Biogeosciences Discuss., 9, C8498–C8508, 2013
www.biogeosciences-discuss.net/9/C8498/2013/

Biogeosciences Discussions

Interactive comment on "An overview of chemosynthetic symbioses in bivalves from the North Atlantic and Mediterranean Sea" *by* S. Duperron et al.

S. Duperron et al.

sduperro@snv.jussieu.fr

Received and published: 25 February 2013

Dear editor, please find below our detailed answers to reviewers comments.

Anonymous Referee #1 Received and published: 17 December 2012 General comments The manuscript "An overview of chemosynthetic symbioses in bivalves from the North Atlantic and Mediterranean Sea" presents a thorough synthesis of the state of current knowledge regarding the ecology, life cycle, and connectivity of five bivalve families (Mytilidae, Vesicomyidae, Solemyidae, Thyasiridae and Lucinidae). As the focus of this manuscript is clearly to review current knowledge, there is little new data presented. Thus, the major contribution of this work is to provide a concise overview

of the current research in this area, which it does quite well. The overall manuscript is well structured and with some additional revision, will be a good contribution to the field. C6649

Thanks for the overall positive comments. Providing an overview, as up-to-date as possible, was the objective of the work, and indeed there is little new data provided (pictures of Fig. 3 mostly). We have reworked the manuscript in order to answer points raised by reviewers, and also to correct errors and add a few references that were not in the former version. We also had the manuscript edited by S. Laming, native English speaker. We hope the new version will be suitable for publication in Biogeosciences.

Specific comments Pg 16830 L16-17 - How is E. guiness typical of vesicomyid symbioses? More specific details would be helpful here.

Details were added “E. guiness was found to display a very typical vesicomyid symbiosis, as documented in many other species around the world (Duperron et al., 2012). This species indeed displays a single symbiont 16S rRNA phylotype, with high similarity to other vesicomyid-associated symbiont sequences available in Genbank, and sulphur metabolism is supported by the presence of the APS reductase encoding gene and by carbon stable isotope values in the range of those reported for seep vesicomyids (Olu et al. 2009).”

Pg 16844 L22-29 - What is it about the 1971 gastropod study that actually provides a viable counterpoint to the 2012 study, given the 40 year time interval? More detail would be helpful here as the comparison is not very convincing as currently presented.

Scheltema demonstrated that gastropod larvae that were planctotroph were able to cross the Atlantic Ocean. Because these larvae present some similarities (shape and size) with bivalve larvae, we cited this study as an example of a work showing that trans-Atlantic dispersal is possible, even if not demonstrated in the case of chemosymbiotic species. We have changed the sentence to “In an early study, Scheltema (1971) had demonstrated that several planktotrophic gastropod larvae, similar in size and

BGD

9, C8498–C8508, 2013

shape, were capable of crossing and dispersing throughout the Atlantic using diverse currents, which indicates that the hypothesis of trans-Atlantic dispersal needs to be considered" and hope this makes it clearer.

Technical corrections In general, the flow of this manuscript would be improved by a detailed review by a native English-speaker. It becomes difficult to read, at times, due to the presence of run-on sentences and somewhat awkward phrasing (e.g. pg 16818 L27-28) The use of semi-colons to break apart some of these long sentences would help improve the flow of the manuscript (e.g., lines 6-13, pg 16823). In some instances, such as pg 16835 L14-21, long lists of information might be better placed in a table.

We have reworked all sentences indicated above. As requested, we have included semi-colons, and cut sentences to make them shorter (see version with changes marked). We also had the ms edited by an Irish colleague to improve the English. We hope this is easier to follow now.

There were also a number of spelling and grammar mistakes (pg 16818 L18,pg 16819 L20, pg 16821 L13 (change to shells), pg 16825 L1 (change someway to somehow?), pg 16829 L24-25, pg 16830 L5 (change symbiont to plural), pg 16831 L16 (symbionts-based to symbiotic), pg 16832 L15-16, pg 16847 L5-7, and pg 16849 L24- 26. Thanks a lot for this detailed editing. We corrected the errors, and carefully checked for other errors.

Anonymous Referee #2 Received and published: 9 January 2013 The manuscript "An overview of chemosynthetic symbioses in bivalves from the North Atlantic and Mediterranean Sea" presents a synthesis of the state of the art regarding the ecology, life cycle, and connectivity of five bivalve families (Mytilidae, Vesicomyidae, Solemyidae, Thyasiridae and Lucinidae). There is barely new data presented, being the manuscript basically a synthesis of the existent data. It is an extensive review, and there are extensive parts that should be concise on a table. Sometimes is difficult to read, and I advise the authors to improve the English, and avoid terms like it seems, probably, etc.

BGD

9, C8498–C8508, 2013

We have edited the manuscript to shorten many sentences, clarify others, and get rid of words like 'it seems, probably", when not necessary. We hope the new version is easier to follow.

There is a lack of illustrations resuming the 3.1 ; 3.2; 3.3; 3.4 sections; A schematic view will help the readers to understand the comparison between the different families, relating with their habitats, symbionts and its functioning.

This criticism is justified, and we have tried to improve illustrations in the new version. We gave up the idea of a short short table summarizing the characteristics of the different families considered in our manuscript because a main point of our study is to emphasize ntra-family variatbility of symbioses, which justifies that studies should not be restricted to a few model species. However we made several changes to improve illustrations. 1) We added some data in the large table 1. 2) To illustrate connectivity, we have added symbols representing trans-Atlantic species complexes to Fig. 1. 3) Finally, we also added two illustrations as a single figure to explain dispersal mechanisms, and symbiont transmission (Fig 4A, and B). These points could appear complex in the text, and we think these illustrations will help reader to better visualize the different pathways of larval dispersal and symbiont transmission. With these new illustrations, we hope we answer this criticism.

Specific comments: Pag.16821 Line 15. This statement (Mussels occur: : :.most anoxic niches) is based on the work of Fisher et al; Desbruyeres et al; etc. and not from the authors work. The references shall be acknowledged.

This is done

pag 16824 Line 26: The authors refer to isotopic data, but no reference is given. Is the statement related to the scientific papers Trask and Vandover 1999 and Colaço et al, 2002?

This statement refers to the previous line (Duperron et al., 2011), this work includes

BGD

9, C8498–C8508, 2013

stable isotope data.

Page 16826 Line 20 What does the authors mean with " none of these seems to harbor methane –oxidizing symbionts"- They have or they do not have? Where is the data?

Sentence was changed to "Interestingly, molecular and microscopic data suggest absence of methane-oxidizing symbionts".

Page 16836 Line 20- "Microscopy indicates possible: : :.which could be epibionts"- this sentence is rather speculative

Yes indeed. Sentence was changed to "Microscopy also indicates possible Spirochete-like morphotypes located extracellularly on the apex of some bacteriocytes."

pag 16844 In this section the authors revise the current knowledge about the reproduction. No data or results are revised by the authors in what concerns Bathymodiolus azoricus, despite the existence of scientific papers from Dixon et al, 2006; Colaço et al; 2006 and Kadar et al, 2006.

in Table 1 we have summarized all the species reviewed in our paper that were either gonochoric or hermaphrodite and as well those that had a seasonality or a continuous breeding period. Bathymodiolus azoricus was documented in Table 1. We have added the example of B. azoricus with its references in the text (Dixon et al, 2006; Colaço et al; 2006)

Figures: Fig. 1. The names of the hydrothermal vents are not well placed. Rainbow is south of Lucky Strike and not North. There is the lack of the Moytirra vent field North of the Azores.

Thanks, this has been corrected. Also, we have added the 'trans-Atlantic' species complexes to the map, to illustrate the part about connectivity as requested in an earlier comment.

Also on the figure 1 caption is hard to understand. Authors shall use MAR- North to

BGD

9, C8498–C8508, 2013

South; Med- East to West; GoM East to West; African Margin- North to South. This way the reader will understand better the figure.

Names are now grouped by region as suggested.

Fig.3 is rather confusing, mixing gill filaments with gonads and juveniles from different species. This figure is not useful to the manuscript.

This figure illustrates some aspects of the association, and of the transmission. It is now supplemented by the two illustrations (Fig. 4) of symbiont transmission and larval dispersal. We think these photos, which illustrate lecithotrophy and planktotrophy side by side, as well as aspect of symbiosis associations, are a good complement to the text, and would prefer to keep them.

P. Dando (Referee) pdando@mba.ac.uk General comments The manuscript "An overview of chemosynthetic symbioses in bivalves from the North Atlantic and Mediterranean Sea" presents a detailed account of current knowledge on symbioses in the Mytilidae, Vesicomyidae, Solemyidae, Thyasiridae and Lucinidae. The review concentrates particularly well on the distribution of the bivalve species and differences in their bacteria. The ecology is les well studied, especially factors affecting competition between species of bivalves with symbionts and parameters controlling bivalve density and biomass. The Summary Table of species for which there is infor- mation about the symbiosis is particularly useful. The final manuscript should be a helpful summary of current knowledge in the field.

Thanks for the overall positive appreciation, and thanks a lot for the very useful and constructive comments provided below. Please find specific answers there. As mentioned, we focused the review on distribution / diversity of symbioses rather than ecological aspects, mainly because relevant ecological background data is often not provided (in particular for deep-sea species), and in most cases, not comparable between species and sites. Indeed physico-chemical data in particular, when present, was obtained using a variety of methods, space and time resolution, which does not allow a proper

BGD

9, C8498–C8508, 2013

comparison. Given the length of the manuscript, we would prefer not to include this data which we think would be more confusing than informative at this stage.

Specific Comments Nucinellidae and Montacutidae (Oliver & Taylor 2012) described two species of the Nucinellidae with bacteriocytes in the gill from an oxygen minimum zone in the Arabian Sea, off Oman, not the Atlantic, as stated on p16833. Although these authors regarded it as probable that the bacteria were sulphur-oxidisers there was no direct evidence for this. Oliver and Taylor (2012) do discuss related species in the Atlantic that might host bacterial symbionts but the gills have not been examined for these. Oliver et al. (2013) report symbiotic bacteria, of more than one morphotype, on the epidermis of specialised bacteriocyte cells in the gills of Syssitomya pourtalesiana (Montacutidae) from the Bay of Biscay, the Norwegian Sea and the Rockall Trough. This bivalve lives on the anal spines of the seep-sea echinoid Pourtalesia miranda. It was proposed that the bacteria obtained nutrients from the anal stream of the echinoid. A further unusual feature is that the bacteria were not covered by microvilli or a glycocalyx and large number of hemocytes were found above the bacteria, suggesting that the bacteria were ingested by hemocytes , for transfer into the bivalve, as well as by phagocytes in the bacteriocytes. These recent discoveries expand the families of bivalves in which symbiotic bacteria have been found and suggest further species and habitats to explore. The general deep-sea environments may prove to have as many symbiont-containing species as the seeps and vents.

Nucinellidae were already mentioned in the ms, and we have expanded a bit the introduction regarding them “Recent discoveries of associated bacteria in two families (Nucinellidae and Montacutidae) suggest further species and habitats should be explored (Oliver and Taylor 2012, Oliver et al 2013” . The Montacutidae are more problematic from our point of view. As pointed, they definitely have bacteria (and this has been added in our introduction). But the role of bacteria is elusive, it is indeed very likely that these are not chemosynthetic, given the type of habitat. Oliver et al actually pointed that in their paper. This is the reason why we did not discuss this symbiosis

BGD

9, C8498–C8508, 2013

any further. And indeed, we agree that there probably exist a diversity of chemosymbiotic species that are not associated with vents and seeps, as illustrated in sections dedicated to Vesicomyidae (genus Vesicomya) and Thyasiridae for example.

Idas The type species is Idas argentius. The recent, cited, paper by Ockelmann & Dinsen (2011) on this species makes it clear that I. simpsoni and related species do not belong in this genus. Until the taxonomy is clarified I suggest that you refer to such species as “Idas”, in quotes. “Idas” simpsoni has been reported from the Mediterranean (Pastorelli et al. 1999) as has another related whale-fall species “I” cylindricus (Pelorce & Poutiers 2009). Another “Idas” species was found, along with Spinaxinus sentosus, on organic cargo in the wreck of the FrancoisVieljeux (Dando et al. 1992). “Idas” simpsoni (and an unidentified “Idas”species) has been found in large numbers on an oil-coated cuttings pile (Hartley & Watson 1993) and it is possible that this species colonises natural oil seeps as well as organic falls.

We acknowledge early on that genera are often not monophyletic. The use of quotes is often recommended, to point that the genus in fact does not really correspond to anything. We acknowledge the use of names can be misleading. However, until a true reassessment and new names are introduced, we think using quotes does not really help readers. For example, the term “Bathymodiolus” or “Idas” (including quotes) can refer to several distinct genera that remain to be defined, so the use of quotes does not tell anything more. Given this limitation, using quotes would lead to a very high density or “” which might make it difficult to read. So if possible, and for readers convenience, we would prefer not to use quotes in the text. Regarding the occurrence of various Idas on other sites, we included these in the new version of the ms (section “Mytilidae): “Other Idas species have been associated with reduced environments. In the Mediterranean I. simpsoni and I. cylindricus have been associated with organic falls (Pastorelli et al 1999; Pelorce and Poutiers 2009). Another unidentified Idas was for example found on organic cargo in the wrecked François Vieljeux ship (Dando et al, 1992).”.

BGD

9, C8498–C8508, 2013

Thyasiridae Symbiosis has been investigated in more than 9 species of thyasirids in the area. (Southward 1986) reported studies 4 unidentified deep-sea species, two of which had symbiotic asociations, each with two morpholgically distinct bacteria. None of these bacteria contained sulphur vesicles and their energy source is unknown. At least some of the thyasirid species without symbionts contain peculiar gill cells with large and very abundant mitochondria, unlike the situation in normal bivalve gills (Southward 1986). These cells were surrounded by smaller cells like the intercalary cells in lucinids. Southward (1986) stated "The mitochondria seem, to some extent, to take the position of the symbiotic bacteria - - ". The 'mitochondria' of Mendicula (Thyasira) ferruginea are very electron dense.(Southward, 2006; Dufour 2005) It is possible that these unusual and numerous mitochondria are chemotrophic, oxidizing reduced compounds from the environment and generating ATP by electron transport phosphorylation, but the gills do not use this ATP to fix CO2. This has been shown for some other bivalves (Parrino et al. 2000), However, the generation of ATP would reduce the reliance on heterotrophic feeding. In the case of Mendicula ferruginea it is possible that the mitochondria generate ATP by the oxidation of Fe++. ATP generation by electron transport phosphorylation coupled to sulphide oxidation has been demonstrated also in mitochondria from some bivalves with symbiotic bacteria (O'Brien & Vetter 1990). Research is needed to explore whether all thyasirids are adapted to exploit reduced environments Reduced sources available to bivalves with sulphur-oxidising symbionts.

Thanks for this comment. We have included some points in the revised version (section Thyasiridae): "In addition, two unidentified species have been reported by Southward (1986) as having symbiotic associations, each with two distinct bacterial morphotypes, none containing sulphur vesicles" and "Another intriguing finding is the presence of peculiar gill cells displaying large and abundant mitochondria, unlike the situation in "normal" bivalve gills (Southward 1986). For example in Mendicula ferruginea, which is devoid of symbionts, it has been hypothesized that these structures might be generating ATP by oxidizing reduced compounds such as reduced iron, although this remains to be proven (Dando, pers. comm., 2013)". However, we did not provide all details not

BGD

9, C8498–C8508, 2013

to increase the length of the ms.

This review concentrates mainly on habitats with high concentrations of dissolved sulphide, whether at seeps, vents or inshore sediments with high organic loading. However, the majority of reducing sediments contain free ferrous ions, resulting in sulphide produced by sulphate-reducing bacteria being rapidly precipitated and low concentrations of dissolved sulphide, often < 0.1_M, within the burrowing range of bivalves. Despite such low concentration, bivalves with sulphur-oxidising symbionts inhabiti such sediments, their tissues being greatly depleted in 13C (Spiro et al. 1986). Many of the bivalves inhabiting such sediments, such as Thyasira flexuosa and Lucinoma borealis, have semi-permeable inhalent tubes. Experimental models, sulphur-isotope studies and microcosm and mesocosm experiments have shown that these bivalves can obtain the reduced sulphur compounds required by their symbionts through the partial oxidation of insoluble iron sulphides in the sediment either side of their inhalent tubes (Dando et al. 1994b, Dando et al. 2004). Lucinoma borelis and Myrtea spinifera are well adapted to this since they reposition theirinhalent tubes every few days, so tht eventually there is an inverted cone of oxidised sediment above the animals (Dando et al. 1986). Geochemical analysis suggests that such a system, of 'mining' the iron sulphides', is also used by the frenulates living on the continental slope (Dando et al. 2008), A habitat that might be exploited by bivalves with sulphur-oxidizing symbionts is the sediments, under the vent plumes, that have high concentrations of sulphide particles. The infauna in these sediments has been poorly sampled.

In the manuscript we do not provide detailed physic-chemical data nor physiology, because we focused more on what could be compared among species, and these data exist only for a few species. All this experimental work on Thyasiridae and Lucinidae is very interesting, and in fact we're currently trying to start experiments on coastal species, as these are less studied these days.

Ecology In the list of Atlantic cold seep sites that have been investigated the Skagerrak seeps, at more than 300 m, might be included. These have been the subject of over six

BGD

9, C8498–C8508, 2013

cruises and publications and are inhabited by the symbiont-containing Thyasira sarsi and T. equalis. The densities of these two species varied dramatically, with sulphide concentrations, over a distance of < 30 cm (Dando et al. 1994a). Similar studies have been made elsewhere, relating bivalve densities to sulphide concentrations. Some comparative data on the biomass of bivalves with chemosythetic bacteria in different Atlantic and Mediterranean habitats would be useful. A neglected area is resource partioning between different bivalve species with symbionts in the same habitat. As many as four such species can be collected in he same core sample at some sites.

Skagerrak has now been added. And regarding resource partitioning, we added a short sentence in the conclusion to emphasize that this question should be addressed in future studies, especially given that new methods (-omics, in situ microsensors) make it tractable. And in fact we're currently trying to address it in a few species (co-occurring mussel species and co-occurring vesicomyids).

Interactive comment on Biogeosciences Discuss., 9, 16815, 2012.