

**The snails' tale at deep-sea habitats**

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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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non-planktotrophic species at the GoC deep-sea habitats and other geographical regions.

## 1 Introduction

Understanding biodiversity, and how the faunal assemblages interact with physico-chemical and geological aspects of the deep-sea, is far from complete. The discovery of highly productive communities at chemosynthetic sites (hydrothermal vents, cold seeps and large organic food falls), and the unsuspected frequency of cold-water coral reefs, where species richness and diversity rivals that of their tropical counterparts, completely changed our perception of the deep-sea environment. The combination of geomorphologic, hydrographic, geochemical and biotic features of continental margins generate habitat heterogeneity at spatial scales ranging from centimetres to kilometres, and tens to hundreds of kilometres (Levin and Sibuet, 2012). According to the habitat heterogeneity hypothesis, structurally complex habitats lead to an increase in species diversity by providing a higher number of distinct niche dimensions and diverse ways of exploiting resources (see Cordes et al., 2010a). This is the case of the Gulf of Cadiz region (NE Atlantic) where the interaction of the structurally complex convergent tectonic setting and hydrographical circulation favour the occurrence of a particularly diverse array of deep-sea habitats; these habitats include mud volcanoes, carbonate concretions and cold-water corals that sustain rich biological communities. Gastropods play a relevant role in this vast seepage region; they account for up to 5 % of total macrofaunal abundance in the best-sampled mud volcanoes and rank among the dominant species in the most active ones (Cunha et al., 2012).

Despite the recognized importance of gastropods in deep-sea communities, both in terms of diversity and biomass (Bernardino et al., 2012; Levin, 2005; Ritt et al., 2012; Decker et al., 2011), very little is known on their distributional patterns. Gastropods are often highly abundant in reducing ecosystems (Sasaki et al., 2010) but while the gastropod vent fauna is fairly well known, the cold seep taxa are less studied, because

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seep gastropods are often part of a vast and more diverse surrounding fauna (Sasaki et al., 2010). Gastropod species are also known from organically enriched habitats such as sunken wood and bones (Sasaki et al., 2010), but there is little information on the gastropod fauna associated with cold-water corals and other hard substrate deep-sea habitats (Young, 2009). Gastropods have been often the focus of studies investigating reproduction and dispersal in the deep-sea environment (Bouchet and Warén, 1994; Rex and Warén, 1982). Life-history traits (e.g. egg size, type of larval development, larval feeding behaviour) can be inferred from the larval shell that remains usually well preserved in the adult (Sasaki et al., 2010). Species with a feeding pelagic larval stage (planktotrophic larvae) are assumed to extend their distributions to wider geographical ranges. By contrast, non-planktotrophic species, which develop using a maternal energy source (e.g. lecithotrophic species, brooders, intracapsular development), have little potential of long-distance dispersal, and therefore, have more restricted distributions (Sasaki et al., 2010). Information on life history traits and dispersal of deep-sea species is vital to understand species distributions and the connectivity of highly patchy and fragmented deep-sea habitats.

Samples collected in the Gulf of Cadiz during the past decade, encompassing various habitats over a large depth range, complemented by in-situ colonization experiments, provided an opportunity to investigate distribution patterns of gastropods and their potential affinity with different substrate types. We compiled information on larval development of each species and inferred their dispersal capabilities. Our working hypothesis is that species distributions are the outcome of the interaction of dispersal capability and habitat selection and/or substrate availability.

## 2 Material and methods

The present work reports on samples collected from mud volcanoes (MVs) and adjacent habitats such as fossil cold-water coral stands, carbonate chimneys and carbonate concretions at depths between 250 and 4000 m along the Moroccan, Spanish and

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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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The bathymetric range of each species in the region was assessed and the total dataset of taxa was used to draw accumulation, loss and turnover curves representing the species replacement with increasing depth (Colwell et al., 2004; Uglund et al., 2003; Hurlbert, 1971). Data on density (ind. m<sup>-2</sup>) of gastropods in quantitative samples (USNEL boxcores; area: 0.25 m<sup>2</sup>) and their relative contribution to the total macrofaunal abundance was obtained from Cunha et al. (2012). Each taxa was then classified into one of five categories of distribution: (i) Singletons – corresponding to single occurrences, (ii) Rare species - two or three individuals found at one substrate type, (iii) Moderate – more than three and less than 10 individuals found in one or more substrate types, (iv) Abundant – taxa with more than 10 individuals found in two substrate types, and (v) Ubiquitous – taxa found at all three substrata.

Finally, distributional patterns were compared for each of three dispersal strategies: planktotrophic, non-planktotrophic and lecithotrophic. Type of larval development was obtained from available data in the literature (Table 2 in the Supplement), or inferred from protoconch morphology using the “Thorson’s apex theory” (Jablonski and Lutz, 1983) and comparisons to closely related taxa with known development mode. We consider that planktotrophic larvae have an obligate feeding pelagic stage, while non-planktotrophs develop using a maternal energy source. Non-planktotrophic strategies include life cycles with a non-feeding pelagic phase (herein designated loosely as lecithotrophic), brooders and intra-capsular development. In some cases, information compiled in the literature allowed to ascribe species to the non-planktotrophic subcategory of “lecithotrophs” (Table 2 in the Supplement).

### 3 Results

A total of 2362 gastropod specimens were examined and ascribed to 65 taxa (Fig. 2). Caenogastropoda is the most diverse subclass (27 species in 15 families), followed by the Vetigastropoda (24 species in 11 families) and the Heterobranchia (9 species in 3 families). Less diverse were the Cocculiniformia with three species all belonging

to the family Cocculinidae, including one new genus that waits formal description and the Patellogastropoda and Neomphalina represented by only one species each. A high proportion (35 %) of taxa were singletons, and more than half (63 %) of the species was recorded in just one or two samples.

The most striking feature of the observed bathymetric distribution of gastropods is the high number of species with overlapping distributions at the middle slope (500–1500 m) contrasting with the scarce number of species at greater depths (Fig. 2). The accumulation, loss and turnover curves (Fig. 3) reflect the scarcity of data at great depths where few locations were sampled, and highlight the three major locations of species replacement: the Mercator MV (EA) (18 species added and 8 lost), the Darwin MV where more species are lost than gained (13 and 10, respectively), and Captain Arutyunov MV where ten species from the shallower areas have their deepest limit, and first occurrence was recorded for six taxa.

### 3.1 Species distributions

The taxonomic composition of gastropod assemblages shows a distinct variation according to the substrate type (Fig. 4a). The number of Vetigastropoda and Heterobranchia taxa showed little variation (7–9 and 2–5 species, respectively) among Hard, Soft and Mixed substrata. On the other hand, the Caenogastropoda were represented by a much higher number of taxa in Soft sediments (19 in opposition to 8 and 10, respectively in “Mixed” and “Hard”), and clearly dominated the assemblage of this substrate type. Mixed sediments showed the most even distribution of the different major taxonomic groups (Fig. 4a) and were the only substrate where Patellogastropoda and Neomphalina occurred. The only sample representing organic substrate (a small wood fall collected at the flanks of Carlos Ribeiro MV) yielded only three species from which two were Cocculiniformia (Cocculinidae n. gen. and *Fedikovella* sp.), a group that was never found in the other substrata. The number of species occurring exclusively in Soft sediments was much higher (22) than the one observed exclusively in Organic (3) or

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Hard (12) substrata. The remaining 22 taxa were found either in Mixed substrate or in more than one type of substrate (7 and 15 respectively).

A total of 21 taxa were found in Hard substrate samples from carbonate and coral habitats usually located in the vicinity of MVs, with little or no influence of the cold seeps (Fig. 4a). Most samples were collected in the Pen Duick Escarpment located in the El Arraiche and several other samples are scattered along the upper slope of the Moroccan and Spanish margins (Table 1 in the Supplement). Very low numbers of individuals were collected from these habitats, and the majority of species were singletons. The Caenogastropoda *Alvania cimicoides* (6 individuals) and *Alvania zylensis* (5), and the Vetigastropoda *Putzeysia wiseri* (6) and *Anatoma* spB (6) were the most common species, but the two Caenogastropoda were restricted to shallower depths.

Mixed and Soft sediments represented respectively by 6 and 34 samples were collected from mud volcano sites (except for one Mixed sample from Pen Duick escarpment). In fact, the mud volcanoes were the main sampling target of this study and their gastropod assemblages were the best characterized, with a total of 42 species collected (Fig. 4b). From these, 14 species were present in EA, 20 in CP and 19 in DF and only eight species were shared between different bathymetric sub-regions. Vetigastropoda were poorly represented in the shallower mud volcanoes (EA: 1 species) that were clearly dominated by Caenogastropoda (10 species; 70 % of the total species richness, Fig. 4b). The carbonate province includes only Mixed sediment samples and therefore shows the most even taxonomic composition of all three mud volcano regions (Fig.4a–b).

Three Caenogastropod species showed a wide bathymetric range and were found across the three sub-regions, *P. porcupinae* (5 samples), *P. echinata* (10 samples) and *A. acutecostata* (11 samples). The major contributors to the species richness in each region were the assemblages from Mercator (EA, 350 m), Darwin (CP, 1100 m) and Captain Arutyunov MVs (DF, 1300 m) with 8, 17 and 11 species, respectively. Marginellidae were always abundant in the faunal assemblages from the crater of Mercator accounting up to 4.9 % of the total abundance (Cunha et al., 2012). The crater of Darwin

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MV is covered with large authigenic carbonate slabs and therefore quantitative samples are not available for estimates of abundance. However the neomphalin *Leptogyra* spA was the most abundant gastropod collected using a suction sampler in mytilid beds from this MV – this gastropod occurred exclusively in this MV. An undetermined vetigastropod (Vetigastropoda spA), the rissoid *Obtusella intersecta* and the xylo-disculid *Xylodiscula* spA were the fourth, fifth and sixth most dominant species in the macrofaunal assemblage associated with gas hydrates in Captain Arutyunov MV (5.7, 4.9 and 2.9% of the total macrofaunal abundance, respectively; Cunha et al., 2012).

### 3.2 Colonization of artificial substrata

CHEMECOLI experiments were densely colonised by gastropods, in particular the wood substrate and the alfalfa grass deployed in Meknès and Darwin. Overall, the colonization experiments showed high diversity at the major taxonomic level (Fig. 4c). Colonization of the carbonate substrata was generally scarce, and only a few gastropod species (9) were collected from the experiments deployed in Mercator (*Pseudosetia* spD, 26 specimens), Meknès (*Xylodiscula* spA, one individual) and Darwin (seven taxa, 15 individuals). The eight samples of experimental organic substrates yielded a total of 17 taxa (Fig. 4c). Pseudococculinids were by large the dominant taxa – *Copulabyssia* spp. was the most abundant taxa especially in Meknès and Darwin with over 1200 individuals collected, followed by the cocculinid *Coccopygia* spp. with a couple of hundred individuals. Much lower numbers (21 *Copulabyssia* spp. and 3 *Coccopygia* spp.) were also collected in Mercator. Preliminary DNA results suggest that two cryptic species may be present in these sites. These species had never been found in typical mud volcano settings in the GoC. Colonization experiments showed that several species (12) occurring in the mud volcanoes can also explore opportunistically organic substrata. These include abundant species such as *Xylodiscula* spA (Mercator, Meknès and Darwin MVs), Marginellidae and *Pseudosetia* spD (Mercator MV), and *Leptogyra* spA (Darwin MV). Interestingly the rissoid *Alvania cimicoides*, found in carbonate and coral sites at Pen Duick Escarpment (in the vicinity of EA MVs), was

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also able to colonize wood and dried alfalfa grass not only in Mercator but also at the deeper Mekkès 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 Mekkès MV.

### 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

5 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  $\mu\text{m}$  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  $\mu\text{m}$  sieves (Ritt et al.,  
10 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.  
15 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.  $\text{m}^{-2}$ ) 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  
20 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 Olimp 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 cofounded 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.

## 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 Meknès 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 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*, *Bathyxylophila* 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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suggested an alternative dispersal strategy by rafting (Sasaki et al., 2010), where individuals could stay afloat and drift a long distance attached to gliding objects (e.g. small wood chips). Another possible explanation for widely distributed non-planktotropic species in deep-sea habitats would be the so-called stepping-stone hypothesis, which relies on the colonization of additional intermediate sites found between distant seeps and/or sunken wood and bones. Considering the size-scale of deep-sea gastropods, and their primary nutrition strategies (grazing and detritus feeding), additional habitats may in fact be very frequent. The possibility of connectedness of reduced sediments is not difficult to envisage; this would provide suitable habitats allowing survival and reproduction of individuals and the persistence of populations. The large number of singletons in our samples suggests that the GoC deep-sea gastropod fauna may be more frequent and diverse than reported here. Consequently, the occurrence of small effective populations may be common; these can serve as larval sources for colonization of highly productive but patchily distributed habitats, such as wood and bone falls and sites with various seepage regimes.

**5 Concluding remarks**

It is expected from its geographical position that Gulf of Cadiz deep-sea gastropod fauna includes species from Atlantic and Mediterranean areas. Our study confirms this hypothesis and gives new evidence for connectivity of deep-sea gastropod communities inhabiting reducing environments. This work also shows that substrate type, with its associated biotic and abiotic characteristics, has a determinant effect on gastropod distribution in the deep-sea, and a diversity of feeding types combined with a variety of dispersal strategies contributes to their successful colonization of deep-sea habitats. Moreover, our work suggests that various deep-sea habitats form a network of suitable environments, which enhances diversity and ensures connectivity of deep-sea gastropod populations. Future research should focus on species-level taxonomy, population dynamics and genetic structure. Mapping of deep-sea habitats and a better

knowledge of local and regional hydrography are also of utmost importance in order to better understand current species distributions and potential population connectivity across ocean basins.

**Supplementary material related to this article is available online at:**

**<http://www.biogeosciences-discuss.net/10/3707/2013/bgd-10-5-3707-2013-supplement.pdf>.**

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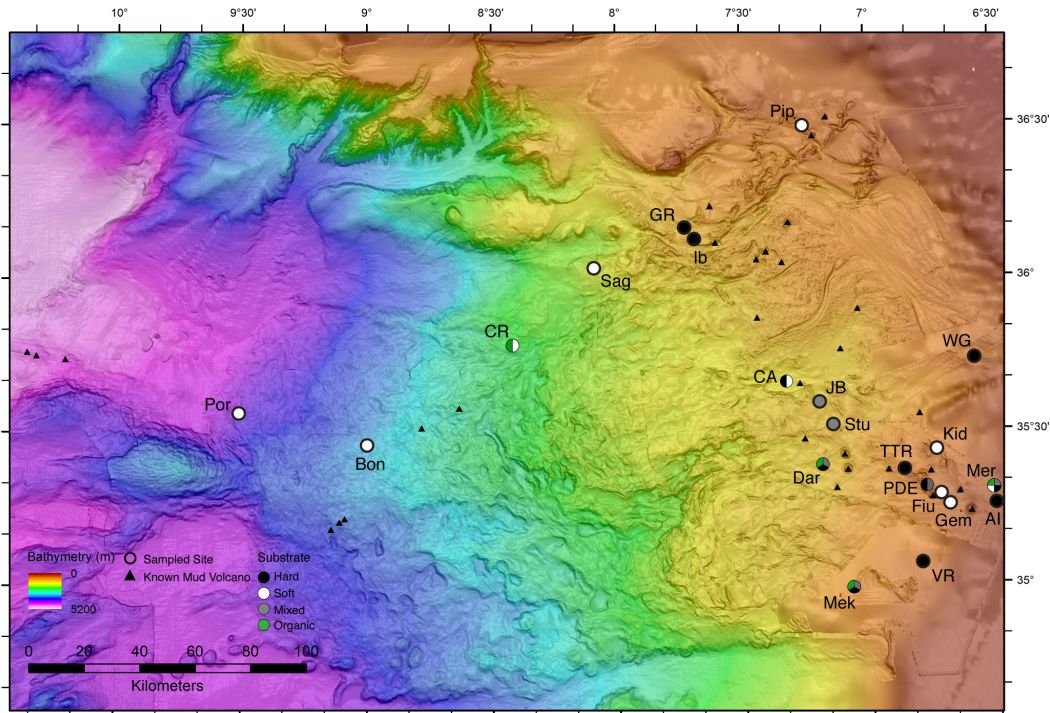
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**Fig. 1.** Map of the study area (Gulf of Cadiz) showing samples locations. Multi-coloured circles represent several samples with different substrate types. Al: Al Idrisi MV; Bon: Bonjardim MV; CA: Captain Arutyunov MV; CR: Carlos Ribeiro MV; Dar: 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; Stu: Student MV; TTR: TTR MV; VR: Vernadsky ridge; WG: West of Gibraltar Strait.

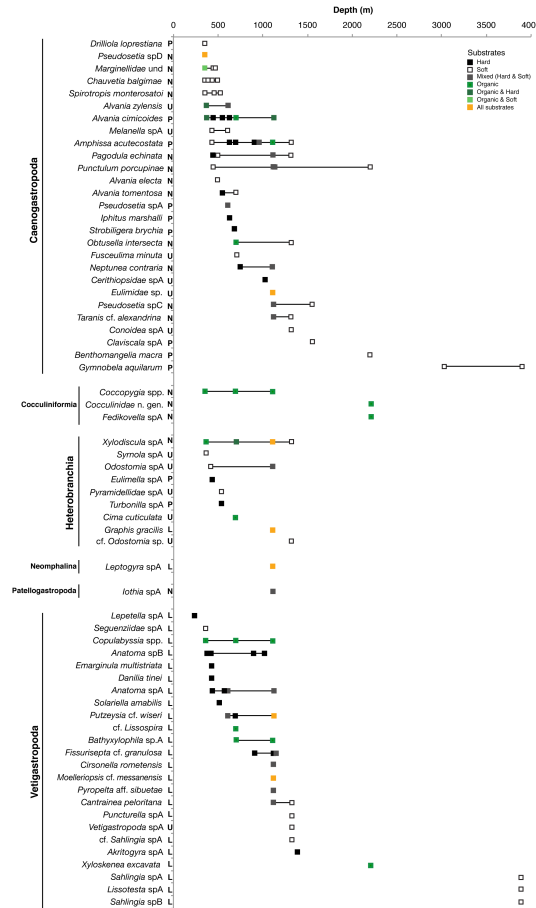
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**Fig. 2.** Bathymetric distribution of the gastropod taxa collected in the Gulf of Cadiz. Type of larval development is indicated after each taxon's name. *P*: planktotrophic; *L*: lecithotrophic; *N*: non-planktotrophic; *U*: unknown.

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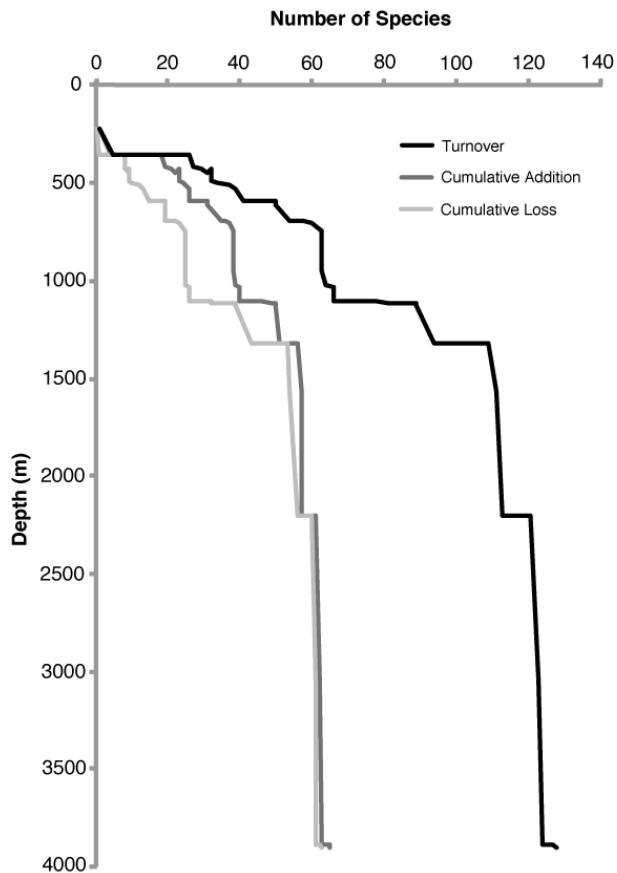
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**Fig. 3.** Regional accumulation, loss and turnover of gastropod taxa along the depth gradient in the Gulf of Cadiz.

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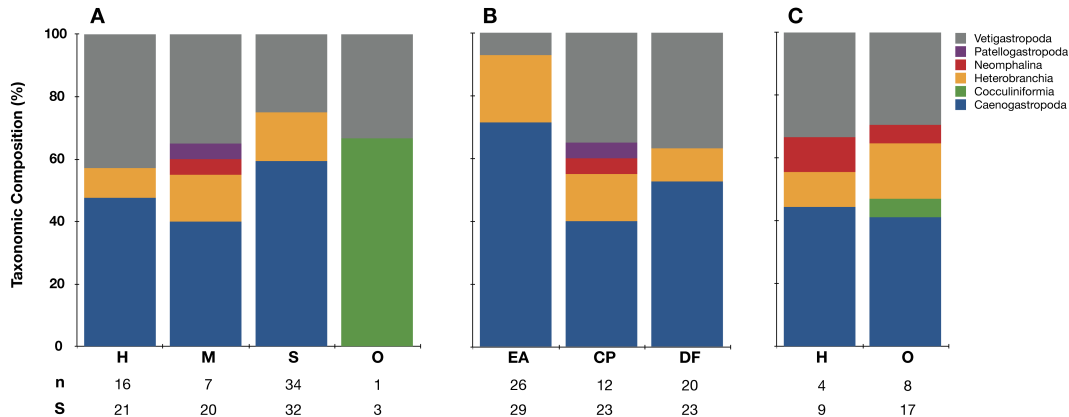
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**Fig. 4.** Taxonomic composition of gastropod assemblages at the Gulf of Cadiz (GoC) deep-sea habitats. **(A)** Comparison between different substrate types. **(B)** Comparison of mud volcano assemblages at different GoC sub-regions. **(C)** Comparison 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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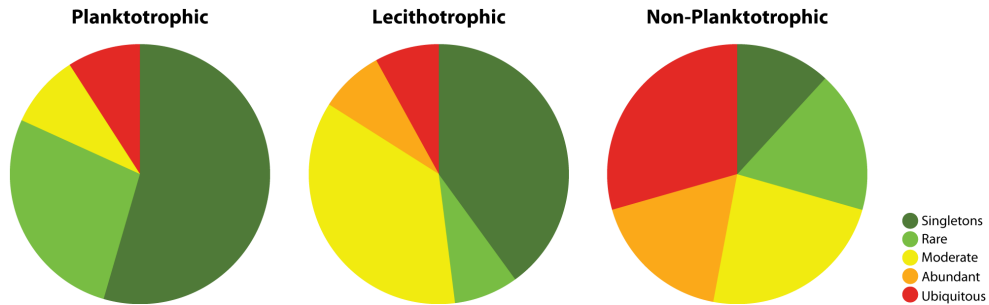
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**Fig. 5.** Distributional patterns of Gulf of Cadiz deep-sea gastropod taxa with distinct larval development types. See text and Supplementary Table 2 for explanation of distribution categories and larval development data.

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