Spondylus crassisquama *Lamarck, 1819 as a microecosystem and the effects of associated macrofauna on its shell integrity: isles of biodiversity or sleeping with the enemy?*

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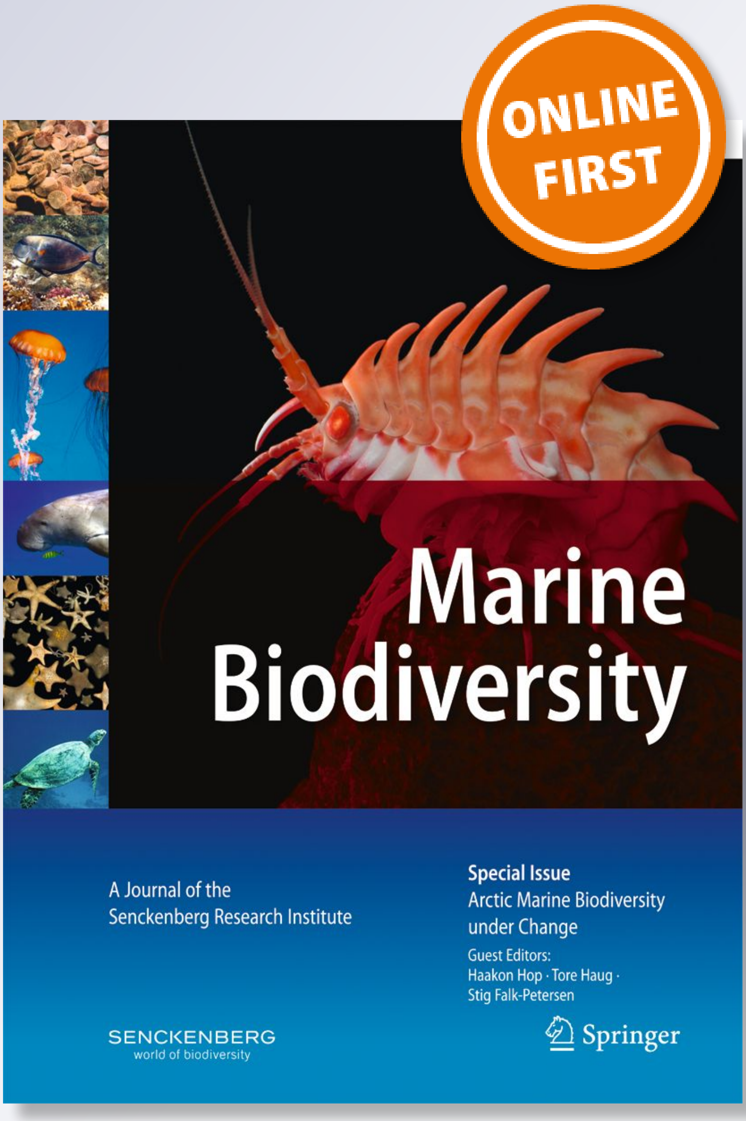

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Spondylus crassisquama Lamarck, 1819 as a microecosystem and the effects of associated macrofauna on its shell integrity: isles of biodiversity or sleeping with the enemy?

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Abstract In May 2009, we studied the bivalve *Spondylus crassisquama* and its relevance for macrobenthic biodiversity off the north Ecuadorian coast. We found that the large and heavy shells offer an exclusive substrate for numerous epibiont species and highly specialized carbonate-drilling endobiont species (71 species in total), which is a distinctly different and much more diverse habitat than the surrounding sandy bottoms (13 species, 4 of them found in both habitats). This is reflected by a Bray–Curtis dissimilarity index of 0.88. We discuss in detail the live habits of all 9 species of drilling endobionts that we found, and conclude that these can be seen as true mutualists, with the exception of boring sipunculids and bivalves. To further illustrate this complex co-existence, we visualize and quantify for the first time the tremendous effects of boring organisms on the shell structure of *S. crassisquama* by means of magnetic resonance imaging and a video appendix is provided.

Keywords *Spondylus crassisquama* · Ecuador · Habitat complexity · Macrofauna · Boring organisms · Nuclear magnetic resonance

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Introduction

"Habitat loss has not been as much a focus of marine science and conservation as in terrestrial environments", stated Airoldi et al. (2008), which they related partly to the limited knowledge of the extent and importance of these losses. Habitat loss is closely connected with the currently accelerated biodiversity loss. There are species in marine environments with roles that reach beyond straightforward functional interactions such as feeding or competition. These constitute key species of the respective community in terms of biodiversity and system functioning, particularly if they provide a unique habitat, i.e. biohabitats facilitating biodiversity. Examples of "large" biohabitats are trees on land or coral reefs in the marine realm that can provide habitat for hundreds of species, and the loss of such habitats has devastating effects on overall biodiversity and ecosystem function. Similar effects have been shown for seagrass beds (Duffy 2006) and kelp forests (Graham 2004). So far, "smaller" biohabitats such as the living space provided by mollusc shells have received less attention, most likely because of their apparently minor importance for maintaining biodiversity. Dead and living shells are abundant in most coastal and shelf systems, and few organisms seem to be confined to live on or in the shells of one particular mollusc species.

Our study targets the possibly unique case of the bivalve *Spondylus crassisquama* Lamarck, 1819, formerly known as *S. princeps* Broderip, 1833, off the Ecuadorian coast[1]. The large (height up to 170 mm) and heavy (over 2 kg)

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[1] See Huber (2009) for a recent scientific revision of the nomenclature of the *Spondylus* species in this area

shells of this species provide a hard substrate in an otherwise soft bottom environment. Moreover, the shell proper serves as an exclusive habitat for highly specialized carbonate-drilling endobiont species, which have hardly any other habitat along the Ecuadorian coast where reef-building corals are restricted to a few areas. During recent years, overexploitation almost wiped out the species in the coastal waters of Ecuador, and a complete fishing ban was announced in October 2009[2] to protect the remaining individuals of *S. crassisquama* and its conspecies *S. limbatus* Sowerby II, 1847, formerly known as *S. calcifer* Carpenter, 1857. Nevertheless, the ecological significance of this decline, particularly for local and regional benthic biodiversity, has not so far been considered.

Spondylus crassisquama is distributed from Baja California in the north to northwest Peru in the south (Lamprell 2006), in water depths down to 30 m, where it attaches to coral rocks, rocks, and occasionally to other shells (Skoglund and Mulliner 1996). In the province of Esmeraldas, *S. crassisquama* is mainly free-living on sandy, muddy, or pebble bottoms. Studies on the biology and ecology of *Spondylus* species are still scarce, though more work has been done on the outer shell structure and the taxonomic composition of shell epibionts and endobionts (Zavarei 1973; Logan 1974; Feifarek 1987; de León-González 1988; de León-González et al. 1993; Castro-Aguirre et al. 1996; Stone 1998; Mienis 2001; Carlson Jones 2003; Linero-Arana and Diaz-Diaz 2006). Yet open questions remain about the nature of the coexistence between *Spondylus* and their associated species: are we dealing with a form of parasitism, commensalism, or is mutualism more likely? Scientific dispute concentrates in particular on the spines, which may serve as direct defence against predators (Zavarei 1973; Logan 1974) or, alternatively, attract epibionts to settle and thereby create camouflage for the shell (Feifarek 1987; Stone 1998; Carlson Jones 2003). The latter hypothesis suggests mutualism between *Spondylus* and the associated species, where *Spondylus* provides habitat and a favorable feeding environment for the epibionts and endobionts in exchange for the effective camouflage. However, is mutualism a proper description regarding the highly active shell-drilling endobiont species? How much damage do they inflict on the shell, and is *Spondylus* able to prevent serious, i.e. life-threatening, shell damage? To facilitate this complex co-existence, we visualize (see 3-D movie in online appendix) and quantify for the first time the tremendous effects of boring organisms on the shell structure of *S. crassisquama* in terms of carbonate loss and shell damage with the help of magnetic resonance imaging.

Materials and methods

Qualitative macrofauna and -flora analysis

We collected ten *Spondylus crassisquama* individuals in two consecutive dives at depths between 17 and 19 m in the shallow waters off the coast of Atacames in the province of Esmeraldas, Ecuador (00°59.829′N, 079°57.531′W; Fig. 1). All individuals were placed in water basins with and oxygen supply, and all living organisms visible on the outer shell surface were collected for identification. The *S. crassisquama* were then sacrificed for a separate study on their reproductive cycle (Mackensen et al. 2011).

We fragmented the shells into pieces of 1 cm or less and collected all animals living inside the shell from the debris. At the same sampling site, we collected ten random samples of the bottom fauna by sampling the sediment within a plastic square with a surface area equivalent to the surface area of our average collected *S. crassisquama* shells down to 2 cm sediment depth into zip-log bags. All material was carefully washed in a 2-mm plastic sieve, sorted, and taxonomically identified as far as possible. All organisms were photographed and then preserved in alcohol (animals) or dried and attached to paper sheets (algae).

We calculated the Bray–Curtis dissimilarity index for the two different types of habitat (shell vs. sediment) with the following equation:

$$BC_{ij} = T_{ij}/S_i + S_j$$

where T_{ij} corresponds with the total number of species unique to each of both habitats and S is the total number of species of one habitat.

MR imaging and quantitative analysis

Due to the extreme laborious analysis listed below, this part of our study comprised three shells. By means of magnetic resonance imaging (MRI), we visualized the meshwork of boreholes and its total volume within the shells of *Spondylus crassisquama*. The dried and cleaned shells were placed in a water-filled exicator to remove all air out of the boreholes and channels of the shells. Subsequently, the water containing one of the shells was poured into a plastic container that was placed inside the MR scanner for MR imaging. A 4.7 T Biospec DBX system (Bruker-Biospin, Ettlingen, Germany) was used for all MRI scans. Signal excitation and reception were acquired using a ^{1}H cylindrical resonator (20 cm diameter) adapted for high conductivity samples. Gradient echo scout scans in all three directions were collected prior to all measurements to correct for the correct position of the shells in the center of the MRI scanner. After all optimizations, three-dimensional multi-slice multi-echo images (3D-

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[2] "Acuerdo Ministerial Nr. 136 publicado en el Registro Oficial Nr. 58 el 30 de octubre de 2009"

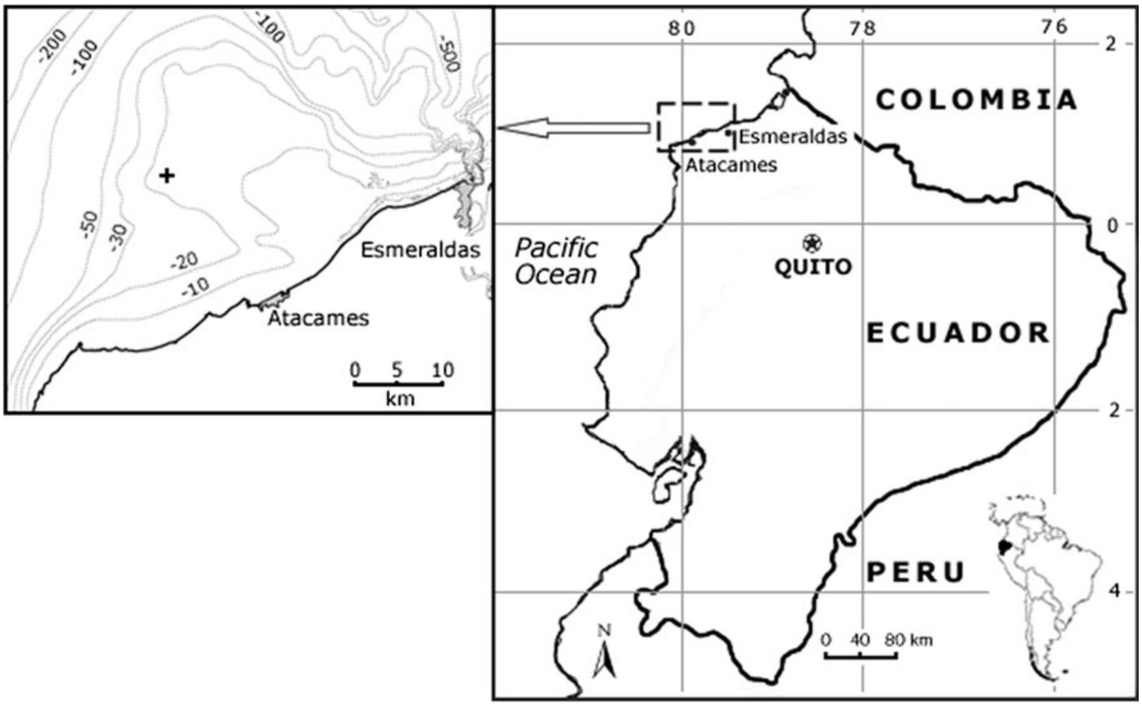

Fig. 1 Northern Ecuador showing the study site (*cross*)

MSME) were collected in a coronal direction using the following parameters: matrix size: 256×256×64; field of view (FOV): 15×15×10 cm; repetition time TR: 1,000 ms; echo time TE: 14.6 ms; resulting scan time 9 h 6 min 8 s, in plane resolution: 586 µm.

Totals of 64 (sample shell 1) to 128 (sample shells 2 and 3) pictures, respectively, were extracted from the particular MR scans for volume analysis. All pictures were individually treated using Adobe Photoshop software to elaborate on shadows and noise, and to finally calculate the calcareous parts and the holes within the shell (Fig. 2).

Results

Qualitative analysis

We found 63 animal species and 8 plant species in or on the *Spondylus* shells (Tables 1, 2). Among them a species new for Ecuador, *Mexichromis antonii*, a nudibranch that has been described no farther south than Panama until now.

In the sediment samples, we found 13 species (Table 3), 4 of them also inhabiting the *Spondylus* shell. These differences regarding the faunistic composition between the two habitats are reflected in the high value of the Bray–Curtis dissimilarity index (0.88). The 4 species living in both habitats are *Ophiothrix spiculata, Polyonyx* sp., *Ambidexter* sp., and an undetermined Balanid.

Quantitative analysis of shell loss

The three shells we analyzed had lost 10.4, 8.5, and 17.6 % of their calcium carbonate, respectively, due to holes and canals drilled by endobionts. These values do not include external abrasion and borings by microendoliths (boreholes of less than 100 µm width).

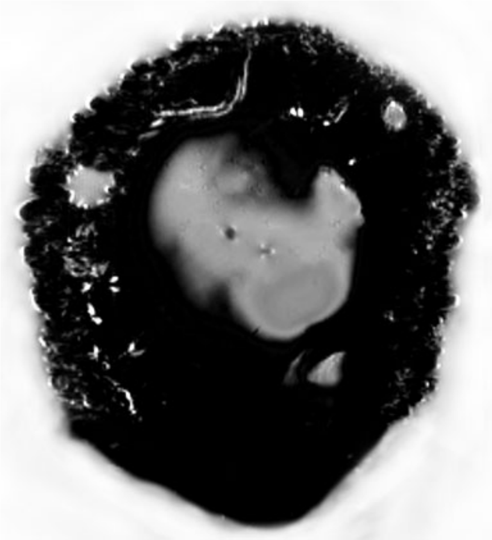

Fig. 2 A single 2-D picture slice of the MR scans after treatment with Adobe Photoshop software ready for the calculation of calcareous parts and holes (the inner gray part is the mantle cavity)

Table 1 List of animal species found in the *Spondylus crassisquama* samples

Animal species
Phylum Porifera
Porifera indet.
Class Demospongidae
Family Clionaidae
Clionaidae indet.
Phylum Cnidaria
Class Anthozoa
Family Gorgoniidae
Leptogorgia chilensis Verrill, 1868
Family Hormathiidae
Calliactis polypus
Phylum Platyhelminthes
Platyhelminthes indet.
Class Rhabditophora
Family Pericelidae
Pericelis sp.
Phylum Nematoda
Nematoda indet.
Phylum Sipuncula
Class Phascolosomatidea
Family Phascolosomatidae
Phascolosoma sp.
Phylum Annelida
Class Clitellata
Family Piscicolidae
Piscicolidae indet.
Class Polychaeta
Family Syllidae
Syllidae indet.
Family Nephtyidae
Nephtyidae indet.
Family Amphinomidae
Amphinomidae indet.
Family Eunicidae
Eunicidae indet.
Family Lumbrineridae
Lumbrineridae indet.
Family Sabellidae
Sabellidae indet.
Family Serpulidae
Serpulidae indet.
Family Flabelligeridae
Flabelligeridae indet.
Family Spionidae
Polydora sp.
Phylum Mollusca
Class Gastropoda
Family Turritellidae
Vermicularia pellucida (Broderip & Sowerby, 1829)
Family Triphoridae
Triphora sp.
Family Calyptraeidae
Crucibulum spinosum (G. B. Sowerby I, 1824)
Family Cypraeidae
Cypraea sp.
Family Buccinidae
Hesperisternia jugosa (C. B. Adams, 1852)
Family Collumbellidae
Anachis gracilis (Adams, 1852)
Columbella fuscata G.B. Sowerby, 1832
Family Muricidae
Trachypollia lugubris (C.B. Adams, 1852)
Stramonita biserialis (Blainville, 1832)
Family Chromodorididae
Mexichromis antonii (Bertsch, 1976)
Family Dendrodorididae
Doriopsilla janaina Er. Marcus & Ev. Marcus, 1967
Class Bivalvia
Family Arcidae
Arca pacifica (G.B. Sowerby I, 1833)
Family Mytilidae
Gregariella coarctata (Carpenter, 1857)
Leiosolenus plumula (Hanley, 1843)
Septifer zeteki Hertlein & Strong, 1946
Family Pectinidae
Spathochlamys vestalis (Reeve, 1853)
Family Chamidae
Chama sordida Broderip, 1835
Family Myidae
Sphenia fragilis (H. Adams & A. Adams, 1854)
Family Gastrochaenidae
Gastrochaena ovata Sowerby I, 1834
Lamychaena truncata (G.B. Sowerby I, 1834)
Family Pholadidae
Pholadidae indet.
Class Cephalopoda
Family Octopodidae
Octopus sp.
Phylum Arthropoda
Class Maxillopoda
Family Balanidae
Balanus trigonus Darwin, 1854
Balanidae indet.
Class Malacostraca
Family Majidae
Microphrys sp.
Mithrax sp.

Table 1 (continued)

Animal species
Majidae indet.
Family Epialtidae
Tyche sp.
Family Xanthidae
Edwardsium lobipes (Rathbun, 1898)
Paractaea sulcata (Stimpson, 1860)
Family Porcellanidae
Petrolisthes edwardsii (de Saussure, 1853)
Polyonyx sp.
Family Alpheidae
Alpheidae indet. 1
Alpheidae indet. 2
Pomagnathus corallinus Chace, 1937b
Family Palaemonidae
Pontonia margarita Verrill, 1869
Family Processidae
Ambidexter sp.
Phylum Echinodermata
Class Ophiuroidea
Family Ophiactidae
Ophiactis sp.
Family Ophiotrichidae
Ophiothrix (Ophiothrix) spiculata Le Conte, 1851
Class Holothuroidea
Family Holothuriidae
Holothuria imitans Ludwig, 1875
Phylum Chordata
Class Ascidiacea
Ascidiacea indet. 1
Ascidiacea indet. 2
Ascidiacea indet. 3
Family Polycitoridae
Cystodytes sp.
Eudistoma sp.

Discussion

The *Spondylus crassisquama* shells of our study area provide a distinctly different and much more diverse habitat (71 species of epibionts and endobionts) than the surrounding sandy bottoms (13 species, of which 4 were also found on the shells). This is reflected by the calculated Bray–Curtis dissimilarity index of 0.88. The majority of the species we found in our shell samples (62, including the epiphyte species) live as true epibionts on the outer shell. From other systems, it is known that epibionts make use of the currents created by filter-feeding organisms such as bivalves, in our case *S. crassisquama*, for better food access (Forester 1979; Laihonen and Furman 1986; Wahl 1989). A classic example for this mode of life would be the barnacles we found on the shells. At the same time, these fouling organisms can "hide" *S. crassisquama* from the tactile and chemical senses of predators such as starfish (Logan 1974; Bloom 1975; Vance 1978). These relationships are thus truly mutualistic.

Table 2 List of plant species found in the *Spondylus crassisquama* samples

Plant species
Division Chlorophyta
Class Bryopsidophyceae
Family Bryopsidaceae
Bryopsis pennata J.V.Lamouroux, 1809
Division Rhodophyta
Class Florideophyceae
Order Corallinales
Corallinales indet.
Family Galaxauraceae
Galaxaura sp.
Family Scinaiaceae
Scinaia sp.
Order Ceramiales
Ceramiales indet.
Family Cystocloniaceae
Hypnea sp.
Family Peyssonneliaceae
Peyssonnelia sp.
Family Sebdeniaceae
Sebdenia flabellata (J.Agardh) P.G.Parkinson, 1980

We found 9 species of drilling endobionts in our bivalve samples. None of them was found in the sediment samples. The relationship between bivalves and drilling endobionts are relatively unknown, apart from a few studies on bivalve species of commercial importance (see "Polychaetes", below). To obtain a more detailed picture of the co-existence between *S. crassisquama* and associated endobionts, we will thus especially discuss the taxa we found that are known for drilling or boring activities and their effects on the *Spondylus* shell:

Sponges

Sponges account for a considerable amount of boring in corals (MacGeachy and Stearn 1976; Sammarco and Risk 1990; Pari et al. 2002). We were not able to identify the sponge species in our samples, but when breaking and analyzing the shells, we found the typical honeycomb boring style reported for the genus *Cliona* (Cobb 1969; Rützler and Rieger 1973; MacGeachy and Stearn 1976), and assume

Table 3 List of all species found in the sediment samples

All species
Phylum Annelida
Class Polychaeta
Family Capitellidae
Capitellidae indet.
Phylum Mollusca
Class Gastropoda
Family Fissurellidae
Leurolepas roseola McLean, 1970
Family Turritellidae
Turritella radula Kiener, 1843
Family Terebridae
Terebra elata Hinds, 1844
Phylum Arthropoda
Class Maxillopoda
Family Balanidae
Balanidae indet.
Class Malacostraca
Family Mithracidae
Mithracidae indet.
Family Porcellanidae
Polyonyx sp.
Family Processidae
Ambidexter sp.
Order Amphipoda
Amphipoda indet.
Phylum Echinodermata
Class Ophiuroidea
Family Ophiotrichidae
Ophiothrix (Ophiothrix) spiculata Le Conte, 1851
Class Asteroidea
Family Asterinidae
Asterina sp.
Class Holothuroidea
Family Sclerodactylidae
Neothyone gibber (Selenka, 1867)
Class Echinoidea
Family Cidaridae
Eucidaris thouarsii (L. Agassiz & Desor, 1846)

that at least one member of that genus was present. Sponges drill delicate networks, but when breaking our thick sample shells, their stability appeared to be little affected even in heavily bored areas. We would thus include sponges in the group of mutualistic endobionts of *S. crassisquama*, since sponges provide tactile and chemical camouflage against certain predatory starfish and sponge–bivalve mutualisms are not uncommon (Bloom 1975 and references therein).

Bivalves

Boring bivalves usually work by a combination of chemical and mechanical means, with one of the methods often being dominant; see Kleemann (1996) and references therein for an in-depth discussion of this topic. We found one species of the genus *Lithophaga*, and two species of the genus *Gastrochaena*, which both drill by mostly chemical means, i.e. are "biocorroders" (Yonge 1955; Warme and Marshall 1969; Scott 1988; Lazar and Loya 1991; Kleemann 1996). Pholadidae (one species in our samples) is also a prominent boring bivalve family (Ansell and Nair 1969; Warme and Marshall 1969; Savazzi 2005), and includes genera of biocorroders and bioabradors (mechanical borers). We found only a few individuals of the four boring bivalve species; however, due to their size, they account for massive cavities in the shells of their hosts (Kiene and Hutchings 1994). We found boreholes up to 2 cm diameter and some that had apparently almost "broken through" to the inner shell surface, upon which this damage had been covered with "extra" layers of calcium carbonate, resulting in distinct blisters (also Mienis 2001). Reports suggest that *Lithophaga* species are capable of boring holes down to 10 cm deep in carbonate substrates (Warme and Marshall 1969). Boring bivalves provide no apparent advantage for *Spondylus*, but instead obvious disadvantages: shell damage (breakthrough to mantle cavity), a coincident cost of shell repair, and the danger of structural weakening of the shell; thus, mutualism is unlikely. We suggest that a classification as "parasites" is also not justified, because calcification appears to be little "costly" when compared to other metabolic costs (Palmer 1992). Additionally, in studies on corals, boring bivalves belonged to the group of later settling epibionts after pioneer species had already discovered suitable habitat and started the first drillings (Kiene and Hutchings 1994). Bivalves and their larvae are thus likely to settle and bore shells at higher ages of *S. crassisquama*, when presumably a smaller fraction of total energy expenditure is put into shell growth.

Sipunculida

We could not identify the sipunculid genus we found; however, the specimens and their boreholes very much resemble examples of the genus *Phascolosoma* given by Rice (1969) and MacGeachy and Stearn (1976). They assume a combination of chemical and mechanical drilling for sipunculids. We are not sure of the maximum size a sipunculid can reach within a shell, nor are we aware of any reported bivalve–sipunculid mutualism. Until a benefit for the bivalve is known, we assume a kind of commensalism with the risk that sipunculid species can reach sizes and boreholes that harm the bivalve by weakening the shell. Rice (1969) studied and described the sipunculid burrows in detail, and found that they instead abruptly change the orientation of a borehole before reaching a surface and opening a second hole. Thus, they would be unlikely to drill an opening to the mantle cavity of *Spondylus*.

Polychaetes

We found members of several polychaete families known for boring; Eunicidae, Sabellidae and Spionidae, represented here by the genus *Polydora* (Haigler 1969; MacGeachy and Stearn 1976; Davies and Hutchings 1983). Previous studies have shown that boring polychaetes can weaken corals (Wielgus et al. 2006) and have deleterious impacts on bivalves and gastropods of economic significance. Oakes and Fields (1996) and Aviles et al. (2007) provide examples for the effects of Sabellidae, while examples for the effects of *Polydora* can be found in Evans (1969) and Handley and Bergquist (1997), as well as in Moreno et al. (2006), who also cover other Spionidae besides *Polydora*. In addition to economical losses, shifts in predator–prey interactions have also been attributed to polychaete borings in non-commercial species such as *Littorina littorea* (Buschbaum et al. 2007). However, all these studies refer to molluscs with a much more delicate shell than those of adult *Spondylus crassisquama*. For example, *Crassostrea virginica* shells can be easily bored through by *Polydora websteri* and the oysters react with “mud blisters” (Haigler 1969). In contrast, *S. crassisquama* develops shells that can be up to some centimetres thick. We presume that adults are not seriously affected by polychaete borings, which we found only in outer shell regions, but instead benefit from the camouflage effect that polychaetes provide. Yet, it remains to be clarified how juvenile shells are impacted, since polychaetes usually belong to the pioneering settling epibionts on corals (Davies and Hutchings 1983; Hutchings et al. 1992; Kiene and Hutchings 1994) and may thus settle on smaller *S. crassisquama* individuals with more delicate shells than those of our samples. Our taxonomic resolution with respect to polychaetes is limited due to the restricted knowledge of occurrences in Ecuador. The only guides with respect to these latitudes we are aware of cover the Galapagos Islands, obviously a very distinct habitat.

None of the floral epibionts we found is considered a bioeroder, i.e. they do not cause carbonate loss. On the contrary, coralline algae, which we also found in our samples, are actually counted as reef building in studies on calcification and bioerosion of coral reefs (Tribollet and Golubic 2005). Boring algae play significant roles in coral reef ecosystems (Verbruggen and Tribollet 2011), but we did not sample microborers in our study, a group that would have probably extended the list of floral species (along with fungi). This should be a concern for future studies since microborers are important bioeroding agents, especially during initial stages. Similar to grazers and macroborers, their share of bioerosion varies over space and time (Tribollet et al. 2002; Tribollet and Golubic 2005).

Conclusions

Besides the bivalves mentioned that more or less “accidentally” might reach the mantle cavity and cause damage, other members of the boring fauna do not substantially weaken the heavy shells of adult *Spondylus crassisquama*. Hence, these findings indicate that the life strategy of *S. crassisquama* involves building up heavy and thick shells with spines that offer attractive hard substrate for fouling organisms in an otherwise soft bottom environment. In return, the shell colonizers provide a camouflage against predators as presumed by Feifarek (1987), i.e. this system represents facultative mutualism. On the other hand, *S. crassisquama* can obviously not control either the number or the identity of the animals that settle and bore, and is thus threatened to a certain extent by deeper and bigger boring bivalve species. Yet, among all the empty shells we inspected during our various diving trips, we have never encountered a shell with a borehole open to the mantle cavity. We can thus assume that *S. crassisquama* can cope with boring bivalves; apparently, the costs involved in preventing breakthroughs to the mantle cavity are sufficiently small compared to the selective advantage of the epibiont camouflage.

The high Bray–Curtis dissimilarity index confirms that *S. crassisquama* provides a very important and distinct habitat type such as reef-building corals in other areas of Ecuador, i.e. it acts as a foundation species. *S. crassisquama* is thus a key vector in maintaining benthic biodiversity. *S. crassisquama* was present in huge beds of hundreds of individuals along the coast of Esmeraldas until 2003 when exploitation started. Consequently, the large part of the habitat suitable for *Spondylus*-associated species was destroyed with those beds during recent years, causing a distinct loss in regional biodiversity. Therefore, conservation measures that aim at the restoration of the diminished population of *S. crassisquama* itself will facilitate regional macrobenthic biodiversity at the same time.

We limit our conclusions at this point because of our restricted sample size. This study must be seen as a preliminary product to value the ecological role of *S. crassisquama*. Even though our results justified other sampling or special replications, we decided against it because no further sampling was needed for our studies on the reproductive cycle and due to the scarcity of the organism.

For the future, we suggest monitoring how *Spondylus* can cope with ocean acidification, assuming that more energy will be needed to follow this life strategy of building up heavy shells to attract and endure fouling organisms. Coral reefs provide a well-studied example for direct and indirect weakening human impacts (over-fishing, rising pCO_2, and rising sea surface temperature), where, as a consequence, the processes of reef growth and loss are no longer in equilibrium as they are in healthy reefs, but, instead, rates of bioerosion substantially exceed rates of reef building (Davies and Hutchings 1983; Kiene and Hutchings 1994; Reaka-Kudla et al. 1996; Pari et al. 1998; Peyrot-Clausade et al. 1999). On the one hand, rates of carbonate dissolution might significantly rise under elevated pCO_2, as the example of the chlorophyte *Ostreobium quekettii* showed (Tribollet et al. 2009). On the other hand, a negative impact of ocean acidification on shellfish calcification even without bioeroding agents has been verified for the edible mussel (*Mytilus edulis*), the Mediterranean mussel (*Mytilus galloprovincialis*), the European flat oyster (*Ostrea edulis*) and the Pacific oyster (*Crassostrea gigas*) (Bamber 1990; Michaelidis et al. 2005; Berge et al. 2006; Gazeau et al. 2007). It should thus be a concern and object of future research to study a possible reaction of *Spondylus* to decreased pH in seawater.

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Conflict of interest The authors declare that they have no conflict of interest.

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