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The snails' tale at deep-sea habitats in the Gulf of Cadiz (NE Atlantic)

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Abstract

Bridging the Atlantic and Mediterranean continental margins, the South Iberian region has recently been the focus for geological and biological investigations. The Gulf of Cadiz (GoC) encompasses a great variety of deep-sea habitats that harbour highly diverse biological communities. In this study, we describe the taxa composition of gastropod assemblages from deep-sea habitats in the GoC and analyse the species distributional patterns in relation to their dispersal capabilities and substrate availability. Distinct gastropod assemblages were found at mud volcanoes, carbonate and coral sites, and organic-falls. Overall, the GoC comprises a high diversity of gastropods that include 65 taxa representing 32 families, 48 genera and 30 named species. The highest number of taxa was found at the highly heterogeneous carbonate province in the middle slope (500–1500 m depth), and higher abundance of individuals was observed in Captain Arutyunov mud volcano, one of the most active sites found in the GoC. Faunal similarities were found with Mediterranean cold-seeps (species- and genus-level) and other chemosynthetic environments in the Atlantic and Pacific Oceans (genus-level). Colonization experiments with organic substrata (wood and alfalfa grass) yielded high abundances of gastropod species. These organic inputs allowed the recruitment of local species but also of wood specialist taxa that were not known to occur in the GoC. Our results suggest that distribution of gastropod assemblages may be primarily determined by the occurrence of suitable habitats probably due to effect of the substrate type on feeding strategies and that larval development is not a limiting factor for colonization of the deep sea. However, the predominance of non-planktotrophy, and especially lecithotrophy, suggests that the trade-off between a more limited dispersal capability and the higher potential for self-recruitment may be favoured by the gastropod species inhabiting reducing environments and other patchily distributed deep-sea habitats. A network of suitable habitats that ensures connectivity of effective populations would explain the predominance and relatively wide distribution of short-distance dispersing

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Portuguese margins of the Gulf of Cadiz (GoC). Herein, we consider three sub-regions characterised by distinct geological, geochemical and biogenic features as described in detail by Rodrigues et al. (2011): the El Arraiche field (EA) encompasses several mud volcanoes in the shallow Moroccan margin; the carbonate province (CP) corresponds to an extensive bathymetric strip (700–1200 m) along the Moroccan and Spanish margins, characterized by the widespread of authigenic carbonates and fossil cold-water coral stands; the deep-water field (DF), mostly within the Portuguese margin includes several of the most active mud volcanoes in the region. Further details on GoC environmental settings are provided in Cunha et al. (2012).

2.1 Sampling

Macrofaunal samples were collected from numerous locations in the Gulf of Cadiz during 14 cruises carried out between 2000 and 2009 using a variety of quantitative and non-quantitative sampling gears and processed on board accordingly (Rodrigues et al., 2011). The material retained by a 500 µm mesh sieve was fixed in 70 or 96 % ethanol for further examination. Overall, gastropods were found in 58 samples from 21 locations (Fig. 1). The metadata of the sampling sites (including the sampling gear) are provided in Table 1 in the Supplement. Each sample was ascribed to one of four categories of substrate: (i) Soft (*S*) – mostly mud breccia from the craters and the flanks of MVs; (ii) Hard (*H*) – carbonate slabs, crusts, and chimneys, rocks (limestones and other lithologies) and coral framework usually collected from the vicinity of MVs; (iii) Mixed (*M*) – a mixture of mud breccia, small carbonate concretions and/or biogenic debris (coral rubble, shell ash) collected in the craters of MVs; and (iv) Organic (*O*) – wood. From the total of 58 samples, 40 were collected from MVs (Soft: 34; Mixed: 6) and were ascribed to one of the three bathymetric sub-regions (EA, CP, DF). Another 17 samples of Hard substrate were obtained from cold-water coral sites and only one sample corresponds to a naturally occurring wood fall (encountered during a ROV dive at the flank of Carlos Ribeiro MV).

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Additional samples were obtained from in situ colonization experiments (CHEMECOLI – CHEMOSYNTHETIC ECOSYSTEM COLONIZATION BY LARVAL INVERTEBRATES, (Gaudron et al., 2010) using three types of substrate – wood, dried alfalfa grass and carbonate. The artificial substrates were included inside Nylon net of 2 mm mesh allowing the colonisation of the substrates by metazoan larvae or juveniles but not by the adults of most species. Four sets of experiments were deployed and recovered after approx. 1 or 2 yr in Mercator (2 sets), Meknès (1 set) and Darwin (1 set) MVs using a ROV. After recovery, the different substrates were sub-sampled and processed for different purposes according a standardised protocol (Gaudron et al., 2010). Two thirds of each sample were kept for biodiversity studies and fixed in 95 % ethanol (one third) and formalin (one third). The whole sub-sample (not sieved) was sorted under a stereomicroscope. Artificial substrates included eight samples of Organic substrata (wood and dried alfalfa grass) and four samples of Hard substrate (carbonates).

2.2 Taxonomic identifications and data analyses

Gastropod specimens were identified to species level whenever possible. Several taxa were not yet matched with a species name but they were all sorted into putative species and ascribed a codename consistent throughout the samples. Therefore the estimated species richness can be considered accurate, although minor changes may be made in the future following more thorough taxonomic revisions of the material. This is the case of the specimens ascribed to the family Marginellidae, and genera *Coccopygia* and *Copulabyssia*, which may include more than one species. Species identifications were based on morphological observations of shells, radula and opercula using optical and scanning electron microscopy and critical point dried soft parts. Specimens were treated according to the methods described in Geiger et al. (2007). In many cases, species identification also requires DNA sequence analyses, which is currently in progress. Taxonomical considerations and descriptions of new taxa are in preparation and will be published elsewhere.

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also able to colonize wood and dried alfalfa grass not only in Mercator but also at the deeper Mecnès and Darwin MVs. *Obtusella intersecta*, on the other hand, occurs in the crater of Capt. Arutyunov MV and was able to colonise dried alfalfa grass in the shallower Mecnès MV.

5 3.3 Larval development

From the 65 gastropod species found in the GoC deep-sea habitats and experimental settings, 25 are lecithotrophs, another 17 species were considered as non-planktotrophic and only 11 species have larval shells typical of planktotrophic development. For the remaining 12 species type of larval development is unknown and could not be inferred from the available specimens (Fig. 2 and Table 2 in the Supplement). Non-planktotrophic species presumably have the lowest dispersal capability, but yet showed to have distributional patterns categorised mostly as Ubiquitous or Abundant (occurring usually in more than one substrate and in relatively high numbers) with only about 30 % classified as Singleton and Rare (Fig. 5). Planktotrophic species, on the other hand, have pelagic-feeding larval phases that are likely to result in greater transport distances. However, 82 % of the gastropod species with this type of development showed restricted distributions and occurred mostly in one type of substrate only as Singleton and Rare taxa (55 % and 27 %, respectively). Because lecithotrophic species have non-feeding pelagic larvae, their dispersal ability is assumed to be intermediate in relation to the other development modes; these species showed in fact a more even balance of Singleton and Moderate distributions (40 % and 36 %, respectively).

Our results do not show a relationship between a large distributional range and a planktotrophic development. The three species exhibiting wider bathymetric ranges (all mud volcano sub-regions) have distinct larval development – *A. acutecostata* is planktotrophic, while *P. echinata* and *P. porcupinae* have non-planktotrophic larvae. None of the four species with distribution ranging the two deeper sub-regions, CP and DF is planktotrophic; only one has lecithotrophic development and three are non-

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planktotrophic. Also most of the species occurring in various substrate types are non-planktotrophic.

4 Discussion

4.1 Abundance and distribution

This study provides the first report on the gastropod assemblages from mud volcanoes and adjacent deep-sea habitats in the Gulf of Cadiz. By using in many cases a 500 μm sieve we may have underestimated the species richness and abundances as most deep-sea gastropods have minute sizes (Geiger et al., 2007). Considerably higher abundances have been recovered from cold seep sites using 250 μm sieves (Ritt et al., 2012; Decker et al., 2011). Nevertheless, gastropods showed diverse assemblages in the GoC and, although practically absent in reference samples (hemipelagic sediments in the vicinity of mud volcanoes), they were among the dominant species in samples from Mercator, Darwin and Capt. Arutyunov MVs; these MVs are thought to be the most active respectively in the EA, CP and DF sub-regions considered in this study. Active gas bubbling was observed both in Mercator and Darwin (Vanreusel et al., 2009) and gas hydrates occur in the near surface at Capt. Arutyunov (Cunha et al., 2012). Gastropods are often found among the dominant taxa in several cold seeps (Levin, 2005 and references therein), but the highest abundances (over 30 000 ind. m^{-2}) were reported from frenalate habitats in the Håkon Mosby MV and Nyegga “pingoes” (Norwegian Margin, Decker et al., 2012). Decker et al. (2011) suggested that the presence of the high densities of gastropods is explained by geochemical conditions rather than by the presence of tubeworms. However, Governor and Fisher (2006) found that the physical structure provided by the tubeworms may be particularly important for the attendant epifauna in areas of high and intermediate fluid flow (more than in low-flow regions).

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Gastropod densities are much more modest in the GoC than in the Håkon Mosby MV but, on the other hand, species richness is among the highest reported from cold seeps. In the GoC a total pool of 43 species were collected from mud breccia and mixed sediments in the MVs' craters; 17 species were recorded in Darwin MV alone, which is more than the total of 11 species reported for the Anaximander and Olimpi regions in the E Mediterranean (ca. 1700–2000 m water depth; Olu-Le Roy et al., 2004). Other studies with species level resolution mention even lower gastropod species richness: five species in the Marmara Sea (Ritt et al., 2012), five species in the Barbados (1000–2000 m, Olu et al., 1997) and eight species in tubeworm and mussel habitats in the Gulf of Mexico (1000–2750 m, Cordes et al., 2010b).

There is a high similarity at genus and even at species level between the gastropod fauna in the seeps of the E Mediterranean (Olu-Le Roy et al., 2004), Marmara Sea (Ritt et al., 2012) and GoC (this study). The trochid species *P. wiseri* appears to be particularly common across these three geographical regions, often associated with carbonates or mixed substrata. Like the majority of gastropod species found in seeps and vents, *P. wiseri* is a presumed grazer that explores opportunistically the increased bacterial biomass. About half of the genera recorded in the GoC (26 out of 48) are also known from other reducing habitats (vent, seep and organic-falls) (reviews by Sasaki et al., 2010; Decker et al., 2011; Ritt et al., 2012). In fact, there is some consensus about the possible, and in some cases confirmed, overlap in the distribution of heterotrophic seep species with other deep-sea environments characterized by sulfidic, low-oxygen, or disturbed sediments (Bernardino et al., 2010; Levin et al., 2009). Apparently many gastropod species in the GoC occurred exclusively in one type of substrate (*H*, *M*, *S*, *O*) but this analysis is confounded by the very high percentage of singletons. If we remove single occurrences the number of species found exclusively in one substrate type is similar to the number of species occurring in two or more substrata. Moreover, the colonization experiments showed that many gastropods (12 species) occurring in the MV sediments and hard substrata were also able to recruit on organic substrata.

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4.2 Species replacement with depth

The patterns of species replacement with depth in the North Atlantic are well documented for several taxa; in general the shelf-slope break shows the most pronounced transition in species composition. A more continuous but high rate of replacement is observed at bathyal depths, and lessens at abyssal depths (Rex, 1981). Regions of conspicuous faunal change have been explained by: (i) temperature mean and variation; (ii) differential adaptation to hydrostatic pressure; (iii) topography; (iv) effects of sedimentary pattern and substrate type on feeding strategies; and (v) the effects of deep boundary currents on larval dispersal (Rex, 1981). For our dataset, the pattern of substrate types (point iv) seems to be of particular relevance. High rates of change in the gastropod assemblages occur at the most active MVs and may be related to the increased availability of food sources for grazers (microorganisms, detritus). A higher trophic diversity can also be sustained by these productive ecosystems: some species are commensals or parasitic on polychaetes (e.g. *Odostomia* spp., *Eulimella* spp., Sasaki et al., 2010) or on echinoderms (e.g. Eulimidae, Sasaki et al., 2010) and large buccinid carnivores are often seen actively foraging at the craters of mud volcanoes (e.g. *Neptunea contraria* at Mekkès MV and an undetermined species at Capt. Arutyunov MV; M. R. Cunha, personal observation, 2006). Moreover, the highest overlap of species distributions is observed at the depth range between 500 and 1500 m coinciding with the increased habitat heterogeneity promoted by the widespread occurrence of carbonate concretions, carbonate chimneys and scleractinean coral framework and rubble. The perception of structurally complex habitats with distinct niche dimensions is dependent on the size, mobility and dispersal capability of the organisms enabling diverse ways of exploiting resources (Cordes et al., 2010a).

4.3 Dispersal and connectivity

The artificial substrata deployed for colonization experiments (CHEMECOLI) proved to be very efficient in the collection of all range of individual sizes, from recruitment

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to reproductive maturity, including a high number of recently settled juvenile stages. CHEMECOLI deployments in the GoC retrieved a higher number of gastropod species than similar experiments in the Håkon Mosby mud volcano (1257 m) and the cold seeps at Nile Deep Sea Fan (1693 m) (Gaudron et al., 2010). Regardless of the differences
5 in sample processing, artificial organic-falls yielded high abundances of gastropod species compared to the numbers obtained in background mud volcano sediments. These organic inputs not only allowed proliferation of species already occurring in their vicinity (e.g. *Pseudosetia* spD and *Xylodiscula* spA), but also favoured the recruitment of species only known from relatively distant MVs (e.g. *A. cimicoides* and *O. intersecta*), and also wood specialist taxa (Cocculinidae, *Copulabyssia*, *Xyloskenea*, *Bathyxyllophila* and cf. *Lissospira*) that were not found in the natural GoC deep-sea habitats. Larval development is known for 17 of the 20 species collected in organic substrates, and only two species are planktotrophic. Remarkably, most of the taxa developing through an obligate feeding pelagic phase were rare in the mud volcano sediments. In contrast, short distance dispersal, resulting into high self-recruitment, may be a favoured strategy at ephemeral, sparsely distributed reducing habitats, as suggested by the predominance and ubiquitous distributions of non-planktotrophic species. As many propagules show a negative exponential survival with distance from the parent, an elevated colonisation rate would be anticipated with proximity to the larval pool, i.e. the parental habitat (MacArthur and Wilson, 1967).

Planktotrophic larvae, transported over large distances by ocean currents, are assumed to allow wider geographical distributions and low genetic differentiation of populations. But a long pelagic duration (planktotrophic) may lead to extremely low propagule concentrations and therefore low levels of recruitment. On the other hand, non-planktotrophic development is often associated with narrow distributions and high levels of endemism (Castelin et al., 2011). These assumptions have proven to be unrealistic for species colonizing deep-sea chemosynthetic habitats. Several examples are found in the literature that showed no noticeable difference in distribution between species with a planktotrophic larvae, a non-feeding dispersal phase or those that crawl
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directly out of the egg-capsule (Sasaki et al., 2010). Although the type of larval development is not a limiting factor for the dispersal of deep-sea gastropods, our results show a preponderance of non-planktotrophic and especially lecithotrophic over planktotrophic development in the gastropod species inhabiting the studied deep-sea habitats. A remarkable discovery of a new development strategy of Provannid gastropods (the Waren's larvae) called attention to how much is yet unknown regarding life histories in the deep-sea, and also challenged the assumption of phylogenetic conservative reproduction and development modes (Reynolds et al., 2010).

Among the gastropod taxa found in the GoC, three species are also found in the Eastern Mediterranean cold seeps, but only *B. macra* is known to have planktotrophic development. The present knowledge of oceanographic circulation indicates that planktonic larvae can be transported into the Mediterranean from the Atlantic by inflowing surface currents, while Mediterranean Outflow water would only allow transport in the opposite direction at 50–300 m depth (Quentel et al., 2011). Mediterranean bottom waters may hinder the successful establishment of species (at the time of metamorphosis or at the time of reproduction) due to its hydrographical characteristics, including high temperature and high salinity. This led Bouchet and Taviani (1992) to postulate that Mediterranean deep-sea fauna represents reproductive sterile pseudopopulations that are constantly dependent on pelagic larval inflow from Atlantic source populations. To understand the consequences of different larval development modes that affect population connectivity, divergence time among populations and changes in effective population sizes must also be considered (Hart and Marko, 2010). Larval dispersal potential and connectivity between populations of marine invertebrates are highly affected by local hydrodynamics that can create significant variability in gene flow and recruitment at different temporal and spatial scales (Bell, 2008).

Colonization of patchy habitats, such as wood and bones, by non-planktotrophic larvae, with limited dispersal ability, is yet rather intriguing. Relying on dispersal by crawling adults does not seem to explain colonization of organic-falls and other reducing habitats, often separated by hundreds or thousands of kilometres. Other authors

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- continental margins, preliminary results of investigations during the TTR-16 cruise of RV Professor Logachev, May–June, 2006, IOC Technical Series, 76, 2008.
- Bell, J. J.: Connectivity between island Marine Protected Areas and the mainland, *Biol. Conserv.*, 141, 2807–2820, 2008.
- 5 Bernardino, A. F., Smith, C. R., Baco, A., Altamira, I., and Sumida, P. Y. G.: Macrofaunal succession in sediments around kelp and wood falls in the deep NE Pacific and community overlap with other reducing habitats, *Deep-Sea Res. I*, 57, 708–723, doi:10.1016/j.dsr.2010.03.004, 2010.
- Bernardino, A., Levin, L., Thurber, A., and Smith, C.: Comparative composition diversity and trophic ecology of sediment macrofauna at vents seeps and organic falls, *Plos One*, 7, e33515, doi:10.1371/journal.pone.0033515, 2012.
- 10 Bouchet, P. and Taviani, M.: The Mediterranean deep-sea fauna: pseudopopulations of Atlantic species?, *Deep-Sea Res. I.*, 39, 169–184, 1992.
- Bouchet, P. and Warén, A.: Ontogenetic migration and dispersal of deep-sea gastropoda larvae, in: *Reproduction, larval biology, and recruitment of the deep-sea benthos*, edited by: Young, C. M. and Eckelbarger, K. J., Columbia University Press, New York, 98–117, 1994.
- 15 Castelin, M., Puillandre, N., Lozouet, P., Sysoev, A., Forges, B., and Samadi, S.: Molluscan species richness and endemism on New Caledonian seamounts: Are they enhanced compared to adjacent slopes?, *Deep-Sea Res. I*, 58, 637–646, 2011.
- 20 Colwell, R. K., Mao, C. X., and Chang, J.: Interpolation, Extrapolating, and comparing incidence-based species accumulation curves, *Ecology*, 85, 2717–2727, doi:10.1890/03-0557, 2004.
- Cordes, E. E., Cunha, M. R., Galeron, J., Mora, C., Olu-Le Roy, K., Sibuet, M., Van Gaever, S., Vanreusel, A., and Levin, L. A.: The influence of geological, geochemical, and biogenic habitat heterogeneity on seep biodiversity, *Mar. Ecol.-Evol. Persp.*, 31, 51–65, doi:10.1111/j.1439-0485.2009.00334.x, 2010a.
- 25 Cordes, E. E., Hourdez, S., and Roberts, H. H.: Unusual habitats and organisms associated with the cold seeps of the Gulf of Mexico, *Topics in Geobiology*, 33, 315–331, doi:10.1007/978-90-481-9572-5_10, 2010b.
- 30 Cunha, M. R., Rodrigues, C. F., Génio, L., Hilário, A., Ravara, A., and Pfannkuche, O.: Macrofaunal assemblages from mud volcanoes in the Gulf of Cadiz: abundance, biodiversity and diversity partitioning across spatial scales, *Biogeosciences Discuss.*, 9, 18331–18369, doi:10.5194/bgd-9-18331-2012, 2012.

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- de Haas, H. and Mienis, F.: Cruise Report R.V. Pelagia Cruise M2005 (64PE237): Cold Water Corals and Carbonate Mound Formation at the Pen Duick Escarpment (Gulf of Cadiz) and Rockall Bank : 19 May–8 June (Leg 1, Lisbon – Galway), 9 June–19 June 2005 (Leg 2, Galway – Galway), Royal NIOZ, 2005.
- 5 Decker, C., Morineaux, M., Van Gaever, S., Caprais, J.-C., Lichtschlag, A., Gauthier, O., Andersen, A. C., and Olu, K.: Habitat heterogeneity influences cold-seep macrofaunal communities within and among seeps along the Norwegian margin. Part 1: macrofaunal community structure, *Marine Ecology*, 33, 205–230, doi:10.1111/j.1439-0485.2011.00503.x, 2011.
- 10 Gaudron, S., Pradillon, F., Pailleret, M., Duperron, S., Le Bris, N., and Gaill, F.: Colonization of organic substrates deployed in deep-sea reducing habitats by symbiotic species and associated fauna, *Mar. Environ. Res.*, 70, 1–12, 2010.
- Geiger, D. L., Marshall, B. A., Ponder, W. F., Sasaki, T., and Warén, A.: Techniques for collecting, handling, preparing, storing and examining small molluscan specimens, *Molluscan Res.*, 27, 1–50, 2007.
- 15 Hart, M. and Marko, P.: It's About Time: Divergence, Demography, and the Evolution of Developmental Modes in Marine Invertebrates, *Integr. Comp. Biol.*, 50, 643–661, 2010.
- Hurlbert, S. H.: The nonconcept of species diversity: a critique and alternative parameter, *Ecology*, 52, 577–586, 1971.
- 20 Ivanov, M., Kenyon, N., Comas, M., Pinheiro, L., and Laberg, J.: Shipboard Scientific Party, 2009. Introduction to the TTR-17 results, Geo-Marine Research on the Mediterranean and European-Atlantic Margins, International Conference and TTR-17 Post-Cruise Meeting of the Training-through-Research Programme, Granada, Spain, 2-5, 2009.
- Jablonski, D. and Lutz, R. A.: Larval Ecology of Marine Benthic Invertebrates – Paleobiological Implications, *Biol. Rev. Camb. Philos.*, 58, 21–89, 1983.
- 25 Kenyon, N., Ivanov, M., Akhmetzhanov, A., and Akhmanov, G.: Interdisciplinary geoscience research on the north east Atlantic margin, Mediterranean Sea and Mid-Atlantic Ridge. Preliminary results of investigations during the TTR-12 cruise of RV “Professor Logachev”, June–August 2002, 2003.
- 30 Kenyon, N., Ivanov, M., Akhmetzhanov, A., and Kozlova, E.: Interdisciplinary geoscience studies of the Gulf of Cadiz and Western Mediterranean basins: preliminary results of investigations during the TTR-14 cruise of RV Professor Logachev July–September, 2004, IOC Technical Series, 70, 2006.

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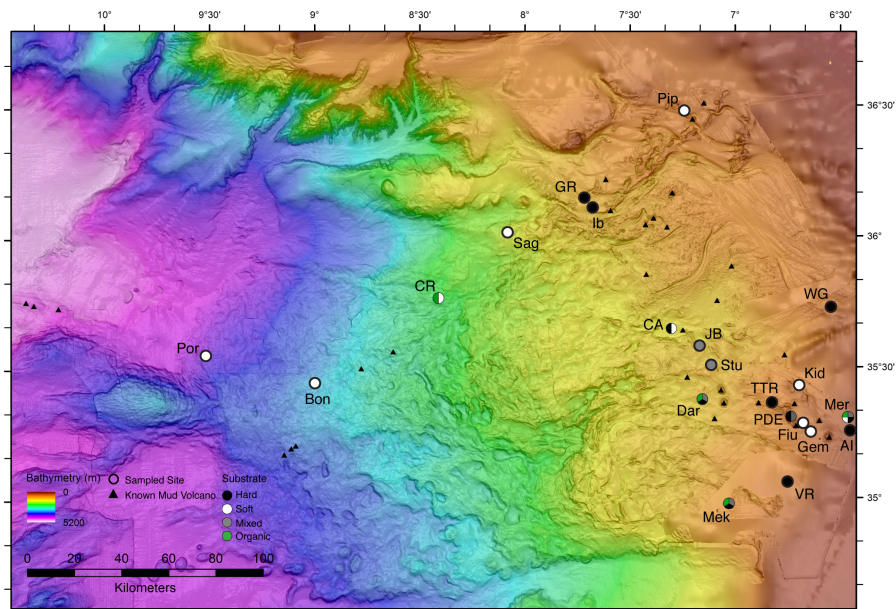


Fig. 1. Map of the study area (Gulf of Cadiz) showing samples locations. Multi-coloured circles represent several samples with different substrate types. Al: Al Idrisi MV; Bon: Bonjardim MV; CA: Captain Arutyunov MV; CR: Carlos Ribeiro MV; Dar: Darwin MV; Fiu: Fiúza MV; Gem: Gemini MV; GR: Gaudalquivir ridge; Ib: Iberico MV; JB: Jesus Baraza MV; Kid: Kidd MV; Mer: Mercator MV; Mek: Meknès MV; PDE: Pen Duick Escarpment; Pip: Pipoca MV; Por: Porto MV; Sag: Sagres MV; Stn: Student MV; TTR: TTR MV; VR: Vernadsky ridge; WG: West of Gibraltar Strait.

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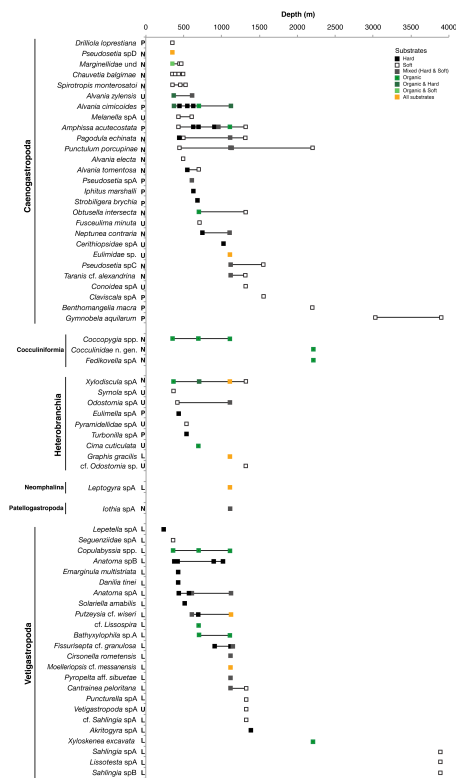


Fig. 2. Bathymetric distribution of the gastropod taxa collected in the Gulf of Cadiz. Type of larval development is indicated after each taxon's name. *P*: planktotrophic; *L*: lecithotrophic; *N*: non-planktotrophic; *U*: unknown.

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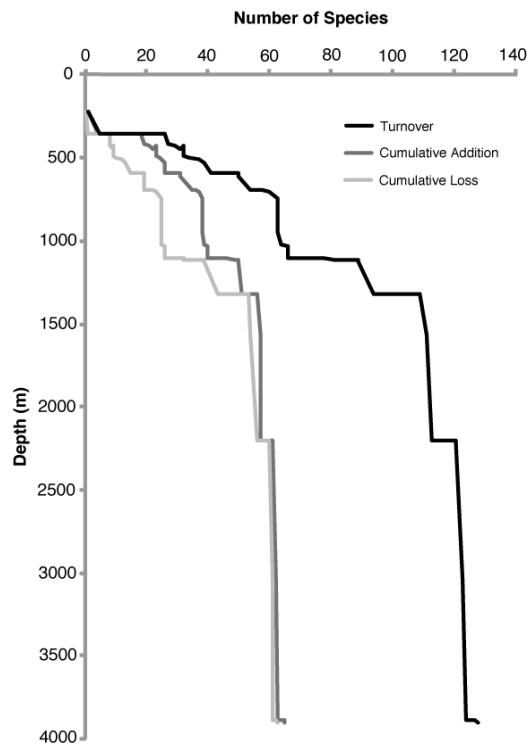


Fig. 3. Regional accumulation, loss and turnover of gastropod taxa along the depth gradient in the Gulf of Cadiz.

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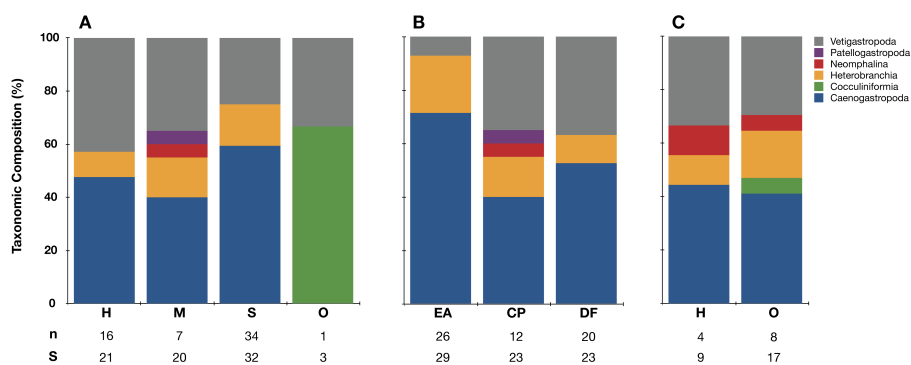


Fig. 4. Taxonomic composition of gastropod assemblages at the Gulf of Cadiz (GoC) deep-sea habitats. **(A)** Comparison between different substrate types. **(B)** Comparison of mud volcano assemblages at different GoC sub-regions. **(C)** Comparison between Hard and Organic artificial substrata from in-situ colonization experiments. Figures below bars indicate the number of samples (n) and the number of species (S) in each assemblage. *H*: Hard; *M*: Mixed; *S*: Soft; *O*: Organic; *EA*: El-Araiche; *CP*: Carbonate Province; *DF*: deep field.

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