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Biogeosciences Discussions

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

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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 information about the symbiosis is particularly useful. The final manuscript should be a helpful summary of current knowledge in the field.

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.

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.

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.

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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 < 0.1μM, 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.

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 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

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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.

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