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Towards sustainable artisanal fisheries for the common pool resource *Spondylus* (Bivalvia, Spondylidae) in Ecuador

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MOST IMPORTANT ABBREVIATIONS AND ACRONYMS

$CaCO_3$	calcium carbonate
CPR	Common Pool Resources
EEZ	Exclusive Economic Zone
ENSO	El Niño Southern Oscillation
FAO	United Nations Food and Agricultural Organization
GNP	Gross National Product
IFA	Inshore Fishing Area
INTQ	Individual No-Transferable Quota
ITCZ	Intertropical Convergence Zone
MEABR	Management and Exploitation Areas for Benthic Resources
MRT	Magnetic Resonance Tomography
NMR	Nuclear Magnetic Resonance
ppt	part per thousand
TURF	Territorial User Rights in Fisheries
VBGF	Von Bertalanffy Growth Function

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SUMMARY

The artisanal fishery for *Spondylus* has a very long tradition in Ecuador but developments in recent years have made it an excellent example of the rapid overharvesting of a Latin American shellfish fishery. In reaction to the declining population status, the Ecuadorian government enacted an official ban on the fishery in October 2009. The ban is intended to be kept in place at least until there is scientific information regarding stock status and basic population parameters that are necessary for a sustainable use of the resource. This study aims to provide the necessary knowledge base to develop a sustainable management program for Ecuadorian *Spondylus* stocks in the future.

Our findings suggest that current population densities will not allow for a recovery without additional measures to support such recuperation. Nevertheless, the parameters we have calculated for growth and fecundity suggest that exploitation of *Spondylus* as a resource is generally possible when undertaken with caution. Under a precautionary approach it is crucial for a future management program to monitor densities of individuals closely, as this study identified recruitment failure as the main factor that has contributed to the collapse of the fishery in the past. Restoration efforts would be of high value for the local ecosystem as this study has also shown that *Spondylus* contributes significantly to the native biodiversity. Their shells provide a three dimensional habitat for a variety of drilling and non-drilling species that are not present without them, thus making *Spondylus* an important foundational species.

Artisanal fisheries make a significant contribution to satisfying the increasing global demand for protein. It is dangerous to assume, that these fisheries operate sustainably *per se* and it is crucial to ensure that they do in the future. Sustainable solutions for artisanal overfishing are urgently needed, because tropical coastal communities are highly dependent on their local resources for their livelihoods and nutrition. The tools for successfully managing a common pool resource such as *Spondylus* through a co-management system are known – we hope these are used in the future in conjunction with the findings of this study to prevent this iconic genus from disappearing.

ZUSAMMENFASSUNG

In Ecuador hat die artisanale Fischerei auf die Muschelgattung *Spondylus* eine jahrhundertealte Tradition. In den letzten Jahren hat sie sich allerdings zu einem Paradebeispiel dafür entwickelt, wie sich Überfischung in den lateinamerikanischen Schalentier-Fischereien ausbreitet. Als Reaktion auf die fallenden Bestandszahlen hat die Ecuadorianische Regierung im Oktober 2009 ein Fischereiverbot für *Spondylus* verhängt. Es soll mindestens bestehen bleiben, bis eine ausreichende wissenschaftliche Beurteilung über den Zustand der Bestände und grundlegende Populationsparameter für eine nachhaltige Nutzung der *Spondylus*-Bestände erarbeitet wurden. Die vorliegende Arbeit zielt darauf, diese notwendigen grundlegenden Erkenntnisse für ein nachhaltiges Management in der Zukunft zusammenzutragen.

Unsere Ergebnisse legen nahe, dass sich die Bestände mit der derzeit geringen Populationsdichte ohne weitere Maßnahmen nicht erholen werden. Die Erkenntnisse dieser Studie zu Wachstums- und Fekunditätsparametern besagen allerdings auch, dass eine nachhaltige *Spondylus*-Befischung unter Berücksichtigung des Vorsorgeprinzips möglich ist. Im Zuge dieses Vorsorgeprinzips ist es unerlässlich, die Populationsdichte zukünftig streng zu überwachen, da diese Studie Nachwuchsausfall als wichtigsten Faktor eines Zusammenbruchs der Fischerei identifiziert. Bemühungen, die ursprünglichen Bestandsdichten wiederherzustellen, wären von großer Wichtigkeit für das lokale Ökosystem, da *Spondylus* einen wesentlichen Beitrag zur Artenvielfalt leistet. Die Schalen stellen für eine Reihe von bohrenden und nicht-bohrenden Organismen ein wertvolles dreidimensionales Habitat dar, sodass *Spondylus* zum wichtigen Typus der „foundation species" gezählt werden sollte.

Artisanale Fischereien liefern einen entscheidenden Beitrag, um den weltweit ansteigenden Proteinbedarf zu bedienen. Es ist falsch, anzunehmen, dass artisanale Fischereien *per se* nachhaltig agieren, und sehr wichtig, dies zukünftig sicherzustellen. Bewältigungsstrategien zur Lösung artisanaler Überfischungproblematik sind dringend notwendig, weil vor allem die tropischen Küstengemeinden auf lokale Resourcen angewiesen sind, um grundlegendste Bedürfnisse zu befriedigen. Strategien, auf deren Basis sich Gemeinschaftsgüter wie *Spondylus* mithilfe eines Ko-Management Systems nachhaltig bewirtschaften lassen, sind bekannt – und wir hoffen, dass sie zukünftig in der Umsetzung der Ergebnisse dieser Studie Anwendung finden, damit *Spondylus* vor dem Verschwinden bewahrt werden kann.

RESUMEN

La extracción artesanal de *Spondylus* en el Ecuador se remonta a épocas precolombinas. Sin embargo, el incremento en la intensidad de su pesquería en las últimas décadas ha convertido a éste en un excelente ejemplo de rápida sobreexplotación de esta concha en América Latina. El Gobierno del Ecuador, en respuesta a la alarmante disminución de las poblaciones, decretó una veda permanente de *Spondylus* a partir de octubre de 2009. La veda será mantenida hasta que se genere la información científica necesaria, acerca del estado del stock y los parámetros poblacionales, para una utilización sustentable del recurso. El presente estudio provée la información básica para desarrollar un programa de manejo de las poblaciones de *Spondylus* en el Ecuador.

Nuestros resultados muestran que las densidades poblaciones actuales son demasiado bajas y que se requieren medidas externas adicionales para permitir la recuperación del recurso. Aún así, los cálculos de los parámetros de crecimiento y fecundidad sugieren que la explotación sustentable de *Spondylus* es posible, siempre y cuando de tomen y se respeten las medidas precautelatorias necesarias. Entre ellas, es crucial el monitoreo de la densidad de individuos, ya que como hemos identificado en este estudio, la falta de reclutamiento es el principal factor del colapso de la pesquería en el pasado. Esfuerzos de restauración pueden tener un gran valor para el ecosistema local y la fauna nativa. Las conchas de *Spondylus* proveen de un hábitat tridimensional para una variedad de especies perforadoras y no perforadoras que de otra manera no sería posible encontrar en un determinado lugar. Este hecho convierte a *Spondylus* en una especie formadora de hábitat.

La pesca artesanal contribuye significativamente a suplir la creciente demanda de proteína a nivel mundial. Sin embargo, sería riesgoso asumir que esta pesquería opera sustentablemente de por sí, al mismo tiempo es sumamente importante asegurar su sustentabilidad en el futuro. Es urgente encontrar soluciones sostenibles para detener y evitar la sobrexplotación por pesca artesanal, ya que el bienestar y la alimentación en las poblaciones costeras de zonas tropicales se basan en el aprovechamiento de los recursos marinos. Las herramientas para manejar de manera exitosa la pesquería de recursos de bien común son conocidas. Esperamos que en el futuro, esas herramientas y los resultados de este estudio sean utilizados en conjunto para prevenir la desaparición de especies icónicas como el *Spondylus*.

“Most small-scale fisheries throughout the world have seen their resources depleted by industrial fishing vessels, notably trawlers, fishing on or near their inshore fishing grounds. Yet this is not the whole story. An ever-increasing number of small-scale fishers operating motorised canoes or similar mobile and versatile crafts can deplete the entire resource available on a country’s continental shelf (…). The local and/or foreign industrial fleets are only accelerating, albeit to a tremendous extent, an overfishing process which, if not controlled, would eventually engulf even the most seemingly benign small-scale fishery”

Pauly, 2006

“Artisanal fisheries have a significant impact on marine ecosystems – overfishing, habitat damage, and bycatch – but, because they are much more efficient than commercial fisheries, they are also our greatest hope for achieving sustainable harvests.”

SAFRN: Small-scale and Artisanal Fisheries Research Network at Scripps 2013

1 GENERAL INTRODUCTION AND CONTEXT OF THE STUDY

1.1 Artisanal fishing

The scientific community has neglected artisanal fishing for many years (Pauly 2011) and similarly policy makers have given preferential treatment to industrial fisheries. Still, artisanal fisheries have expanded continuously (Allison and Ellis 2001) and nowadays amount to a catch of about approximately 30 million tons, approximately the same amount of fish for human consumption that is caught by industrial fleets (Jacquet and Pauly 2008).

One of the factors that can lead to the depletion of fishery resources is the underestimation of fishing pressure (Teh and Sumaila 2013) and it is thus important that the scientific community has developed an interest in the matter. The extent and significance of the artisanal sector is increasingly being recognised. The social weight is shown by the fact that 22 ± 0.6 million people are engaged in small-scale fishing, which refers to 44% of the estimated 50 million fishers in the primary production sector (Teh and Sumaila 2013). Though the recent interest helps in understanding the sector, general studies/ conclusions are complicated by the versatile nature of artisanal fishing practises. The struggle already begins with a proper definition of artisanal and/ or small-scale fisheries (Allison and Ellis 2001; Defeo and Castilla 2005; Carvalho et al. 2011). The United Nations Food and Agricultural Organisation (FAO) has addressed this problem and their definition is highly applicable to *Spondylus* fisheries in Ecuador. The FAO glossary defines artisanal fisheries as:

> *"traditional fisheries involving fishing households (as opposed to commercial companies), using relatively small amount of capital and energy, relatively small fishing vessels (if any), making short fishing trips, close to shore, mainly for local consumption. In practice, definition varies between countries, e.g. from gleaning or a one-man canoe in poor developing countries, to more than 20-m. trawlers, seiners, or long-liners in developed ones. Artisanal fisheries can be subsistence or commercial fisheries, providing for local consumption or export. They are sometimes referred to as small-scale fisheries."*
>
> (FAO 2013)

Although the scientific and non-governmental community has come to generally acknowledge the role that artisanal fisheries play with respect to their economic importance, food security and livelihoods, as well as cultural and social integrity of fishing communities (Allison and Ellis 2001; Berkes et al. 2001; Béné et al. 2004; Granzotto et al. 2004; Blount 2005; Sadovy 2005; Salmi 2005; Chuenpagdee et al. 2006; Pauly 2006; Andrew et al. 2007), it is still mainly the industrial fisheries that are associated with a global trend of overfishing and thus the focus of controversial debates about potential solutions (Pauly et al. 2002; Hilborn et al. 2003; Myers and Worm 2003; Rosenberg 2003; Worm et al. 2009). In this discussion, artisanal fishing is often still perceived as a quaint, romantic and retrograde activity. This perception is far from the truth (Allison and Ellis 2001); and this study provides an excellent example how a drastic short-term increase in artisanal fishing effort can deplete a highly-valued shellfish resource within a relatively short period of time.

1.2 Latin American fisheries and *Spondylus* in Ecuador

In developing countries such as Ecuador and other Latin American countries, a higher relative share of fisheries belongs to the artisanal sector (Andrew et al. 2007) and they are mostly unregulated (Defeo and Castilla 2005). Landings are rarely controlled because this would mean huge enforcement costs for countries where surveillance is a task for governmental agencies (Defeo and Castilla 2005). This leads to a severe underrepresentation of small-scale fisheries data passed from national agencies to the FAO (Jacquet et al. 2010) and their statistics should thus be used with caution.

Because of the dependence of coastal communities on their local resources with respect to economic welfare and sustenance, sustainable solutions for artisanal overfishing are of even greater urgency than for industrial fisheries (Defeo and Castilla 2005; Andrew et al. 2007). The socioeconomic implications of Latin American artisanal fisheries on wild benthic invertebrates are especially critical, as these fisheries are often based on high-value species and from stocks that are increasingly being depleted (Castilla and Defeo 2001). They follow a general trend of rapid expansion and, in some cases, serial depletion of global invertebrate fisheries (Anderson et al. 2011). Because of the functional roles that invertebrates often play, this has serious implications for the marine ecosystems of which they are a part (Anderson et al. 2011).

All this holds true for *Spondylus* in Ecuador: it is a *de facto* unregulated fishery of which official landings were never controlled or recorded and stocks have been depleted with problematic consequences for the ecosystem, as we will show in this thesis.

Fisheries are a key sector for the Ecuadorian economy, generating around 1 billion $ from exports, of which 540 million $ are derived from small-scale fisheries exports alone (FAO 2011). Around 1981, the number of artisanal fishers was estimated to be around 1,500 (Herdson et al. 1982). Estimated numbers increased to 11,000 - 18,000 in the late 1980s (Epler and Olsen 1993) and may have been as high as 44,000 (Martínez 1987) depending on the data source (and whether fishing was defined as a temporary or permanent activity). Ecuador has now the largest artisanal fishing fleet of all countries in the Southeast Pacific (Félix et al. 2006). Around 169,000 artisanal fishers are officially registered in Ecuador (FAO 2011) and more work without registration (pers. observation). It is noteworthy, that Ecuador has reserved small-scale fisheries for its own citizens only (WTO 2004). Todays Ecuadorian *Spondylus* fishery is undertaken with a fibreglass boat of 6-8 metres, usually with a 75 hp outboard engine operated by three people: a captain to navigate and handle the air compressor on the boat while two hookah (Esmeraldas) or scuba (Manabí, Santa Elena) divers go down to maximum depths of 25-30 meters and collect the bivalves manually (pers. observation). As is the case in many other artisanal fisheries, *Spondylus* is fished under open access conditions, a fact that may have contributed to the overexploitation of the stock (but see the section on common pool resources in the discussion).

The Ecuadorian *Spondylus* fishery has a long tradition in coastal Ecuador and early signs of *Spondylus* trade date back to sometime between 2600 and 2000 BC (Solís 2005; Solís 2006). Extensive literature is available on the history and traditional use of *Spondylus* for ceremonial and ritual purposes in pre-Hispanic contexts [(Paulsen 1974; Murra 1975; Marcos and Norton 1984; Marcos 1986a; Marcos 1986b; Hocquenghem and Ruiz 1994; Blower 1995; Bauer 2007; Bauer and Lunniss 2010) but see Carter 2011) for an excellent updated discussion].

It is noteworthy that after being almost completely forgotten a long time, it was most likely an American archaeologist, who restored traditional use in the memories of local divers in Salango (Richard Lunniss pers. comm.; Bauer and Lunniss 2010). As recently as the 1980s, *Spondylus* appeared on menus of restaurants in the Province of Manabí. Their value was rediscovered and the exploitation of *Spondylus* accelerated with drastic consequences for the standing stock. This eventually resulted in a *de jure* ban of the fishery in October 2009 (see Appendix: Registro Oficial No. 58). Fishermen in Manabí reported that 3-4 dives yielded a catch of about 150 kg (muscle only!) in 1990. In

2002, the same effort yielded a maximum of only 5 kg (Fabara 2003). A similar decline was observed when the interest spread further north to Esmeraldas 5-8 years later. In addition to the direct use of *Spondylus* for human consumption, demand was further fuelled by the use of their colourful shells for jewellery, both locally and in Peru (Fig. 1).

Fig. 1: Typical jewellery made of *Spondylus*

1.3 Bivalves in science and fisheries

The phylum Mollusca is one of the largest, most diverse and important groups in the animal kingdom. There are more than 50,000 described species of which around 30,000 are marine. Part of this phylum is the class Bivalvia with about 7500 species, many of which are commercially important, such as mussels, clams, scallops and oysters (Gosling 2003). Some bivalves adopt a burrowing lifestyle; another large group live by attaching themselves to a variety of surfaces. The attachment can either be provided by byssus threads or, like *Spondylus*, by a cement-like substance that fixes one of the valves to a substrate (Gosling 2003).

Due to their shells, bivalves are the subject of studies from various fields of science. The main component of bivalve shells is calcium carbonate ($CaCO_3$) and the shells longevity as fossils helps archaeologists and anthropologists to understand old trade routes, rituals and traditions. Geologists use fossil shells to date rock layers and formations, and also recent shells are often well suited for (long-term) environmental reconstructions. Many bivalve shells display growth rings that are formed due to changes in environmental parameters such as water temperature, salinity and light, which influence the availability of food and therefore the metabolism and the growth of the animal. Stable isotopes of bivalve shells can provide proxies for high-resolution records of environmental parameters (Goodwin et al. 2001; Schöne et al. 2002; Schöne 2003; Schöne et al. 2003; Carré et al. 2005; Schöne et al. 2005).

Besides their value for the different fields of scientific research, bivalves also play an important role in human consumption and catches have increased consistently since 1950, peaking in 1984 at approximately 2.2 Million tonnes (Fig. 2). Catches have subsequently fallen, which has been associated with a worldwide trend of overharvesting invertebrate stocks (Anderson et al. 2011).

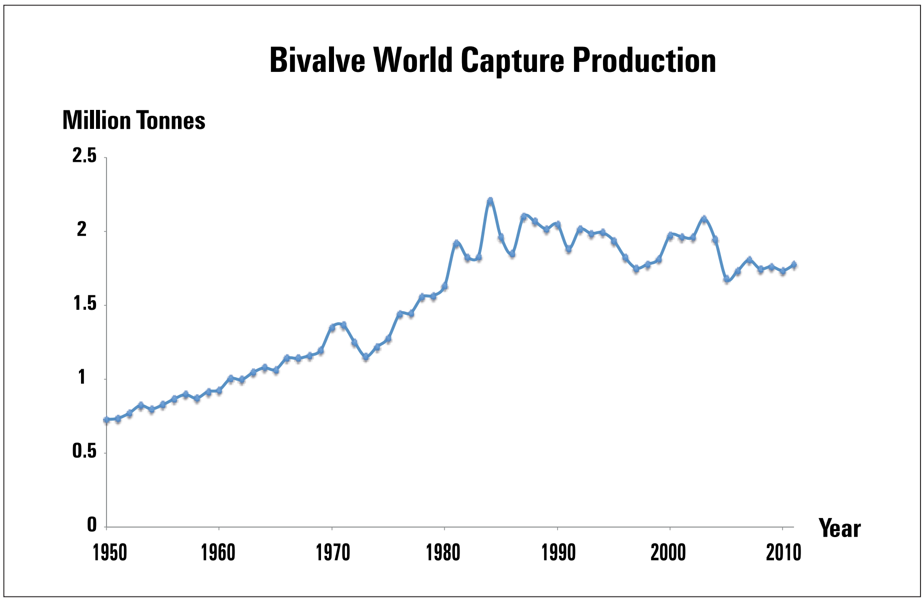

Fig. 2: FAO Statistics of marine bivalve captures worldwide 1950 - 2011

1.3.1 The family Spondylidae with its single genus *Spondylus*

The family Spondylidae (Gray 1826) consists of a single but rather conspicuous genus: *Spondylus* (Linnaeus 1758), also known as “thorny” or “spiny oysters”. There are an estimated 76 species living in tropical and subtropical waters worldwide (Lamprell 2006). Spondylidae are closely related to the *Pectinidae* with whom they share the complex eyes around the mantle and a relatively well developed nervous system. In contrast to the overall biology and ecology of the genus, the general anatomy and morphology are well known and documented (Dakin 1928a; Dakin 1928b; Yonge 1973; Zavarei 1973; Logan 1974; Lamprell 2006). Spondylidae exhibit medium-sized to large shells with prominent radial (spiny) ribs. Crossed-lamellar aragonite is the dominant substance, covering the hinge plate and extending outside the pallial line almost reaching the edges (Waller 1978).

The hinge shows two large isodont teeth and the ligament is sunken in a triangular slot (Fig. 3). The shell has unequal valves of which both or at least the left (top) valve

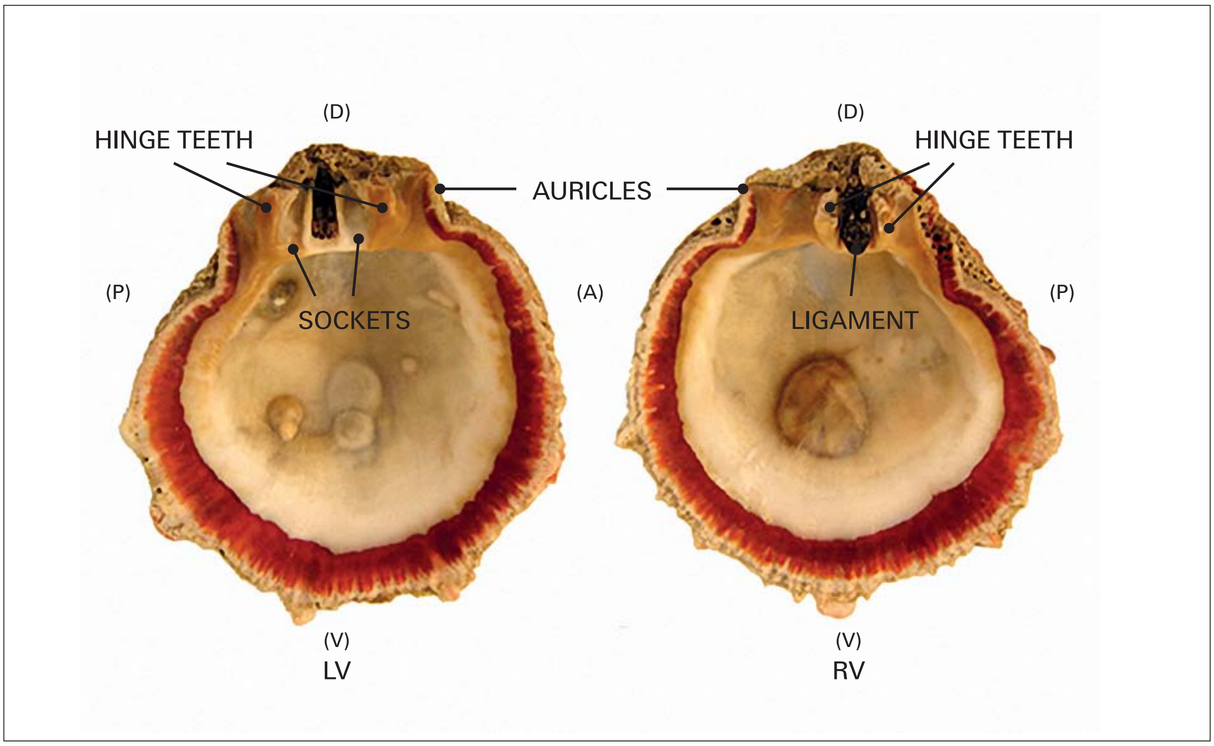

Fig. 3: Internal view of the left or upper valve (LV) and right or lower valve (RV) of *Spondylus crassisquama* (Lamarck, 1819). Dorsal (D), ventral (V), anterior (A) and posterior (P) orientation is given in brackets for each valve. Modified from Lamprell (2006)

feature prominent auricles (Figs. 3 & 4). All Spondylids are monomyarian, with a large (rather posterior) muscle that consists of two sub-equal parts: a striated quick and a non-striated, smooth catch muscle. Also common among all species of *Spondylus* is the cementation to a substrate for at least a part of their lifecycle (Logan 1974) and the lack of a byssal notch in adults. They pass through a byssate stage only in early ontogeny (Harper 1991). Despite their abundance and economic importance in parts of the world, studies on the biology and ecology of Spondylidae are rather underrepresented. Spondylids are gonochoric (or more rarely hermaphroditic) and broadcast spawners (Parnell 2002), i.e. gametes are released into the water column and fertilization occurs externally. The massive, thick shells have received considerable scientific interest and their microstructure was analysed in detail (Carter 1990). However basic growth parameters are still unknown and attempts at aging Spondylidae have differed considerably in their results (Fabara 2003; Cudney-Bueno and Rowell 2008).

Owing to their generally large intraspecific variability (Whitehead 1989), the taxonomy of *Spondylus* is under permanent revision and the potential for hybridisation

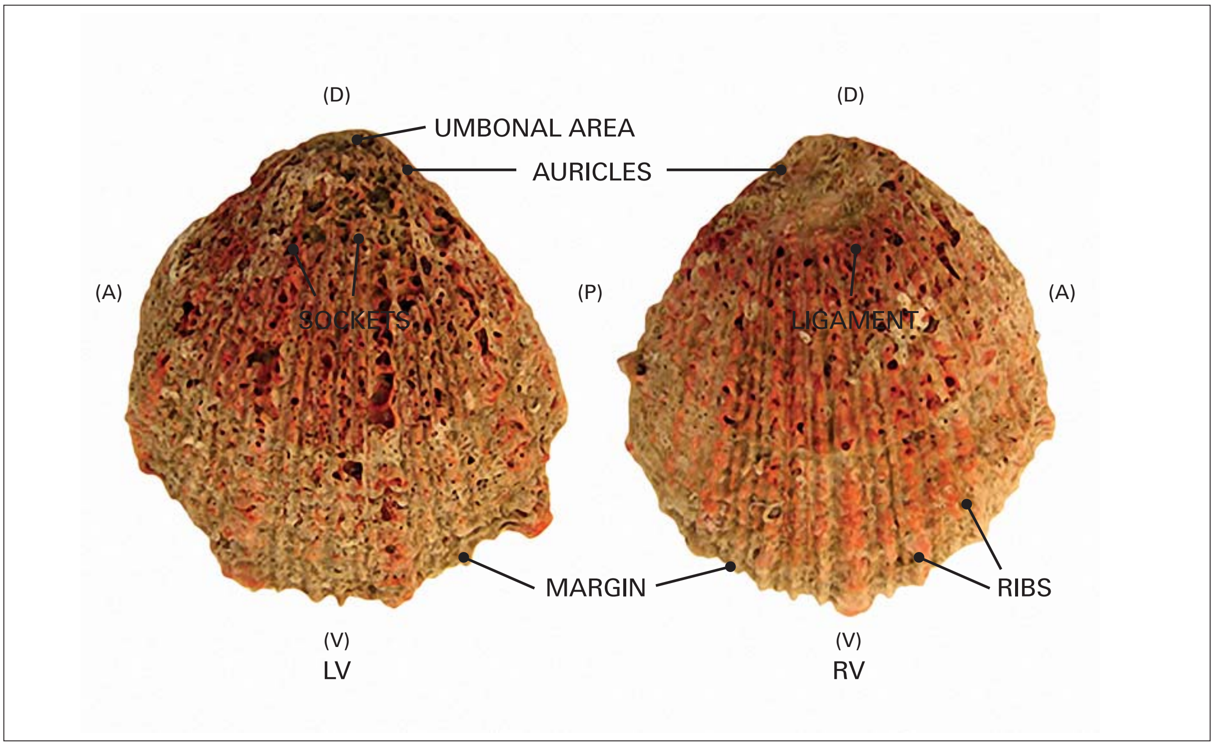

Fig. 4: External view of the left or upper valve (LV) and right or lower valve (RV) of *Spondylus crassisquama* (Lamarck, 1819). Dorsal (D), ventral (V), anterior (A) and posterior (P) orientation is given in brackets for each valve. Modified from Lamprell (2006)

is assumed (Lamprell 2006). Widespread confusion exists as to the officially acknowledged species (and names) for the three species found along the mainland coast of Ecuador. They have undergone various scientific revisions, the most recent by Huber (2009). Due to this recent confusion and because formerly accepted names were used in the first manuscript of this thesis (manuscript 2.1) as well as in the official governmental documents, clarification on the three Ecuadorian species is provided here:

■ *Spondylus limbatus* (G. B. Sowerby II, 1847)
was formerly known as *S. calcifer* (Carpenter, 1857) and corrected to the earlier name by Lamprell (2006). He found this species distributed from the Sea of Cortez/ Mexico in the north to Ecuador in the south. According to Keen (1971), *S. limbatus* is by far the largest of west American thorny oysters and reaches lengths up to 249 mm. The external structure is often heavily eroded when it ages (Fig. 5). We found *S. limbatus* in Ecuador usually attached with almost the entire right valve and thus very variably taking the form of the rock or crevice where it attaches. According to Lamprell (2006), *S. limbatus* is found from the intertidal to a depth of 30 metres and can live in tidal as well as in quiet, silty conditions which are unsuitable for the other two species described below. In our dives, we never found individuals in the intertidal zone, nor in depths less than 12 metres, most likely because these shallow waters had been deprived of *Spondylus* long ago.

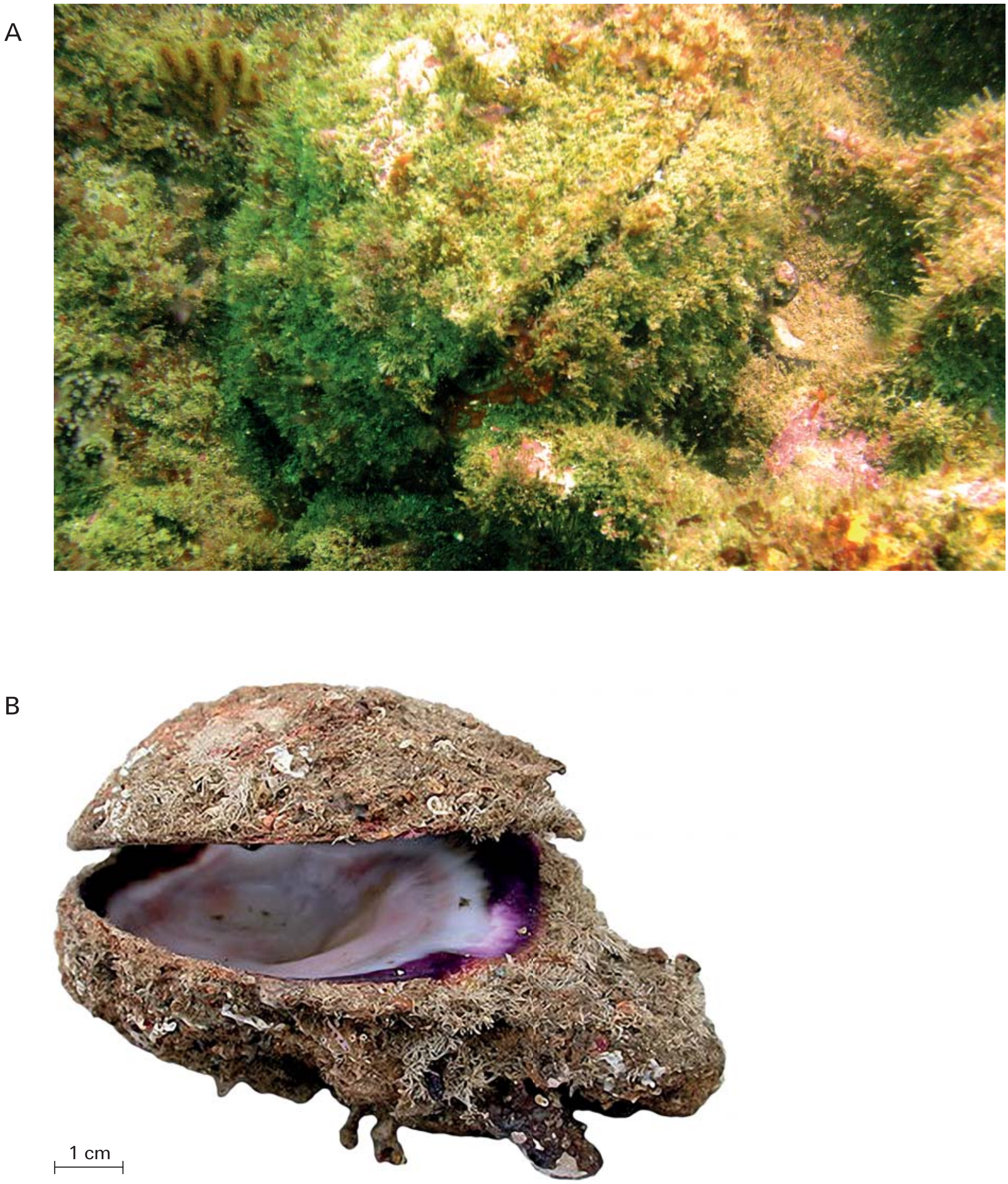

Fig. 5: *Spondylus limbatus in situ* (A) and one specimen from Ayangue (B), the lower valve is deformed due to growth along a rock and the outer parts of the valves show typical signs of age: lack of spines and overgrowing by encrusting structures such as sponges.

Spondylus crassisquama (Lamarck, 1819)
is the earlier and thus correct name of what has for a very long time been famously known as *S. princep*s (Broderip, 1833). A false location given for the lectotype of *S. crassisquama* led to the newer nomenclature before Huber (2009) clarified the identification. Lamprell (2006) corrected the previously documented distribution between Baja California in the north and Isla de la Plata, Ecuador in the south (Skoglund and Mulliner 1996): according to his findings, *S. crassisquama* occurs much further south down to northwest Peru. We consider this distribution to be more appropriate as we came across *S. crassisquama* shells sold in the stores of Salinas, southern Ecuador (Fig. 8), which were bought from local divers and local sites (pers. comm.). We found specimens up to a height of 170 mm, with the bigger (older) animals of our collection lacking the spines of younger conspecifics (similar to *S. limbatus*). The attachment area is usually much smaller than in *S. limbatus* allowing the valves to grow in a more roundish shape (Fig. 6) than *S. limbatus*. The habitat is usually described as rocks, dead corals and shells as attachment objects in depths between 3 and 28 (Skoglund and Mulliner 1996) or between 5 and 35 metres (Lamprell 2006). At our study sites in Esmeraldas, we found *S. crassisquama* as a free-living species on sandy or pebble bottoms lacking (former) attachments.

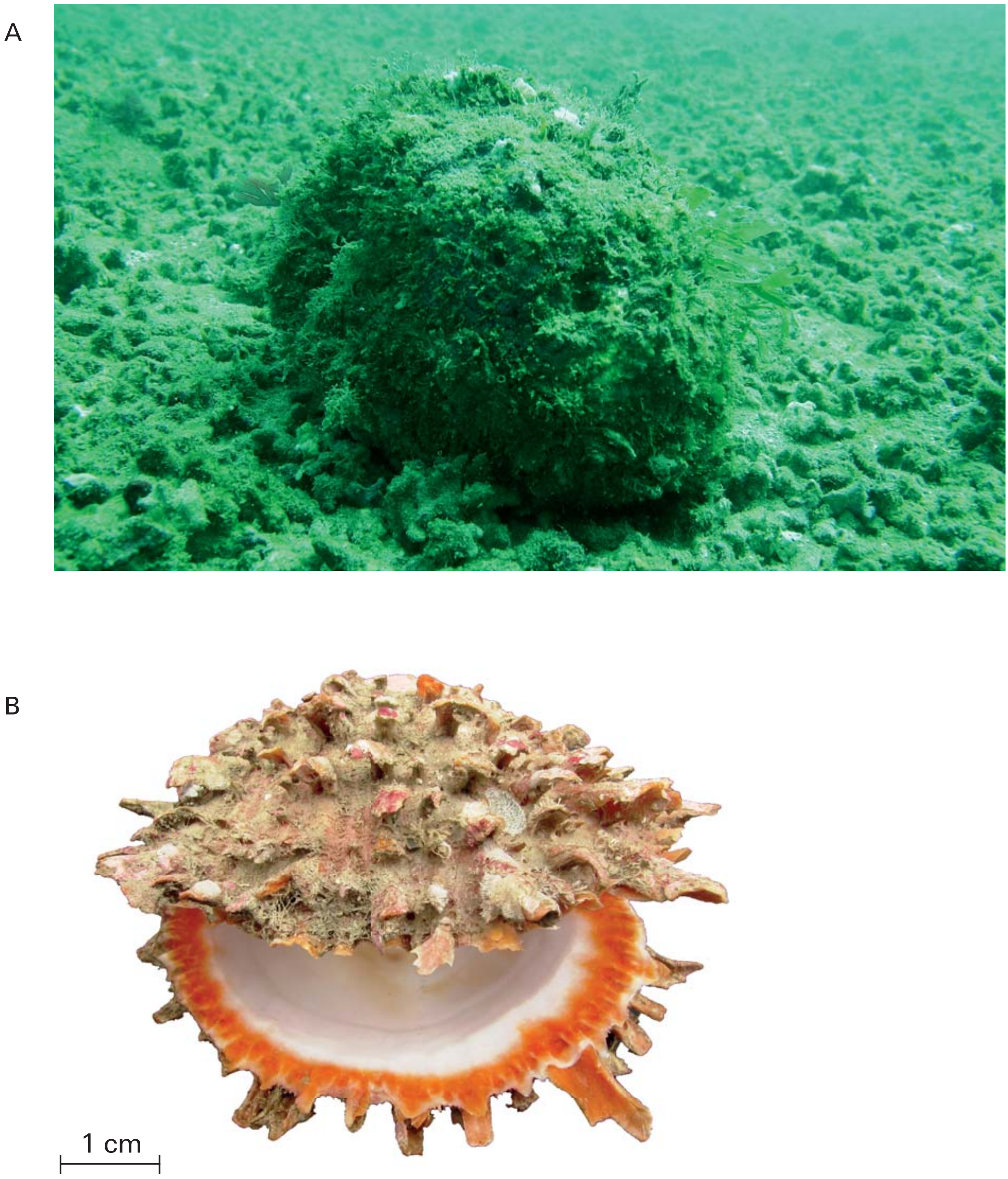

Fig. 6: *Spondylus crassisquama in situ* (A) and cleaned for selling in a jewellery store in Quito (B).

Spondylus leucacanthus (Broderip, 1833)
has been confirmed by Huber (2009) as a correctly named, valid species. The distinction between *S. crassisquama* and *S. leucacanthus* has been documented by Skoglund and Mulliner (1996). The distribution ranges from Baja California in the north to Isla de la Plata, Ecuador in the south. I never came across a single specimen of *S. leucacanthus* in all my dives in Esmeraldas, Manabí or Santa Elena. They are assumed to share a similar habitat type with *S. crassisquama*, but range much deeper. I would confirm the latter assumption, since our dives in Esmeraldas and elsewhere were usually limited to a depth of 30 metres and my only observed catch of *S. leucacanthus* was from the by-catch of a trawl net, fishing in depths between 50 and 90 metres. We excluded this species from our studies due to the difficult access, general low quantities and lesser importance on the local markets.

1.4 Ecuador and the main research areas

Ecuador features a coastline of 2859 km along the equatorial Pacific (Coayla Berroa and Rivera Miranda 2008) with an Exclusive Economic Zone (EEZ) of 236,597 km^2 of which 23,894 km^2 are Inshore Fishing Area (IFA[1]). The equatorial Pacific is a high-nitrate, low chlorophyll region where productivity is generally limited by iron (Behrenfeld et al. 2006). The coasts of Ecuador and Peru provide distinctive oceanographic conditions owing to their low latitude. In comparison with similar winds at higher latitudes, the diminished Coriolis force allows constant winds towards the equator to drive larger Ekman transports and upwelling (Strub et al. 1998). The offshore region north of the equator (Panama Basin) and the region between 0° and 15° South (Peru Basin) are divided by the Carnegie Ridge, which stretches westwards to the Galapagos Islands. The coastal zones of Ecuador are under the influence of a complex system of three currents: Warm waters (over 25° C) of low salinity (less than 33.5 ppt) are transported from the north with the Panama Current and form a tropical zone down to the 1-2° South latitude. The Humboldt Current influences the Ecuadorian coastal systems with cold (18-20° C) waters from the south. This builds a temperate

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[1] The Inshore Fishing Area (IFA) represents the area between the shoreline and either 200 m depth or 50 km distance from shore, whichever comes first (Sea around us 2013).

zone up to the 4° S latitude, which occasionally (depending on the season) reaches up to the Santa Elena tip or even the centre of the Ecuadorian coastline. The conjunction of these two current systems forms a front of mixed waters with high marine productivity. The Equatorial Undercurrent or Cromwell Current reaches the Galapagos Islands and the mainland from the west and combines high salinity with high oxygen and low nutrient values (Tsuchiya 1985). This current runs below and counter to the prevalent course of the Humboldt Current (Epler and Olsen 1993). Still, net primary production is high along the equatorial line due to the equatorial upwelling (Saba et al. 2008). The circulation system becomes even more complex when seasonality is considered [see Wyrtki (1966) for details]. In conclusion, all the different water masses (Fig. 7), together with the related climate conditions and marked oceanographic fluctuations during (austral) summer and winter all combine to provide ideal conditions for a large number of distinct climates and habitats. Furthermore, Ecuador forms part of the ENSO (El Niño Southern Oscillation) impact zone.

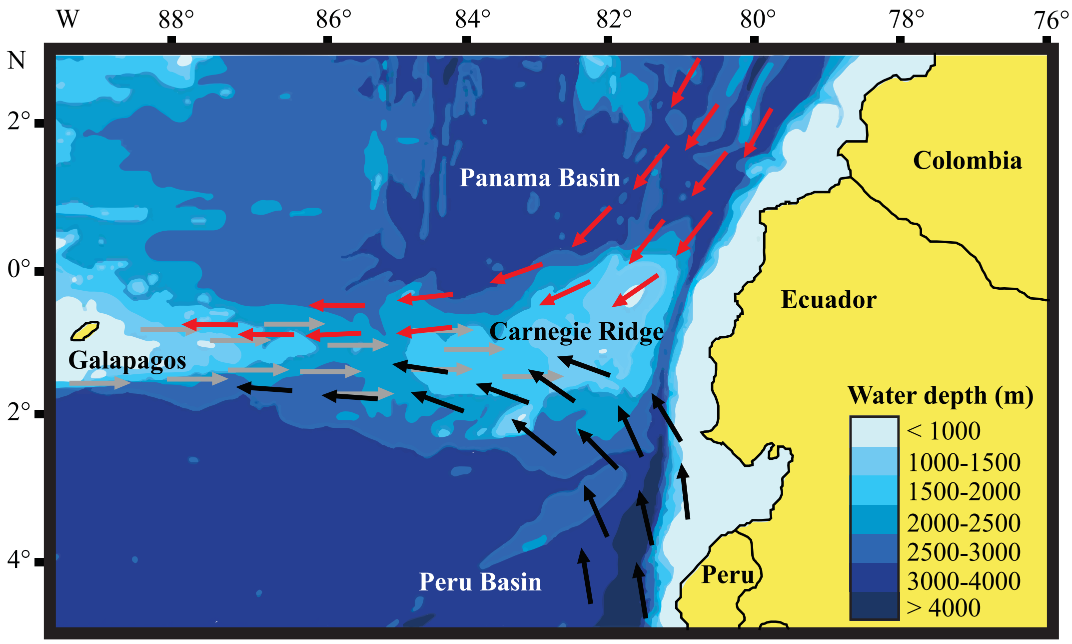

Fig. 7: Simplified overview on the oceanographic conditions off the Ecuadorian coast showing the main currents and their directions marked as red (warm Panama Current from the North), black (cold Humboldt Current from the South) and grey arrows (Cromwell Current flowing eastwards beneath the former two).

1.4.1 Study site off Atacames in the province of Esmeraldas

The oceanographic characteristics in Esmeraldas are very different from the rest of the Ecuadorian coast. Warm waters between 22 ° and 27 ° C (annual mean 24.5 ° C) are present almost throughout the year and make this a zone of tropical influence. This is largely reflected by the local biodiversity with many flora and fauna representatives of the tropical countries further north (Reck and Hurtado 1993). The river Esmeraldas reaches the ocean at N 0°59′54.1″-W 79°38′37.7″ and its freshwater and sedimentation has a large impact on the area. Until the late 1980s almost one third of the mangrove cover in the area Atacames – Sua – Muisne was removed to construct shrimp basins (Programa de Manejo de Recursos Costeros 1993). This has not led to the intended reduction in poverty and the province of Esmeraldas is still one of the poorest in the country: the lowest GNP at $670 per capita (43% lower than national average) is found here (UNDP 2012). Esmeraldas is also one of three key provinces for artisanal fisheries in Ecuador (FAO 2011) and the areas off the coast of Atacames where our study site is located, are targeted by divers and fishermen for their "bajos" (shallow waters).

Fig. 8: Map of Ecuador with the respective study sites in the provinces of Esmeraldas in the North and Santa Elena in the South (study sites are depicted in red)

1.4.2 Study site off Ayangue in the province of Santa Elena

Cold waters originating from the Humboldt Current are the main influence for the southern coast of Ecuador, including the province of Santa Elena. The offshore temperature ranges between 17 and 22° C, with an annual mean of 19.5° C in years with no El Niño activity. The province was founded in 2007 and thus most data with respect to ecology or socio-economy is lumped together with the province of Guayas of which it was formerly part of.

1.5 Concept of the thesis

In October 2009, an official ban was declared for the fishery on *Spondylus calcifer* (i.e. *S. limbatus*) and *S. princeps* (i.e. *S. crassisquama*) (Acuerdo ministerial No 136, see Appendix). No further capture, transport, commercialisation and consumption were allowed beginning 15 days after publication of the Registro Oficial No. 58, the document containing the declaration (Ma. Christina Puente pers. comm.). This was followed by a public campaign against the consumption and purchase of *Spondylus* and its products (see appendix).

This fishery ban went into effect without an official ending date announced; the document says instead that the ban should be in place as long as there are no scientific studies on the population and on sustainable use that provide the measures necessary to establish a responsible fishery:

> *"Art. 1.- Declarar una veda permanente del recurso concha Spondylus Calcifer y Spondylus Princeps sobre cualquier forma de captura, transporte, comercialización y consumo, hasta que no existan estudios científicos de población y aprovechamiento sustentable que sustenten las medidas de ordenamiento necesarias para establecer una pesca responsable."*
>
> (Acuerdo ministerial No 136, see Appendix)

The objective of this thesis was thus to develop the knowledge base required for the management and sustainable use of *Spondylus* resources in Ecuador. These include basic knowledge of population dynamics such as the parameters for reproductive effort and growth. We also included ecological questions on the functional role of *Spondylus* to provide a broad picture of this poorly studied genus. The three manuscripts that describe the key investigations of this thesis are as follows:

Manuscript I

We assessed the reproductive cycle of *Spondylus limbatus* and *S. crassisquama* and the respective environmental triggers and compared them with studies on the same species under different environmental conditions (Mexico). Additionally, we evaluated whether the current population status and reproductive effort of these two species allow a recovery on its own on the basis of their distinct fecundity estimates and discuss if/what further measures are necessary before a possible reopening of the fishery.

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Chapter 2.1: The Fate of *Spondylus* stocks (Bivalvia: Spondylidae) in Ecuador: is Recovery likely?

Manuscript II

We determined the growth parameters (K and S_{00}) for *Spondylus limbatus* and *S. crassisquama* for the first time and by means of the von Bertalanffy growth equation. To ensure species distinction, both encountered *Spondylus* morphotypes were tested for DNA differences. Additionally, we evaluate the potential of *Spondylus* to provide estimates of the environmental history of this area with the help of a stable isotope analysis.

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Chapter 2.2: Towards Individual Growth Models for *Spondylus limbatus* G. B. Sowerby II, 1847 and *S. crassiquama* Lamarck, 1819

Manuscript III

We evaluated the ecological importance of *Spondylus crassisquama* and the functional role as a foundational species (responsible for providing the foundation of a habitat) for a variety of drilling and non-drilling organisms and defined these functional threads. Additionally, we evaluate for the first time the impact of the associated organisms on the shell structure of *S. crassisquama* by means of a three-dimensional MRT video.

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Chapter 2.3: *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?

2 MANUSCRIPTS

The following chapters are manuscripts already published (2.1 + 2.3) or ready for submission (2.2). The respective contributions of the authors are listed below each title:

2.1 The Fate of *Spondylus* stocks (Bivalvia: Spondylidae) in Ecuador: is Recovery likely?

Annika K. Mackensen, Thomas Brey, Stanislaus Sonnenholzner

AKM was responsible for the study design, sampling, histological and all other lab work and measurements, data analysis/ interpretation and manuscript writing; TB supported the statistical data analysis and commented on the manuscript; SS provided comments on the manuscript.
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THE FATE OF *SPONDYLUS* STOCKS (BIVALVIA: SPONDYLIDAE) IN ECUADOR: IS RECOVERY LIKELY?

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ABSTRACT The bivalve genus *Spondylus*, with its large and magnificent shells, has played an important cultural and economic role in coastal Ecuador that reaches back to Valdivian and Incan times. At least 2 of the 3 occurring species lately faced exploitation rates that the populations could not sustain, and a fishing ban for *Spondylus calcifer* and *Spondylus princeps* was announced in October 2009. The objective of this study is to evaluate the recovery potential of the stocks that are still present. We analyzed the reproductive cycle of *S. calcifer* in the area of Ayangue (Santa Elena Province), and its relation to temperature and food abundance. In addition, we calculated fecundity values for the two threatened species. Our results show that *S. calcifer* in Ayangue reproduces year-round, although with a peak in October to December, when temperature is low and chlorophyll concentration is high. The total fecundity increases with soft body mass and is significantly higher in *S. calcifer* than in *S. princeps*. The individual fecundity levels in our study range from 2.2–8.3 million eggs in *S. princeps*, and from 2.9–35 million eggs in *S. calcifer*, which is in the range of better studied oyster and scallop species. With the latest observations on current densities of both species, we conclude that these have long fallen below the reproduction thresholds for other broadcast spawning invertebrates, and possibly for positive net recruitment rates. Because broadcast spawners are susceptible to mate limitation (which is the dominant cause of Allee effects in aquatic invertebrates), the reproductive asynchrony we found in *Spondylus* populations in Ecuador further increases the significance of potential depensatory mechanisms and of nearest neighbor distance.

KEY WORDS: reproductive cycle, fecundity, overfishing, broadcast spawners, recruitment failure, Allee effect, depensation

INTRODUCTION

The family Spondylidae (Gray, 1826) consists of only one genus—*Spondylus* (Linnaeus, 1758)—commonly also called *thorny oysters*, with about 76 living species worldwide (Lamprell 2006). Spondylidae are closely related to the Pectinidae, with whom they share the complex eyes around the mantle and a relatively well-developed nervous system. Three species can be found along the Ecuadorian coast: *Spondylus princeps* (Broderip, 1833) and *Spondylus leucacanthus* (Broderip, 1833), whose distinction has been documented by Skoglund and Mulliner (1996); and *Spondylus. calcifer* (Carpenter, 1857), which is by far the largest west American thorny oyster. Lamprell (2006) found this to be a synonymy of the earlier name *Spondylus limbatus* (Sowerby, 1847). However, as long as the ICZN has not officially made a decision on the scientific name, we continue to use *S. calcifer*. This species is distributed from the Gulf of California to Peru and can be found from intertidal to subtidal zones, attached by the right valve to exposed boulders or under rock ledges (Skoglund & Mulliner 1996).

The large and magnificent *Spondylus* shells have a long history in South American culture as ceremonial offerings and currency, reaching back to Valdivian and Incan times (Paulsen 1974). Beginning in 1990s, after centuries of oblivion, *S. calcifer* and *S. princeps* have made a comeback as a valuable resource in coastal Ecuador. The reinvention of handicrafts (jewelry) using *Spondylus* and its recent fame as a delicacy, probably resulting from a misinterpretation of the nickname *manjar de los dioses* (‘‘food of the gods’’; most likely for their ancient use as ceremonial offerings); fostered a rapid decline of the stocks in Manabí.

Authorities never recorded official landings; we are only aware of unpublished figures from a conference in 1998, when annual landings of more than 150,000 lb. (68,040 kg) of *Spondylus* flesh were reported for only the four villages of Salango, Puerto Lopez, Machalilla, and Puerto Cayo (Manabí) (Ma. Cecilia Téran, Instituto Nazca, pers. comm., February 2009). Anecdotal evidence indicates the susceptibility of *Spondylus* to fisheries. In Esmeraldas, divers started to collect *S. princeps* in 2000, mainly for the demand of arriving Peruvian artisans (who reported their own *Spondylus* stocks as already being depleted). When they first began diving for *Spondylus*, a fisherman could easily collect around 300 animals per day at certain sites. After less than 7 y, with only 3–4 operating boats and a yearly ‘‘natural’’ closed season from December to April (resulting from turbid waters and a shift to other target species), divers stated that it was already not worth paying the fuel to search for *Spondylus*, because they had become so scarce.

Obviously, exploitation rates were way too high along the entire Ecuadorian coast. In October 2009, the subsecretary of fishery resources in Ecuador finally took action and announced a complete closure of *S. calcifer* and *S. princeps* fisheries (Subsecretaria de Recursos Pesqueros, registro oficial no. 58), at least until the current state of the population is evaluated. The subsecretary also recommended identifying and fostering measures for a sustainable use of *Spondylus* resources. The Instituto Nacional de Pesca (INP) is currently undertaking investigative efforts on the densities of both *Spondylus* species. However, when monitoring six formerly known *Spondylus* fishing sites of 100 m^2 in the coastal waters of Santa Elena during April 2010, not a single living specimen was found (INP 2010). At other sites, only a few individuals were located. If undiscovered populations are found, one must ascertain whether it is possible to turn *Spondylus* fisheries into a continuous source of income

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for the artisanal sector at local/regional scales by means of an appropriate and sustainable management scheme. We cannot determine this question yet, because next to nothing is known about the biology and population dynamics of *Spondylus* spp. in Ecuador, and very little is known the about biology and ecology of this genus in general. This study will provide basic information on the reproduction of *Spondylus* in Ecuadorian waters; this information is essential for the development of a sustainable management scheme.

There is extensive literature on bivalve reproduction (e.g., Giese & Pearse 1974, Sastry 1979, Barber & Blake 1983, Gosling 2003), showing that reproduction is controlled by a complex interchange of exogenous factors such as temperature, food, salinity, and light, with endogenous regulations such as nervous and/or neuroendocrine control systems and genotype. Only one study clearly focused on the reproduction of *S. calcifer*, and documented a well-pronounced seasonality for Bahía de Loreto, Mexico, a place where the annual amplitude in SST is about 10°C (Villalejo-Fuerte et al. 2002). According to that study, this species is gonochoric and, unlike in other bivalves, spawning takes place during times of low food availability. Temperature increase was found to initiate gonad maturation, and a threshold water temperature of 29°C was linked with spawning. A more recent but less detailed study from Mexico concludes a similar reproductive strategy for *S. princeps* (Villalejo-Fuerte et al. 2005). Our study area for *S. calcifer* in the province of Santa Elena is characterized by a much lower annual SST amplitude (23–27°C) and overall lower temperature.

In the current study we evaluate whether reproduction of *Spondylus* in Ecuadorian tropical waters is seasonal and, if so, whether it is possible to identify drivers of the gonad cycle. In addition, we quantify gonad output and discuss whether population fecundity at the current low abundance level is still sufficiently high to enable stocks to recover.

MATERIALS AND METHODS

Sampling was conducted near Ayangue in the province of Santa Elena (Fig. 1, site A), Ecuador (the members of the fishing community usually do not reveal exact coordinates). Local divers collected 126 adult specimen of *S. calcifer* on 15 sample trips with monthly intervals from October 2007 to April 2009. No samples were collected in January 2008 and December 2008/ January 2009 because of turbulent water conditions. *Spondylus* was already considered to be scarce and difficult to find at that time; thus, the number of individuals per sampling date was kept low (4 in October and November 2007, 5 in December 2007 and February 2008, 10 in March 2008 to February 2009, and 7 in March 2009). In addition, we collected 68 *S. princeps* near Atacames in the province of Esmeraldas (Fig. 1, site B; 12 in November 2007, 9 in June 2008, 8 in August 2008, 9 in February 2009, and 10 each in March, April, and May 2009).

The height, length, and weight of each bivalve shell were recorded, and the soft part of the animal was extracted and fixed in Davidson solution (Howard & Smith 1983) for 24 h. *Spondylus* has anatomically distinct gonads that can be removed intact from dead animals. Wet weight of gonads, muscle, and remaining soft parts were recorded. Gonads were dehydrated in an alcohol series and prepared according to standard histological processes. Four-micrometer sections were placed on slides and stained with hematoxylin–eosin. Each gonadal slide was analyzed microscopically, sex was determined, and a gonadal stage was assigned. The gonad developmental stages were defined, and an index was assigned to each stage ranging from 0–1 using the following categories:

Figure 1. Study sites in the 2 provinces of Esmeraldas and Santa Elena.

Cytolized (indifferent): index 0; sex determination difficult
Preactive: index 0.5; evident follicular development, interfollicular conjunctive tissue present
Active: index 1; interfollicular conjunctive tissue absent or scarce, follicles full of ripe gametes, spermatozoa in order and oriented with the flagella toward the center of the follicle, oocytes in polygonal shape pressed against each other
Spawning: index 0.5; ripe gametes released through gonoduct, conjunctive tissue scarce and scattered, groups of spermatocytes in central position in the tubules, remaining oocytes still polygonal, free or attached at one side of the follicle

The mean condition index (CI) for each monthly sample was calculated as follows:

$$CI = (N_{preact} \times 0.5 + N_{act} \times 1 + N_{spawn} \times 0.5)/(N_{indif} + N_{preact} + N_{act} + N_{spawn})$$

Quantitative analysis provided further information on the reproductive state. In each female (except for cytolized animals), the diameter of at least 100 randomly selected oocytes was measured (Grant & Tyler 1983). Because female acini tend to have irregular shapes, the longest dimension was recorded and defined as "diameter." Oocyte size frequency distributions per female and per sampling date were established from these data. Last, a gonad index (GI) was computed from the ratio of the wet weight of the gonads to the total animal wet mass (Giese & Pearse 1974):

$$GI = (M_{gonad}/M_{total}) \times 100$$

Temperature data for Santa Elena were obtained from the station "El Pelado". We used chlorophyll concentration as a measure for food availability. The chlorophyll series is a merged product from several satellites: SeaWiFS (NASA), MODIS (NASA), MERIS (ESA) (http://hermes.acri.fr/GlobColour/index.php).

We calculated the mean fecundity N_{egg} of each species of various size classes (16 *S. calcifer* from the Ayangue area and 23 *S. princeps* from the Atacames area) with the gravimetric method used in finfish on the basis of gonad weight and oocyte density (Murua et al. 2003). We tested for significant differences in N_{egg} between the two species via ANCOVA of eggs per female versus species, with a covariate of total soft body mass.

RESULTS

During reproductive development and activity, the *Spondylus* gonad is white to cream in males and orange to red in females. Of the 126 specimens of *S. calcifer* examined, 54 were males, 44 were females, and 24 were animals in the indifferent stage. We found four hermaphroditic individuals, with one recognizable during dissection because of orange gonads exhibiting white spots. For a comparative study, we took samples of *S. princeps* in Esmeraldas. Of the 68 specimens of *S. princeps* examined, 28 were males, 34 were females, 4 were hermaphrodites, and 2 were animals in the indifferent stage.

Gonad Development

Gonad stage distribution in *S. calcifer* at Ayangue was highly variable between samples (Fig. 2B). Preactive organisms were present in all the months sampled, besides October to December 2007, when the number of sampled individuals per month was 4 and 5, respectively. Only 3 individuals of all samples were found in the spawning stage (1 in each sample in July 2008, and February and March 2009). The share of animals in the active stage was highest in October 2007 (100%) and October 2009 (70%), respectively. Most animals in the cytolized stage were found during the highest temperatures in February 2008 (80%) and March 2009 (83%).

The CI for *S. calcifer* in Ayangue attained maximum values in October 2007 and minimum values in February/March 2008 and March 2009 (Fig. 2C), during times of lower temperatures and higher chlorophyll concentrations. The GI showed a similar pattern, with the ratio of gonad to total weight increasing from March to October and decreasing slightly thereafter (Fig. 2D; please note that the first months of sampling were excluded from this analysis because of a different dissection technique). Multiple linear regression identified a significant positive effect of temperature on the CI ($n = 17$, $P = 0.025$, $r^2 = 0.399$) as well as on GI ($n = 102$, $P = 0.017$, $r^2 = 0.048$), whereas chlorophyll concentration affected neither CI ($n = 17$, $P = 0.520$, $r^2 = 0.038$) nor GI ($n = 102$, $P = 0.165$, $r^2 = 0.012$). Mean oocyte diameter showed a less distinct seasonal pattern (Fig. 2E). Nevertheless, oocyte diameter was significantly affected by temperature ($P < 0.001$), by chlorophyll concentration ($P = 0.008$), and by the interaction between the 2 parameters.

$$\begin{aligned} \mathrm{OD} = {} & 110.819 - 2.533 \times \mathrm{T} + 0.883 \times \mathrm{Chl} + 1.480 \\ & \times (\mathrm{T} - 24.800) \times (\mathrm{Chl} - 1.891); \\ & (n = 3{,}947,\ r^2 = 0.059,\ P < 0.001,\ \mathrm{F} = 82.446) \end{aligned}$$

Note that temperature (T) and chlorophyll (Chl) are adjusted to a mean of 0 in the interaction term to make the test for the main effects independent of the test for interaction (centered polynomials). The corresponding contour plot illustrates the overall strong negative relationship between temperature and oocyte diameter, whereas the positive effect of chlorophyll becomes apparent at higher temperatures only (Fig. 3).

Most of our gonad preparations of *S. princeps* from Atacames got lost during a robbery; hence, only a few months could be analyzed (Fig. 4). These data indicate a high share of active animals during February, March, and April 2009 (67%, 90%, and 100%, respectively), coinciding with months of high chlorophyll concentrations (unfortunately, SST data were not available for Atacames).

Individual fecundity ranged from 2.2–8.3 million eggs in *S. princeps* and from 2.9–35 million eggs in *S calcifer*. Total fecundity increased with soft body mass and was significantly higher in *S. calcifer* than in *S. princeps*.

$$\begin{aligned} N_{\mathrm{egg}} = {} & -3{,}907{,}819 + 136{,}234.543 \times \mathrm{M} \\ & + \mathrm{X}_{\mathrm{taxon}} \times 2{,}191{,}962.423 \\ & (n = 39,\ r^2 = 0.539,\ P < 0.001,\ \mathrm{F} = 21.047) \end{aligned}$$

where $\mathrm{X}_{\mathrm{taxon}}$ is –1 for *S. calcifer* and +1 for *S. princeps*. The interaction effect of taxon × body mass was not significant ($P = 0.457$).

DISCUSSION

All reproductive parameters analyzed here—histological sections (Fig. 2B), gonad condition (Fig. 2C (generally considered to be the most sensitive to changes in the reproductive development), gonadosomatic index (Fig. 2D), and oocyte diameter (Fig. 2E)—showed a consistent picture of the reproductive development of *Spondylus calcifer*. This species reproduces year-round in Ayangue, with a peak in October to December, when temperature is low and chlorophyll concentration is high (Fig. 2A). During times of higher temperature, the season with less activity was reflected by smaller oocytes, whereas the largest oocytes (associated with highest reproductive activity) were present during times of low temperature and high chlorophyll values (Oct. 2007 and September/October to December 2008). The overall small proportion of animals found in the spawning stage indicates that *S. calcifer* individuals from Ayangue are distinct batch spawners (i.e., all gametes are released in a short period of time).

Parnell (2002) reports that larvae of *Spondylus tenebrosus* are common throughout the year in Hawaiian waters, and concludes that this species is likely to spawn more than once a year, as do many other tropical pectinids (Baqueiro Cárdenas & Aldana Aranda 2000). Temperature is the exogenous factor that is most often cited as influencing gametogenesis in bivalves. Gosling (2003), on the other hand, concluded that food, rather than temperature, is the major factor determining the timing of gametogenesis in many bivalve species. In general we know that marine benthic invertebrates with planktotrophic larvae tend to adjust both width and temporal position of the "spawning window" to the seasonal availability of food supply for the larvae, because their survival is strongly affected by food limitation (Bos et al. 2006). Villalejo-Fuerte et al. (2002) found that in Bahía de Loreto, Mexico, *S. calcifer* exhibits a distinct spawning season from August to October that coincides with high water temperature and low chlorophyll concentrations. They presume that *S. calcifer* need high phytoplankton

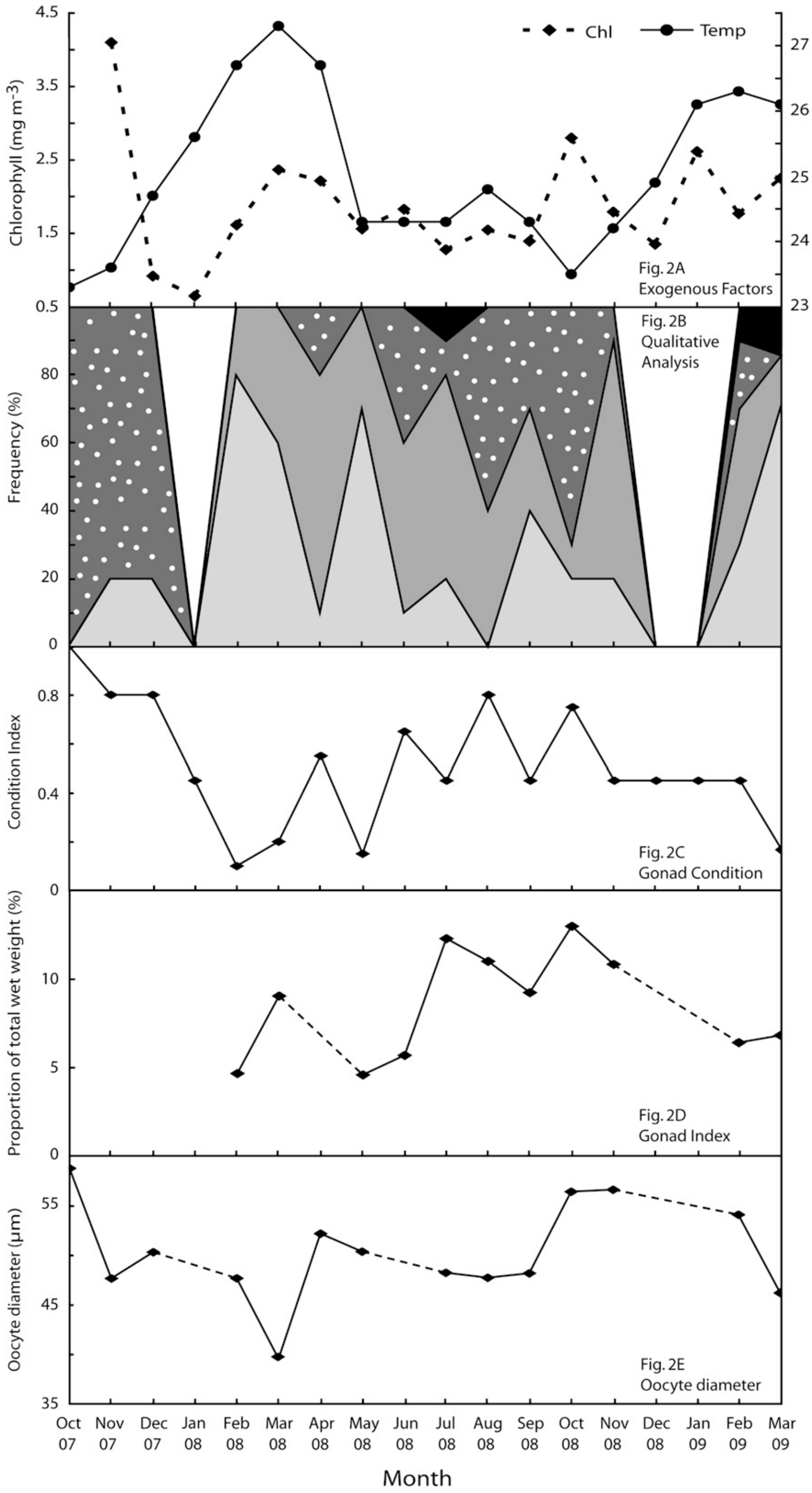

Figure 2. Different parameters of the reproductive cycle of *Spondylus calcifer* in Ayangue. Gonad stages were cytolized (□), preactive (▨), active (▩), and spawning ( ). (A) Exogenous factors. (B) Qualitative analysis. (C) Gonad condition. (D) Gonad index. (E) Oocyte diameter.

concentrations during the time of oocyte ripening, and that 29°C is the threshold temperature at which spawning occurs. Temperature conditions in our study area (23.3–27.3°C) are comparable with Hawaiian conditions (23.3–27.5°C). In other words, the annual amplitude is much lower than the 10°C range (19–29°C) in the study area of Villalejo-Fuerte et al. (2002).

In our study we worked with *Spondylus* populations that obviously do not require such an extreme thermal trigger for

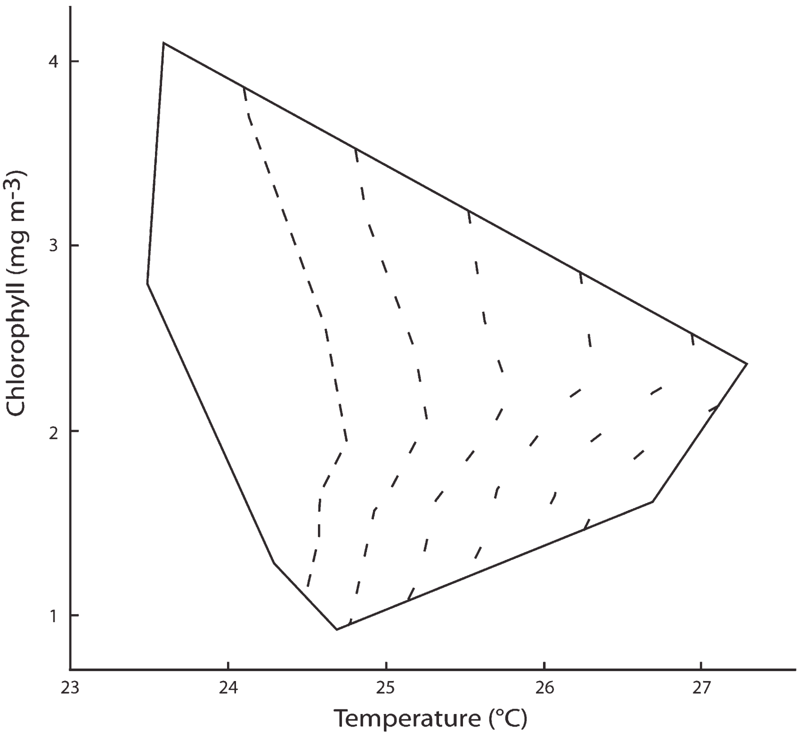

Figure 3. The contour plot illustrates the overall strong negative relationship between temperature and oocyte diameter, whereas the positive effect of chlorophyll becomes apparent at higher temperatures only.

spawning. The annual range of chlorophyll concentration is quite similar in Bahía de Loreto (monthly mean, 0.25–2.15 mg chlorophyll/m^3) and Ayangue, Santa Elena (0.6–2.8 mg chlorophyll/ m^3), with the difference that our investigation area shows a 10–month period of values over 1 mg chlorophyll/m^3 compared with 4 mo only in Bahía de Loreto. Because food supply in our study area seems secured most of the year, there is no need to accumulate and transfer nutrient reserves from the digestive gland to the gonads, as was suggested for the Bahía de Loreto population (Villalejo-Fuerte et al. 2002). Hence, we interpret the annual spawning pattern of *S. calcifer* in Ayangue (year-round with a peak between October and December) as an adaptation to the local pattern of food availability for the larvae. The Humboldt Current seasonally influences our study sites with cold, nutrient-rich waters, and the active period in both species apparently precedes the chlorophyll peak slightly (Figs. 2 and 4). It is yet to be unresolved which signal may trigger the ripening process, because chlorophyll concentrations are just a proxy for primary production.

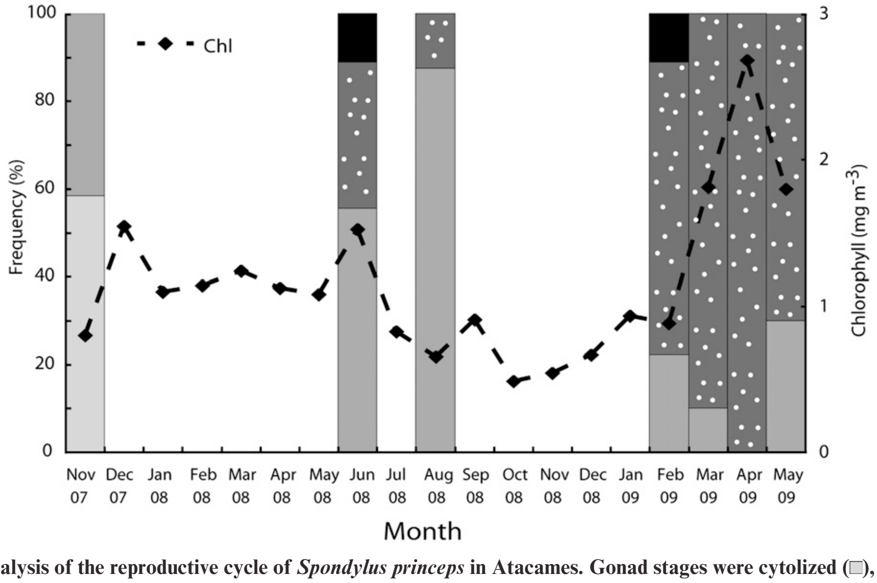

Figure 4. Qualitative analysis of the reproductive cycle of *Spondylus princeps* in Atacames. Gonad stages were cytolized (□), preactive (■), active (▨), and spawning ( ).

Reports from fishermen indicate a high sensitivity of *Spondylus* species to fishery pressure in Ecuadorian waters, as yields diminished rapidly despite a comparably low fishing effort. Fecundity of both *S. calcifer* and *S. princeps* is within the range of better studied oyster and scallop species (Helm et al. 2004), but fecundity by itself is a poor trait to predict species vulnerability to exploitation (Dulvy et al. 2003). Net recruitment rate would be the parameter of interest, but these data are lacking completely. This is most necessary, because all *Spondylus* species are broadcast spawners (Parnell 2002). Broadcast spawners are especially vulnerable to Allee effects (we follow the definition given by Stephens et al. (1999), which describes the Allee effect as "a positive relationship between any component of individual fitness" [in our case, reproduction] "and either numbers or density of conspecifics", p. 186), because fertilization success depends on the concentration of sperm and eggs in the water column (Gascoigne & Lipcius 2004a) and because broadcast spawners are more susceptible to mate limitation (Gascoigne et al. 2009), which is the dominant cause of Allee effects in aquatic invertebrates (Kramer et al. 2009). The fact that *S. princeps* and *S. calcifer* are dioecious (Villalejo-Fuerte et al. 2002; Villalejo-Fuerte et al. 2005), as well as the less synchronized reproduction as we found it at our Ecuadorian study sites, further increases the significance of potentially depensatory mechanisms and the importance of nearest neighbor distance (Babcock & Keesing 1999). Asynchrony in reproduction generally promotes Allee effects at low densities for species for which asynchrony at high densities is evolutionary beneficial (Calabrese & Fagan 2004, Levitan & McGovern 2005), and possibly augments the susceptibility of Ecuadorian *Spondylus* populations to fishery pressure in comparison with the population in Bahía de Loreto with synchronized spawning.

High exploitation rates together with Allee effects have been proved to cause fatal consequences for invertebrate populations to the point of extinction (e.g., in queen conchs (*Strombus gigas*) (Stoner & Ray-Culp 2000, Gascoigne & Lipcius 2004b), white abalone (*Haliotis sorensi*) (Hobday et al. 2001) greenlip abalone (*Haliotis laevigata*) (Babcock & Keesing 1999), and in giant clams and sea cucumbers (Roberts & Hawkins 1999)). For the greenlip abalone, fertilization rates drop rapidly when individuals are separated by 1–4 m (Babcock & Keesing 1999). Levitan and McGovern (2005) found that, for many species, sperm limitation is likely when males are more than a few meters away from a female.

Natural densities of several *Spondylus* specimens per square meter must have been common according to observations from fishermen. Our overall findings raise the suspicion that current densities of both *Spondylus* species in previously densely populated areas have long fallen below the aforementioned thresholds for other broadcast-spawning invertebrates and possibly for positive net recruitment rates. Consequently, passive measures such as protected areas and nonfishing periods may not lead to a recovery of the stock. We can show this for *S. princeps* in Atacames, even though the loss of samples does not allow establishing the complete reproductive cycle. We found many animals in the active state between February 2009 and April 2009 (Fig. 4), which happens to be the months when divers from Atacames and surrounding areas head for other target species during times of heavy rainfall and bad visibility (the times of highest values in chlorophyll concentrations in this area): December until May. We can conclude that *S. princeps* is basically undisturbed during peak reproduction times and that lack of food for larvae is not a limiting factor (Bos et al. 2006). As mentioned, we lack statistics for the *Spondylus* fishery in Ecuador, but anecdotal evidence (reports from fishermen) and market observance (amount of shells traded locally) leave no doubt that populations are nonetheless dwindling in the Atacames area as well. A closure during peak recruitment time has already proved insufficient as a measure to protect the reproductive potential of the stock.

With the latest INP reports, it seems unlikely that *Spondylus* will recuperate on its own. Artificial aggregating as a conservation measure to facilitate fertilization and reproduction should be worth a trial, ensuring, of course, that these sites remain undisturbed. In addition, further investigations for possible cultivation and eventual repopulation of former *S. calcifer* and *S. princeps* sites should be considered. Experience with restoration programs for bivalves with the help of aquaculture already exist (Manzi et al. 1986, Arnold 2001, Rossi-Snook et al. 2010) and especially experiments with hatchery produced spat of the bay scallop (*Argopecten irridians*) yielded promising results in enhancing natural populations (Tettelbach & Wenczel 1993, Peterson et al. 1996, Lu & Blake 1997, Goldberg et al. 2000, Tettelbach et al. 2002, Arnold et al. 2005, Leverone et al. 2010). Soria et al. (2010) have succeeded in a first attempt to culture larvae of S. *calcifer* and their results can be helpful in an Ecuadorian restoration program for this traditional resource.

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2.2 Towards Individual Growth Models for *Spondylus limbatus* G. B. Sowerby II, 1847 and *S. crassiquama* Lamarck, 1819

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AKM was responsible for the study design, sampling, measurements, data analysis/interpretation and manuscript writing; TB suggested data treatment and commented on the manuscript.

TOWARDS INDIVIDUAL GROWTH MODELS FOR *SPONDYLUS LIMBATUS* G. B. SOWERBY II, 1847 AND *S. CRASSIQUAMA* LAMARCK, 1819

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Abstract

Despite the economic importance, investigations on population dynamics of the bivalve genus *Spondylus* have been limited. Knowledge of individual growth is the basic prerequisite for stock assessment, and the estimation of mortality and effort parameters. Thus far, no *Spondylus* growth models have been published. This study provides first estimates for the growth parameters K and asymptotic shell length Loo for both *S. crassiquama* (K = 0.08/ Loo = 11.7 cm) and *S. limbatus* (K = 0.03/ Loo of 9.93 cm) by means of a van Bertalanffy growth model. Different morphotypes were analysed with PCR runs of fragments of the mitochondrial 16S rDNA gene to confirm the two distinct species.

Introduction

The bivalve family Spondylidae (Gray, 1826) consists of only one genus: *Spondylus* (Linnaeus, 1758), commonly also called thorny or spiny oysters, with about 76 living species worldwide (Lamprell 2006). They are closely related to the Pectinidae with whom they share the complex eyes around the mantle and a relatively well developed nervous system. An outer foliated layer composed of calcite and including the spines, a middle aragonitic layer forming the hinge and teeth and an innermost, crossed-lamellar aragonite layer characterize the shells (Taylor et al. 1969).

Three species can be found along the Ecuadorian coast: *Spondylus crassisquama* (Lamarck, 1819), formerly known as *S. princeps* (Broderip, 1833)[1] and *S. leucacanthus* (Broderip, 1833), whose distinction has been documented by Skoglund and Mulliner (1996). The third species is *S. limbatus* (G. B. Sowerby II, 1847), formerly famous as *S. calcifer* (Carpenter, 1857), which is by far the largest west American spiny oyster. This species is distributed from the Gulf of California to Peru and can be found from intertidal to subtidal zones, attached by the right valve to exposed boulders or under rock ledges (Skoglund and Mulliner 1996).

In Ecuador, *Spondylus* was a valuable source of income for local fishermen until an official fishery-ban ("Acuerdo Ministerial Nr. 136 publicado en Registro Oficial Nr. 58 el 30 de octubre de 2009") was installed to prevent the dwindling population from being eradicated. Due to their biological features, local *Spondylus* species are very susceptible to fishery pressure (Mackensen et al. 2011), and a good management system thus needs to be installed for the time when the fishery-ban will have expired. Knowledge of individual growth is the basic prerequisite for stock assessment, and the estimation of mortality and effort parameters. Thus far, no *Spondylus* growth models have been published, despite the economic significance of this taxon in the region.

Bivalve growth is usually measured as an increase in either valve length or valve height over time, though shell growth is not perfectly synchronized with soft body growth (Gosling 2003). The time can be either inferred from natural, regular shell growth marks such as annual growth bands caused by seasonal changes in growth or from mark-recapture experiments. Growth band formation intervals must be verified either by direct observation or by post-growth analysis of seasonally triggered geochemical markers in the shell, e.g., temperature dependent stable oxygen istotope ratio $\delta^{18}O$ (Clédon et al. 2005).

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[1] For a recent revision of the names of panamic Spondylids see Huber (2009)

Establishing a growth model for *Spondylus* species is a very challenging task, reflected by the lack of published studies and likely due to a very high inter-individual variability in shell forms as well as growth rates and patterns. Moreover, the outer shell region of older (and for growth models valuable) specimen is usually deformed and destroyed by drilling organisms.

This study aims to provide a first estimate of the growth parameters of the two species *Spondylus limbatus* and *S. crassisquama* in Ecuador and to develop growth models to be used for a future management. Additionally we want to provide estimates of the age of the studied specimen by using the growth rings that are formed due to changes in environmental parameters such as water temperature, salinity, depth and light which influence the availability of food and therefore the metabolism and the growth of the animal. As these growth lines are not reliable by themselves; they have to be validated with an analysis of the time intervals at which they occur with the help of a stable oxygen isotope analysis. Finally, we wanted to base all these analyses on a clear distinction between the two investigated species, which due to their morphological variety, can be hard to distinguish.

Fig. 1: Map of Ecuador with the respective study sites in the provinces of Esmeraldas in the North and Santa Elena in the South

Material and Methods

Study area and species collection

Monthly samplings of *Spondylus crassisquama* were performed at depths between 12- 15 meters North 01 05 316 East 079 53 907 off Atacames, in the province of Esmeraldas (Fig. 1). This is an area with high fishing activities, as divers and other fishermen know and value this zone for various easily accessible "bajos" (shallow water zones).

The Ecuadorian coast from the Colombian border in the north, to Punta Galera in the south (about 1°N) is part of the Panama bight, which stretches further north to the isthmus of Panama (about 9°N) and to about 81°W westwards (Cucalón 1987). This typical tropical water is warm and salinity is low; during austral summer, surface temperatures vary between 26 and 28° C and salinities between 32.5 and 34 ppt (in years with El Niño events, these waters appear to be advected further south). Annual fluctuations of the intertropical convergence zone (ITCZ) are the main influence on the seasonally different weather conditions in the bight, e.g. during austral summer, when the ITCZ moves to the equator and the rainy season reaches the coast of Esmeraldas (Cucalón 1987).

Additionally, we investigated shells of *Spondylus limbatus* from the Cenaim (Centro Nacional de Aqcuicultura e Investigaciones Marinas), which were provided by divers from the village of Ayangue. Ayangue is located in the coastal province of Santa Elena (Fig. 1), which is much more influenced by the colder waters of the Humboldt Current. We have no detailed information on the location of the study site, as local fishermen usually do not enclose their fishing grounds. But we know that divers in Ayangue are used to work with scuba gear including tanks and may thus reach deeper areas than the hookah divers from Esmeraldas.

Spondylus leucacanthus are not regularly fished (and not mentioned in the ministerial decree) and thus excluded from our study. *S. leucacanthus* are much more difficult to obtain as they inhabit deeper regions between 25 to 90 m, rarely as shallow as 15 m (Skoglund and Mulliner 1996). While they can sometimes be found for sale in local shops where the date of death is unknown and the shell is therefore of limited value, we only came across a few living specimen once in the net of a trawler from a reported depth of around 50 m.

Species validation

This study investigated *Spondylus* spp. shells from two different study sites. Although morphological analyses have proven to be useful in distinguishing species of other bivalves (Silina 2011), we wanted to ensure we do not work with different morphotypes (due to different environmental or physical conditions) of the same species as intraspecific variation is extremely high in *Spondylus* species (Whitehead 1989). DNA was extracted from muscle and mantel tissues of 8 specimens (4 specimens from each of the locations) using the Qiagen DNeasy Mini Kit according to the standard tissue protocol. Only 100 µL of elution buffer were used to increase DNA concentration. The universal primers 16Sar (5'-CGCCTGTTTATCAAAAACAT-3') and 16Sbr (5'-CCGGTCTGAACTCAGATCACGT-3') (Palumbi 1991) were used for the PCR (polymerase chain reaction) amplification of a fragment of the mitochondrial 16S rDNA gene. Reactions were carried out in 25 µl volumes with 1xHotMaster Taq (Eppendorf, 5-Prime). The PCR reaction conditions were, initial denaturation for 2 min at 94° C followed by 36 cycles of 20s at 94° C, 15s at 46° C and 80s at 65° C plus a final elongation step of 5 min at 65° C. PCR products were then checked for quality on a 2% agarose gel, stained with ethidium bromide, by loading a 5 µL of each of the amplified products mixed with 1 µL of loading dye. Additionally, a low range DNA ladder (FastRuler, ThermoFisher Scientific Inc.) was added to the gel to determine the size of the products.

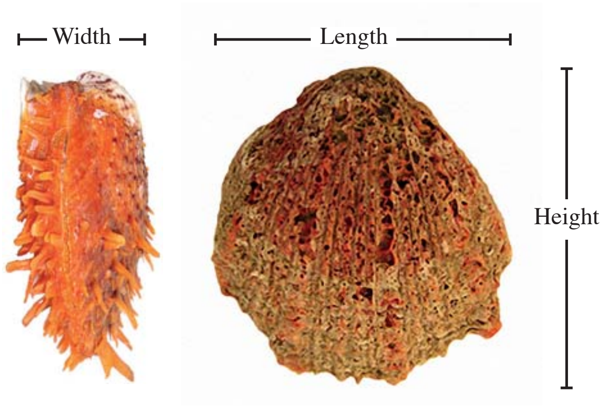

Fig. 2: Scheme of the recorded morphometric valve measurements.

Morphometry

Monthly collected animals of *Spondylus limbatus* and *S. crassisquama* for a study on the reproductive cycle were used, the flesh was sacrificed and shell morphology was recorded. Additionally, one hookah diver from Atacames allowed us to conduct basic morphometric measurements with empty *S. crassisquama* shells before these were sold. The measures included total shell weight, measured with a spring balance with the two valves still attached to each other, as well as length, height and widths, all measured with a vernier calliper to the nearest 0.1 mm (Fig. 2). All calliper measurements were taken without considering overlapping spines. A total of 279 shells of *S. crassisquama* and 121 shells of *S. limbatus* were measured and recorded.

Tagging and recapture experiment

Tagging and recapture is a labour intensive, but usually a reliable method to estimate growth rates. In bivalves, internal fluorescent shell markers like calcein and tetracycline can be used for such experiments (Day et al. 1995). We collected 20 S. crassisquama on January 5th, 2009 at North 00 59 815 East 079 57 509, kept them overnight (14 hours) in aerated seawater with 50 mg calcein ($C_{30}H_{26}N_2O_{13}$) L^{-1} and returned them to their natural habitat. We recovered 12 of the tagged animals on April 19th, 2009 used the soft body parts for other studies and stored the valves in a dark box (protected from sunlight) before they were brought to the AWI facilities where the valves were cut (see method below).

Growth and aging

Spondylus is usually attached with the right valve, and especially *Spondylus limbatus* shapes its growth along the substrate, so we used the left valves to look for internal growth bands. Shells were cut through the umbonal zone along the line of strongest growth (Fig. 3).

Fig. 3: Valve of *Spondylus crassisquama* with the line of strongest growth (LSG) through the umbo.

The cut surface was polished on a Buehler low and high speed grinder and polisher using various degrees of fine-grained sandpapers (P400, P1000, P2400, P4000) and subsequently finished with polycrystalline diamond suspension (1 and 0.1 µm) to obtain a highly reflective surface. We inspected all shell sections with the help of a reflected-light stereomicroscope (Olympus SZX12) connected to a camera (Olympus Colorview 1). We followed the advice of Lutz (1976) that counts should be made close by or directly at the umbo if internal growth lines from the shell are used, as this is the only region of the nacreous layer that contains a relatively complete record of growth. From the specimen without clear growth bands, one shell section was immersed for a trial in Mutvei's

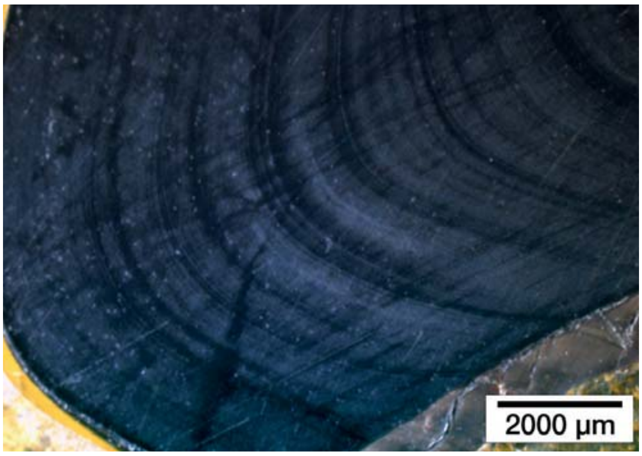

Fig. 4: Picture of a ligament with visible banding.

solution for 20 min at 37°-39° C, following the protocol of Schöne et al. (2005a). The etched section was rinsed with demineralized water afterwards and left to dry; yet growth bands did not become visible. A second immersion of the same shell for another 20 (10+10) min did not yield better results. Other shell samples were cut and used for further tests with X-Ray, Microfocus X-ray Computer Tomography and Confocal Raman Microscopy but did not yield a better visibility of growth bands.

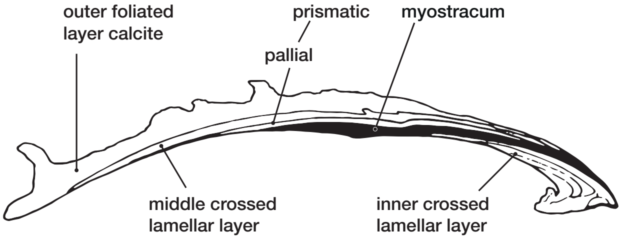

Fig. 5: Scheme of a *Spondylus* shell [taken from (Taylor et al. 1969)]

We also used the ligaments for a similar treatment of cutting and polishing on Buehler wheels after ligaments were embedded in transparent epoxy resin, but even though bands were visible under the microscope (Fig. 4), we were not able to interpret the growth band pattern in a meaningful way.

We verified the temporal pattern of growth bands by stable isotope analyses. We used two different techniques to sample $CaCO_3$ powder from the aragonitic layer of *Spondylus crassisquama* shells. After polishing and grinding the shells, we cut out the isolated umbo part for easier handling and used a hand-held micro-drilling device (with a 300 µm engraving bit). From the inner aragonite layer, sampling was conducted along the darker middle layer of aragonite, which forms hinge and teeth (Fig. 5 and 6).

We took two samples, one of from each opaque and each translucent part, which together form a visible growth band. These resulted in 24 samples from one shell and 39 from another shell, respectively. We could not sample the full growth spectrum though, as drilling epibionts heavily infested the outer shell part, which is a common problem when working with *Spondylus* shells (Fig. 6).

For the second analysis technique, we used a slice of the umbo section of a S. crassisquama shell, mounted it on a carrier glass and grinded down to 1 cm thickness for the use with a computer operated Merchantek MicroMill (New Wave Research). The automatic drill was set (software 1.5.1) to run along the growth lines following Maier and Titschack (2010).

Fig. 6: Scheme of our hand made drill holes in the umbo of a *Spondylus crassisquama* shell. The outer shell region had been infested by boring epibionts.

We started drilling at the inner, i.e. last precipitated shell region moving then further out to the older shell parts (but note that the graph of Fig. 10 shows the results after the isotope analysis in reversed order). The drill was set at a pass depth of 50 µm, retracing each track 6 times. The first 20 cuts were set to a width of 20 µm, the next 20 cuts to 30 µm, the next 20 cuts to 40 µm, the next 7 cuts in the outer region of the shell with visibly broader growth bands were set to a width of 50 µm and the last two to a cut width of 60 µm (Fig. 7). Drill speed was set at 100 %. A total of 70 $CaCO_3$ samples were obtained this way.

All were acidified with 100 % phosphoric acid. The stable isotope ratios of the resulting carbon dioxide were analysed with an isotope ratio mass spectrometer (IRMS) MAT 251 of Thermo Finnigan, coupled with an automated carbonate preparation device. The IRMS was calibrated via international standard NBS-19 to the Pee Dee belemnite (PDB) scale, and

Fig. 7: Simplified scheme of our automated milling lines, starting with lines very close to each other at the most recent formed parts of the shell and then moving further outside to the oldest parts of the shell with wider growth bands where we also increased the distance between the milling lines. We sampled twice per growth band: one sample from the opaque and one sample from the translucent part.

results are given in d-notation versus Vienna-PDB (VPDB) by

$$\delta = [(R_{sample} / R_{standard}) - 1] * 1000 \qquad (1)$$

where R_{sample} and $R_{standard}$ are the isotopic ratios of the sample and of the standard, respectively. The precision of $\delta^{13}C$ and $\delta^{18}O$ measurements, based on an internal laboratory standard (Solnhofen limestone) measured over a one-year period together with samples, was better than ±0.06 and 0.08 ‰, respectively.

The $\delta^{18}O$ values were converted into water temperature by the equation of Dettman et al. (1999):

$$T(°C) = 20.6 - (4.34 * (\delta\, ^{18}O_{shell} - (\delta\, ^{18}O_{water} - 0.27))) \qquad (2)$$

Not every shell provided visible bands; those with clear bands were chosen (*Spondylus limbatus* n = 4; S. crassisquama n = 14), individual growth increments were counted and distances between each increment measured using the image analysis software "analySIS 5.0" (Soft Imaging System). We fitted a von Bertalanffy growth model (VBGM) to these data (von Bertalanffy 1938):

$$S_t = S_{oo} * (1 - e^{-K * (t - to)}) \qquad (3)$$

where S_t is the size (e.g. length) at time t, S_{oo} is the asymptotic size, K represents the growth rate and t_0 is the age at which size would be zero.

To obtain the parameters of the VBGF, we applied the Gulland & Holt (1959) model to our data:

$$(S_{t+1}-St)/(t_{+1} - t) = a – K * S_{oo} \qquad (4)$$

where S_t and S_{t+1} represent size at time t and t+1, respectively. For S_t, we used the cumulative size of all increments from the first to increment t.

We then used a regression to define the causal relationship between the figures for S_{oo} derived from the growth measurements of increments and the absolute values of shell sizes.

Results

Species validation

All the 8 specimens showed bright and distinct bands on the agarose gel indicating the successful amplification of the 16S rDNA fragment (Fig 8). Two distinct sizes, which correspond to the different sampling locations, were observed. While the specimens from Ayangue (supposedly *Spondylus limbatus*) showed a band at ~500 bp (base pairs), the specimens from Atacames (supposedly *S. crassisquama*) showed a band at ~550 bp. This difference in sizes is a result of an insertion/ deletion event, which indicates the presence of two distinct genetic clusters.

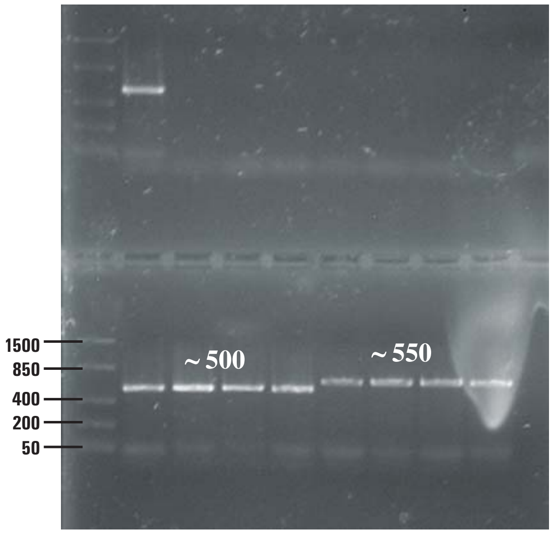

Fig. 8: Picture of the gel with the PCR results for 4 specimens from each site. On the left the 4 bands at ~500bp for the specimens from Ayangue (*Spondylus limbatus*) and on the right with 4 bands at ~550 bp, the specimens from Atacames (*S. crassisquama*).

Tagging and recapture experiment

Unfortunately, we could not detect any calcein marks after cutting the valves.

Morphometry

Both *Spondylus crassisquama* and *S. limbatus* exhibit high variance in the relationship between shell morphometric parameters, i.e. a large variability in shell shape and shell size – mass relationship, especially *S. limbatus* (Fig. 9).

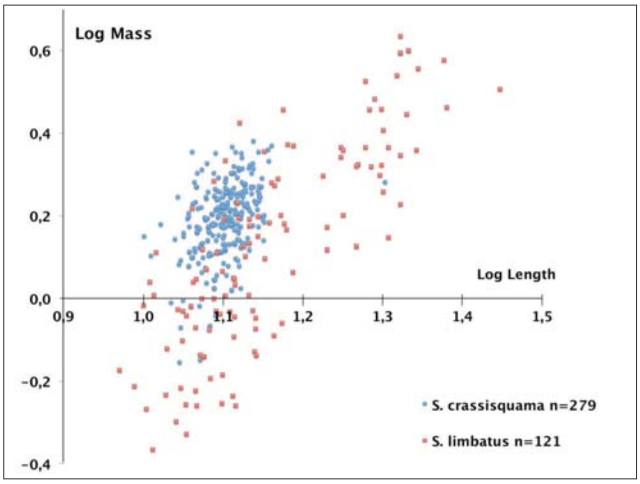

Fig 9: Log10 length plotted against log10 mass exemplarily shows the morphometric variety in *Spondylus limbatus* (red squares) in comparison with *S. crassisquama* (blue circles). The graphs for log10 width and log10 height plotted against log10 mass look similar with respect to variability.

Growth and age

Given that growth bands build up on an annual basis (Cudney-Bueno and Rowell 2008), counting the number of growth increments provided age estimates that range from 6 to 24 years in *Spondylus crassisquama* (n = 14) and from 6 to 22 in *S. limbatus* (n = 4).

Von Bertalanffy growth parameters for *Spondylus crassisquama* were estimated to K = 0.08 and S_{oo} = 31746.86 µm by the Gulland and Holt plot. By means of the relationship between increment trajectory size S and shell length L (y = 0.5398x – 5.4329), S_{oo} translates into an asymptotic shell length of L_{oo} = 11.7 cm for *S. crassisquama*. With K = 0.03 and a relative L_{oo} = 87633.96 µm for *S. limbatus* we calculated a mean absolute L_{oo} of 9.93 cm (y = 0.10762x + 0.50153).

Stable isotope analyses

Manual drilling: Our manual drilling did not result in a resolution high enough to reveal the whole range of temperature considering that the $\delta^{18}O$ curve reflects mainly the temperature, the shells were exposed to.

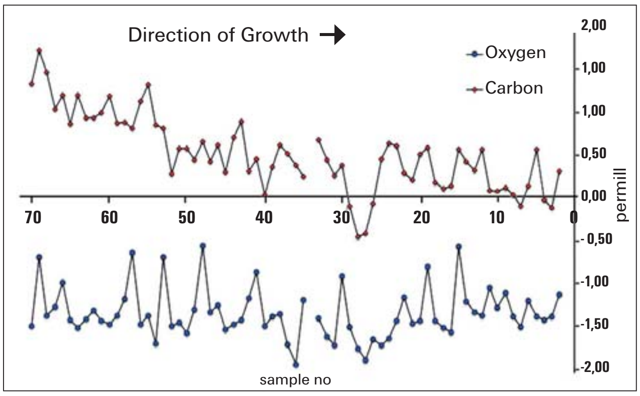

Fig. 10: Stable isotope ratios of δ ^{18}O and δ ^{13}C from our micromill drilling calcium carbonate samples after analysis with an isotope ratio mass spectrometer

MicroMill drilling: Two samples of 70 were below the minimum-needed 60 µg and could thus not be analysed. The sampling was effective though: our results reflect the whole range of temperatures the shell was presumably exposed to (Figs. 10 and 11).

Discussion

Species validation

We can conclude that the two units we tested (corresponding with the two different morphotypes) are genetically distinct and we treat these as two different species in our study. Such large differences in size (~10%) for mitochondrial genes are rare, however whether these correspond to interspecific differences cannot be said with absolute certainty and would need sequencing. The challenges many researchers face when dealing with *Spondylus* species is that their intraspecific morphology is highly variable (Whitehead 1989). Furthermore, features such as the number of spines and ribs are used for identification purposes (Lamprell 2006) and the shell abrasion in older animals adds further difficulties. Our quick validation thus proves to be a useful help in this context.

Tagging and recapture experiment

We had to take the animals from their original location and kept them in artificial tanks during the dyeing process, the stress might have induced a slowed down metabolism. A longer immersion in Calcein is recommended to ensure that the fluorescent dye is really taken up.

Shell morphometry

From a certain length on, the *Spondylus* species we worked with mainly build up shell mass, which means that assumptions related to size may lead to imprecise conclusions. While it may be appropriate in smaller size classes to define e.g. a size for maturity, the age cannot be derived only from size measurements in bigger size classes. The difficult relationship between size and weight also inhibits a straightforward procedure to calculate growth parameters (see below) especially for *S. limbatus* due to the higher variability (Fig. 9).

Growth and age

Many more *Spondylus limbatus* shells had to be omitted for our growth band reading due to the absence of visible growth lines than in *S. crassisquama*. Various methods to help with the visibility/ analysis of growth bands have been tried and failed including the Acetate peel method, IMAGEPRO computer imaging and electron microprobe analysis (EMPA), scanning electron microprobe (SEM) testing, backscatter imaging (Fabara 2003), X-rays, counting/ measuring internal ligament lines, Mutvei solution, Microfocus X-ray Computer Tomography, Confocal Raman Microscopy (all tried for this study).

Since growth models are essential for fisheries management purposes, we publish our results as a first approximation hoping that they will be complemented by further studies from other climatic regions to better understand what factors mainly drive the assumed variability of growth parameters in *Spondylus* and other bivalves (Lomovasky et al. 2008). Additionally it should be considered, that other bivalves have groups of individuals with different growth speed (de Sousa et al. 2011), a possibility that can only be considered when the *Spondylus* population size has build up again and allows for larger sampling.

Our K values are biased to some extend as our study lacks representation of smaller size classes (under 6 years), which are usually the age classes of strongest growth (Ridgway et al. 2011). Growth often slows down when maturation begins; a process that is estimated to start with 2.5 – 4 years in *Spondylus limbatus* (Cudney-Bueno and Rowell 2008). Our S_{oo} values do not seem to reflect the full growth potential, as our VBGM values do not present a true "plateau-phase". Though for *S. crassisquama*, we had specimens as big as the maximum size mentioned in literature [e.g. Skoglund and Mulliner (1996) and others], we can assume that these authors did not adequately consider the fisheries impact that is adherent to *Spondylus* since a long time ago. Our sampling was conducted in an area with high fishing activity. Therefore and because of the nonlinearity of the growth process, caution is needed when comparing our values with growth parameters of other bivalves. Our K value for *S. crassisquama* is in line with reports about other bivalves that reach impressive maximum sizes: *Tridacna maxima* (Smith 2011), which are also known to grow highly variable *in situ* (K values from 0.07 – 0.26). Cudney-Bueno and Rowell (2008) also report a high variability for *S. limbatus* (growth of 25.7 mm y-1 in one animal and 5.9 mm y-1), however they do not provide growth parameters. Our growth parameters for *S. limbatus* provide a low reliability due to the small sample size and the much higher morphological variabiliy and should be complemented by another study with higher quantities.

The oldest animals found in our sampling were 24 (*S. crassisquama*) and 22 (*S. limbatus*) years old, respectively, though we assume that much older animals were present in our samples due to bigger sizes but we were not able to age them due to absent growth bands and/ or due to heavily infested outer shell regions.

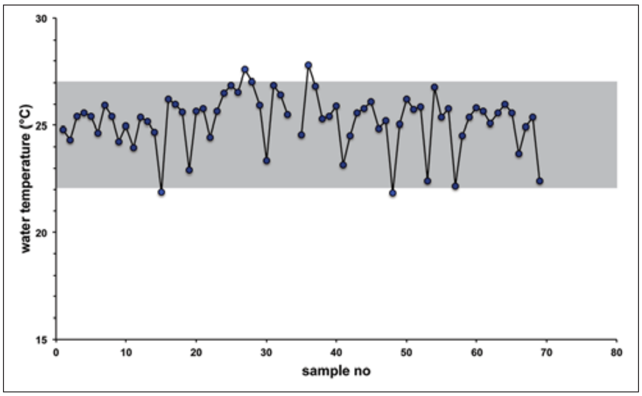

Fig. 11: Conversion of our $\delta^{18}O$ values into temperature data according to the paleo-temperature equation of Dettmann et al. (1999): $20.6 - (4.34 * (\delta\,^{18}O_{shell} - (\delta\,^{18}O_{water} - 0.27)))$. The grey bar in the background shows the range of mean annual temperature at the study site in Atacames (22-27 °C).

Many animal groups show an inversely correlated relationship between growth rate and life span, as it is true for bivalves (Ridgway et al. 2011). Our fairly low growth rates thus also lead to assume that older, i.e. larger/ heavier specimen should exist or have at least existed (Ridgway et al. 2011). A comprehensive assessment of the current number and distribution of *Spondylus crassisquama* and *S. limbatus* would help in this regard, as there is no information available in the country. This would also be necessary to regularly report on the conservation status of the species currently under protection and decide if/ when to switch from a general ban to a proper fishery management.

Stable isotope analyses

As mentioned above, physical data such as temperature and salinity are essential for an in-depth analysis of growth performance and stable isotopes. Our data logging instruments were stolen, so we have to rely on the scarce data provided by scientific literature about the area.

Depletion of $\delta^{13}C$ as a matter of age has been reported by various authors (Maier and Titschack 2010 and therein) while Schöne (2005b) has disputed this as a matter of natural fluctuations of carbon. However, our curve shows a clear trend of decreasing values with age. The decrease is relatively high with approximately 1.5 ‰ over time and best explained by a change of the metabolism of the animal when it ages.

Our results show that a high resolution is crucial to obtain good results and our last data points do not provide this necessary high resolution. These samples were taken at the inside of the umbo, the area where growth bands are narrowest. In general, our results show that this method has a lot of potential, because even with a relatively simple exercise we could display the whole variability of temperatures. Future studies must closely monitor salinity to take this variable adequately into account because a pattern oscillating similarly to the temperature is based on a relatively constant salinity (Clédon et al. 2005). The ratio of ^{18}O and ^{16}O isotopes of marine carbonate remains is controlled by temperature and the oxygen isotope composition of the surrounding seawater (Epstein and Mayeda 1953).

The eastern tropical pacific is a key climate sector and Ecuador forms part of the ENSO (El Niño Southern Oscillation) impact zone. Skeletal remains of calcifying marine organisms can provide high-resolution records of environmental parameters, but reef-building corals are limited to the Galapagos Islands (a very distinct climate sector) and very few areas along the Ecuadorian mainland coast. The stable isotopes of *Spondylus* shells may thus be a useful alternative proxy to the coral archive. Local *Spondylus* species as possible climate tracers pose various advantages over other bivalve species because: i) the thick, massive shells of *Spondylus* have a high potential to remain preserved during the ages compared to other, more fragile calcifying organisms for sklerochronological research; ii) due to the historical importance of *Spondylus* since pre-Colombian times, well-preserved ancient shells are available from archaeological excavations of various eras and may be useful for reconstructing past climate events; iii) large shells can be found, of which a lifespan of several decades or more is presumed [this needs further verification, as it is still under controversial interpretation (Fabara 2003; Cudney-Bueno and Rowell 2008 and this study) although it is hard to estimate maximum life spans and large sample sizes would be essential (Beukema 1989)].

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2.3 *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?

Annika K. Mackensen, Thomas Brey, Christian Bock, Soledad Luna

AKM was responsible for the study design, sampling, species identification, video-data analyses, calculations and manuscript writing; TB commented on the manuscript and conceived of the idea to use NMR; CB was responsible for the NMR measurements/ video and commented on the manuscript; SL helped with sampling and species identification and provided comments on the manuscript.

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ORIGINAL PAPER

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?

Annika K. Mackensen · Thomas Brey · Christian Bock · Soledad Luna

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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:

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

where $\mathrm{T_{ij}}$ 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”

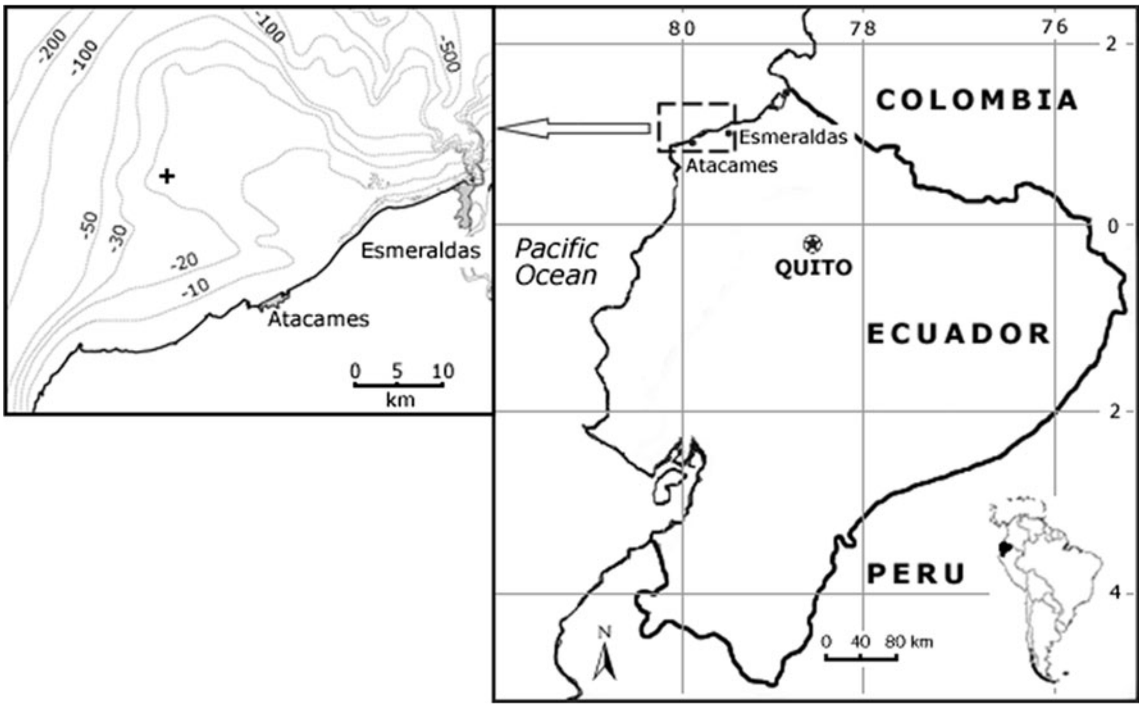

Fig. 1 Northern Ecuador showing the study site (*cross*)

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).

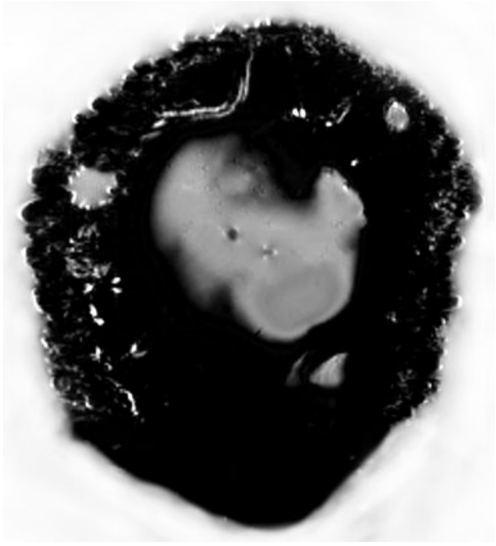

Fig. 2 A single 2-D picture slice of the MR scans after treatment with Adobe Photoshop software ready for the calculation of calcareous parts and holes (the inner gray part is the mantle cavity)

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.

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

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.

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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3 DISCUSSION

The Ecuadorian *Spondylus* fishery is a prime example of Defeo's case b) "of an unmanaged species showing overexploitation portrayed in the so called three collapsing-fishery phases" on his list of Latin American shellfish fisheries (2005). The phases depicted are as follows: "an initial stage for small shellfish catches (sustained in time, linked to local/ national consumption; followed by a rapid catch expansion (sometimes linked to exportation; in our case Peru), which ends in a final overexploitation stage" [(Castilla and Defeo 2001; Hobday et al. 2001) in (Defeo and Castilla 2005)]. Latin American coastal fisheries such as the *Spondylus* fishery generally face a number of challenges related to the amount of work involved, the social implications due to the high dependence on local resources, the absence of policy support, as well as the marginalization of many fishing communities due to remoteness and economic disempowerment (Agüero 1988; Pauly 1997; Thorpe et al. 2000). Solutions to these issues are difficult to find: in most cases, fisheries institutes in Latin American countries were created in the 1960s with the aim to do research, however given the economic realities in the region, they rarely established sufficient human and technical capacity (Agüero 2007). Furthermore it was and still is difficult to measure fishing effort properly because fishermen switch between various fishery resources using different techniques or gears throughout the year (Salas et al. 2011).

Between 1950 and 1992, the population of Ecuador tripled, while the coastal population increased fourfold (Epler and Olsen 1993). Ecuador is an example of the general trend of increasing human populations along the coastlines of the world (Ferrol-Schulte et al. 2013). This leads to ever more fishing pressure, especially in the largely biologically diverse, but economically impoverished, tropical countries. There is thus no alternative to responsible management schemes to continue to provide the necessary protein for human consumption. Unfortunately, invertebrate species are increasingly exploited in cases where stock and ecosystem-impact assessments are limited and greater management attention is needed to avoid negative impacts for both human well-being and ocean ecosystems (Anderson et al. 2011). In addition to their value as an exploited commodity, shellfish beds also play a variety of important roles in aquatic ecosystems (Gutierrez et al. 2003). Shellfish reefs or beds facilitate in- and epifauna and –flora (Commito et al. 2008) and thus are of similar ecological importance as corals, seagrass and kelp species that provide three-dimensional habitats for a variety of mutualistic and/ or commensalistic species. As we have shown in our section on the functional role of *S. crassisquama* (manuscript 2.3), this species needs to be considered as an important ecosystem engineer and foundational species, adding significantly to the biodiversity of the area. Besides providing structural habitats for other marine organisms and stabilising habitats and shorelines, turbidity and nitrification can be reduced by the filtration of suspension-feeding bivalves (Ocean Studies Board 2010). Thus even when no destructive fishing method takes place, overharvesting of these invertebrates can have drastic implications for the ecosystem (Anderson et al. 2011).

It is nearly impossible to prove that species are disappearing due to the frequent lack of data on current and historical abundance, which leads to a general tendency to underestimate marine extinction (Roberts and Hawkins 1999). Even though an area might seem large, bottom-living species usually have a much more limited area that they can occupy (Roberts and Hawkins 1999). Up to now, the recovery of *Spondylus* populations following the ban on fishing has not been assessed and recent word of mouth does not support the hope for recovery. A baseline population assessment is still missing and furthermore, it is not even clear whether the ban was *de facto* put into force, e.g. if violations have been documented or penalties issued. In spite of these difficulties, I hope that this study can contribute to shedding light on some of the very basic parameters necessary to develop a sustainable management of this fishery in the future.

3.1 Recommendations for a future *Spondylus* management

It is of crucial importance to develop baseline estimates of population densities that can be monitored in the future. Though marine invertebrates have long been seen as far too fecund to face extinction risks, recent studies have proven this perception wrong when considering the dynamics of populations at low densities. Models suggest that broadcast spawning invertebrates like *Spondylus* spp. are particularly vulnerable to anthropogenic impacts such as fishing pressure (Gascoigne and Lipcius 2004a), because a minimum density of reproductive individuals is necessary to allow for successful fertilization between egg and sperm to occur (Hobday et al. 2001). The results from our studies on fecundity and growth are within the range of better-studied bivalve species that can sustain commercial exploitation (see discussions in manuscripts 2.1 and 2.2). However, when we analysed the reproductive cycle of *S. limbatus* in the area of Ayangue (manuscript 2.1), we found that reproduction occurs year-round, with a peak in October to December, when temperature is low and chlorophyll concentration is high. This differs substantially from the results of studies from Mexico on *S. limbatus*, where temperature increase initiates simultaneous gonad maturation and reproduction occurs when food availability is low (Villalejo-Fuerte et al. 2002). The asynchronous spawning we observed in the Ecuadorian population makes it much more susceptible to mate limitation (Babcock and Keesing 1999), the most important cause for Allee effects in aquatic invertebrates (Kramer et al. 2009): when the population density is reduced due to fishing pressure and nearest neighbour distance increases, it is crucial that the closest neighbour does not mature with a time lag (even more in dioecious species such as *Spondylus*). Asynchrony in reproduction was found to generally promote Allee effects at low densities even for species where asynchrony at high densities is evolutionary beneficial (Calabrese and Fagan 2004; Levitan and McGovern 2005). Heavy exploitation rates together with Allee effects have been shown to have fatal consequences for invertebrates, potentially to the point of extinction, e.g. in queen conchs (*Strombus gigas*) (Stoner and Ray-Culp 2000; Gascoigne and Lipcius 2004b), in white (*Haliotis sorensi*) (Hobday et al. 2001) and greenlip abalone (*Haliotis laevigata*) (Babcock and Keesing 1999), giant clams and sea cucumbers (Roberts and Hawkins 1999). Current densities from our observations are below the reproductive thresholds reported for other broadcast spawning invertebrates (Babcock and Keesing 1999; Stoner and Ray-Culp 2000; Levitan and McGovern 2005) and some former *Spondylus* sites have even been fished down to zero (Subsecretaría de Recursos Pesqueros 2010). As discussed in detail in manuscript 2.1, we doubt that the Ecuadorian *Spondylus* population will be able to recover without additional actions. Furthermore we have shown that passive management measures such as a closed season did not sufficiently restrain the fishery. Necessary measures in the future must be targeted toward increasing spawning stock densities. Experiments in *Spondylus* rearing have proven to be costly and difficult (pers. comm. Cenaim) and have therefore not been followed up on recently. When restoration efforts are not only focussing on habitat destruction that limits restoration success (Supan et al. 1999), many different methods are available (Manzi et al. 1986; Tettelbach and Wenczel 1993; Peterson et al. 1996; Lu and Blake 1997; Arnold 2001; Tettelbach et al. 2002; Arnold et al. 2005; Brumbaugh et al. 2006; Arnold 2008; Leverone et al. 2010; Rossi-Snook et al. 2010) but see Caddy and Defeo (2003) on how to assess the ecological and economic feasibility of the different techniques.

A very important aspect of management efforts in artisanal fisheries is to involve the different interest groups and bring them together, because restoring shellfish populations requires consent and cooperation of all stakeholders (Arnold 2001). This, above all is our most important recommendation for achieving sustainability for the *Spondylus* fishery. During my interviews with fishers of Atacames who had witnessed and contributed to the decline of *Spondylus* it turned out, that they had not spoken to each other for years. Instead, every single one of them kept accusing the others of overharvesting and thus responsibility for the decline.

What is commonly perceived of as “the tragedy of the commons”[2] (Hardin 1968) has often been a misuse of a famous phrase that has been taken out of context to promote the solutions of individual researchers (Hawkshaw et al. 2012). More importantly: numerous studies have shown that a “tragedy of the commons” is not at all inevitable (Feeny et al. 1990; Feeny et al. 1996; Ostrom et al. 1999; Johannes 2002; McClanahan et al. 2009). Managing common pool resources requires a clear framework, however the necessary guiding principles and processes are much better understood today (Adams et al. 2003; Dietz et al. 2003; Ostrom 2009a; Ostrom 2009b). Furthermore, there is sufficient experience with a number of co-management schemes in Latin America including TURFs (Territorial User Rights in Fisheries), INTQs (Individual No-Transferable Quota), MEABRs (Management and Exploitation Areas for Benthic Resources) and others to show that co-management of common pool resources can be successful (Castilla and Defeo 2001; Defeo and Castilla 2005; Carranza et al. 2009). We find that the necessary knowledge is there, but facilitation is needed to bring the different stakeholders together to use the findings of this study to establish commonly accepted rules for users. The fact that the number of *Spondylus* fishers operating in each of the respective fishing areas is relatively small (e.g. less than 20 people at our study site in Atacames) should reduce potential for conflicts (Santos and Pacheco 2011). After all, it was the local association of Salango divers (Asociación de Buzos de Salango), which got together and decided to voluntarily ban fishing for *Spondylus* and to push for an official ban at the governmental level. This effort was successful and the resulting momentum must be channelled into similar actions in other areas.

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[2] Nowadays usually referred to as common pool resources (CPR) and defined as those “in which (i) exclusion of beneficiaries through physical and institutional means is especially costly, and (ii) exploitation by one user reduces resource availability for others.” (Ostrom et al. 1999)

3.2 Perspectives for future *Spondylus* research

Spondylus is a poorly studied genus and a significant amount of additional research needs to be done. Acknowledging that financial resources for scientific research in Ecuador are limited, I wish to highlight what I perceive as very urgent matters for future research.

The rise of atmospheric carbon dioxide (CO_2) concentrations has caused a greater CO_2 uptake by the oceans and their saturation state regarding $CaCO_3$ particles has consequently changed due to this acidification process (Feely et al. 2004). Calcareous marine organisms such as bivalves depend on the precipitation of $CaCO_3$ to produce their skeletons. The shift in inorganic carbon equilibrium towards higher CO_2 and lower carbonate ion (CO_3^{2-}) is regarded as a potential threat for calcifying organisms (Orr et al. 2005; Guinotte and Fabry 2008; Kroeker et al. 2010). As we have shown in manuscript 2.3, *Spondylus*' individual survival and functional role depends very much on building up thick, massive shells. Studies on the ability of *Spondylus* to cope with ocean acidification are thus of great importance.

As this work was focussed to develop baseline knowledge, we have excluded potential ENSO effects on *Spondylus* ecology and thus *Spondylus* fisheries in this discussion. However an ENSO effect on Ecuadorian fisheries has been shown for other species, e.g. the significant decline in captures of pelagics during El Niño years (Epler and Olsen 1993). Given the socioeconomic implications that the fishery has in Ecuador, and the fact that other bivalve (fisheries) are influenced by ENSO dynamics (Arntz et al. 1988; Mendo and Wolff 2003; Garcia-Cuellar et al. 2004; Riascos 2006; Riascos et al. 2007), *Spondylus´* response to ENSO variability should be the subject of future research.

I hope this research has contributed to the baseline knowledge of basic biological and ecological features of *Spondylus*, but also has provided some background on artisanal *Spondylus* fisheries in Ecuador. This part of research should also be continued as it is always necessary to understand not only biological and technological aspects of small-scale fisheries but the socio-cultural, institutional and economic factors as well (Pauly and Agüero 1988).

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ROSA LUXEMBURG STIFTUNG

Ministerio de Agricultura, Ganadería, Acuacultura y Pesca

SRP
Subsecretaría de Recursos Pesqueros

VEDA INDEFINIDA DE LA CONCHA SPONDYLUS

POR UNA PESCA RESPONSABLE

NO

*** LA EXTRAIGA, COMERCIALICE NI LA CONSUMA**

Recuperar la población de spondylus
en Ecuador tomará décadas.
No permitas que este histórico
recurso se extinga de nuestro mar.

¡¡TODOS A RESPETAR LA VEDA DE LA SPONDYLUS!!

ACUERDO MINISTERIAL 136 DEL 2 DE OCTUBRE DE 2009

Registro Oficial No. 58 - Viernes 30 de Octubre de 2009

REGISTRO OFICIAL
Administración del Señor Ec. Rafael Correa Delgado
Presidente Constitucional de la República del Ecuador
Viernes, 30 de Octubre de 2009 - R. O. No. 58

FUNCION EJECUTIVA

DECRETOS:
101......... Declárase el estado de excepción en la Empresa Estatal Petróleos del Ecuador, PETROECUADOR y sus empresas filiales permanentes que tiene la empresa para cada una de las actividades operativas: a) Exploración y producción; b) Industrialización; y, c) Comercialización y transporte de petróleo

102......... Dase por concluido el encargo conferido al doctor Alexis Rivas Toledo y nómbrase a la doctora María Fernanda Espinosa Garcés, Ministra Coordinadora de Patrimonio

103......... Agrégase al Decreto Ejecutivo Nº 42 del 10 de septiembre del 2009, con la que se creó la Secretaría Nacional de Gestión de Riesgos

ACUERDOS:

MINISTERIO DE FINANZAS:

069 MF-2009 Delégase al señor Antonio Grijalva, funcionario de la Subsecretaría de Crédito Público, para que represente a la señora Ministra en la sesión ordinaria del Directorio del Banco del Estado

070......... Incorpóranse varios códigos al Catálogo General de Cuentas

MINISTERIO DE GOBIERNO:

0131....... Sanciónase la Ordenanza para la elaboración, ejecución, control y rendición de cuentas de los presupuestos participativos parroquiales, rurales en el Gobierno de la Provincia de Pichincha

0197....... Apruébase la reforma y codificación de los estatutos de la Iglesia Evangélica Pentecostés Misionera “Retorno de Cristo”, con domicilio en el cantón Quito, provincia de Pichincha

MINISTERIO DE RELACIONES
EXTERIORES:

-.......... Convenio Básico de Cooperación Técnica y Funcionamiento entre el Gobierno del Ecuador y Naturaleza y Cultura Internacional

SUBSECRETARIA DE RECURSOS PESQUEROS:

136......... Declárase una veda permanente del recurso concha Spondylus Calcifer y Spondylus Princeps sobre cualquier forma de captura, transporte, comercialización y consumo, hasta que no existan estudios científicos de población y aprovecha-miento sustentable que sustenten las medidas de ordenamiento necesarias para establecer una pesca responsable

RESOLUCIONES:

CONSEJO DIRECTIVO DEL
INSTITUTO ECUATORIANO
DE SEGURIDAD SOCIAL:

C.D.282.. Refórmase el Reglamento Interno del Régimen de Transición del Seguro de Invalidez, Vejez y Muerte
C.D.283.. Expídese el Reglamento para compensación de gastos ocasionados por urgencias y emergencias atendidas en unidades de salud ajenas al IESS

INSTITUTO ECUATORIANO DE LA
PROPIEDAD INTELECTUAL,
DIRECCION NACIONAL DE
OBTENCIONES VEGETALES:

001-2009 DNOV-IEPI Deléganse facultades a los abogados Wilson Usiña Reina y Santiago Cevallos Mena, funcionarios del IEPI

002-2009 DNOV-IEPI Deléganse facultades a la abogada Nora Roxana Chang Chang, Experta Principal en Oposiciones y Tutelas Administrativas (E)

SECRETARIA NACIONAL DE
TRANSPARENCIA DE GESTION:

SNTG-011-09 Deléganse atribuciones al Subsecretario Nacional Técnico de Transparencia de Gestión

SERVICIO DE RENTAS INTERNAS:

NAC-DGERCGC09-00704 Refórmase el Art. 2 de la Resolución No. NAC-DGER2008-0182 de 21 de febrero del 2008, publicado en el Suplemento del Registro Oficial Nº 285 de 29 de febrero del 2008

TRIBUNAL CONTENCIOSO
ELECTORAL:

-.......... Expídese el Reglamento para el uso de vacaciones, licencias, cesación de funciones y designación de juezas y jueces del TCE para el período de transición

EXTRACTO:

CORTE CONSTITUCIONAL
PARA EL PERIODO DE TRANSICION

f.) Renzo Paladines Puertas, representante legal.

Certifico que es fiel copia del documento original que se encuentra en los archivos de la Dirección General de Tratados del Ministerio de Relaciones Exteriores.- Quito, a 29 de septiembre del 2009.- f.) Leonardo Arízaga S., Director General de Tratados (E).

Nº 136

EL SUBSECRETARIO DE RECURSOS PESQUEROS

Considerando:

Que el artículo primero de la Ley de Pesca y Desarrollo Pesquero establece que los recursos bioacuáticos existentes en el mar territorial, en las aguas marítimas interiores, en los ríos, en los lagos o canales naturales y artificiales, son bienes nacionales cuyo racional aprovechamiento será regulado y controlado por el Estado de acuerdo con sus intereses;

Que el 24 de abril del 2009 se realizó el taller sobre “Medidas de Ordenamiento para el Recurso Spondylus” ante la explotación indiscriminada del recurso Spondylus, con la participación de representantes de la Subsecretaría de Recursos Pesqueros, del Instituto Nacional de Pesca, de la Asociación de Buzos de la Pesca Artesanal “Puerto Salango” de la provincia de Manabí, y la Agrupación de Buzos, Ostreros y Pulperos “29 de Julio” de la provincia de Santa Elena;

Que la Asociación de Buzos de la Pesca Artesanal “Puerto Salango” de la provincia de Manabí que extraen el recurso Spondylus se comprometieron a no extraer el recurso y solicitaron a la autoridad pesquera ejecutar talleres sobre las medidas de ordenamiento para el recurso Spondylus en todo el perfil costero ecuatoriano;

Que dicha asociación comprometida a la no extracción del recurso, expresa su preocupación por la demanda agresiva de comerciantes y abastecedores de restaurantes, de la concha Spondylus, a buzos que no pertenecen a sus organizaciones y extraen especies juveniles sin ningún control;

Que existen estudios técnicos superficiales sobre el recurso Spondylus que recomiendan medidas de ordenamiento y vedas sobre este recurso; ante lo cual, la Dirección de Gestión y Desarrollo Sustentable Pesquero de la Subsecretaría de Recursos Pesqueros, en el informe técnico contenido en el memorando Nº DGDSP-612-09 de 24 de agosto del 2009, recomienda la declaratoria de una veda permanente sobre el recurso concha Spondylus Calcifer y Spondylus Princep, así como, el inicio inmediato de estudios técnicos que sirvan para establecer el estado poblacional y medidas de ordenamiento para la protección, conservación y explotación sustentable sobre este recurso;

Que la Constitución Política de la República, en su artículo 396 estipula que en caso de duda sobre el impacto ambiental de una acción u omisión, aunque no exista evidencia científica del daño el Estado adoptará medidas protectoras, eficaces y oportunas;

Que el artículo 13 de la Ley de Pesca y Desarrollo Pesquero determina que el Ministro del ramo queda facultado para resolver y reglamentar los casos especiales y los no previstos que se suscitaren en la aplicación de esta ley; y,

En ejercicio de las facultades delegadas que le confiere la letra a) del artículo 1 del Acuerdo Ministerial número 074, publicado en el Registro Oficial número 84 del 15 de mayo del 2007,

Acuerda:

Art. 1.- Declarar una veda permanente del recurso concha Spondylus Calcifer y Spondylus Princeps sobre cualquier forma de captura, transporte, comercialización y consumo, hasta que no existan estudios científicos de población y aprovechamiento sustentable que sustenten las medidas de ordenamiento necesarias para establecer una pesca responsable.

Art. 2.-Los lugares de expendio de alimentos a base del recurso Spondylus deberán agotar su reserva dentro de los quince días subsiguientes contados a partir de la fecha de publicación del presente acuerdo.

Art. 3.- El Instituto Nacional de Pesca, con la participación de las asociaciones de buzos, demás actores involucrados, y en coordinación con la Dirección General de Pesca iniciará inmediatamente los estudios necesarios para que la Subsecretaría de Recursos Pesqueros establezca un plan de manejo y conservación del recurso concha Spondylus de las especies mencionadas en el artículo primero.

Art. 4.-Quienes infringieren la veda dispuesta mediante el presente acuerdo, serán sancionados de conformidad con la Ley de Pesca y Desarrollo Pesquero.

Art. 5.- El presente acuerdo entrará en vigencia a partir de su publicación en el Registro Oficial y de su ejecución encárguese la Dirección General de Pesca, el Instituto Nacional de Pesca, en coordinación con la Dirección Nacional de Espacios Acuáticos (DIRNEA).

Notifíquese y publíquese.- Dado en Manta, el 2 de octubre del 2009.

f.) Ing. Guillermo Morán Velásquez, Subsecretario de Recursos Pesqueros.

Subsecretaría de Recursos Pesqueros.- Secretaría.- Certifico: Que la copia que antecede es conforme al original.- f.) Ilegible.

No. C.D.282

EL CONSEJO DIRECTIVO DEL INSTITUTO ECUATORIANO DE SEGURIDAD SOCIAL