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Interactive comment on "The snails' tale at deep-sea habitats in the Gulf of Cadiz (NE Atlantic)" *by* L. Génio et al.

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We would like to acknowledge the comments and useful suggestions of the anonymous reviewer and we hope to respond satisfactorily to his criticism. Our answers to each of his specific comments are given below.

R1: General Comment: Although I thought that this paper could be an interesting contribution, as it reports a number of gastropod taxa from different types of environments and depth in the gulf of Cadiz where gastropod fauna is poorly known, this paper has still many weaknesses that required clarifications and analyses. The paper focus on mud volcano gastropod fauna, but some of them are presently inactive in the Gulf of Cadiz, and therefore the study includes a wide heterogeneity of habitats, much higher than in most of the other cold-seep studies focussing on active seepages.

AU: The Gulf of Cadiz includes in fact a wide heterogeneity of habitats and this what makes it so interesting. All the mud volcanoes that we mention in our ms are active as proven by the diversity of chemosymbiotic species (see Rodrigues et al. in this special issue of Biogeosciences), the presence of fresh mud breccia at or very near the surface (see Supplementary Table 1) and the geochemical characteristics of their sediments and pore water (see Cunha et al. in this special issue of Biogeosciences and references therein). The seepage is, in most cases, much milder than in other geographical regions, but during the explorations of the Gulf of Cadiz the mud volcano label was only ascribed after detecting at least some of these characteristics. Inactive structures (no seepage) were named “mounds” or “diapirs” depending on their characteristics.

R1: Moreover, data include sampled in “adjacent habitats” mainly represented by carbonate outcrops likely resulting from old seepages. This should be better considered in the different sections of the paper, in order to compare the observed gastropod fauna not only with active seep habitats, but also with other deep-sea environments, including soft and hard substrata.

AU: The age of the carbonates is irrelevant for the purpose of this paper because we are focusing on the influence of the type of substrate (hard, soft/sedimentary, organic). The variations in properties and intensity of seepage are not sufficiently well documented (at the sample level) to be taken into account with detail.

R1: I am very disappointed to see any consideration to my first comments (short review) with the most important are: - Site description: because of the very high heterogeneity at different spatial scales, it is important to give more information about the sites and habitats, even if chemical or visual observation is not available (e.g. did the cores from the mud volcanoes indicated a sulfidic environement: sulphide smell, black sediments?), in which habitats have the experimental devices been deployed.

AU: Because we have 22 different sites and to avoid a lengthy paper, the description of the study area is referred to previous publications of the team (Rodrigues et al. 2011

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and Cunha et al 2013). We modified the text in Material and Methods in order to include some additional information but the available details on each specific sample are given in Supplementary Table 1. Sulphide smell is not mentioned although the occurrence of mud breccia is almost always associated with variable intensities of sulphide smell. Chemical information from the studied MVs was obtained from gravity cores which were taken at variable distance from the biological samples. Due to the high spatial variability even within a single MV these measurements may be taken only as indicative of the conditions in each MV. The colonization experiments were always deployed in the craters of the MVs – this is indicated in Supplementary Table 1 and now also clarified in material and methods: "Four sets of experiments were deployed on the craters of Mercator (2 sets), Meknès (1 set) and Darwin MVs (1 set), and recovered after approx. 1 or 2 years using a ROV."

R1: The mixing of results from samples taken in the natural environment and from experiments that should be presented separately before comparison. It is not possible to distinguish both sources of samples in the results (Table 1, Fig 1, Fig 3, Fig4). It is interesting to present together both set of data but it should be clearer of which data is considered for each analysis.

AU: As requested by the reviewer we separated the experimental samples in the first revision of the ms; this can be verified in the material and methods and Fig. 4 (Fig.4A is the comparison between substrate types of the 58 samples from the natural environment; Fig 4B is the comparison of the three sub-groups of MV samples only and Fig 4.C is the comparison between hard and organic substrata in colonization experiments only. We have now extensively revised the Material and Methods sections 2.1 and 2.2, and caption of Fig 4 to make this clearer. In relation to Figs 2 and 3 it makes no sense to separate the different samples because we are representing the bathymetric distributions of each species. Fig 1 is a map of the 22 sites (some with more than on sample). Substrate types are indicated but it would result into a very busy figure to represent also here each individual sample (58 + colonization experiments). Again

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we revised the text in Material and Methods for clarification and we added more information to Fig. captions: Fig 1 we added “Colonization experiments were deployed in Mercator, Meknès and Darwin MVs”. Fig2 and 3 we added: “Data from all samples and experiments are included”

R1: The sampling effort has to be estimated in order to validate or discuss more carefully the results (e.g. high % of singletons): was the diversity completely sampled? (rarefaction curves based on area of sampling, or on number of individuals)

AU: Diversity is hardly ever completely sampled especially in such a rich area. The high percentage of singletons may be by itself an indication that the sampling effort must be increased, but taking into account that we have 58 gastropod samples in 22 sites we think that this is a good sampling effort for deep-sea standards. Also, the 58 samples are only the ones yielding gastropods – we collected over 250 samples in the region (this information is now included in the ms – section 2.1. Sampling) We are not using rarefaction curves here because the focus of the ms in on the analysis of distributional patterns- the abundance-occupancy relationships, species ranges and their affinity to the substrate types and for this objective it is more useful to include all information available albeit the inevitable heterogeneity. A paper on taxonomical aspects will be prepared in the future and we hope to include some biodiversity analyses- e.g. rarefaction curves. However these will have to be performed on selected subsets of the gastropod data in order to restrain the influence of sampling heterogeneity.

R1: Diversity analyses (accumulation, loss and turnover curves representing the species replacement with increasing depth: fig.3) have been performed on the total dataset of taxa. However, quantitative data are only available for 14 of the 58 samples (USNEL cores) and the sampling effort is highly heterogeneous between sub-regions, depths and substrata types. Several conclusions are based on this sampling bias (influence of depth, substrata, sub-region, mud volcano, on species turnover, species richness). The diversity cannot be compared if it is not related to sampling effort (sampling area, or at least number of samples or number of sampled individuals).

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AU: Turnover is envisaged as an assessment of the distributional pattern of gastropod assemblages resulting from the overlap of the species bathymetric ranges. Quantitative samples are not required to describe bathymetric ranges, the simple information on presence/absence is sufficient. Also, the carbonates and corals occur only within a certain bathymetric range and MVs are much less in the deeper field: Yes, our results are constrained by the distribution of the studied habitats because these are also affecting our sampling effort along the bathymetric gradient. But the distribution patterns will always be conditioned by the distribution of the study habitats themselves and our focus is on the mud volcanoes and their adjacent habitats. Note also that: 1) our total macrofaunal set is much larger; 2) the number of gastropod samples in each substrate type and in each mud volcano is mentioned (e.g. numbers below graphs in fig.4); 3) the number of mud volcanoes in each sub-region is rather balanced (4, 4, 5). We now added in several occasions throughout the text the number of samples to which values of species richness refer to.

R1: Specific comments Introduction P3709 line 8 If they have been recognized as biodiversity hotspots with enhanced species richness and evenness as well as distinct composition (e.g (Henry & Roberts 2007), coral reefs cannot be considered as "where species richness and diversity rivals that of their tropical counterparts, completely changed our perception of the deep-sea environment

AU: Although we do not understand the incompatibility in the phrasing, the statement "where species richness and diversity rivals that of their tropical counterparts" can be removed. We propose to change the text to: "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 completely changed our perception of the deep-sea environment."

R1: P3710 Line 7 Other reference about reproduction and dispersal of seep gastropods could be added: - Eckelbarger KJ, Young CM (1997) Ultrastructure of the ovary and oogenesis in the methane-seep mollusc Bathynerita naticoidea (Gastropoda: Neritidae)

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from the Louisiana slope. Invertebrate Biology 116:299-312 - Hodgson AN, Eckelbarger KJ, Young CM (1998) Sperm morphology and spermiogenesis in the methane-seep mollusc Bathynerita naticoidea (Gastropoda: Neritacea) from the Louisiana slope. Invertebrates Biology 117:199-207 - Young CM, al. (2012) Dispersal of Deep-Sea Larvae from the Intra-American Seas: Simulations of Trajectories using Ocean Models. Integrative and Comparative Biology 52:483-496

AU: References have been added.

R1: P3710, line 11 Although discussed later in the paper, the authors present here a very simplified contrasted situation of planktotrophic vs non-planktotrophic species regarding their potential of dispersal (planktotrophs dispersing more than lecitotrophs) and inferred the dispersal capabilities of the different species based on the above simplified statement (lines 20-23). Nevertheless this is not always the case in the deep-sea, as said by (Sasaki et al. 2010), or before by Tyler and Young 2009. There are several hypotheses for long distance dispersal of lecitotrophic larvae (see Sasaki) particularly for vent and seep species.

AU: In order to accommodate the reviewer concerns, in the introduction we replaced "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)." by "A feeding pelagic larval stage (planktotrophic larvae) is frequently assumed to favour widespread geographical distributions while larval retention would be more compatible with non-planktotrophic species, which develop using a maternal energy source (e.g. lecithotrophic species, brooders, intracapsular development) (Sasaki et al., 2010). However both long distance dispersal (enabling high rates of habitat occupancy) and self-recruitment owing to local larval retention (enabling high local abundances) are possible in planktotrophic and lecitotrophic dispersers (Shiling & Manahan, 1994;

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Young 1999, 2003; Pradillon et al, 2001; Swearer et al. 2002). Yet for brooders dispersal is often limited by the foraging range of adults."

R1: Material and Methods There are several problems in the site description and habitat characterisation: One is the hard substrate that is sometime attributed to carbonates (that may be related to cold seep)s or corals, and later to the CWC only.

AU: The Reviewer is right – this has been corrected.

R1: Another one is the description of the three sub-regions: the El Arraiche field (EA) and the deep-water field (DF) are described as mud volcanoes with the most active in the DF region. In contrast, the carbonate province (CP) is presented as a fossil area with carbonates and CWC.

AU: The sub-regions are only used for the Mud volcano samples. The text in Material and methods has been revised to clarify the categorization of samples.

R1: However, as seen in Table 1, Mussel beds (Bathymodiolus sp. I assume) have been described from some of the mud volcanoes of this area, so active seeps. I understand that the authors have chosen to separate the sub-regions according to substrate dominance but the occurrence of active seepage could be as important as substrate to understand fauna distribution.These 3 sub-regions should be indicated in Fig1, where only the mud volcano names are reported

AU: The caption of Figure 1 was altered: "The mud volcanoes are included in three sub-regions: i) El Arraiche: Al: Al Idrisi*; Fiu: Fiúza MV; Gem: Gemini MV; MV; Kid: Kidd MV; Mer: Mercator MV; ii) Carbonate Province: Dar: Darwin MV; Ib: Iberico MV*; JB: Jesus Baraza MV; Mek: Meknès* MV; Pip: Pipoca MV; Stu: Student MV; TTR: TTR MV*; and iii) Deep-water Field: Bon: Bonjardim MV; CA: Captain Arutyunov MV; CR: Carlos Ribeiro MV; Por: Porto MV; Sag: Sagres MV. In the MVs marked with * gastropods were only found in samples from hard substrata in adjacent habitats. The sites GR: Gaudalquivir Ridge; PDE: Pen Duick Escarpment; VR: Vernadsky ridge; WG:

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West of Gibraltar Strait are sites of accumulation of carbonate chimneys and concretions, and dead scleractinean framework."

R1: Are these regions corresponding to geographic areas? For some of them it seems (the carbonate province) but for other not (adjacent habitats). This has to be clarified.

AU: Bathymetric sub-regions (EA, CP, DF) are only used for mud volcano samples (sedimentary environment). Most samples from "adjacent habitats" are from depths shallower than 1200 m as the formation of authigenic carbonates and scleractinean skeletons are conditioned at greater depths (the carbonate accumulation rate decrease with increasing depth). The text in Material Methods has been revised for clarification.

R1: P3715, line 18 Sub-regions are described as "bathymetric sub-regions". However, adjacent habitats are not included in the first 3 sub-regions and encompasses the whole bathymetric gradient. The comparison of the number of species, or species composition between sub-regions, or along depth is therefore confusing (p3715 lines17-21)

AU: This paragraph refers only to the mud volcano samples. The paragraph has been revised for clarification: "Mud volcano samples consisted of Mixed (6 samples) and Soft sediments (34 samples). 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 – mud volcano samples only). From these, 14 species were present in EA (4 MVs; 15 samples), 20 in CP (4 MVs; 7 samples) and 19 in DF (5MVs; 18 samples) 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 Caenogastropods (10 species; 70% of the total species richness, Fig. 4B). In the deeper mud volcano sub-regions (CP and DF) the contribution of Caenogastropoda and Vetigastropoda was more balanced, but the highest diversity at the sub-class level (also at species level) was observed in the group of mud volcanoes from the Carbonate Province (Fig.4B)." The number of samples mentioned below Fig 4B was incorrect which may have added to the confu-

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sion – this has been now corrected and the caption of Fig. 4.B was also revised for clarification.

R1: Other inconsistencies: “flanks” are sometimes considered as “adjacent habitats”, sometimes in others (Mvs). E.g. Carlos Ribeiro JC10 54 MC 27.05.07 35_47.30’ 08_25.22’ 2179 Flank; Coral site NE; Hemipelagic sediments with coral debris Soft is in Deep field”/ Why not in Carbonate province? And why substrate is classified as “soft”? It seems rather “mixed?”

AU: The term flank is used as a topographical indication of the sample location not as a habitat. Therefore we have “Mud volcano” samples from the flank (soft sediments) and “Adjacent habitat” samples from the flanks (whenever rocks, carbonate concretions or coral framework were collected from these locations) – Supplementary Table 1 categorizes and describes very clearly each individual sample. Note that nowhere in the ms “flank” is used as describing a habitat type. The sample mentioned by the reviewer is from the flank of Carlos Ribeiro. It was collected from an area with Isidellidae bushes and numerous fragments of living octocoral were collected in the sample (the description in Supplementary Table 1 is now more precise and refers to octocoral fragments) – there is no doubt about the classification of the sample as “soft sediments”. Carlos Ribeiro is located at 2200m and therefore it is included in the Deep Field – the Carbonate Province includes the MVs within the bathymetric strip of 600-1200m.

R1: P3711, lines 24-25 This is unclear if hard samples are only from Cold Water Coral sites or also Carbonates from mud volcanoes: it has to be clarified.

AU: This has been clarified in the revised Material and Methods.

R1: There is also a confusion between the Mud Volcano (EA) and the carbonate (CP) provinces

AU: As explained in the categorization of samples the sub-regions are only used for the “mud volcano” samples. This has been clarified in the revised Material and Methods.

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R1: Material & Methods & Results The diversity cannot be compared if it is not related to sampling effort (sampling area, or at least number of samples or number of sampled individuals). - Diversity analyses (accumulation, loss and turnover curves representing the species replacement with increasing depth: Fig. 3 has been performed on “the total dataset of taxa”. However, quantitative data are only available for 14 of the 58 samples (USNEL cores) and the sampling effort is heterogeneous between sub-regions, depth and substrate type.

AU: This has been answered above - Turnover is envisaged as an assessment of the distributional pattern of gastropod assemblages resulting from the overlap of the species bathymetric ranges. Quantitative samples are not required to describe bathymetric ranges, the simple information on presence/absence is sufficient. Also, the carbonates and corals occur only within a certain bathymetric range and MVs are much less in the deeper field: Yes, our results are constrained by the distribution of the studied habitats because these are also affecting our sampling effort along the bathymetric gradient. But the distribution patterns will always be conditioned by the distribution of the study habitats themselves and our focus is on the mud volcanoes and their adjacent habitats. Note also that: 1) our total macrofaunal set is much larger; 2) the number of gastropod samples in each substrate type and in each mud volcano is mentioned (e.g. numbers below graphs in fig.4); 3) the number of mud volcanoes in each sub-region is rather balanced (4, 4, 5). We now added in several occasions throughout the text the number of samples to which values of species richness refer to.

R1: These curves highlight that “the three major locations of species replacement are the Mercator MV, the Darwin MV and Captain Arutyunov MV, that are the three sites with the highest sampling effort, what is not really surprising.

AU: Not all results are surprising but they still have to be described and demonstrated. Note that: 1) in Darwin MV we had only four samples with gastropods (plus colonization experiments) while for instance Meknès MV from the same sub-region was one of the best sampled (several boxcores –see Cunha et al. 2013- plus colonization exper-

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iments) and it showed low gastropod richness. 2) turnover curves are built from the overlap of species bathymetric ranges - it means that each species is “checked in” at the shallowest depth where it occurs” and checked out” at the greatest depth where it occurs regardless of the irregularities of its distribution in between these depths.

R1: In the same way, the fact that “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” has to be discussed according to the sampling effort

AU: The number of samples was added to the phrase. This statement is relative and not absolute: of course these are the MVs with more samples with gastropods in each one of the three sub-regions but, as mentioned above, other MVs may have more samples albeit without gastropods (e.g. Meknès in CP and Porto in the DF).

R1: Again, the comparison of species richness among substrate type is not valid, for the same sampling bias. P3714, lines 26: from the dataset, it is observed that “the number of species occurring exclusively in Soft sediments was much higher (22) than the one observed exclusively in Organic (3) or Hard (12) Substrata”. However, there are more samples from Soft sediments (34) than from other substrate. This is not surprising that the diversity is higher and then the number of species occurring exclusively in this substrate higher.

AU: Changed to: “The number of species occurring exclusively in Soft sediments was higher (22 out of 32) than the one observed exclusively on Hard substrata (12 out of 21)." However, exclusivity is not necessarily correlated with richness within each group of samples (alfa-diversity); when the two groups are compared exclusivity reflects the degree of beta-diversity - if beta-diversity is high then the two groups groups are dissimilar and exclusivity is likely higher. Therefore by describing exclusivity we are informing on the degree of (dis)similarity between the groups of samples.

R1: The colonisation experiment revealed that some species may have a larger bathy-

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metric range that observed by sampling in natural environment (page 3716, from line 25 to end of the paragraph). These observations have to be considered in discussing the results. May be the favourable habitat is absent, but may be it has not been sampled.

AU: This is discussed in section 4.3.: "Considering the size-scale of deep-sea gastropods, and their primary feeding habits (bacterial grazing and detritus feeding), additional habitats may in fact be very frequent. As demonstrated by our colonization experiments gastropod species that are common in the mud volcanoes are also able to colonize organic falls. Also, some of the species that colonised these organic substrata were previously known only from relatively distant location in the Gulf of Cadiz (i.e. they were not known to occur in the local background fauna). The possibility of connectedness of adequate habitats for deep-sea gastropods is therefore not difficult to envisage; this would allow survival and reproduction of individuals and the persistence of populations."

R1: Concluding remarks From concluding remarks list, those are supported by the data, other not. 1. 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. Yes

AU: We agree

R1: 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. NO, as sampling effort inappropriate (too heterogeneous)

AU: The text has been changed to: "Our results also support the hypothesis that the highest biodiversity of gastropods at the upper bathyal region is related to the strong

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gradients and habitat heterogeneity at these depths. Different substrate types, in particular, are determinant for the structural complexity of the habitat and/or availability of food sources and are successfully colonized by gastropods with different larval development modes and feeding types."

R1: 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. Yes, with combination of experimental and sampling approaches.

AU: We agree.

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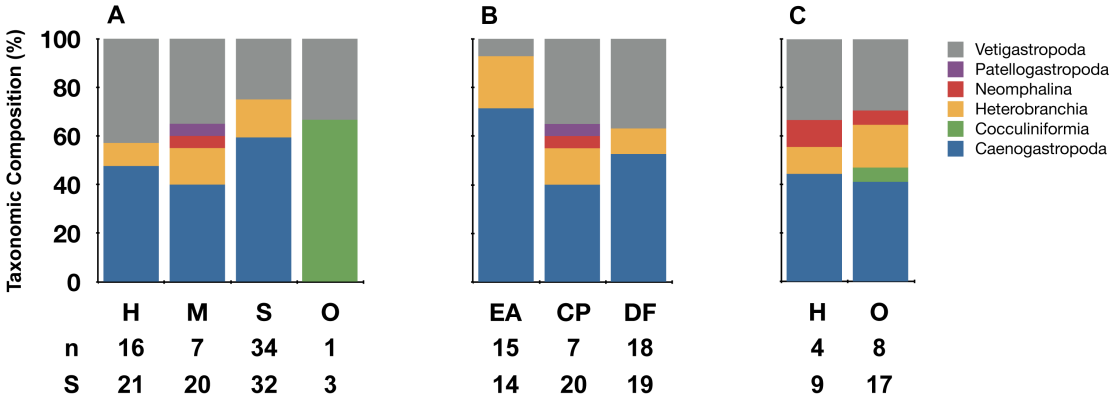

Fig. 1. New Figure 4

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