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Distribution and biogeographic trends of decapod assemblages from Galicia Bank (NE Atlantic) at depths between 700 and 1800 m, with connexions to regional water masses

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ABSTRACT

The Galicia Bank (NE Atlantic, 42°67'N–11°74'W) is an isolated seamount, near NW Spain, a complex geomorphological and sedimentary structure that receives influences from contrasting water masses of both northern and southern origins. Within the project INDEMARES, three cruises were performed on the bank in 2009 (Ecomarg0709), 2010 (BanGal0810) and 2011 (BanGal0811) all in July–August. Decapods and other macrobenthic crustaceans (eucarids and peracarids) were collected with different sampling systems, mainly beam trawls (BT, 10 mm of mesh size at codend) and a GOC73 otter trawl (20 mm mesh size). Sixty-seven species of decapod crustaceans, 6 euphausiids, 19 peracarids and 1 ostracod were collected at depths between 744 and 1808 m. We found two new species, one a member of the Chirostylidae, *Uroptychus cartesi* Baba & Macpherson, 2012, the other of the Petalophthalmidae (Mysida) *Petalophthalmus* sp. A, in addition to a number of new biogeographic species records for European or Iberian waters. An analysis of assemblages showed a generalized species renewal with depth, with different assemblages between 744 and ca. 1400 m (the seamount top assemblage, STA) and between ca. 1500 and 1800 m (the deep-slope assemblage over seamount flanks, DSA). These were respectively associated with Mediterranean outflow waters (MOW) and with Labrador Sea Water (LSW). Another significant factor separating different assemblages over the Galician Bank was the co-occurrence of corals (both colonies of hard corals such as *Lophelia pertusa* and *Madrepora oculata* and/or gorgonians) in hauls. Munidopsids (*Munidopsis* spp.), chirostylids (*Uroptychus* spp.), and the homolodromiid *Dicranodromia mahieuxii* formed a part of this coral-associated assemblage. Dominant species at the STA were the pandalid *Plesionika martia* (a shrimp of subtropical-southern distribution) and the crabs *Bathynectes maravigna* and *Polybius henslowii*, whereas dominant species in the DSA were of northern origin, the lithodid *Neolithodes grimaldii* and the crangonid *Glyphocrangon longiristris*, likely associated with LSW. The diversity (*H* and *J*) of small crustaceans (collected with BT) seemed to be controlled by the phytoplankton blooms (satellite Chl *a* data) over bank surface 3 months before the samplings, both at the top (Spearman $r=0.57$, $p=0.03$) and on the flanks ($r=0.74$, $p=0.02$) of Galicia Bank, while no significant relationships with Chl *a* were found for the larger decapods collected with GOC73, on average they feed at the higher trophic levels than those collected with BT.

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1. Introduction

The idea of the deep sea as a stable and even monotonous system is progressively changing due to increased attention on (i) studies on deep communities (e.g. over submarine mounts)

showing the patchy distribution of assemblages (Gage and Tyler, 1991; Stuart et al., 2003; Baco, 2007); (ii) the use of visual techniques (e.g. ROVs, multi-beam sonars) showing new structures in the marine relief (seamounts, knolls, banks); (iii) long term studies revealing changes of water mass conditions (e.g. changes in S and T in the deep Mediterranean: Skliris et al., 2007; Cartes et al., 2011a,b) related to the drop in abundance of dominant species; and (iv) a number of human-induced factors (e.g. trawling) that have changed communities (Fossà et al., 2002) and have

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reduced fish populations (Hopper, 1995; Koslow, 1997). The deep-sea is now viewed as a complex patchwork of distinctive habitats (Stuart et al., 2003), comprising seamounts, deep coral reefs and submarine canyons, among others. Even habitats seeming to be monotonous a priori, particularly muddy bottoms are submitted at different (meso and small) scales to varying environmental factors (bottom currents, sediment type, etc.) and gradients (depth) that provoke changes in benthos composition and dispersal capability as cited for macro and megafauna (Jumars and Ekman, 1983; Gage and Tyler, 1991; Cartes et al., 2009a).

Seamounts (and similar submarine habitats such as banks) are described from all over the world oceans (Rogers, 1994; Butler et al., 2001; Gubbay, 2003; Baco, 2007), including small, semi-enclosed, peripheral seas such as the deep Mediterranean (Mitchell and Lofi, 2008). These systems are sometimes characterized by high biodiversity, significant levels of endemisms and relatively high production, which can support productive fisheries (Rogers, 1994; Koslow et al., 2000). However, valuable aspects of such systems, like endemicity of fauna, depend of a series of factors ultimately conditioning the dispersal capability of species (Samadi et al., 2006). The responses of the fauna depend on taxon (e.g. ophiuroids: O'Hara, 2007; Galatheididae and Chirostylidae: Samadi et al., 2006), on the specific mode of biological development of each taxon (e.g. peracarids vs. eucarids, as discussed by Cartes et al., 2007a) and on local surface production. Rarely, the variety, nature and origin of water masses surrounding seamounts have been considered as a variable explaining seamount diversity, although it was related with fish assemblages dwelling insular areas (around the Azores: Menezes et al., 2006). The influences of surface production and hydrography on fauna depend crucially on the depths at the top of mounts, ranging widely between only 275 m for the Great Meteor Seamount (Fock et al., 2002) to 1700 m in Tasmanian waters (Butler et al., 2001). Often associated with submarine relief, deep-coral reefs also attract particular interest because they support high biodiversity (Butler et al., 2001; Gubbay, 2003). Reefs generate habitat for a variety of species and can serve as refuges for adults and recruits of the target-species of fisheries in surrounding areas. Colonies of deep-corals (*Lophelia pertusa*, *Madrepora oculata*) and gorgonians emerge as reefs in different areas of the North Atlantic Ocean (Wilson, 1979; Frederiksen et al., 1992; Sherwood et al., 2005; Sánchez et al., 2008) at ca. 300–800 m, including on Galicia Bank (León et al., 2010).

In allocthonous system such as, in general, deep sea seamounts, dynamics, ecology and structure of faunal assemblages ultimately depend on surface primary production. Seamounts also generate their own hydrographic surroundings (Taylor columns: Roden, 1986), capable of enhancing local productivity by accumulation of zooplankton (White et al., 2007). Despite this enhanced productivity, populations of these ecosystems have suffered over-exploitation after only short periods of fishery activity (Koslow et al., 2000). So, neither the structure of seamount communities (e.g. faunal distribution and zonation) nor their functioning (dynamics, factors enhancing diversity) is well enough known in order to manage them correctly or to protect them. Megafauna composition differs on the summits of seamounts in comparison to surrounding areas (Probert et al., 1997). This is the case for fish (i.e. at Great Meteor Seamount: Fock et al., 2002) and decapod crustacean (Cartes et al., 2007a) assemblages with characteristic deep sea-families (hakes and macrourids) lacking. The factors controlling diversity and composition are almost unknown.

The bank of Galicia is a large isolated seamount, with a diverse soft-bottom community of megafauna, composed of fish and decapod crustaceans (Piñeiro et al., 2001). As shown by the analysis of decapod assemblages over Le Danois bank (Cartes et al., 2007a,b), though the group is rather low in biomass, they are highly diversified

and widely distributed in slope ecosystems. They have, together with other crustaceans such as mysids a significant role in trophic webs, as prey of fish (Carrasón and Cartes, 2002; Preciado et al., 2009; Fanelli and Cartes, 2010). The Cantabrian Sea and, in general, the Bay of Biscay is an interesting area in a biogeographical perspective, because some species of subtropical shrimps (e.g. *Plesionika martia*, *Aristeus antennatus*, *Aristaeomorpha foliacea*) reach their northernmost latitudes (Lagardère, 1977), increasing species richness in areas where they coincide with temperate species (e.g. *Pasiphaea tarda*, *Ephyrina figueirai*). Decapods also have a significant trophic role, feeding across a wide range of trophic levels (from phytodetritus to benthos or zooplankton: Cartes et al., 2007b; Fanelli et al., 2011a,b). Thus, the study of distributional patterns of decapods can give us important information on ecological factors conditioning the diversity over seamounts. The Galicia Bank constitutes an optimal scenario for the study of biodiversity in open waters and causes controlling it. Apart from its complex geomorphological and sedimentary structure (Ercilla et al., 2011) the region of the Galicia continental margin is influenced by contrasting water masses from northern and southern origins at different levels: below the surface waters and down 500–600 m there is the East North Atlantic Central Water (ENACW), formed by winter mixing and subduction in a region northeast of Azores to the western European margin (Pollard and Pu, 1985; Pollard et al., 1996). This upper layer circulation to the west of the British Isles and in the Bay of Biscay was measured by Pingree (1993). Below it lies the Mediterranean Water (MW or MOW depending on authors), that is formed in the Gulf of Cádiz and progresses northwards as a high salinity vein along western Iberia with its core at 1000–1200 m (Pingree, 1973; Pingree and Morrison, 1973; Danialt et al., 1994; Iorga and Lozier, 1999). Below it appears the Labrador Sea Water (LSW), spreading from the northwest with its core locally placed at about 1800–1900 m (Pingree, 1973; Van Aken, 2000; Johnson et al., 2005).

The aim of this study is to give some initial evidence about the structural and functional community characteristics of the Galicia Bank through study of its macro and megabenthic crustaceans, one of the most diversified faunal groups inhabiting this special environment. Based on a multidisciplinary sampling study covering most of the depth range (710–1805 m) occupied by this bank, our specific objectives are (1) to identify assemblages and to establish zonation patterns for decapod crustaceans dwelling on Galicia Bank and (2) to identify environmental factors conditioning changes in assemblage composition. The roles of trophic (e.g. food availability), hydrological, and biogeographical factors in structuring the distributions of Galicia Bank decapods are also discussed.

2. Materials and methods

2.1. Study area and sampling

The Bank of Galicia is a large seamount located at 42°67' N–11°74' W, ca. 200 km to the W of the Galician coast (NW of Iberian Peninsula). The bank encompasses about 6250 km², with a channel of 2500 m depth separating it from the mainland shelf and with minimum (in the Eastern zone of the bank) of ca. 600 m. Within the LIFE+INDEMARES project (EC contract INDEMARES-LIFE, 07/NAT/E/000732) three cruises were performed around the Galicia Bank (NW Iberian peninsula, NE Atlantic) in 2009, 2010 and 2011 (Ecomarg0709: 22–23/07/2009; BanGal0810: 8–24/08/2010; BanGal0811: 26/07–9/08/2011). Decapods and other macrobenthic crustaceans (eucarids and some peracarids) were collected with different sampling systems (Fig. 1), basically beam trawls (BT) and otter trawls. In addition, some information was obtained in two hauls performed with a 1 m² WP2 plankton net with 0.5 mm mesh and in two hauls with a rock dredge of 80 cm × 30 cm mouth size

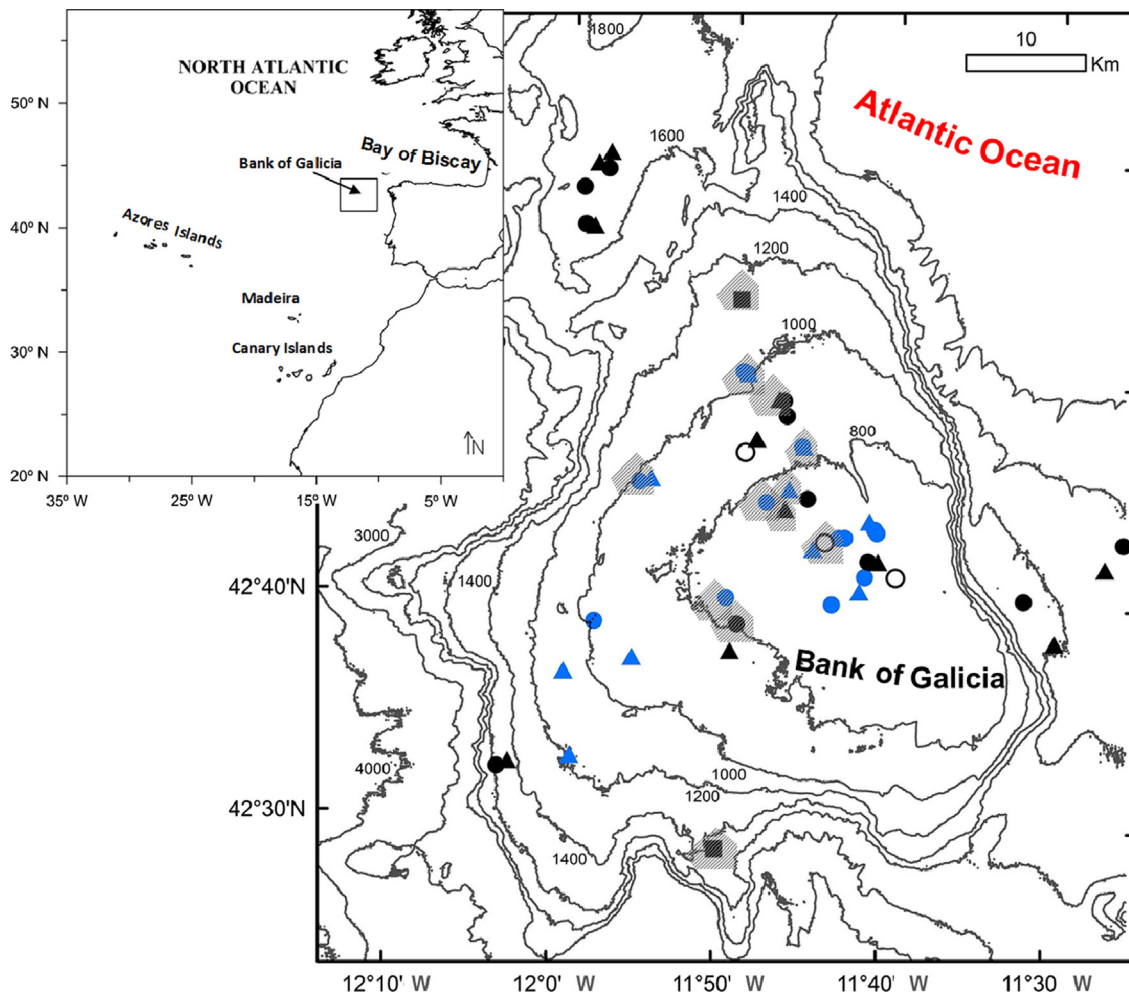


Fig. 1. Map of the Galicia Bank, indicating the location of hauls performed (●, ○, ▲: GOC, ▲: beam trawls, and ■: rock sledges). Empty symbols, 2009 hauls; gray symbols, 2010 hauls; black symbols, 2011 hauls, shaded areas indicate those hauls where corals (alive or dead remains) were collected.

and 8 mm mesh. Beam trawls are optimal gear for collecting small epibenthic invertebrates. It is formed by two steel skids joined by a 3.5 m horizontal bar with a vertical opening of 1 m and mesh size of 10 mm. Trawling was carried out during 15 min at an average speed of 2 knots. The otter trawl used was a standardized GOC73 bottom trawl used in monitoring programs in the Mediterranean (Bertrand et al., 2002). It is a 2-warp trawl used by I.E.O. on MEDITS cruises, with two doors, 35.7 m headline length, 30 m bridles, a vertical height or opening of 2.7 m and 20 mm mesh at the codend. Haul duration was 1 h at 2.8–2.9 knots. Trawl openings were recorded by means of SCANMAR and Simrad ITI Trawl monitoring sensors mounted in the mouths of the trawls.

The sampling was at depths between 751 and 1808 m for GOC hauls and between 744 and 1720 m for the BT. Decapod and macro-crustacean composition tables were constructed from 25 GOC trawls and 22 BT hauls. During 2009 only 3 GOC hauls were performed on the summit of the bank (between 760 and 859 m), in 2010 13 GOC and 9 BT hauls were performed between 764–1101 m and 768–1187 m, respectively, while in 2011 9 GOC and 12 BT hauls were performed between 751–1764 m and 744–1720 m, respectively. So, in 2009 and 2010 sampling was performed over the top of the bank (at ca. 620 m depth: Ercilla et al., 2011), while in 2011 sampling also included the flanks at maximum depths of 1808 m. In addition, two of the rock dredge tows in which crustaceans were captured were used for the analysis of decapod composition (see below). Sampling was performed on board R/Vs

Cornide de Saavedra in 2009 (66.7 m long, 1120 kW), Thalassa in 2010 (73.6 m long, 2200 kW), and Miguel Oliver in 2011 (70 m long, 2000 kW).

2.2. Environmental data

The hydrographical structure of the Bank of Galicia was characterized in all cruises, though for the purpose of the present work (to identify water masses surrounding the bank) it is enough to analyze only a single year, in this case the sampling performed during BanGal0810 (7–24 August 2010). During this cruise a grid of 56 hydrographic profiles down to 2200 m or near the bottom at shallower areas (ca. 10 m above bottom) covered the area of the Bank and its surroundings (42°20′–43°10′N and 11–12°30′W) including all the area in Fig. 1 for the biological sampling. The sampling was performed by a CTD model Seabird-911 provided with external oxygen sensors embedded in an oceanographic rosette. T (temperature in °C), S (salinity in pss), and O₂ (oxygen concentration in ml/l) were recorded. Values for S and O₂ were profiled at 24 data records/s. The same hydrographic sampling was performed on July–August 2011 cruise, however, for the purposes of our analysis only data of 2010 are presented. Warming and increased salinity of intermediate waters in recent decades have been reported west of Iberia and in the SE Bay of Biscay (Potter and Lozier, 2004, González-Pola et al., 2005), though no significant differences in structure in the Bay of Biscay below deep winter

Table 1
List of macroplanktonic and benthopelagic crustaceans collected in the Galicia Bank during BANGAL cruises. *n*: number of individuals; %F: frequency of occurrence of each species (in their respective depth range).

Species	Author	<i>n</i>	Depth range (m)	%F
Decapoda				
<i>Aristaeopsis edwardsiana</i>	(Johnson, 1867)	32	765–1683	26.1
<i>Aristeus antennatus</i>	(Risso, 1816)	21	764–1565	21.2
<i>Aristaeomorpha foliacea</i>	(Risso, 1827)	1	768	9.1
<i>Gennadas elegans</i>	(S.I. Smith, 1882)	65	761–1764	30.4
<i>Gennadas valens</i>	(S.I. Smith, 1884)	10	788–1565	6.1
<i>Gennadas</i> sp.		4	1565	14.3
<i>Bentheogennema intermedia</i>	(Bate, 1888)	4	1462–1701	8.3
<i>Funchalia woodwardi</i>	Johnson, 1868	2	766–775	3.4
<i>Hymenopenaeus affinis</i>	(Bouvier, 1906)	2	779–782	6.7
<i>Hymenopenaeus debilis</i>	S.I. Smith, 1882	2	779–1094	5.7
<i>Sergestes arcticus</i>	Krøyer, 1855	7	859–1092	13.3
<i>Sergestes armatus</i>	Krøyer, 1855	1	1091–1092	3.3
<i>Sergia robusta</i>	(S.I. Smith, 1882)	113	761–1631	43.9
<i>Sergia japonica</i>	(Bate, 1881)	3	1700–1808	20.0
<i>Parapasiphaea sulcatifrons</i> ^a	S.I. Smith, 1884	1	1764	20.0
<i>Pasiphaea ecarina</i>	Crosnier, 1969	4	1565–1683	20.0
<i>Pasiphaea hoplocerca</i>	Chace 1940	1	909	3.3
<i>Pasiphaea multidentata</i>	Esmark, 1866	42	751–1092	23.3
<i>Pasiphaea sivado</i>	(Risso, 1816)	157	761–1764	54.3
<i>Pasiphaea tarda</i>	Krøyer, 1845	8	909–1706	15.4
<i>Acanthephyra eximia</i>	S.I. Smith, 1884	22	1672–1683	37.5
<i>Acanthephyra pelagica</i>	(Risso, 1816)	28	785–1706	21.7
<i>Acanthephyra purpurea</i>	A. Milne-Edwards, 1881	29	818–1720	12.5
<i>Ephyrina figueirai</i>	Crosnier and Forest, 1973	7	1101–1706	27.8
<i>Hymenodora gracilis</i>	S.I. Smith, 1886	4	1670	12.5
<i>Oplophorus spinosus</i>	(Brullé, 1839)	5	764–1079	15.4
<i>Systellaspis debilis</i>	(A. Milne-Edwards, 1881)	385	761–1706	81.8
<i>Nematocarcinus exilis</i>	(Bate, 1888)	21	1485–1720	50.0
<i>Bresilia atlantica</i>	Calman, 1896	1	1631	11.1
<i>Alpheus</i> cf. <i>macrocheles</i>	(Hailstone, 1835)	27	761–909	28.0
<i>Caridion gordonii</i>	(Bate, 1858)	1	768	5.6
<i>Lebbeus microceros</i>	(Krøyer, 1841)	1	1485	10.0
<i>Dichelopandalus bonnierii</i>	Caullery, 1896	20	766–847	22.2
<i>Plesionika martia</i>	A. Milne-Edwards, 1883	382	761–793	53.3
<i>Glyphocrangon longirostris</i>	(S. I. Smith, 1882)	119	1565–1764	70.0
<i>Philocheras echinulatus</i>	(M. Sars, 1861)	1	791	3.2
<i>Sabinea hystrix</i>	(A. Milne-Edwards, 1881)	1	1631–1720	33.3
<i>Calocaris</i> cf. <i>templemani</i>	Squires, 1965	1	1720	20.0
<i>Richardina</i> cf. <i>spincincta</i>	A. Milne-Edwards, 1881	90	788–909	17.6
<i>Spongicoloides koehleri</i>	(Caullery, 1896)	1	847	3.1
<i>Polycheles typhlops</i>	Heller, 1862	146	764–1041	58.3
<i>Polycheles</i> (<i>Pentacheles</i>) <i>laevis</i>	Bate, 1878	40	1485–1764	81.8
<i>Stereomastix sculpta</i>	(S. I. Smith, 1880)	1	1631	12.5
<i>Stereomastix nana</i>	(S. I. Smith, 1884)	7	1565–1764	70.0
<i>Neolithodes grimaldii</i>	(A. Milne-Edwards & Bouvier, 1894)	30	(768)1565–1764	70.0
<i>Gastroptychus formosus</i>	(Filhol, 1884)	3	761–1410	10.7
<i>Uroptychus bouvieri</i>	Caullery, 1896	3	867–909	18.2
<i>Uroptychus rubrovittatus</i>	A. Milne-Edwards, 1881	67	761–1041	27.8
<i>Uroptychus cartesi</i>	Baba & Macpherson, 2012	7	1410	–
<i>Uroptychus concolor</i> ^b	A. Milne-Edwards & Bouvier, 1894	147	950–1651	35.3
<i>Galathea machadoi</i>	Barrois, 1888	2	785–788	13.3
<i>Munida microphthalma</i> ^b	A. Milne-Edwards, 1880	1	1401–1423	–
<i>Munida sarsi</i>	Huus, 1935	51	764–793	46.2
<i>Munida tenuimana</i>	G.O. Sars, 1872	219	761–1092	40.5
<i>Munidopsis serricornis</i>	(Lovén, 1852)	131	761–1041	31.6
<i>Munidopsis acutispina</i>	Benedict, 1902	3	909–1101	27.3
<i>Dicranodromia mahieuxii</i>	A. Milne Edwards, 1883	2	1410	–
<i>Parapagurus pilosimanus</i>	S.I. Smith, 1879	33	1187–1764	50.0
<i>Pagurus alatus</i>	(J.C. Fabricius, 1775)	131	744–1187	55.6
<i>Paromola cuvieri</i>	(Risso, 1816)	2	771–789	7.7
<i>Ebalia nux</i>	A. Milne Edwards, 1883	2	818–867	10.0
<i>Cymonomus normanii</i>	Lankester, 1903	3	1462–1631	33.3
<i>Dorhynchus thomsoni</i>	Wyville Thomson, 1873	239	744–1485	30.8
<i>Ergasticus clouei</i>	A. Milne-Edwards, 1882	2	744–768	11.1
<i>Cancer bellianus</i>	Johnson, 1861	169	744–950	52.8
<i>Chaceon affinis</i>	(A. Milne-Edwards & Bouvier, 1894)	45	744–1631	48.6
<i>Bathynectes maravigna</i>	(Prestandrea, 1839)	377	761–1100	62.2
<i>Polybius henslowii</i>	Leach, 1820	78	761–1094	47.4
Euphausiacea				
<i>Nematobrachion boopis</i>	(Calman, 1905)	12	(357–404)	–
<i>Euphausia krohni</i>	(Brandt, 1851)	3	(357)–1701	–
<i>Meganctiphanes norvegica</i>	(M. Sars, 1857)	9674	764–1720	63.0

Table 1 (continued)

Species	Author	n	Depth range (m)	%F
<i>Thysanopoda acutifrons</i>	Holt and Tattersall, 1905	2	770–1041	10.0
<i>Nematoscelis megalops</i>	G.O. Sars, 1883	120	1041–1701	25.0
<i>Stylocheiron maximum</i>	Hansen, 1908	2	909–1631	12.5
Lophogastrida				
<i>Gnathophausia zoea</i>	Willemoes-Suhm, 1873	158	744–1720	73.9
<i>Gnathophausia ingens</i>	(Dohrn, 1870)	1	1462	14.3
<i>Eucopia grimaldii</i>	Nouvel 1942	16	785–1701	4.7
<i>Eucopia hanseni</i>	Nouvel 1942	39	818–1764	45.8
<i>Eucopia sculpticauda</i>	Faxon, 1893	17	1041–1701	27.3
Mysida				
<i>Petalophthalmus</i> sp. A		12	1565–1764	40.0
<i>Boreomysis arctica</i>	(Krøyer, 1861)	117	744–1706	66.7
<i>Boreomysis tridens</i>	G. O. Sars, 1870	27	770–1092	20.0
<i>Boreomysis microps</i>	G. O. Sars, 1884	1	1706	12.5
Amphipoda				
<i>Cyphocaris anonyx</i>	Boeck, 1871	1	1631	14.3
<i>Themisto compressa</i>	Goes, 1865	490	928–1701	52.2
<i>Phronima sedentaria</i>	(Forskål, 1775)	20	751–1701	10.9
<i>Tmetonyx</i> sp.		5	1462–1565	50
<i>Hippomedon</i> sp.		4	1565	9.1
<i>Rhachotropis palporum</i>	Stebbing, 1909	2	1462	–
<i>Nicippe tumida</i>	Bruzelius, 1859	1	1565	–
<i>Cystisoma latipes</i> ^a	(Stephensen, 1918)	1	(0–688)	–
<i>Trischizostoma raschi</i>	Esmark & Boeck, 1861	1	909	–
Isopoda				
<i>Aegiochus ventrosa</i>	(M. Sars, 1859)	4	775–1706	9.3
Ostracoda				
<i>Gigantocypris muelleri</i>	Skogsberg, 1920	1	1041	5.0

^a Species collected with a WP2 zooplankton net.

^b Species collected with rock dredge.

mixing (to depths of 4000 m) were found between 1967 and 1987 (Pingree and Le Cann, 1990); so, in the 2–3 years of the current study we assumed no influence of such long-term T–S trends on the structure of water masses and hence in our analysis. As the region of the Galicia continental margin is influenced by contrasting water masses of different origins (summarized by Ercilla et al., 2011), hydrographic variability was considered as a factor in multivariate analyses.

Phytoplankton pigment concentration at the ocean surface (*ppc*, mg Chl *a* m⁻³) was obtained from <http://reason.gsfc.nasa.gov/Giovanni> for each LAT-LONG haul location. This variable was used as an indicator of the productivity in the area. Monthly average values of *ppc* for the positions of hauls were downloaded for different time lags: simultaneously and 1, 2 and 3 months before sampling. Monthly NAO indices (<http://www.cru.uea.ac.uk>) were also downloaded for similar time lags (from May to July) as *ppc* data in order to have an idea about interannual variation.

Total organic matter (%OM) was calculated after collecting sediments with a mega Box-Corer *ca.* over each sampling station. %OM was calculated by loss on ignition by ashing *ca.* 4 g of dry sediment (dry weight at 60 °C until reaching constant weight) for 2 h at 550 °C. Detailed results will be done in future INDEMARES publications. We used here data only for GLM models (see below).

2.3. Data analysis

Depth-related trends in terms of appearance/disappearance of species vs. depth were analyzed by plotting the cumulative number of species appearing and disappearing as a function of increasing depth. First appearances and disappearances were collected for each species along the depth range analyzed (Gage and Tyler, 1991). We plotted GOC and BT results separately knowing that, due basically to mouth-trawl dimensions and mesh

size, we worked with two gear types of quite different catching efficiency. The GOC trawl captured mostly larger decapods, while the BT caught smaller decapods and the other crustacean taxa listed in Table 1. In the BT analysis, we included results of the two rock-dredge hauls. Due to similar mesh size and mouth framed shape we assumed that the catch of these two gears is comparable at qualitative level (occurrence/absence of species).

All crustaceans were sorted and identified to the lowest feasible taxonomic level. Both abundance (number of individuals/ha) calculated from swept area and raw numbers (total individuals collected per haul) were considered for nMDS analysis. Data matrices (species vs. hauls) were analyzed by multivariate techniques. Non-metric Multidimensional Scaling (nMDS) was performed using both Bray–Curtis distances (after log-transformation of the data) and non-parametric Spearman-rank correlation indices (based on the rank, i.e. the 1st, 2nd, 3th, ..., *n*th position of species by decreasing number in hauls). Always, species with low frequency of occurrence (that is, once only) were removed from matrices. Analyses performed on GOC data were based only on decapod crustaceans and were done with Bray–Curtis distance, while analysis of BT data (including also information from the two rock dredges) was performed on macrocrustaceans in general, and we used Spearman-rank distance in MDS. We used the Spearman rank distance in order to minimize differences between both gears (basically consisting in a fixed frame with a net of similar mesh size: 8–10 mm) because it is based on species rank in hauls (not in species abundance).

PERMANOVA tests (distance-based permutational multivariate analysis of variance; Anderson et al., 2008) were performed on the same matrices. The PERMANOVA designs were based for both GOC and BT data on two factors: Factor 1 was depth intervals, with two levels according to the water masses in which hauls were performed (Ercilla et al., 2011). These groupings were (i) Mediterranean

outflow waters (MOW), comprising hauls performed between 744 and 1500 m (1500 m, being the lower boundary observed for MOW) and ii) Labrador Sea Water (LSW) comprising hauls below 1500 m (to the maximum depths sampled of 1808 m). Factor 2 was LAT (latitude), with two levels comprising hauls taken north and south of latitude 42.7°N (Fig. 1). Another MDS analysis was performed only on hauls collected at the top of seamount, hence at the MOW domain. Factors considered in the two-way PERMANOVA were (i) the co-occurrence in hauls of corals (in a wide sense, including remains of live colonies of both hard corals such as *L. pertusa* and *M. oculata* and/or gorgonians) with two categories of hauls (with or without corals) and (ii) LONG (longitude), with two levels comprising hauls taken east and west of longitude 11.45°W. The taxonomical and detailed ecological study of coral assemblages is unknown in the area and it will be done in the future from parallel studies. We only considered this aspect as a factor here because deep corals constitute the habitat of a variety of epibiotic crustaceans (Buhl Mortensen and Mortensen, 2005; Carlier et al., 2009, among others). “Corals” and “No Corals” were considered as independent factors in the two-way PERMANOVA design, because corals appeared in hauls performed exclusively at depths < 1500 m (see Fig. 1).

A SIMPER (SIMilarity of PERcentages) routine was used to identify species dominant in terms of abundance within the significant factors explored. All the analyses were performed using PRIMER 6 plus PERMANOVA (Clarke and Warwick, 1995; Anderson et al., 2008) and STATISTICA 6.1 software.

Species diversity indices (*S*, number of species; *H'*, Shannon–Wiener index in log_e; *J*, evenness) were calculated for each haul (separately for GOC and BT).

2.4. Environmental factors controlling diversity

We examined the correlation of crustacean diversity with the environmental information available using non-parametric Spearman rank correlation indices.

Relationships between decapod assemblages (numerical composition based on GOC hauls) and environmental variables were explored by the multivariate Canonical Correspondence Analysis technique (CCA: Ter Braak, 1986). CCA is a multivariate scheme for extracting synthetic environmental gradients from ecological data (Ter Braak and Verdonschot, 1995). Ordination axes in CCA are linear combinations of environmental variables that are represented on plots by arrows. Arrow lengths are proportional to the importance of each variable for explaining diversity/biomass variability (Ter Braak, 1986). Data were log-transformed. The software XLStat (AddinSoft Inc.) was used for CCA.

Diversity and biomass (g/ha) from GOC and BT were also evaluated as functions of environmental explanatory variables using generalized linear models (GLMs) (Gill, 2000). Generalized linear models (GLM) are flexible generalizations of ordinary least squares regressions. GLMs identified the environmental, explanatory, variables significantly related to the distributions of the dependent variables (diversity and biomass of crustaceans in this case) in our sampling. A GLM allows the linear model to be related to the response variable based on a link function and relates the variance of each measurement with a function of its predicted value. To test these relationships a GLM based on a Gaussian distribution and a log link were used. Selection of best-fit models was based on minimizing Akaike's Information Criterion (AIC). GLMs were built using the software R for statistical computing (see <http://www.r-project.org>).

Explanatory variables included in GLM models are: LAT, LONG, T, S, Chl *a* 1, 2 and 3 months before cruises and %OM.

3. Results

3.1. Species composition, taxonomic remarks and biogeographic aspects

Sixty-seven species of decapod crustaceans were collected in the depth range between 751 and 1808 m over Galicia Bank, 9 of them were Dendrobranchiata, 27 Caridea, 2 Stenopodidea, 1 Thalassinidea, 4 Eryoneida (Polychelidae), 16 Anomura and 8 Brachyura. The rest of macrocrustaceans were represented by 6 Euphausiacea, 5 Lophogastrida, 4 Mysida, no less than 6 Amphipoda Gammaridea and 3 Amphipoda Hyperidea, 1 Isopoda and 1 Ostracoda (Table 1).

We found two new species: the Chirostylidae *Uroptychus cartesii* and the Petalophthalmidae (Mysidacea) *Petalophthalmus* sp. A., (under description), *U. cartesii* was represented by seven specimens collected at 1410 m in a single haul. Twelve specimens of the new mysid were collected at depths between 1565 and 1764 m, occurring in 40% of samples collected in this depth range with trawls (Table 1). Other species would probably merit closer examination in order to establish whether they could be new species. That is the case for *Alpheus* cf. *macrocheles*, collected at the top of the seamount between 761 and 909 and showing different chela morphology than that of *A. macrocheles*. *Calocaris* cf. *templemani* showed some differences in the spinulation of the telson compared with Squires's (1990) description. Also, two specimens of the Homolodromiidae *Dicranodromia mahieuxii* were collected for the second time after its original description (Milne Edwards, 1883) at 1410 m.

In addition, a number of species constituted rare biogeographic findings. *Hymenopenaeus affinis* and *Sergestes armatus* have not been cited previously at European latitudes. Both are species of southern origin, the first described from Cape Verde (Crosnier and Forest, 1973) while *S. armatus* is distributed from Morocco to the Azores, Madeira and Canary Islands (Udekem d' Acoz, 1999). *Hymenopenaeus debilis* was also collected north of its previously known distribution (south of Portugal, southwest of Spain, Alboran Sea (Cartes et al., 2000), as occurred with *Oplophorus spinosus* and *Pasiphaea hoplocerca*. All these species were found only at the seamount top.

By contrast a number of species of northern origin were collected for the first time in Iberian waters. The most remarkable, because it was a dominant species (30 specimens collected between 1565 and 1764 m, excluding a small specimen collected at 768 m) over the slope flanks was the Lithodidae *Neolithodes grimaldii*. Other species of North Atlantic (Labrador, Newfoundland and other Canadian waters: Squires, 1990) origin were the Hippolytidae *Caridion gordonii* and *Lebbeus microceros* and the Crangonidae *Sabinea hystrix*. All these species were mainly collected at depths below 1400 m. *L. microceros* is a new species record for European waters. The species did not have colored integument as described by Squires (1990), but it had all of the characteristics described by Jensen (2006) regarding the antennular spinulation, short rostrum, pleuron shape and epipods on the three first pereopods described for a number of *Lebbeus* species, among which *L. microceros* was included. A specimen of *Bresilia* captured was classified as *B. atlantica*, in agreement with the comparative characteristics given by Calado et al. (2004) for known *Bresilia* species.

3.2. Species renewal with depth

We found a generalized species substitution with depth. Only 12 species of decapods were distributed along 75% or more of the depth range explored, and only 13 occurred in at least 50% of samples performed (Table 1).

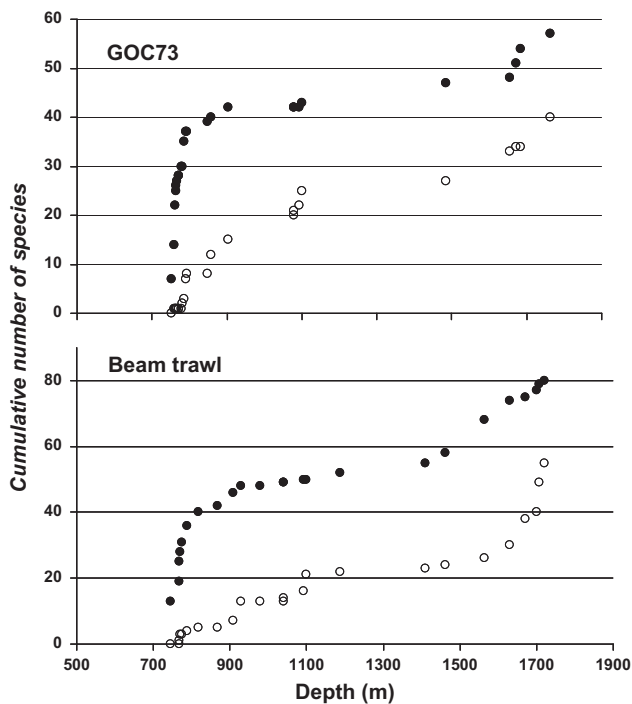


Fig. 2. Appearance (●) and disappearance (○) of accumulative number of species (decapods) as a function of depth on the Galicia Bank for cruises performed in July–August 2009, 2010 and 2011.

After plotting species (first) appearance/disappearance vs. depth (Fig. 2), we identified boundaries characterized by the higher species renewal or substitution. In GOC hauls, there was a progressive appearance of new species with depth from 751 to 793–903 m, while in the interval 1079–1656 m scarcely any new species appeared. In spite of the sampling gap at between 1101 and 1485 m, the stabilization in the appearance of new species occurred already at 793–903 m. Below 1656 m we found a new sharp increase in species appearance. Disappearance of species with increasing depth was progressive to 1101 m, negligible between 1101 and 1485 m, and then increased again below this depth.

Results with BT were similar (Fig. 2); the community sampled with this type of gear is composed by decapod crustaceans and by the other macro-crustacean taxa cited above. Species appearance was sharp from 744 to 928 m, being more progressive to 1410 m and sharply increasing again to the maximum depth sampled (1720 m). The disappearance of species followed the same trend, it was more progressive than species appearance, but followed a clear positive tendency to 1100 m, it was very slight between 1100 and 1565 m, increasing again deeper.

In summary, combining trends of both samplers, we found a community over the top of the seamount, between ca. 750 and 1100 m, characterized by sharp species appearances and more progressive species disappearance, an intermediate belt with scarcely any species renewal to 1400–1500 m and below 1500 m a new deep-slope assemblage dwelling on bottoms to the maximum depths sampled (ca. to 1800 m).

The nMDS results (Fig. 3) were in general similar to those from the appearance/disappearance plots. In short, GOC hauls from the seamount top, influenced by Mediterranean outflow waters (MOW), indicated the habitat of a *seamount top assemblage* (STA). That had a quite different composition from GOC hauls taken between ca. 1500 and 1800 m, where a *deep-slope assemblage* (DSA) was found on the seamount flanks (PERMANOVA pseudo- $F=9.69$; $p=0.001$). The variable LAT had no significant influence (pseudo- $F=0.124$; $p=0.974$) on assemblage composition. Similar results were found for decapods

collected with BT (Fig. 3). STA was significantly different from DSA (pseudo- $F=10.917$; $p=0.001$; and there was no significant influence from LAT: pseudo- $F=0.626$; $p=0.694$).

The influence of factor “corals” was significant when it was tested on the STA hauls, both among large decapods collected with GOC (pseudo- $F=3.990$; $p=0.002$) and smaller species caught with BT (pseudo- $F=6.760$; $p=0.0004$). In this 2-way design LONG was also considered as a factor and was significant for large decapods (pseudo- $F=1.527$; $p=0.01$) and close to the $p=0.05$ level for BT decapods (pseudo- $F=2.092$; $p=0.07$).

SIMPER analysis evidenced quite different composition of species in the assemblages at the top of Galicia Bank (STA) from those over the deep flanks of the seamount (DSA), both on GOC and BT results. In short, STA assemblage (GOC) was composed (to 51% of abundance) by the shrimp *P. martia*, the swimming crab *Polybius henslowii* and the benthic crabs *Bathynectes maravigna* and *Cancer bellianus* (Table 2). At DSA dominant species (to 65% of abundance) were the anomuran *N. grimaldii*, the crangonid *Glyphocrangon longirostris*, two polychelid lobsters (*Polycheles laevis* and *Stromastis nana*) and the shrimp *Pasiphaea sivado*. STA and DSA were highly dissimilar (92.7%). Dissimilarity between STA and DSA was also very high (90.4%) based on BT hauls (Table 2). STA assemblage (GOC) was composed (to 63% of abundance) by the hermit crab *Pagurus alatus*, the bathypelagic shrimp *Systellaspis debilis* and by *Polycheles typhlops*. At DSA *S. debilis* and *P. typhlops* (together with *G. longirostris* and *Acanthephyra purpurea*) accumulated also 62% of similarity.

SIMPER analysis on STA also evidenced quite different composition of species in the assemblages in where live corals were collected (*corals* assemblage) compared to soft-bottoms (those without corals, Table 3), with a high dissimilarity (68.6%) between them. The small munidopsid crab *Munidopsis serricornis* is the most abundant species in the *corals* assemblage, with the small shrimp, an associated-sponges living species, *Richardina cf. spinicineta*. Other epibionts often associated to corals and other sessile organism are *Dorhynchus thomsoni* and *Urotychus rubrovittatus*. However, as we swept in *coral* trawls areas with and without sessile organisms, in this same assemblage we found also large (not epibiont) crabs (*B. maravigna*, *Munida tenuimana*) even, some mud-living species such as *P. alatus*.

Diversity was calculated separately for the STA and DSA groups. We did not find any significant difference of *S*, *J* and *H* between the two assemblages, either for large decapods collected with GOC or the small-epibenthic decapods caught with BT (Table 4). Only the “other” crustaceans (mainly euphausiids and mysids) showed higher *S* and *H* in the deeper assemblage (DSA) with lower evenness. That tendency is due to the higher diversification of mysids below 1400 m.

3.3. Environmental factors controlling diversity

Fig. 4 provides meridional and zonal sections across the Bank axis of two key properties for water masses identification, salinity and dissolved oxygen. The lower bound of ENACW is characterized by a relative salinity minimum (35.50–35.55, practical salinity scale) at around 500 m (above the bank summit) and defines the beginning of the area of influence of MOW waters. The seamount top assemblage (STA), i.e. between 700 and 1400 m, comprises the whole level of influence of MOW, characterized by high salinity (> 36) and low dissolved O_2 (< 4.4 ml/l). In addition, we found at STA relatively high potential temperature (10.5–11.0 °C, author's data). The MOW core is, as expected from the literature (Pingree, 1995; González-Pola et al., 2005; Ercilla et al., 2011), located around 1000–1200 m, but due to the intense mesoscale activity fluctuations in the salinity and O_2 fields are evident. Below 1400 m there is a sharp gradient in all properties towards the core of LSW at 1800–1900 m, characterized by low salinity (< 35.10), and very

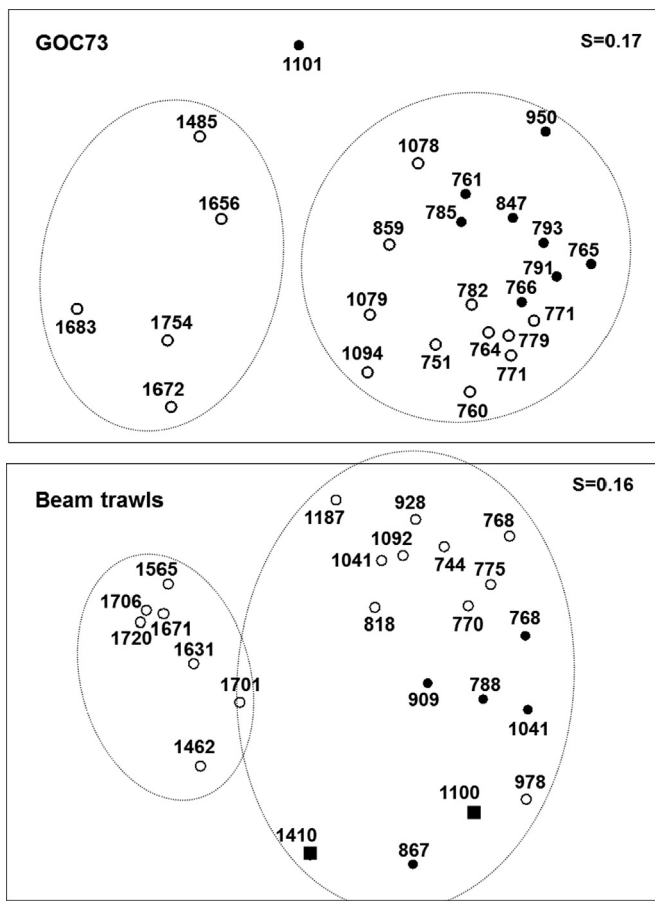


Fig. 3. MDS analyses performed on decapods collected during BanGal cruises (●: 2009–2010 cruise, ○: 2011 cruise, and ■: 2 rock sledges added to the beam trawl analyses). Mean depth of each haul above their respective symbol. S, stress.

Table 2
SIMPER analysis indicating dominant species of decapods collected with GOC and beam trawls along the gradient 744–1808 m. STA: seamount top assemblage from DSA (deep-slope assemblage).

GOC73			Beam trawls		
Species	Av. abund	Cum.%	Species	Av. abund	Cum.%
Group STA (744 to ca. 1400 m)			Group STA (744 to ca. 1400 m)		
Average similarity: 35.81			Average similarity: 18.88		
<i>Plesionika martia</i>	1.88	15.63	<i>Pagurus alatus</i>	7.29	28.21
<i>Polybius henslowii</i>	1.24	27.88	<i>Systellaspis debilis</i>	17.72	51.11
<i>Bathynectes maravigna</i>	1.62	39.76	<i>Polycheles typhlops</i>	6.65	63.35
<i>Cancer bellianus</i>	1.44	50.95	<i>Bathynectes maravigna</i>	4.53	73.55
<i>Sergia robusta</i>	1.06	60.6	<i>Munida tenuimana</i>	2.59	79.27
<i>Systellaspis debilis</i>	0.79	69.1	<i>Pasiphaea sivado</i>	2.29	84.43
<i>Chaceon affinis</i>	0.73	75.67	<i>Sergia robusta</i>	0.88	88.3
<i>Pasiphaea sivado</i>	0.86	81.31	<i>Munidopsis serricornis</i>	6.65	90.42
<i>Munida tenuimana</i>	1.06	85.08			
<i>Uroptychus rubrovittatus</i>	0.66	87.63			
<i>Polycheles typhlops</i>	0.51	89.74			
<i>Munidopsis serricornis</i>	0.40	91.09			
Group DSA (ca. 1500–1800 m)			Group DSA (ca. 1500–1800 m)		
Average similarity: 24.47			Average similarity: 29.09		
<i>Neolithodes grimaldii</i>	1.18	16.5	<i>Systellaspis debilis</i>	6.71	23.03
<i>Glyphocrangon longirostris</i>	1.51	31.84	<i>Glyphocrangon longirostris</i>	7.86	39.62
<i>Polycheles granulatus</i>	0.64	45.48	<i>Acanthephyra purpurea</i>	2	51.81
<i>Pasiphaea sivado</i>	0.74	55.32	<i>Polycheles granulatus</i>	5	62.15
<i>Stereomastis grimaldii</i>	0.42	64.51	<i>Gennadas elegans</i>	5.14	69.83
<i>Gennadas elegans</i>	0.50	72.61	<i>Parapagurus pilosimanus</i>	3.57	77.11
<i>Acanthephyra purpurea</i>	0.50	79.15	<i>Uroptychus concolor</i>	3.43	82.88
<i>Nematocarcinus ensifer</i>	0.50	85.7	<i>Pasiphaea sivado</i>	2.71	87.18
<i>Parapagurus pilosimanus</i>	0.60	89.86	<i>Acanthephyra pelagica</i>	0.86	89.54
<i>Systellaspis debilis</i>	0.28	93.14	<i>Nematocarcinus ensifer</i>	2.43	91.86

high dissolved O₂ contents (up to 6.2 ml/l). Also, we found low potential temperature (< 4 °C, data not plotted). The core of LSW coincides with the maximum depth trawled.

We found significantly positive correlations between diversity (*J* and *H*) of small epibenthic decapods collected with BT and phytoplankton standing stock at the surface 2 and 3 months before sampling (Table 5) (*J* vs. Chl *a*_{2 months} $\rho=0.493$, $p=0.016$, $n=23$; *H* vs. Chl *a*_{2 months} $\rho=0.487$, $p=0.018$, $n=23$; *H* vs. Chl *a*_{3 months} $\rho=0.428$, $p=0.041$, $n=23$), and also for other crustaceans (mainly euphausiids/mysids) (*H* vs. Chl *a*_{2 months} $\rho=0.469$, $p=0.038$, $n=20$). The mean of Chl *a*_{3 months} records (this was in April–May) taken over the bank (corresponding to LAT, LONG of all samples) was 0.749 mg/m³, decreasing to 0.321 mg/m³ 2 months before cruises, to 0.217 mg/m³ 1 month before cruises and to 0.160 mg/m³ in July–August. Similarly significant tendencies were found for epibenthic decapods when correlations were calculated for STA and DSA assemblages separately, in both cases with Chl *a*_{3 months} (Table 5). In contrast no significant tendency was found for large benthopelagic decapods collected with the otter trawl GOC. We did a joint analysis of the dataset for the 3 years sampled, in fact mainly 2010–2011. Although some interannual changes cannot be fully excluded, the monthly NAO was always negative for 2009, 2010 and 2011 (respectively −2.45, −4, −3.89), being practically identical between 2010 and 2011.

CCA related species (and hauls) with environmental variables influencing their distributions (Fig. 5). CCA evidenced quite different distributions of species in the assemblages at the top of Galicia Bank (STA) from those over the deep flanks of the seamount (DSA). STA species were distributed on the left on the plot, related with values of *T* and *S*. DSA species (e.g. *Acanthephyra pelagica*, *G. longirostris*, *N. grimaldii*, *Nematocarcinus ensifer* and *Acanthephyra eximia*) were at the right of the plot, linked to low *T* and *S*. Within STA, species associated with corals (the clearest examples: *U. rubrovittatus* and *M. serricornis*) were grouped in the left upper part of the CCA plot (Fig. 5). The CCA results suggested a more delayed response to Chl *a* with increasing depth; the simultaneous and 1 month lag Chl *a* values

Table 3
SIMPER analysis of dominant species of decapods collected at STA as a function of the co-occurrence of corals in hauls.

Beam trawls		
Species	Av. abund	Cum.%
Group STA (744 to ca. 1400 m)		
Soft-bottoms		
Average similarity: 27.43		
<i>Pagurus alatus</i>	9.9	38.79
<i>Systellaspis debilis</i>	26.22	67.3
<i>Polycheles typhlops</i>	5.8	77.05
<i>Pasiphaea sivado</i>	3.2	84.35
<i>Sergia robusta</i>	1.1	89.24
<i>Aristaeopsis edwardsianus</i>	0.9	91.56
<i>Bathynectes maravigna</i>	1.0	93.08
<i>Pasiphaea multidentata</i>	3.0	94.52
<i>Munida sarsi</i>	1.5	95.96
Corals		
Average similarity: 17.01		
<i>Bathynectes maravigna</i>	9.57	34.35
<i>Munidopsis serricornis</i>	16.14	49.59
<i>Munida tenuimana</i>	5.0	62.98
<i>Polycheles typhlops</i>	7.86	71.4
<i>Dorhynchus thomsoni</i>	2.43	78.78
<i>Systellaspis debilis</i>	5.57	85.31
<i>Pagurus alatus</i>	3.57	90.6
<i>Richardina cf. spinicincta</i>	12.86	92.4
<i>Gennadas elegans</i>	1.0	94.14
<i>Uroptychus rubrovittatus</i>	2.57	95.64

Table 4
Species richness (*S*) and diversity (*J*, *H*) at the two assemblages (STA, DSA) identified on the Galicia Bank for decapods and other macrocrustaceans as function of the trawl type used.

	<i>S</i>	<i>J</i>	<i>H</i>
Decapoda			
GOC73			
STA	10.75	0.74	2.40
DSA	8.60	0.72	1.99
Beam trawl			
STA	10.21	0.77	2.52
DSA	11.00	0.75	2.57
Other Crustacea			
STA	3.86	0.69	0.71
DSA	6.75	0.59	1.02

were more linked to STA, and Chl *a* 3 months before sampling was related to DSA species. The CCA explained 76.5% of the system variance in the first two axes plotted.

The GLM models pointed to possible explanatory variables for the distribution of diversity and biomass of decapods over Galicia Bank (Table 6). The GLM for decapod diversity caught with the GOC trawls explained between 43.8% and 25.1% of the deviance for two GLMs based on *J*, and 15.9% for a GLM based on *H*. Explanatory variables for *J* were LONG and LAT (GLM₁) and salinity (*S*) close to the bottom (GLM₂). In GLM₁, *J* was higher with higher LAT (in the north) and higher LONG (to the west areas) into the Bank. In GLM₂, *J* was higher at depths with lower *S*, i.e. deeper, a result of the negative correlation between *S* and depth ($\rho = -0.429$; $p = 0.03$). The only variable changing significantly in GLMs with *H* was %OM (organic matter), showing a positive relationship. The %OM was higher below 1400 m depths in the depth range studied. Biomass of GOC decapods was also related with LONG, and near-bottom T and *S* in GLM₄. That model explained 42.9% of total variance.

Biomass was significantly higher to the west on the bank and at shallower depths where the higher T and *S* were recorded.

GLMs were also performed on crustaceans collected with BT. A GLM explained between 18.5% (*J*, GLM₅) and 31.0% (*H*, GLM₆) of diversity variation. Explanatory variables were Chl *a* recorded 2 months before the cruises, both for *J* and *H*, and LONG for *H*. The smaller fraction of the decapod community (those collected with BT) was, therefore, more diverse (in terms of *H* and evenness) when records of surface Chl *a* 2 months before sampling were greater and also to the west on the bank. A GLM for biomass was positively related with *S*, accumulating 22.3% of variance. As in the case of biomass estimated with GOC, this means greater biomass at shallower depths with higher *S*.

4. Discussion

The depths explored (744–1808 m) during INDEMARES cruises did not cover all habitats of the Galicia Bank (GB), the slopes of which reach abyssal depths to 5000 m (Ercilla et al., 2011). Despite this, we found high species richness, *S*, among macrobenthic crustaceans, especially among decapods (67 species). At least two new species (potentially endemic) and a number of new biogeographic records, new species for European or Iberian waters, were found. Comparison of diversity with studies done at other seamounts and in neighboring areas depends, among other factors, on the trawl type used, which can impose important bias on diversity estimates (Cartes et al., 2009b), also on the number of samples (and the area swept), that in our study were in general high compared with other studies on seamounts. Studies on deep-sea decapods with similar trawl types (at comparable depths: 750–2000 m) and sampling intensity have been performed in the Cantabrian Sea and the western Mediterranean, showing in general that GB is a highly diversified marine area. We avoided the use of the term “hotspot” of diversity for Galicia Bank because this term has a specific definition related with terrestrial communities and endemism (Myers et al., 2000).

In terms of γ -diversity the higher *S* at GB can be attributed to first order on the distance from the bank to the nearest coast: 220 km to the northwestern Iberian Peninsula. Distance from the coast (to the continental shelf) was one of the main factors explaining biological variability of Seamounts in New Zealand region (Rowden et al., 2005). Over Le Danois Bank, situated only to 25 km from the Cantabrian shelf (Cartes et al., 2007a), some new species, to date endemics, were found exclusively among peracarid crustaceans (e.g. Guerra-García et al., 2008; Frutos and Sorbe, 2010, 2012; San Vicente et al., 2013) with no new decapod crustaceans. Peracarids have a conservative life style, with females bearing embryos in marsupial pouches in contrast to decapods having free-living larvae. The new chirostyliid crab described from the GB (*U. cartesi*) belongs to a family with large eggs and lecithotrophic, well developed larvae probably having relatively low dispersal capability and high potential capacity for speciation. Over New Caledonian seamounts nearly all endemic species of gastropods (close to 38 species) have lecithotrophic larval development (Castelin et al., 2011). The other potentially endemic species on GB was a mysid, *Petalophthalmus* sp. A (Frutos et al., 2012). It was not collected at the top of bank but deeper, away from the possible retention effect caused by Taylor columns described at the top of the bank (Ercilla et al., 2011). So, possible endemism of *Petalophthalmus* sp. A at GB seems rather a consequence of the suprabenthic behavior of the species (Frutos et al., 2012), together with the low dispersal capability of peracarids above mentioned. Estimates of *S* were also higher at GB than in the deep Balearic Basin (western Mediterranean) at comparable depths > 700 m (*S*=58), that have been intensely sampled for

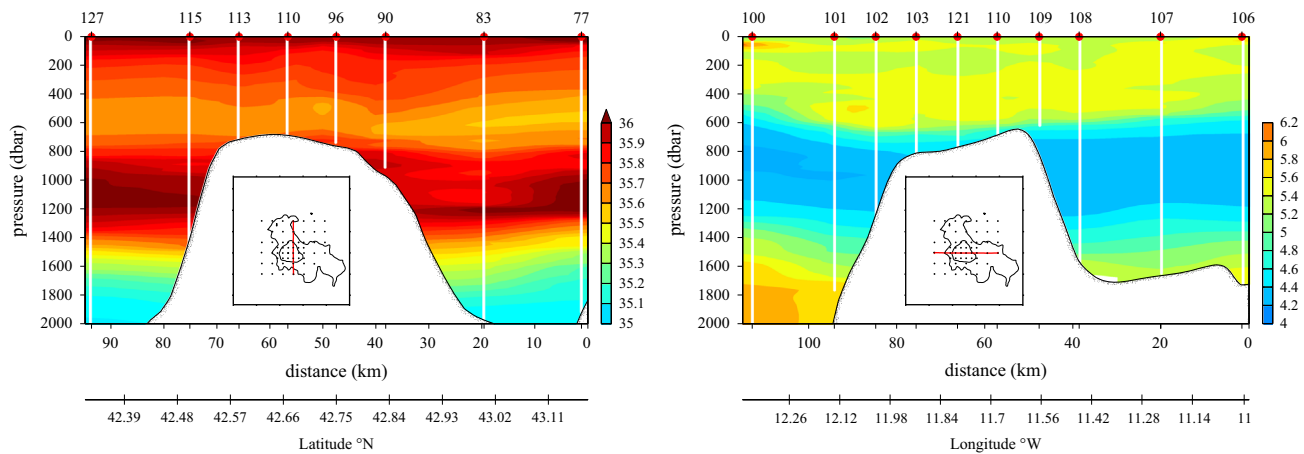


Fig. 4. Left: vertical section of salinity (PSU) along a meridional section crossing the main axis of the Galician Bank on August 2010. Right: dissolved oxygen (ml/l) along a zonal section crossing the main axis of the Galician Bank. Maps showing the Galician Bank isobaths of 1000 and 2000 m with the section tracks shown.

Table 5

Spearman rank correlations between diversity (J and H) and the primary production at surface 2 and 3 months before sampling, for decapods collected with beam trawls and GOC and for other macrocrustaceans (e.g. euphausiids, mysids) in the summit, flanks and whole mount of the Galicia Bank.

	<i>n</i>	<i>r</i>	<i>P</i>
Decapods			
Beam trawl			
Seamount			
<i>J</i> vs. Chl <i>a</i> 2	23	0.494	0.017
<i>H</i> vs. Chl <i>a</i> 2	23	0.487	0.018
<i>H</i> vs. Chl <i>a</i> 3	23	0.428	0.042
Mount summit			
<i>H</i> vs. Chl <i>a</i> 3	14	0.574	0.032
Mount flanks			
<i>H</i> vs. Chl <i>a</i> 3	9	0.745	0.021
GOC73	Any significant <i>r</i>		
Other Crustacea			
Beam trawl			
Seamount			
<i>J</i> vs. Chl <i>a</i> 2	20	0.469	0.037

20 years (Cartes et al., 2009a). In the deep Mediterranean the low number of species is attributable to the particular paleoecological conditions that have occurred there and to low food availability (Pérès, 1985; Cartes, 1993) linked to relatively high temperature in the water masses below 150 m, which may favor OM degradation (Wishner, 1980).

At GB we found a mixture of species that, depending of depth, were of southern or northern origin. Thus, over the top of the seamount (STA assemblage) we found both frequent (*P. martia* and *A. antennatus*) and rare (*H. debilis*, *H. affinis*, *S. armatus*, *P. hoplocerca*) species with distributions centered well to the south. Our hydrographic data is consistent with the well-known distribution of water masses in the area (summarized for example by Ercilla et al., 2011). To our purpose the main outcome is the clear distinction of levels influenced by the Mediterranean outflow waters (MOW) at the top of Galicia Bank and by Labrador Sea Water (LSW) distributed below 1400 m. This water mass originates from the deep outflow of water from the Mediterranean Sea into the Atlantic Ocean through the Strait of Gibraltar (Pingree and Morrison, 1973; Danialt et al., 1994; Iorga and Lozier, 1999; González-Pola et al., 2005), but only the dominant shrimps cited above (*P. martia* and *A. antennatus*) are also abundant in deep waters of the Mediterranean (Cartes et al., 2009a). The other species are not found (or scarcely found: Cartes et al., 2000) in the Mediterranean, and they probably reach the GB thanks to entrainment in the northward flow of MOW along Portuguese

coasts, where this mass may reach velocities of 5–10 cm/s (Iorga and Lozier, 1999). Our assemblage analysis showed generalized species renewal at depths of ca. 1500 separating the STA from the DSA assemblage. The DSA belt is surrounded by Labrador Sea Water (LSW), of northern (near Greenland, and eastern Canada) origin (Yashayaev and Loder, 2009). LSW occupies depths between 1600 and 2500 m with its core at 1800 m (Pingree, 1973; Pingree and Morrison, 1973; Huthnance et al., 2002; Van Aken et al., 2011). The occurrence of *N. grimaldii*, at the GB, with well established populations (including adult males and females) seems linked to the influx of LSW on the flanks of Galicia Bank. This is consistent with the greater abundance of *N. grimaldii* in our sampling on the Galicia Bank walls exposed to northern currents (Fig. 6). It is also consistent with the depth range inhabited by *N. grimaldii* in the Bay of Biscay and Galician waters generally (1565–2480 m). Offshore of Labrador *N. grimaldii* is distributed at shallower depths (ca. 800–1400 m: Squires, 1990; He, 2005) roughly coinciding with the LSW depth range in that region (400–1600 m: Yashayaev and Loder, 2009). Similar northern origins and distributions would be valid for other species (i.e. *L. microceros* and *Calocaris templemani*, the two crangonids *S. hystrix* and *G. longirostris*). The first two have not been reported previously in European waters (Udekem d'Acoz, 1999), while *S. hystrix* has had a reported distribution limited to the west of Brittany (48°41'N–10°53'W). That area is close to the Charcot Seamounts (45°N–11.5°W), where LSW seems to be confined after crossing the Mid-Atlantic Ridge at 50°N, then spreading farther eastward and southward (Paillet et al., 1998). *G. longirostris* showed higher abundance at Galicia Bank on the wall exposed to northern currents (Fig. 6), as remarked for *N. grimaldii*. We should distinguish between dominant species at GB, often epibenthic species, and the occurrence of rare species, particularly bathypelagic or benthopelagic species including *Hymenopenaeus* spp., *S. armatus* and *P. hoplocerca*. The last of those can sporadically arrive at GB, perhaps depending on interannual variations in current intensity.

Comparing assemblage richness (α -diversity) the STA assemblage has similar *S* to the inner Basin assemblage described for Le Danois Bank (at 630–1050 m), although in terms of functional diversity (trophic guilds of species) the assemblages were quite different (see below). Richness, *S*, was also similar between the DSA of the GB compared to the mainland slope of the Cantabrian Sea below 1500 m (*S* range: 11–23 species: de Saint Laurent, 1985; Alcázar et al., 1992). The DSA was highly diverse in comparison to the lower slope assemblages in the Mediterranean (Cartes, 1993; Cartes and Sardà, 1993; Fanelli et al., 2013), where for paleoecological reasons (see Pérès, 1985; Cartes, 1993) entire families as lithodids are absent, while others (crangonids,

polychelids, oplophorids) are often represented by a single or a few species.

Over the GB, a highly diverse decapod fauna was found associated with cold corals (*L. pertusa*, gorgonians, etc.) forming reefs with no fewer than six munidopsid and chirostyliid crabs (*Munidopsis* spp., *Uroptychus* spp., and *Gastroptychus formosus*) or the homolodromiid *D. mahieuxii*. By contrast, richness, *S*, of fauna associated with deep corals was low over both Le Danois Bank and especially in the Mediterranean, where only a few species are regularly found: (i) the majid *Rochinia (Anamathia) rissoana* (on *Isidella elongata*; Dieuzeide, 1960; Maynou and Cartes, 2011; on *L. pertusa* in Santa Maria de Leuca; Carlier et al., 2009) and (ii) *M. serricornis* found on isolated *Lophogorgia* colonies on muddy bottoms (Cartes, 1993). This may depend on coral density and morphology (low forming habitat capacity by *I. elongata* in the deep Mediterranean; Cartes et al., 2013a) in addition to paleoecological history of the deep Mediterranean, considered as an impoverished Atlantic ecosystem (Pérès, 1985). The occurrence of deep-water corals may not always result in increasing diversity of associated fauna (Metaxas and Davis, 2005). Diversity of decapod species associated with corals is high in a variety of habitats, from shallow (Snelgrove and Lewis, 1989) to deeper waters (Jensen and Frederiksen, 1992), while in other locations decapod diversity is low (Buhl Mortensen and Mortensen, 2005). Galatheid (Munidopsid) and chirostyliid crabs are not exclusively decapod-associated corals, but they are diverse over other hard benthic structures such as hydrothermal vents (Macpherson and Segonzac, 2005; Martin and Haney, 2005).

4.1. Trophic factors controlling diversity

Some benthic feeders typically dwelling on muddy bottoms of continental margins in the Atlantic and Mediterranean (e.g. *Pontophilus norvegicus*, *Geryon trispinosus*) were completely absent from our GB samples, and this is likely related to the low %OM in sediments (1.36–2.03% at 683–1343 m; S. Parra, unpublished data) with very low benthos biomass on sediments (S. Parra, personal communication). These species were common on Le Danois Bank, with %OM ranging between ca. 4% and 7% (Cartes et al., 2007b). Large crabs (*Chaceon affinis* and *C. bellianus* in the STA and *N. grimaldii* in the DSA) may feed on epibenthic invertebrates (as do taxonomically neighboring species; Cartes, 1993, Domingos et al., 2008). While dominant in biomass at GB, they have low metabolic and feeding rates (0.061 %DW/WW for *Geryon longipes*; Maynou and Cartes, 1998). By contrast other benthos feeders, such

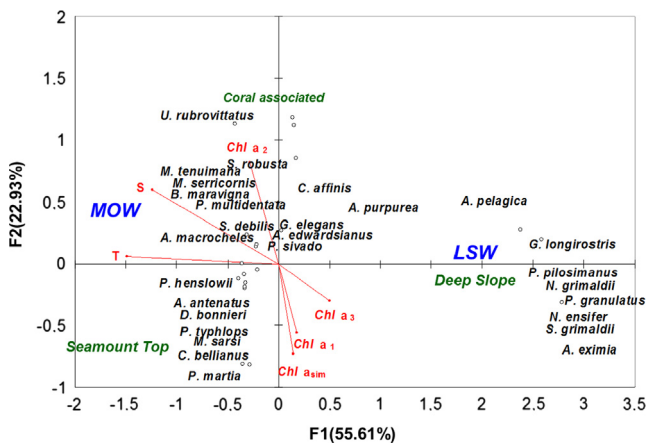


Fig. 5. CCA of decapod species collected over the Galicia Bank as a function of environmental variables (T, temperature; S, salinity; Chl a_{sim}, 1, 2, 3, satellite records of Chl a taken at the intervals simultaneous, 1, 2 and 3 months before sampling). Empty circles represented hauls.

Table 6
GLMs performed on diversity (J and H) and biomass (g/ha) of decapod crustaceans captured with beam trawls and with an otter trawl GOC over the Galicia Bank.

Variable	Estimate	Explained deviance	Residual deviance	% expl. deviance	p	Variable	Estimate	Explained deviance	Residual deviance	% expl. deviance	p
1	J NULL Chl a _{2mo} AIC: 2.625	0.208	1.164 0.956 Total	17.9 17.9	0.03	J	GOC73	0.141	0.464	30.4	5.8e-4
						LONG	0.660	0.323	0.323	13.1	0.02
						LAT	0.335	0.262	0.262	43.5	
						AIC: -31.53		Total	0.464	25.0	0.006
						S	-0.015	0.348	0.348	25.0	
						AIC: -26.52		Total	0.348	25.0	
2	H NULL LONG Chl a _{2mo} AIC: 66.07	3.517 3.369	22.25 18.73 15.36 Total	15.8 15.1 30.9	0.02 0.04	H	GOC73	1.692	7.365	23.0	0.03
						%OM	1.021	5.673	5.673	23.0	
						AIC: 43.65		Total	7.365	23.0	
3	Biomass NULL LONG T S AIC: 337.94	19.758	88.75 69.00 Total	22.3 22.3	0.02	Biomass	GOC73	32.066	220.3	14.6	0.02
						LONG	-8.066	188.2	188.2	15.3	0.04
						T	0.464	154.5	154.5	13.1	0.03
						S	0.064	125.7	125.7	13.1	
						AIC: 471.97		Total	88.75	42.9	

Explanatory variables included in the models are: LAT, LONG, T, S, Chl a₁, 2 and 3 months before cruises and %OM. Df, degree of freedom; AIC, Akaike index, a relative measure of fit goodness of models.

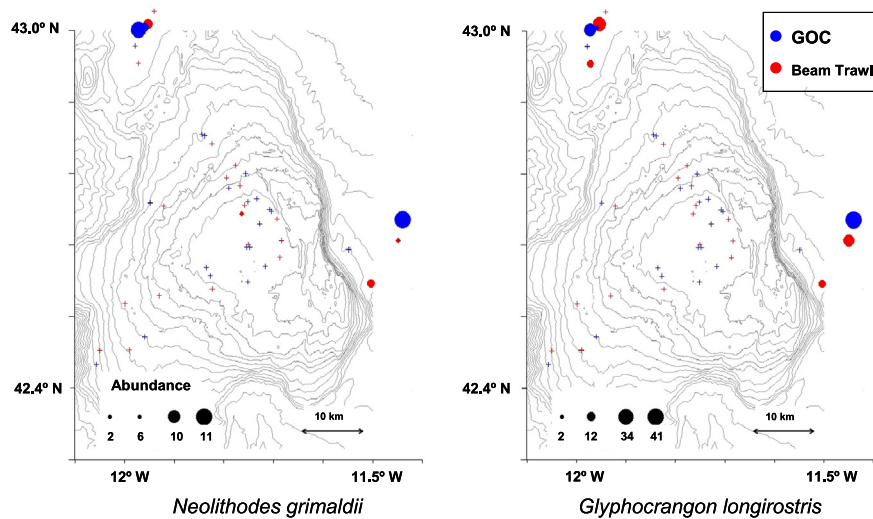


Fig. 6. Distribution of abundance of the two most abundant species of northern origin on the Galicia Bank: *Neolithodes grimaldii* and *Glyphocrangon longirostris*. + indicates hauls where a species was not caught; circle (•) size is proportional to the abundance of species in hauls.

as large shrimps (*A. antennatus* and *Aristaeopsis edwardsianus*; Lagardere, 1972; Cartes et al., 2007b; authors unpublished data), with higher feeding rates were rather not dominant. Rather low O_2 concentration at the level of the STA assemblage may also favor low benthos density in addition to effects of low %OM in sediments. In fact the STA assemblage was dominated at GB by such zooplankton feeders as *P. martia* (Cartes, 1993; Fanelli and Cartes, 2008), *P. henslowii* (Signa et al., 2008) and *S. debilis*. These species have high feeding rates (0.442%DW/WW for *P. martia*; Maynou and Cartes, 1998) or high gut fullness (as for *P. henslowii*, Signa et al., 2008). They feed on migratory zooplankton (euphausiids, small decapods) that probably are more abundant in the water column over the GB, where O_2 concentration increased to 5.2–5.8 ml/l and greater fluorescence (phytoplankton stock) was found in the photic zone (unpublished data INDEMARES0810). The lowest zooplankton density was found over Galicia Bank at MOW core (1000–1200 m, author's unpublished data) where O_2 concentration decreased to <4.4 ml/l. This confirmed the positive relationships found between O_2 and near-bottom zooplankton found in the deep Mediterranean (Cartes et al., 2013b).

The diversity (H and J) of small crustaceans (collected with beam trawls) seems controlled by the phytoplankton blooms over the bank, indicated by elevated surface Chl a 2–3 months before the samplings, both at the top (Spearman's $r=0.57$, $p=0.03$) and over the flanks ($r=0.74$, $p=0.02$) of Galicia Bank, whereas no significant relationships with Chl a were found for larger decapods (collected with GOC), located on average in higher trophic levels than those collected with BT (see stable isotope results from Le Danois Bank: Cartes et al., 2007b). By contrast, those factors explaining GOC decapod diversity (and biomass) were related with LAT, LONG, and S (in turn dependent on depth), that is, with spatial variables, rather than temporal ones. This further suggests the influence on the GB decapod communities of water masses of northern/southern origin arriving at different depths along the bank surface.

In conclusion, the decapod fauna the Galicia Bank can be cataloged as a site of high diversity (S) in terms of γ -diversity. In terms of α -diversity, however, the decapods of GB had similar S to surrounding areas in the Bay of Biscay. This high γ -diversity of the GB decapods is attributable to the different geographic origins of the water masses reaching this seamount at different depths, more than to variety in available trophic resources (basically of pelagic origin). Although detailed trophic analyses are still pending, the low %OM of the sediments and the correlation of decapod

diversity with surface Chl a points to zooplankton as the main (if not the only) food source for megafauna species on the top and flanks of the GB, in agreement with the results found over other seamounts (Fock et al., 2002; Genin and Dower, 2007).

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