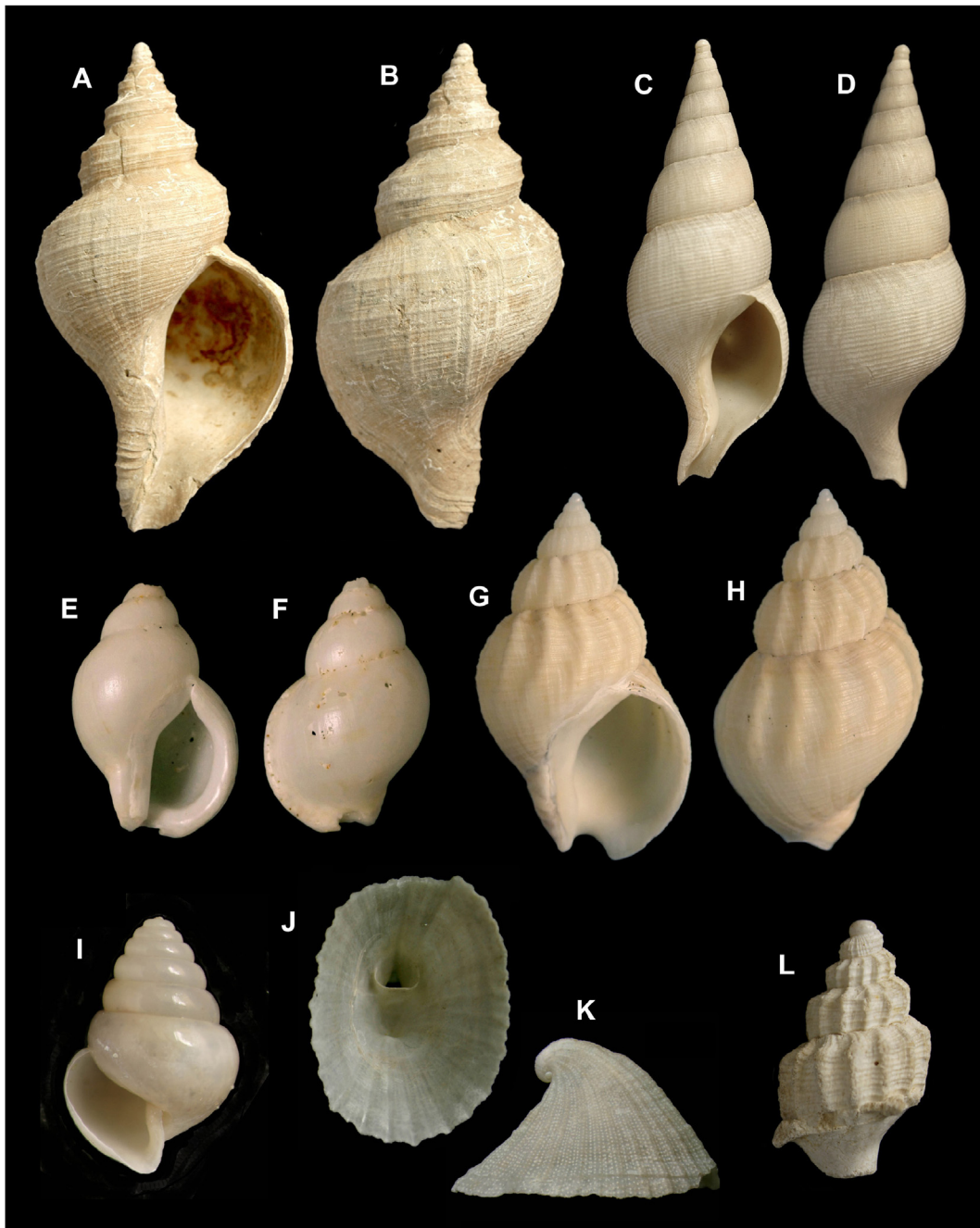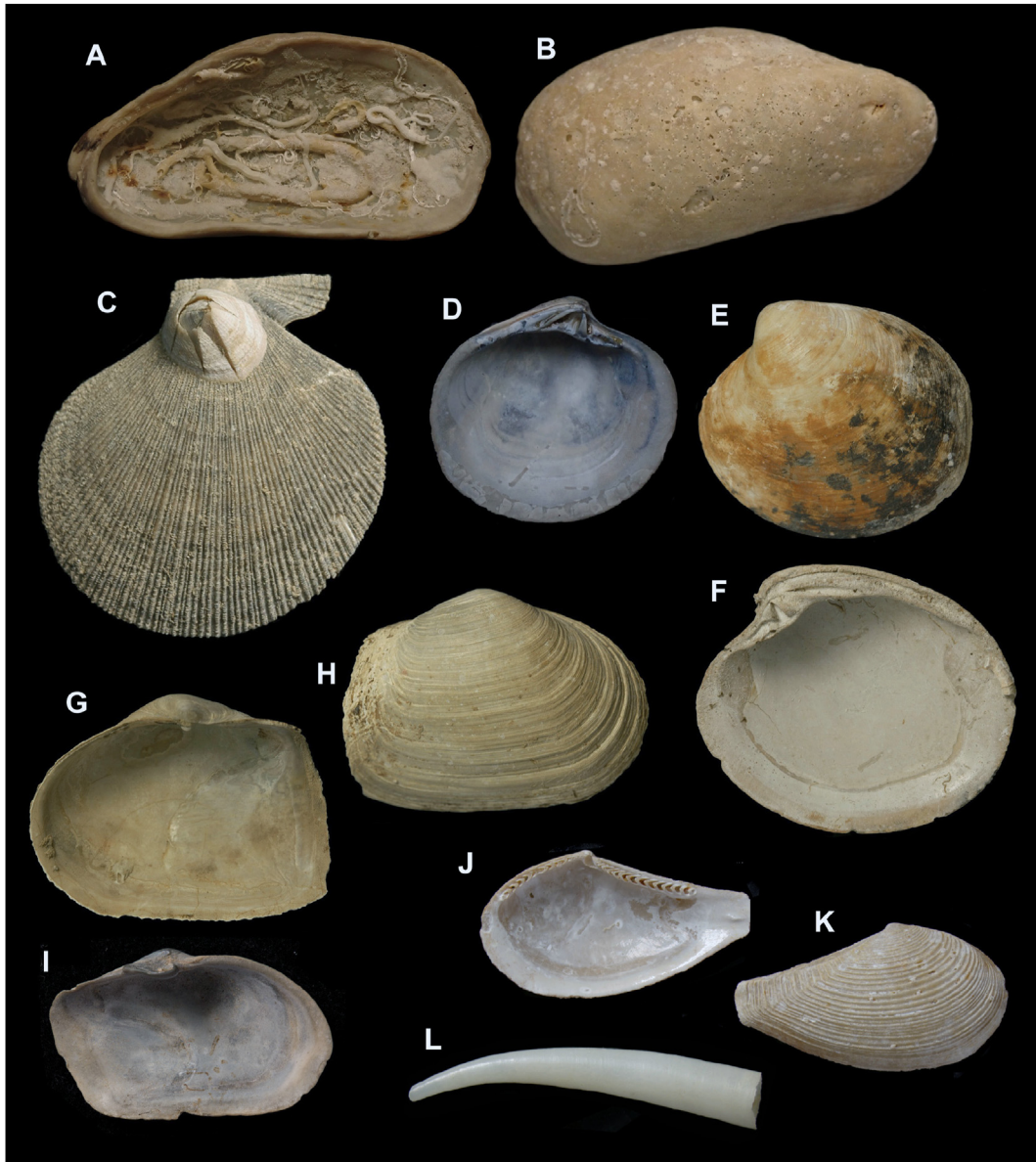
Fig. 2. Representative specimens of gastropods found in the thanatocoenosis dredged in the Gulf of Cadiz (species currently restricted to higher latitudes), with indication of the area and depth where the specimens were collected. A−B: *Neptunea antiqua*, Hespérides diapir/mud volcano complex (DMV), ANASTASYA 09/99 DA06/5, 721 mwd (101 mm). C−D: *Colus gracilis*, Pipoca mud volcano (MV), INDEMARES 0211 DA19, 656 mwd (67 mm). E−F: *Liomesus ovum*, western approaches of the Strait of Gibraltar, CIRCASUR 2020 BT32-52, 617 mwd (24 mm). G−H: *Buccinum undatum*, same locality and sample (42 mm). I: *Limacina retroversa*, Almazán MV, INDEMARES 0211 DA42, 903 mwd (2.5 mm). J−K: *Puncturella noachina*, same locality and sample (7.0 mm). L: *Propebela turricula*, Gusano channel, INDEMARES 0412 BC11, 558 mwd (incomplete shell).

therein). Nevertheless, it extends southwards to Mauritania and Senegal, and it is still found alive in the Alboran Sea (Cosel and Gofas, 2019). Compared to live-taken specimens of *P. peslutrae* from the Alboran Sea, the valves found in the thanatocoenoses were larger and more heavily sculptured, therefore most of the individuals with the "sculptured form" could also be interpreted as BGs.

Neptunea contraria is the most "southern" of the northern guests, its main populations occurring nowadays off NW Spain at 100−200 mwd, and not further north in Bay of Biscay. *Neptunea contraria* and *Troschelia berniciensis* currently do not enter the Mediterranean Sea, but live-taken specimens of both species have been collected in the southern part of the GoC, not influenced by the MOW but in contact with the AAIW. In this line, one live

Fig. 3. Representative specimens of bivalves and scaphopod found in the thanatocoenosis dredged in the Gulf of Cadiz (species currently restricted to higher latitudes), with indication of the area and depth where the specimens were collected. A−B: *Modiolus modiolus*, western approaches of the Strait of Gibraltar, CIRCASUR 2020 BT10-54, 526 mwd (69 mm). C: *Chlamys islandica*, Gazul mud volcano (MV), INDEMARES 0610 DA11, 462 mwd (61 mm). D: *Arctica islandica*, head of Portimão canyon, TALISMAN 1883 D02, 99 mwd (40 mm). E−F: *A. islandica*, Albolote diapir/MV complex (DMV), INDEMARES 0610 BT09, 380 mwd (79 and 85 mm; specimens used for age determination). G−H: *Mya truncata*, Gazul MV, INDEMARES 0211 DA26, 455 mwd (55 mm). I: *M. truncata*, head of Portimão canyon, TALISMAN 1883 D02, 99 mwd (25 mm). J−K: *Nuculana pernula*, Gazul MV, INDEMARES 0610 DA07, 495 mwd (9.7 mm). L: *Antalis entalis*, Geraldine DMV, INDEMARES 0211 DA31, 742 mwd (20.5 mm).

specimen of *N. contraria* was collected off Casablanca (Morocco) at 650 mwd in 1971 (Gofas, unpublished data), and another one was collected off Rabat by the BALGIM expedition haul CP86 (34.250°N, 07.350°W, 512 mwd), being these specimens deposited in the Muséum National d'Histoire Naturelle (MNHN) of Paris. On the contrary, no live-taken specimens of *N. contraria* were collected in the different INDEMARES/CHICA expeditions and in the ARSA expeditions for monitoring epibenthic and demersal commercial resources in Spanish waters of the GoC using an otter trawl (two expeditions during each year since the 1990s) (Rueda, unpublished data). Only empty shells occurred in the INDEMARES/CHICA material and the two shells of *N. contraria* submitted to age

determination were dated from the LGM.

Colus islandicus was reported as reaching the NW African coast off Morocco by Bouchet and Warén (1985). Its presence is confirmed by a live-taken specimen collected by the BALGIM expedition in haul CP156 (1135 mwd, specimen deposited in MNHN), a puzzling occurrence right in the pathway of the MOW. This may be explained by the depth of the site, where the MOW outflow may be situated far above the sea bottom (Gasser et al., 2017) and also by the situation in the western part of the GoC, at the longitude of Faro, where mixing with Atlantic intermediate water (Iorga and Lozier, 1999) will have reduced temperature and salinity of the MOW. *Turrisipho fenestratus* is ambiguous, because it
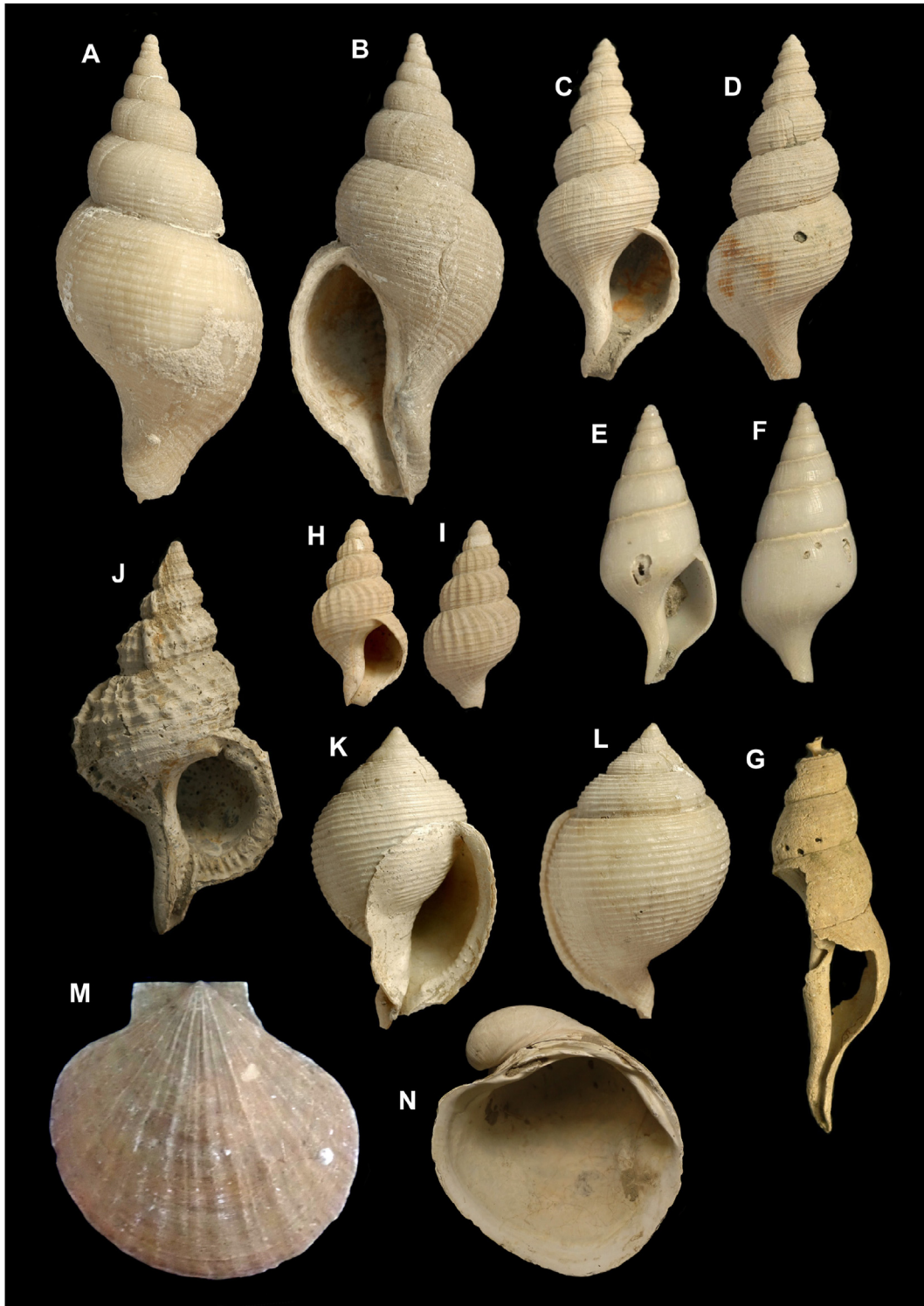
Fig. 4. Representative specimens of molluscs found in the thanatocoenosis dredged in the Gulf of Cadiz (species that are still living in the Gulf of Cadiz; more information in the discussion section), with indication of the area and depth where the specimens were collected. A−B: *Neptunea contraria*, Pipoca mud volcano (MV), INDEMARES 0211 DA17, 599 mwd (98 mm). C−D: *Troschelia berniciensis*, Hespérides diapir/MV complex (DMV), ANASTASYA 09/99 DA06/5, 721 mwd (81 mm). E−F: *Colus jeffreysianus*, Pipoca MV, INDEMARES 0211 DA19, 656 mwd (34 mm). G: *Colus islandicus*, Hespérides DMV, ANASTASYA 09/99 DA06/5, 721 mwd (92 mm). H−I: *Turrisipho fenestratus*, Pipoca MV, INDEMARES 0211 DA19, 656 mwd (20 mm). J: *Ranella olearium*, Albolote DMV, INDEMARES 0211 DA01, 339 mwd (123 mm). K−L: *Galeodea rugosa*, Pipoca MV, INDEMARES 0211 DA17, 599 mwd (77 mm). M: *Pseudamussium peslutrae* (sculptured form), western approaches of the Strait of Gibraltar, CIRCASUR 2020 BT10-54, 526 mwd (55 mm). N: *Glossus humanus*, western approaches of the Strait of Gibraltar, CIRCASUR 2020 BT17-26, 570 mwd (66 mm).

was also stated as extending to NW Morocco by Bouchet and Warén (1985), but their report is based on Locard (1897) who had only shells which could be suspected to be a BG.

The fine fractions of the GoC samples contain several undoubted BGs, including the gastropod *Puncturella noachina* and the scaphopod *Antalis entalis* (Malatesta and Zarlenga, 1986), and three
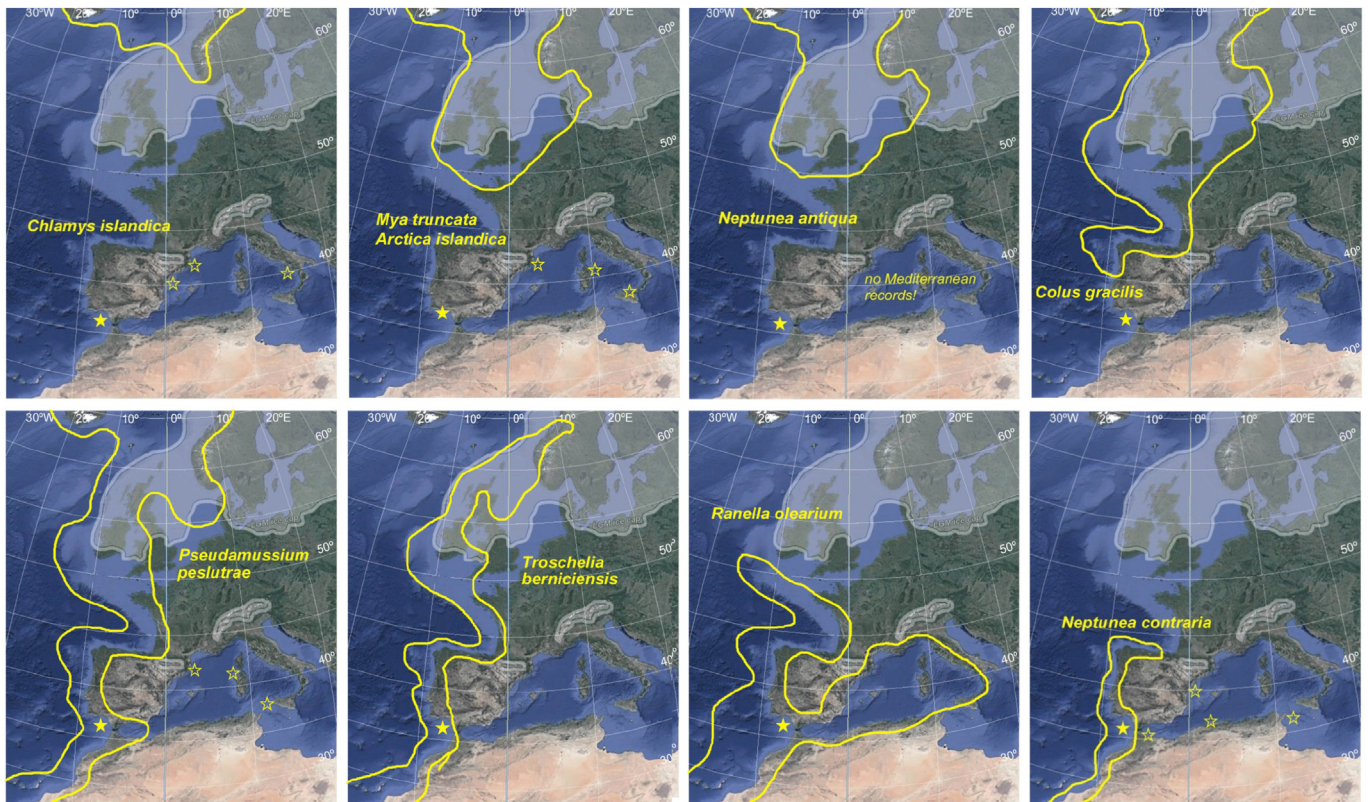
Fig. 5. Outline of current biogeographical distributions (solid yellow line) of some of the main species of molluscs found in the thanatocoenosis dredged in Gulf of Cadiz. The occurrence in the thanatocoenosis from our data is represented with a solid star, whereas literature data is represented with void stars. The northern shaded area outlines ice sheets of the Last Glacial Maximum after Mangerud et al. (2004).

Table 4
AMS ^{14}C dates determined on molluscan specimens found in the thanatocoenosis dredged on mud volcanoes (MVs) and diapir/MV complexes (DMVs) in the Spanish waters of the Gulf of Cadiz, with indication of the fluid venting submarine structure (FVSS) and depth interval where the specimen was collected. The AMS ^{14}C ages have been corrected for ^{13}C and a mean ΔR value for closest known localities in the northern Gulf of Cadiz, and have been converted into calendar years using the Marine20 calibration curve of the CALIB 8.2 calibration software. Sample J-082 of *Neptunea antiqua* was dated twice.

Sample ID	Mollusc species	FVSS	Depth (mwd)	^{14}C age (yr B.P.)	1σ error (yr B.P.)	ΔR	2σ range cal. age (cal. yr B.P.)	Calibrated ^{14}C age (cal. yr B.P.)
AI-01	*Arctica islandica*	Albolote DMV	339−388	14640	±46	100 ± 100	16405−17096	16770
AI-02	*Arctica islandica*	Albolote DMV	339−388	14812	±45	100 ± 100	16638−17323	16980
J-061	*Neptunea contraria*	Pipoca MV	599−684	18524	±56	100 ± 100	20962−21782	21370
J-062	*Neptunea contraria*	Pipoca MV	599−684	22907	±70	100 ± 100	25830−26447	26140
J-063	*Neptunea antiqua*	Pipoca MV	599−684	18914	±52	100 ± 100	21478−22202	21880
J-071	*Neptunea antiqua*	Hespérides DMV	714−1047	13461	±38	100 ± 100	14917−15598	15250
J-081	*Neptunea antiqua*	Pipoca MV	599−684	14928	±40	100 ± 100	16777−17457	17120
J-082	*Neptunea antiqua*	Pipoca MV	599−684	13030	±37	100 ± 100	14160−15000	14600
J-082	*Neptunea antiqua*	Pipoca MV	599−684	13020	±36	100 ± 100	14147−14985	14590
J-084	*Neptunea antiqua*	Pipoca MV	599−684	14460	±50	100 ± 100	16198−16913	16550

more species which have never been reported as BGs in the Mediterranean are here documented for the first time in the GoC waters, the bivalve *Nuculana pernula* and the gastropods *Propebela turricula* and *Curtitoma trevelliana*. Abundant shells of the pteropod *Limacina retroversa*, common in North Atlantic water bodies, were found well preserved in the sediment inside a shell of *Colus gracilis*, and more specimens were detected in scattered samples. The modern distributional limit of this species is unclear from the literature. It was depicted to reach the western Iberian margin to the south (van der Spoel and Heyman, 1983, map reproduced in Biekart, 1989) but this map may be skewed southwards with

occurrences based on shells deposited during cold episodes. In the North East Atlantic, high quantities of *Limacina retroversa* are characteristic of the subarctic waters north of 53°N (Pafort-Van Iersel, 1986), although Morton (1954) reported this species to live as far South as the English Channel (49.5°N). In the North West Atlantic, Chen and Bé (1964) report it as dominant in subarctic waters of the Labrador Sea, and still abundant in the transitional zone where Gulf Stream mixes with Subarctic waters around 45°N. This pteropod species has been found with high dominance values in sediments from the last glaciation in the Western Mediterranean (Froget, 1967) and the Tyrrhenian Sea (Biekart, 1989) where it is no

Table 5
Current distribution (1: documented presence as living; * rebutted reports, not based on live-taken specimens and presumably based on Boreal Guest shells) of some of the main species of molluscs found in the thanatocoenosis dredged in the Gulf of Cadiz. ARC, Arctic; GRE, Greenland; ICE, Iceland; Eastern Atlantic: FAR, Faroes; NOR, Norway; BRI, British Isles; GAL, Galicia and Northern Spain; POR, Portugal; MED, Mediterranean (at least Alboran Sea); Western Atlantic: NSC, Nova Scotia to Cape Cod; VIR, Cape Cod to Cape Hatteras; CRL, Carolinas and Georgia. Upper thirteen rows are Boreal Guests, lower rows are species still living in the area. For the detail of sources, see the World Register of Marine Species (WoRMS Editorial Board, 2023), "Documented distributions" tab.

Species	ARC	GRE	ICE	FAR	NOR	BRI	GAL	POR	MED	NSC	VIR	CRL
Buccinum undatum Linnaeus, 1758	1	1	1	1	1	1	*	*		1	1	
Colus gracilis (da Costa, 1778)		1		1	1	1	1	1				
Liomesus ovum (Turton, 1825)			1		1	1						
Neptunea antiqua (Linnaeus, 1758)				1	1	1	*	*				
Arctica islandica (Linnaeus, 1767)			1	1	1	1		*		1	1	*
Chlamys islandica (O.F. Müller, 1776)	1	1	1	1	1	1				1		
Modiolus modiolus (Linnaeus, 1758)			1	1	1	1				1	*	
Mya truncata Linnaeus, 1758	1	1	1	1	1	1				1	1	
Antalis entalis (Linnaeus, 1758)		1	1	1	1	1			*	1		
Curtitoma trevelliana (W. Turton, 1834)			1	1	1	1				1		
Nuculana pernula (O.F. Müller, 1779)	1	1	1	1	1	*				1		
Propebela turricula (Montagu, 1803)	1	1		1	1	1				1		
Limacina retroversa (J. Fleming, 1823)				1	1	1				1		
Puncturella noachina (Linnaeus, 1771)	1	1	1	1	1	1	*	*	*	1	1	
	ARC	GRE	ICE	FAR	NOR	BRI	GAL	POR	MED	NSC	VIR	CRL
Acesta excavata (Fabricius, 1779)			1	1	1	1	1	1	1			
Ampulla priamus (Gmelin, 1791)								1				
Buccinum humphreysianum Bennett, 1824					1	1	1	1	1			
Buccinum oblitum Sykes, 1911					1	1		1				
Colus islandicus (Mohr, 1786)	1	1	1	1	1	1	1	1		1		
Colus jeffreysianus (P. Fischer, 1868)						1	1	1	1			
Galeodea rugosa (Linnaeus, 1771)						1	1	1	1			
Glossus humanus (Linnaeus, 1758)						1	1	1	1			
Lutraria lutraria (Linnaeus, 1758)						1	1	1	1			
Neptunea contraria (Linnaeus, 1771)							1	1				
Pseudamussium peslutrae (Linnaeus, 1771)			1	1	1	1				1		
Ranella olearium (Linnaeus, 1758)						1	1	1	1			
Troschelia berniciensis (W. King, 1846)				1	1	1	1	1				
Turrisipho fenestratus (W. Turton, 1834)		1	1	1	1	1	1					

longer living. In core MD99-2341 situated at 582 mwd in the main channel of MOW outflow, Ducassou et al. (2018) found *L. retroversa* only during Henrich Stadials 1 and 2 and to a lesser extent during Younger Dryas, coupled with or slightly posterior to the peaks of the polar planktonic foraminifer *Neogloboquadrina pachyderma*.

The current distribution of the monoplacophoran *Veleropilina reticulata* is not known, but this species was originally described from cold-water deposits of the Mediterranean and is treated as a BG (Warén and Gofas, 1996).

Only the larger species (>5 cm) were commonly collected whereas smaller BG species (e.g. *Nuculana pernula*) were extremely scarce. This is not a collecting artefact, since all the dredge hauls in which definite larger BGs were registered were scrutinized, searching for more species in the smaller fractions. Instead, we hypothesize that this is a post-depositional artefact due to the context of strong currents which shaped the contouritic complex, where smaller fractions were winnowed away during the erosional process whereas larger shells would remain *in situ*. This is consistent with the view of Sierro et al. (1999) that the sand layer episodes are "condensed layers originating during times of rapid warming and relative sea-level rise within the last deglaciation".

5.2. The dynamics of faunal shifts

Driving factors for changes in the geographical distributions of species involve (1) the ability of individuals to reach new areas and (2) the possibility for those individuals to originate perennial populations. The ability of marine benthic invertebrates in general (and molluscs in particular) for dispersal is in part determined by their larval stage (Thorson, 1950; Hansen, 1980; Jablonski and Lutz, 1983). Some species (e.g. the bivalves *Arctica islandica*, *Chlamys islandica*, *Pseudamussium peslutrae*, *Modiolus modiolus*, *Mya truncata*) have larvae which feed in the plankton (planktotrophic) and remain pelagic for usually several weeks, being then transported by surficial currents. Others (e.g. all buccinoid gastropods *Buccinum undatum*, *Colus gracilis*, *C. islandicus*, *C. jeffreysianus*, *Liomesus ovum*, *Troschelia berniciensis*, *Neptunea antiqua*, *N. contraria*) develop inside egg-capsules deposited on the sea-bottom and supposedly undergo very little dispersal (except if the egg-capsules are rafted by bottom currents). Protobranch bivalves such as *Nuculana pernula* and Vetigastropoda such as *Puncturella noachina* present an intermediate condition, in which larvae are released in the plankton but do not feed and have to settle after a few days. Pteropods such as *Limacina retroversa* are holoplanktonic and therefore constrained by water masses and their circulation.

The second and crucial stage of establishing reproducing populations requires that the environmental setting in the newly reached area provides suitable conditions for the species to live there and reproduce. Temperature is usually critical (Belanger et al., 2012) but other factors such as salinity, food resources and substrate type may also play a role. Table 6 displays some environmental data within the current distributional area of some of the BGs reported in this work. Admittedly, some of those values recorded in shallow bays do not represent the highest possible temperature and salinity, whereas the values stated for the Faroes (Sneli et al., 2005: their Table 4) are best representative of the open ocean. In any case, it is clear that similar conditions are not met with at present in any part of the GoC or the Mediterranean sea.

Surprisingly, most of the reported BGs (with or without planktotrophic larvae) currently have an amphiatlantic range, whereas all but one of the species still living in the GoC do not (Table 5). However, we believe that this is not the effect of a better dispersal capacity, but rather a consequence of the shorter distances to be bridged between Scandinavia, the Faroes, Iceland, Greenland and North America, compared to the broad oceanic barrier which is present further south.

5.3. Dated shells, geographical distribution and palaeoceanographic implications

Radiocarbon ages determined on *C. islandica* and *M. modiolus* in the western approach of the Strait of Gibraltar by Taviani et al. (1991) span the period 27−12.5 kyr B.P., which brackets our range of 26.5 and 14.5 kyr B.P. on *Neptunea* spp. and *A. islandica* (Fig. 6). Nevertheless, their age determinations on *Buccinum undatum* in the same area was only 7.5 kyr B.P., and those made on species still living in the area (*P. peslutrae*, *Buccinum oblitum* and *B. humpreysianum*) resulted in even younger ages. Age determinations within the Mediterranean (Gulf of Lion) by Froget et al. (1972) on *A. islandica*, *M. modiolus* and *B. undatum* are also younger than LGM (from 13.1 to 9.8 kyr B.P., broadly bracketing the Younger Dryas). This provides clear evidence that the local extinction of BGs may not have occurred simultaneously, but rather progressively with some species lagging behind.

Most of the locations where BGs were found during the present study are currently situated at 600−1000 mwd on the pathway of the MOW. Exceptions include the shallow Albolote DMV and Gazul MV, which occasionally receive MOW upwellings (Sánchez-Leal pers. comm.), and the deep Hespérides DMV and Almazán MV, where occasional events of very low energy may occur (Sánchez-Leal pers. comm.). Today, the seafloor affected by the MOW is known to host an impoverished fauna (Salas, 1996, based on bivalves), compared to the upper slope at similar depths on the Moroccan margin, where the bottom is in contact with the much less saline North Atlantic Central Water (NACW) formed along the

Azores Front (Ríos et al., 1992) and penetrating the GoC in the 250−700 mwd range. Even attenuated by subsequent mixing with Atlantic intermediate waters, the present-day salinity (38.45) and temperature (12.9 °C) of the MOW are not suitable for the truly boreal species that were living along its current pathway during the last glaciation. Therefore, the presence of these species must be explained by a drastically different palaeoceanographic setting in the GoC.

An abrupt change in environmental conditions on the GoC seabed under the direct influence of the MOW might be behind the absence of truly BGs in the last ca. 13 kyr (at least in the areas studied so far). Living populations of boreal molluscs located in the NE Atlantic are mainly found with seawater temperatures below 10 °C and salinity values lower than 36 (Table 6 above, and references therein), contrasting sharply with the current conditions prevailing in the MOW, with warmer (12.9 °C) and saltier (38.45) waters cascading into the GoC (Sánchez-Leal et al., 2017).

During the last glaciation, the prevailing conditions in the GoC and the MOW were controlled by the conditions within the Mediterranean Sea. In this regard, Sierro et al. (2020) have stated that there have been long periods of high impact of bottom currents in the GoC over the last 20 kyr, including part of Heinrich Stadial 1 (ca. 16−14.5 kyr B.P.), during which most of the age values presented here are situated. The presence of BGs in the current pathway of the MOW would have been possible either if the MOW were suppressed (a hypothesis not supported by current literature) or displaced towards deeper parts of the GoC, or if the outflowing Mediterranean waters had sufficiently low temperature and salinity to accommodate the requirements of those boreal species. Even if the estimated palaeotemperatures in the Western Mediterranean (Cacho et al., 2000, and others) at the time of maximum cooling events are compatible with the persistence of the abovementioned species, the salinity of the outflow may have been even higher than today (Voelker et al., 2006) due to more saline inflowing Atlantic water and to more arid and windy conditions around the Mediterranean Sea margins. Therefore, the most likely factor that would have favoured the thriving BGs in the investigated

Table 6
Examples of the environmental settings and types of larval development where living populations of the Gulf of Cadiz Boreal Guests have been studied. SST, sea surface temperature; EBT, estimated sea-bottom temperature. Additional references for larval development (NF: non-feeding): [1] Thorson (1950); [2] Lutz et al. (1982); [3] Gruffydd (1976); [4] De Schweinitz and Lutz (1976).

| Species	Locality	Temperature	Salinity	References	Larval development
Buccinum undatum	S England	4−22 °C (reproducing 4−10 °C)	<34.9−>35.1	Smith et al. (2013)	Intracapsular [1]
	E Irish Sea	7−16 °C		Emmerson et al. (2020)	
	Faroes	0.9−9.1 °C (EBT)	<34.9−>35.1	Sneli et al. (2005)	
Colus islandicus	Faroes	0.9−8.5 °C (EBT)	<34.9−>35.1	Sneli et al. (2005)	
	Faroes	0−8 °C		Jordan (1890)	
	W Ireland	3.2−9.8 °C (EBT)		Jordan (1890)	
	Bristol Channel	10.5−11 °C (EBT)		Jordan (1890)	
Colus gracilis	Faroes	0.9−8.8 °C (EBT)	<34.9−>35.1	Sneli et al. (2005)	Intracapsular [1]
Neptunea antiqua	W Irish Sea	7.6−15 °C (SST)		Power and Keegan (2001)	Intracapsular [1]
		7.6 °C (EBT)	>35.1	Sneli et al. (2005)	
Arctica islandica	North Sea	5−8 °C		Witbaard and Bergman (2003)	Planktotroph [2]
	White Sea		<20	Filippova (2013)	
	Faroes	6.7−8.3 °C (EBT)	<34.9−>35.1	Sneli et al. (2005)	
Chlamys islandica	W Norway	3.5−5.5 °C		Greve and Samuelsen (1970)	Planktotroph [3]
Modiolus modiolus	W Norway	4.5−13.8 °C	ca. 30	Brown (1984)	Planktotroph [4]
	W Sweden	3.5−16 °C	<20	Brown (1984)	
	N Norway	2−8 °C	32−33	Brown (1984)	
	N Ireland	7−15.5 °C	32−34	Brown (1984)	
	Faroes	3.0−9.1 °C (EBT)	<34.9−>35.1	Sneli et al. (2005)	
Mya truncata	S North Sea	5−10 °C		Amaro et al. (2005) (T from De Wilde et al., 1984)	Planktotroph [1]
	Faroes	8.2 °C	>35.1	Sneli et al. (2005)	
Nuculana pernula	White Sea	6 °C max	<30	Berger and Naumov (2001)	NF planktonic
	Faroes	7.6 °C	>35.1	Sneli et al. (2005)	
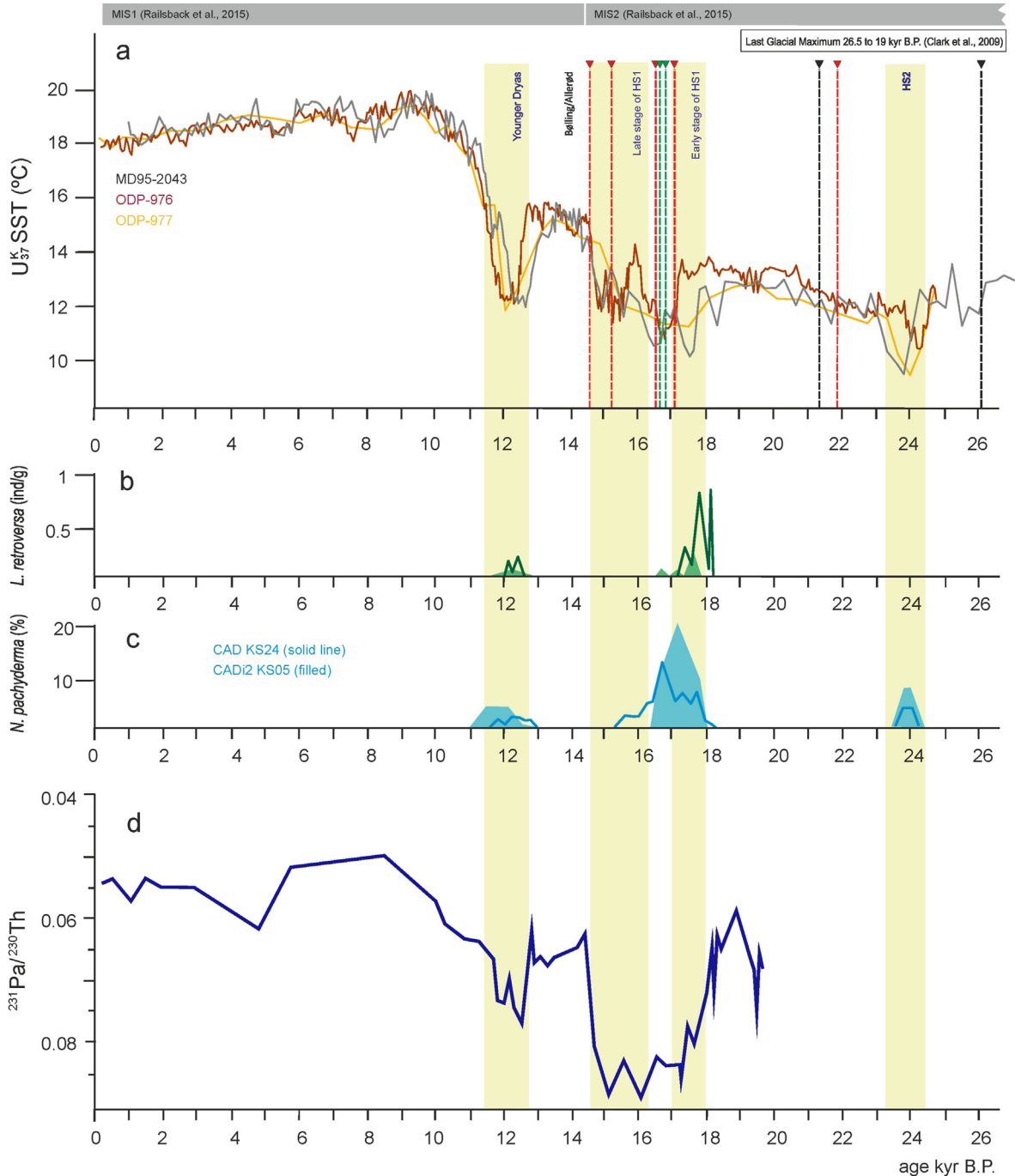
Fig. 6. Chronologic framework for AMS ^{14}C dates determined on molluscan specimens found in the thanatocoenosis dredged in the Spanish waters of the Gulf of Cadiz. Vertical dashed bars topped with triangles (red: *Neptunea antiqua*; black: *N. contraria*; green: *Arctica islandica*) indicate AMS ^{14}C ages (calendar years B.P.) presented in this study. From top to bottom: (a) SST reconstructed from alkenone unsaturated ratios in marine cores ODP-976, ODP-977 and MD95-2043 (Alboran Sea) (redrawn from Cacho et al., 1999; Martrat et al., 2014); (b) Peaks of abundance of the subpolar pteropod *Limacina retroversa* in cores CADKS24 and CADI2KS05 and (c) peaks of the polar foraminifer *Neogloboquadrina pachyderma* in the same cores (redrawn from Ducassou et al., 2018); (d) Pa/Th 232-based as Atlantic meridional overturning circulation (AMOC) intensity proxy (redrawn from McManus et al., 2004). Shaded vertical bars represent Younger Dryas (YD), Heinrich Stadial 1 (HS1) and Heinrich Stadial 2 (HS2) events.

area is the shift to greater depth of the main Mediterranean outflow (enhanced by the drop of ca. 100 mwd in sea level), which would have allowed more appropriate Atlantic intermediate waters to be in contact with the upper slope. The alternative hypothesis of a suppressed or superficial MOW is not supported by the wealth of studies now available on the GoC contourite depositional systems (Hernández-Molina et al., 2003; Llave et al., 2006).

Our findings raise the question of why certain species present in the GoC during the last glaciation (*Neptunea antiqua, Colus islandicus, C. gracilis, Liomesus ovum, Troschelia berniciensis, Turrisipho fenestratus, Nuculana pernula, Propebela turricula, Antalis entalis*) never colonized the Mediterranean, while others were widely distributed throughout the basin. Predictably, the holoplanktonic *Limacina* and the bivalves with planktotrophic larvae all penetrated

the Mediterranean at some time, but the buccinids *Buccinum undatum* and *Neptunea contraria* also did so despite lacking planktonic larvae. Reasons for other species not succeeding in doing so could be that those live in deeper water and the temperature and salinity in the Mediterranean would be low enough only in the relatively shallow subtidal environments which harbour the commonly recorded BGs (*Arctica islandica, Buccinum undatum, Chlamys islandica, Neptunea contraria, Mya truncata*). In fact, most of the BGs reported in the Mediterranean are constrained to the upper 200 mwd corresponding to the nearshore habitats and shallow continental shelf during the deposition period. An alternative explanation for the absence of the deeper water species as BGs in the Mediterranean is that the shallow Camarinal sill (currently 284 mwd, ca. 100 m shallower during LGM) acted as a barrier against the species with a bathymetric range restricted to the slope.

6. Conclusions

The palaeontological and chronological data presented here provide evidence of the continuity of the faunal shift of BGs, well documented inside the Mediterranean Sea, and here reported along the south-western Iberian Peninsula. Our data, which report thriving molluscs in the current pathway of the MOW suggest that either the MOW was strongly reduced along the slope during the last glacial, or more likely shifted to a deeper level, allowing the upper slope to remain in contact with suitable Atlantic intermediate waters. Boreal Guests of marked palaeoclimatic significance, such as *Colus gracilis*, *Neptunea antiqua* and *Liomesus ovum*, are reported for the first time in the GoC and have never been reported in Mediterranean fossil deposits. The BG species collected were mostly large (>5 cm) whereas smaller boreal species were extremely scarce, probably winnowed away by strong bottom currents. Definitely, the faunal remains from the last glaciation rule out the existence of a strong, warm, hypersaline MOW along the upper slope like it is as present. Species still living in the Gulf of Cadiz and the Alboran Sea nevertheless account for 84.6% of specimens among the larger species.

Credit author statement

Javier Urra, Olga Utrilla & Serge Gofas: Conceptualization, Methodology, Writing - Original draft; Visualization, Investigation, Reviewing and Editing; & Conceptualization, Methodology, Investigation, Reviewing and Editing; Victor A. Valencia: Methodology, Resources; José L. Rueda, Carlos Farias, Emilio González-García, Nieves López-González & Luis M. Fernández-Salas: Reviewing and Editing.

Free format author statement

This subject is part of the doctoral dissertation of Olga Utrilla, supervised by Javier Urra and Serge Gofas. All three, together with José Luis Rueda, collaborated in the processing of the samples obtained in four deep-sea cruises, and in the conceptualization and writing of the first draft. In addition, Javier Urra selected and prepared samples for dating, obtained the funding for these and arranged for the analyses be done by Victor A. Valencia. Nieves López-González and Luis M. Fernández-Salas were expedition leaders in the INDEMARES deep-sea cruises and Javier Urra, Serge Gofas, Carlos Farias, Emilio González-García and José Luis Rueda participated in sample collection in one or another of the expeditions. These coauthors from IEO also contributed the discussions relating the fauna to oceanographic and geological factors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are included in the tables of the article

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