The Fate of *Spondylus* Stocks (Bivalvia: Spondylidae) in Ecuador: Is Recovery Likely?

Author(s): Annika K. Mackensen, Thomas Brey and Stanislaus Sonnenholzner

Source: Journal of Shellfish Research, 30(1):115-121. 2011.
Published By: National Shellfisheries Association
DOI: 10.2983/035.030.0117
URL: http://www.bioone.org/doi/full/10.2983/035.030.0117

Journal of Shellfish Research, Vol. 30, No. 1, 115–121, 2011.

THE FATE OF *SPONDYLUS* STOCKS (BIVALVIA: SPONDYLIDAE) IN ECUADOR: IS RECOVERY LIKELY?

ANNIKA K. MACKENSEN,[1,2]* THOMAS BREY[2] AND STANISLAUS SONNENHOLZNER[3]

[1]*Nazca Institute for Marine Research, Quito, Ecuador;* [2]*Alfred Wegener Institute for Polar and Marine Research (AWI), Bremerhaven, Germany;* [3]*Centro Nacional de Acuicultura e Investigaciones Marinas, San Pedro- Manglaralto, Ecuador*

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

---

*Corresponding author. E-mail: amackensen@institutonazca.org

DOI: 10.2983/035.030.0117

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*.

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

where X_{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

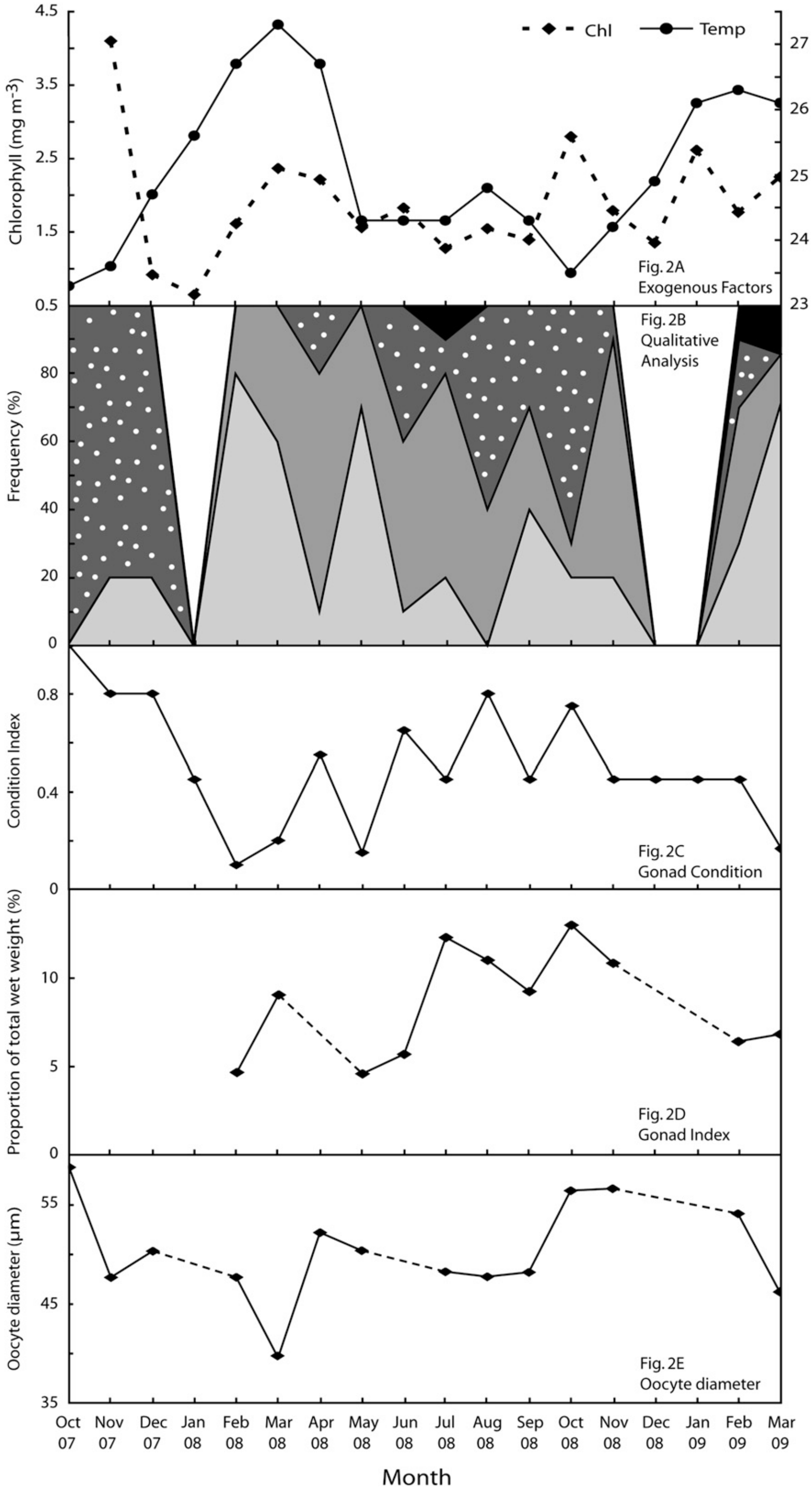

Figure 2. Different parameters of the reproductive cycle of *Spondylus calcifer* in Ayangue. Gonad stages were cytolized (□), preactive (▩), active (▦), and spawning (■). (A) Exogenous factors. (B) Qualitative analysis. (C) Gonad condition. (D) Gonad index. (E) Oocyte diameter.

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

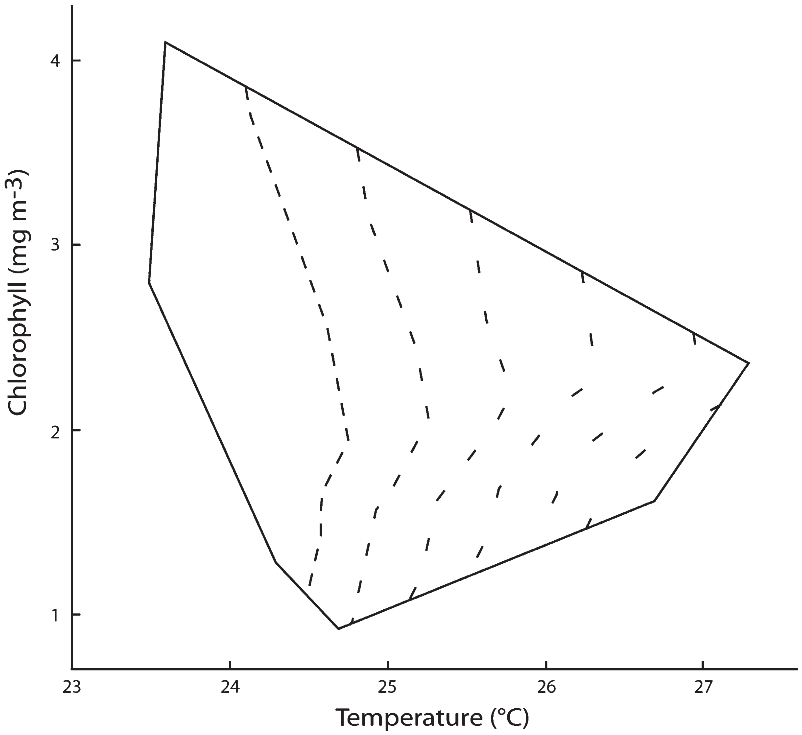

Figure 3. The contour plot illustrates the overall strong negative relationship between temperature and oocyte diameter, whereas the positive effect of chlorophyll becomes apparent at higher temperatures only.

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.

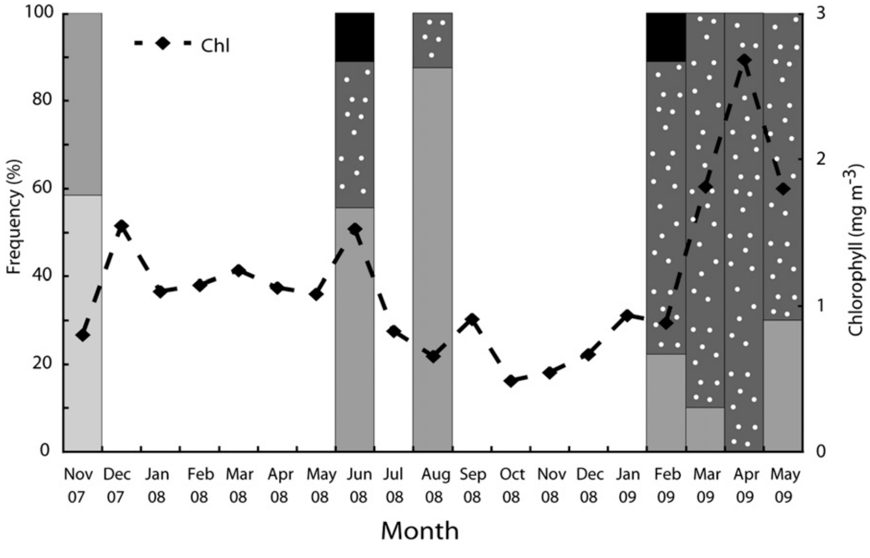

Figure 4. Qualitative analysis of the reproductive cycle of *Spondylus princeps* in Atacames. Gonad stages were cytolized (□), preactive (▩), active (▨), and spawning (■).

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.

ACKNOWLEDGMENTS

This study was possible as a result of a full doctoral scholarship for A. M. provided by the Rosa Luxemburg Foundation, Germany. We thank Jürgen Laudien (AWI) for his advice on the categories of the reproductive cycle. Thanks are due to the CENAIM for providing facilities and helpful staff, namely we owe Fanny Panchana for teaching histological practices, and Wilfrido Argüello and José Luis Vélez for organizing logistics and fixation. Thanks to Marc Taylor (AWI) for processing chlorophyll data. The Ecuadorian Ministry of Environment provided the permits for the collection of *Spondylus* individuals (nos. 028 IC-FAU-DNBAPVS/MA and 015-09 IC-FAU-DNB/MA).

LITERATURE CITED

Babcock, R. & J. Keesing. 1999. Fertilization biology of the Abalone *Haliotis laevigata*: laboratory and field studies. *Can. J. Fish. Aquat. Sci.* 56:1668–1678.

Baqueiro Cárdenas, E. & D. Aldana Aranda. 2000. A review of reproductive patterns of bivalve mollusks from Mexico. *Bull. Mar. Sci.* 66:13–27.

Barber, B. J. & N. J. Blake. 1983. Growth and reproduction of the bay scallop *Argopecten irradians* (Lamarck) at its southern distributional limit. *J. Exp. Mar. Biol. Ecol.* 66:247–256.

Bos, O., I. Hendriks, M. Strasser, P. Dolmer & P. Kamermans. 2006. Estimation of food limitation of bivalve larvae in coastal waters of north-western Europe. *J. Sea Res.* 55:191–206.

Calabrese, J. & W. Fagan. 2004. Lost in time, lonely, and single: reproductive asynchrony and the Allee effect. *Am. Nat.* 164:25–37.

Dulvy, N., Y. Sadovy & J. Reynolds. 2003. Extinction vulnerability in marine populations. *Fish Fish.* 4:25–64.

Gascoigne, J., L. Berec, S. Gregory & F. Courchamp. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Popul. Ecol.* 51:355–372.

Gascoigne, J. & R. N. Lipcius. 2004a. Allee effects in marine systems. *Mar. Ecol. Prog. Ser.* 269:49–59.

Gascoigne, J. & R. N. Lipcius. 2004b. Conserving populations at low abundance: delayed functional maturity and Allee effects in reproductive behaviour of the queen conch *Strombus gigas*. *Mar. Ecol. Prog. Ser.* 284:185–194.

Giese, A. C. & J. S. Pearse. 1974. Introduction: general principles. In: A. C. Giese & J. S. Pearse, editors. Reproduction of marine invertebrates. New York: Academic Press. pp. 1–49.

Goldberg, R., J. Pereira & P. Clark. 2000. Strategies for enhancement of natural bay scallop, *Argopecten irradians irradians*, populations; a case study in the Niantic river estuary, Connecticut, USA. *Aquacult. Int.* 8:139–158.

Gosling, E. M. 2003. Bivalve molluscs: biology, ecology and culture. Oxford: Wiley-Blackwell. 456 pp.

Grant, A. & P. A. Tyler. 1983. The analysis of data in studies of invertebrate reproduction. II. The analysis of oocyte size/frequency data, and comparison of different types of data. *Int. J. Invert. Reprod.* 6:271–283.

Helm, M. M., N. Bourne & A. Lovatelli. 2004. Hatchery culture of bivalves. FAO fisheries technical paper no. 471. Rome: FAO. 177 pp.

Hobday, A. J., M. J. Tegner & P. L. Haaker. 2001. Over-exploitation of a broadcast spawning marine invertebrate: decline of the white abalone. *Rev. Fish Biol. Fish.* 10:493–514.

Howard, D. & C. Smith. 1983. Histological techniques for marine bivalve mollusks. NOAA technical memorandum NMFS-F/NEC-25, pp. 97. Accessed March 1, 2011. <http://www.nefsc.noaa.gov/nefsc/publications/tm/pdfs/tmfnec25.pdf>.

Kramer, A. M., B. Dennis, A. M. Liebhold & J. M. Drake. 2009. The evidence for Allee effects. *Popul. Ecol.* 51:337–340.

Lamprell, K. 2006. Spiny oysters: a revision of the living *Spondylus* species of the world. Brisbane: Jean Lamprell. 119 pp.

Leverone, J. R., S. P. Geiger, S. P. Stephenson & W. S. Arnold. 2010. Increase in bay scallop (*Argopecten irradians*) populations following releases of competent larvae in two west Florida estuaries. *J. Shellfish Res.* 29:395–406.

Levitan, D. & T. McGovern. 2005. The Allee effect in the sea. In: E. A. Norse & L. B. Crowder, editors. Marine conservation biology: the science of maintaining the sea's biodiversity. Washington: Island Press. pp. 47–57.

Lu, Y. T. & N. J. Blake. 1997. The culture of the southern bay scallop in Tampa Bay, an urban Florida estuary. *Aquacult. Int.* 5:439–450.

Manzi, J., N. Hadley & M. Maddox. 1986. Seed clam, *Mercenaria mercenaria*, culture in an experimental-scale upflow nursery system. *Aquaculture* 54:301–311.

Murua, H., G. Kraus, F. Saborido-Rey, P. Witthames, A. Thorsen & S. Junquera. 2003. Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *J. Northwest Atl. Fish. Sci.* 33:33–54.

Parnell, P. E. 2002. Larval development, precompetent period, and a natural spawning event of the pectinacean bivalve *Spondylus tenebrosus* (Reeve, 1856). *Veliger* 45:58–64.

Paulsen, A. C. 1974. The thorny oyster and the voice of God: *Spondylus* and *Strombus* in Andean prehistory. *Am. Antiq.* 39:597–607.

Peterson, C., H. Summerson & R. Luettich. 1996. Response of bay scallops to spawner transplants: A test of recruitment limitation. *Mar. Ecol. Prog. Ser.* 132:93–107.

Roberts, C. M. & J. P. Hawkins. 1999. Extinction risk in the sea. *Trends Ecol. Evol.* 14:241–246.

Rossi-Snook, K., G. Ozbay & F. Marenghi. 2010. Oyster (*Crassostrea virginica*) gardening program for restoration in Delaware's inland bays, USA. *Aquacult. Int.* 18:61–67.

Sastry, A. N. 1979. Pelecypoda (excluding Ostreidae). In: A. C. Giese & J. S. Pearse, editors. Reproduction of marine invertebrates. New York: Academic Press. pp. 113–292.

Skoglund, C. & D. K. Mulliner. 1996. The genus *Spondylus* (Bivalvia: Spondylidae) of the Panamic Province. *Festivus* 28:93–107.

Soria, G., J. Tordecillas-Guillen, R. Cudney-Bueno & W. Shaw. 2010. Spawning induction, fecundity estimation, and larval culture of *Spondylus calcifer* (Carpenter, 1857) (Bivalvia: Spondylidae). *J. Shellfish Res.* 29:143–149.

Stephens, P., W. Sutherland & R. Freckleton. 1999. What is the Allee effect? *Oikos* 87:185–190.

Stoner, A. W. & M. Ray-Culp. 2000. Evidence for Allee effects in an over-harvested marine gastropod: density-dependent mating and egg production. *Mar. Ecol. Prog. Ser.* 202:297–302.

Subsecretaría de Recursos Pesqueros Ecuador 2010. Investigan situación de concha *Spondylus*. Accessed January 24, 2011. <http://www.subpesca.gob.ec/subpesca323-investigan-situacion-de-concha-spondylus.html>.

Tettelbach, S., C. Smith, P. Wenczel & E. Decort. 2002. Reproduction of hatchery-reared and transplanted wild bay scallops, *Argopecten irradians irradians*, relative to natural populations. *Aquacult. Int.* 10:279–296.

Tettelbach, S. & P. Wenczel. 1993. Reseeding efforts and the status of bay scallop *Argopecten irradians* (Lamarck, 1819) populations in New York following the occurrence of brown tide algal blooms. *J. Shellfish Res.* 12:423–431.

Villalejo-Fuerte, M., M. Arellano-Martínez, B. P. Ceballos-Vázquez & F. García-Domínguez. 2002. Reproductive cycle of *Spondylus calcifer* Carpenter, 1857 (Bivalvia: Spondylidae) in the "Bahía de Loreto" National Park, Gulf of California, Mexico. *J. Shellfish Res.* 21:103–108.

Villalejo-Fuerte, M., A. Tripp-Quezada & F. García-Domínguez. 2005. Varición de los índices gonádico, de rendimiento muscular y de la glándula digestiva de *Spondylus princeps* (Gray, 1825) (Mollusca: Bivalvia) en Isla Cedros y Punta Eugenia, México. *Rev. Biol. Mar. Ocean.* 40:87–90.