Reproductive cycle of the rock oyster, *Hyotissa hyotis* (Linné 1758) (Mollusca, Bivalvia, Gryphaeidae) during El Niño 1997-98 and La Niña 1998-99 events at La Ballena Island, Gulf of California, Mexico

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Abstract. The reproductive cycle of *Hyotissa hyotis* during El Niño 1997-98 and La Niña 1998-99 events in La Ballena Island, Gulf of California, Mexico was examined in relation to sea water temperature and chlorophyll *a* concentration. Every month, from January 1997 to December 1999, 30 adult specimens of *H. hyotis* were collected at 10 m depth by scuba diving. The specimens' gonads were subjected to histological analyses and the gonadosomatic index was determined. Spawning occurs during the summer in relation to high temperature, becomes more intense during El Niño and decreases during La Niña events. Sea water temperature was the main factor regulating spawning during these events. The gonadosomatic index is an indicator of gametogenic activity whereas food availability is closely related to gonadic development.

Key words: Reproduction, spawning, honeycomb oyster, temperature, Bivalvia

Resumen. Ciclo reproductivo de la ostra de roca *Hyotissa hyotis* (Linné, 1758) (Mollusca, Bivalvia, Gryphaeidae) durante eventos de El Niño 1997-98 y La Niña 1998-99 en Isla La Ballena, Golfo de California, Mejico. Se estudió mediante un análisis histológico de las gónadas y la determinación del índice gonadosomático el ciclo reproductivo de *Hyotissa hyotis* en la isla La Ballena, Golfo de California, México durante El Niño 1997-98 y La Niña 1998-99, en relación con la temperatura y la concentración de clorofila *a*. De enero de 1997 a diciembre de 1999 se recolectaron al azar 30 organismos adultos por mes de *H. hyotis* mediante buceo autónomo a 10 m de profundidad. Se encontró que el desove se presenta en los meses de verano en relación con las temperaturas altas, que su intensidad se incrementa durante El Niño y que disminuye durante La Niña, además de que la temperatura del mar fue el principal factor que regulo el desove durante ambos eventos, que el índice gonadosomático es un indicador de actividad gametogénica y que la disponibilidad de alimento está relacionada con el desarrollo gonádico.

Palabras clave: Reproducción, desove, ostión de roca, temperatura, Bivalvia

Introduction

El Niño Southern Oscillation (ENSO) and La Niña weather phenomena occur every 3 to 7 years with varying intensity. Their main effect in the Latin American Pacific coast is a temperature increase and a lowering of the thermocline which lead to a collapse in primary productivity (Barber & Chavez 1986, Arntz & Fahrbach 1996). The 1997-98

El Niño event has been the most intense ever recorded in the tropical Eastern Pacific and the one that has had the greatest impact on global weather (McPhaden 1999), and has thus been named the "El Niño of the century" (Wolter & Timlin 1998). In the Gulf of California, positive temperature anomalies larger than 3°C were recorded during the 97-98 El Niño and negative temperature anomalies larger than −1.0 °C were recorded during the 98-99 La Niña event (Lavín *et al*. 2003).

Learning how environmental changes affect the reproduction of marine bivalves is important as it has been widely documented that temperature and food availability are the most important factors affecting seasonal variations in the reproductive activity of these organisms (Suárez *et al*. 2005, Morriconi *et al*. 2007). However, the effects of El Niño and/or La Niña have only been studied in some species of the Western coast of South America, such as *Mesodesma donaciun* (Barriga & Quiroy 2002), *Aulacomya ater* (Gamarra & Cornejo 2002), *Gari solida* (Urban & Tarazona 1996) and *Tagelus dombeii* (Ishiyama & Shiga 1998) in Peru; *Donax dentifer* (Riascos 2006) and *Cardita affinis* (Riascos *et al*. 2008) in Colombia; *Argopecten purpuratus* (Cantillanez *et al*. 2005, Avendaño *et al*. 2006) in Chile and *Pinctada mazatlanica* (García-Cuellar *et al*. 2004) in the Gulf of California, Mexico.

Knowledge of the reproductive cycles of marine invertebrates is relevant for the management of wild populations, as well as for the development of aquacultural activities (Gaspar-Soria *et al*. 2002). Studying the reproductive patterns of species such as the oyster, *Hyotissa hyotis* (Linné, 1758), is important as it is commercially exploited in the Indo-Pacific (Carriker & Gaffney 1996) and the Eastern Pacific (Holguin-Quiñones 1976).

The rock oyster is circumtropical in distribution; it has been recorded in the tropics in the Indo-Pacific and the Eastern Pacific (Carriker & Gaffney 1996), the Caribbean (Sevilla 1993), Florida (Bieler *et al*. 2004), and south east coast of India (Stella *et al*. 2010). It is common in rocky coasts as well as in coral reefs (Harry 1985, Carriker & Gaffney 1996). In the Pacific coasts of the Americas, it is found from the South end of the Gulf of California to the Ecuador, including the Galapagos Islands. However, it is only abundant in the Gulf of California (Keen 1971), where banks with densities up to 50 individuals/m^2 can be found in some islands (Duprat-Bertazzi & García-Domínguez 2005).

Overall, *H. hyotis* has been little studied. Studies of its taxonomy (Sevilla *et al*. 1998), feeding habits in relation to the breeding season

(Villalejo-Fuerte *et al*. 2005), and the relationship between breeding and biochemical composition (Rodríguez-Astudillo *et al*. 2005) have been conducted in Mexico. Reproductive patterns have only been studied in La Ballena Island (Duprat-Bertazzi & García-Domínguez 2005), between August 1995 and December 1996, a period which, according to the Oceanic Niño Index (ONI) values, was coincident with a La Niña event occurring from October 1995 through March 1996 (Climate Prediction Center 2008). Based on Multivariate ENSO Index (MEI) values, the period from March 1995 through December 1996 was normal, except for the months from September 1995 through February 1996 when a weak La Niña event occurred (Wolter & Timlin 1998). This study examines the effects of El Niño 1997-98 and La Niña 1998-99 events on the reproductive cycle of *H. hyotis* through changes in sea surface temperature and food availability.

Materials and methods

The study was conducted on samples from a wild population collected in an oyster reef located off La Ballena Island (24° 29' 20" N, 110° 24' 31" W), part of the Espiritu Santo archipelago at La Paz Bay, Baja California Sur, Mexico. Every month, from January 1997 to December 1999, 30 adult specimens of *H. hyotis* were collected at 10 m depth by scuba diving. In the laboratory, the shell length (SL) of each specimen was measured, to the nearest 1mm, with a calliper. Then, the specimens were dissected and the fresh weights of both, the soft body parts and the gonad, were recorded to the nearest 0.1g. All the specimens examined were between 130 and 230 mm SL (average = 185 mm SL).

For histological analysis, a 1 cm³ gonad segment was fixed in a buffered 10% formaldehyde solution for 48 h, dehydrated in ethylic alcohol, cleared in Hemo-De, and embedded in paraplast. Sections 6 µm thick were cut on a rotatory microtome, placed on slides and stained with Harris hematoxylin-eosin (Humason 1979). To study the gonadal cycle, gonad preparations were examined under the microscope and assigned to a development stage using categories previously defined for this same species (Duprat-Bertazzi & García-Domínguez 2005): undifferent, developing, ripe, partially spawned, and spent.

The gonadosomatic index (GSI) was evaluated following the Sastry & Blake (1970)'s criterion, which expresses the gonad weight as a percentage of the shell-less body weight. The resulting GSI curve was then interpreted following

Villalejo-Fuerte & Ceballos-Vázquez (1996)'s criteria. The lowest values were considered as evidence of post-spawning or gametogenic inactivity, whereas a sustained increase in the GSI values denotes gametogenic activity. Peaks in the curve were considered as denoting maturity while a sustained decrease in the GSI values was considered as evidence of population spawning.

Sea surface temperature (SST) values were obtained from the National Oceanic and Atmospheric Administration (NOAA)'s Coastal Zone Colour Scanner (CZCS). Chlorophyll *a* concentration data for La Paz Bay for the period January 1997 through December 1999 were taken from Kahru *et al.* (2004). Time periods influenced by El Niño and La Niña events were delimited based on García-Cuellar *et al.* (2004)'s criterion who, based on positive and negative temperature anomalies for the same locality. El Niño-influenced period (characterized by positive anomalies) going from May 1997 through October 1998 and the La Niña-influenced period (negative anomalies) going from November 1998 through November 1999.

To test for significant differences in the gonadosomatic index (GSI) values, a one-way analysis of variance (ANOVA) was applied, followed by a Tukey's multiple range test. The same approach was followed to test for between-years differences in the monthly proportions of ripe and spawning individuals in the population. Spearman's rank correlation analyses were used to examine the relationships between GSI values and temperature, chlorophyll *a* concentration (mg/chl) and the proportions of mature and spawning individuals. The same analysis was also used to examine the relationship between the proportion of undifferentiated individuals and chlorophyll *a* concentration (mg/chl).

Percentage data were first subjected to an arcsine transformation in order to reduce the dependency on the sample variance in intermediate values and to normalize the data (Zar 1999). A significance level of $\alpha = 0.05$ was used in all statistical tests.

Results
Temperature and anomalies

SST values ranged from 19 to 30.8 °C. During El Niño, SST ranged from 21.6 to 30.8 °C with a maximum anomaly of +2.82 °C in January 1998. During La Niña, SST values varied from 19 to 28.2 °C, with a maximum anomaly of -1.36 °C in February 1999. SST values and anomalies are shown in Figure 1.
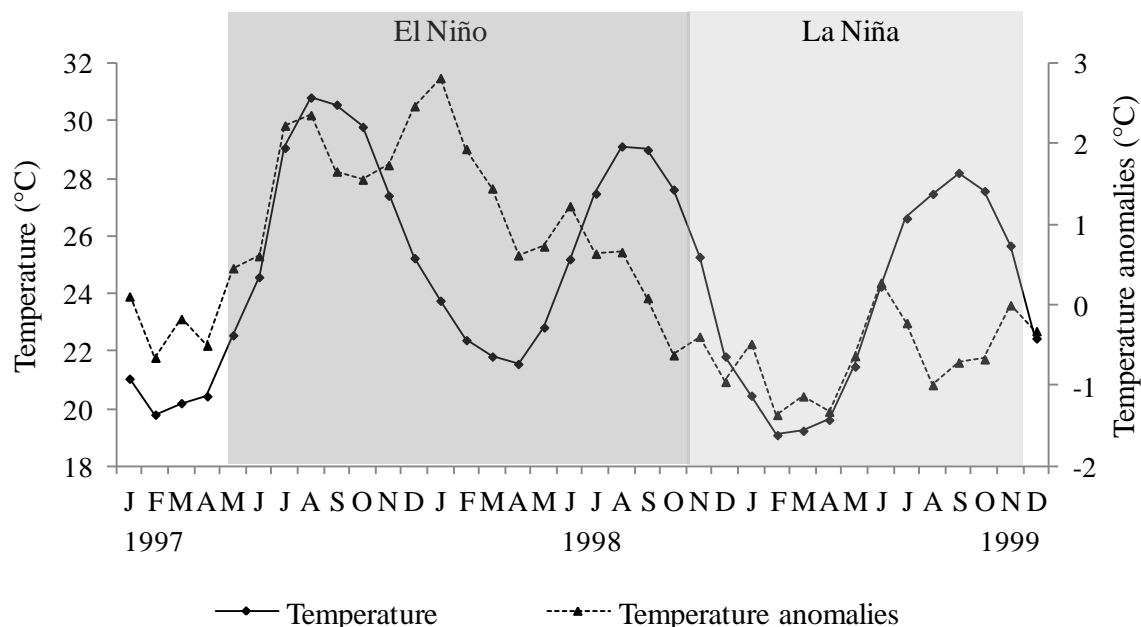

Figure 1. Monthly averages of sea surface temperature and temperature anomalies from January 1997 to December 1999 at La Ballena Island, Gulf of California, Mexico. El Niño from May 1997 to October 1998 (positive anomalies), La Niña from November 1998 to November 1999 (negative anomalies).

Reproductive cycle

Histological analyses showed that the spawning of *H. hyotis* occurred from May to September in 1997 and from April to October in

both, 1998 and 1999 (Fig. 2). In those three years, the highest frequency of spawning individuals was recorded in August (91.6, 80 and 76.4%, respectively). Ripe specimens were observed from May through July in 1997, from April through October in 1998 and between April and September in 1999. The highest frequency of ripe individuals was observed in May 1997 (47%), July 1998

(68.4%) and May 1999 (75%). Undifferentiated individuals were observed from January to June in 1997, between October 1997 and February 1998 and from September 1998 through April 1999. The highest frequency of undifferentiated organisms was observed in January in both, 1997 and 1998 (75 and 82%, respectively), and in February and December in 1999 (90 and 70%, respectively).
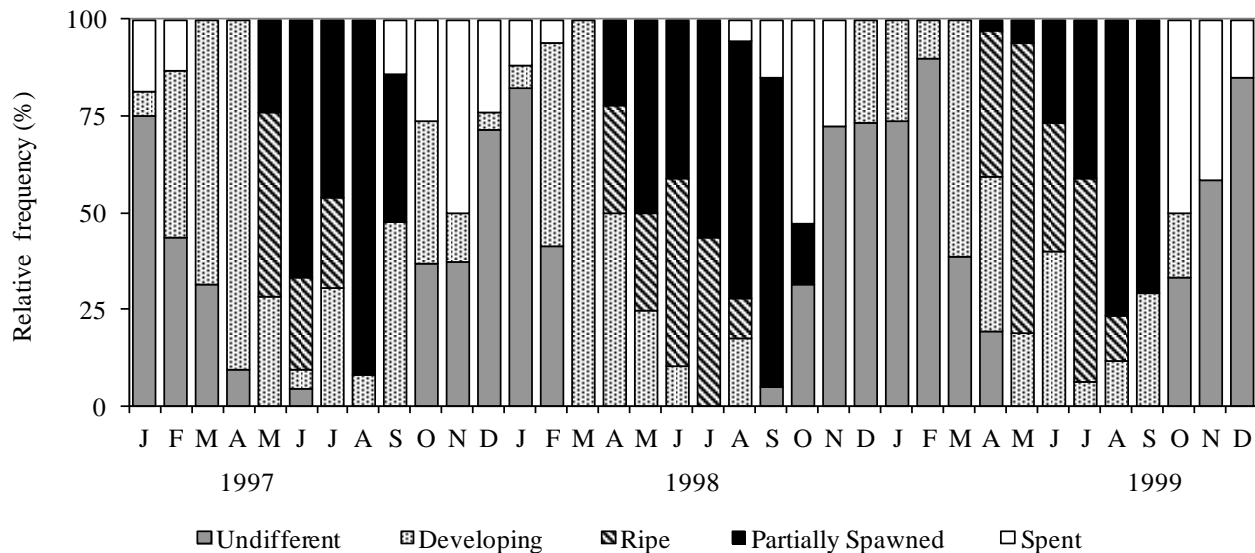

Figure 2. Reproductive cycle of *Hyotissa hyotis* from January 1997 through December 1999 at La Ballena Island, Gulf of California, Mexico.

Gonadosomatic index

    Gonadosomatic index values showed a clearly seasonal pattern with statistically significant differences (one-way ANOVA, $P < 0.05$) throughout the study period (Fig. 3). GSI values were low in January - March 1997 (2.0% - 2.4%), October 1997 - February 1998 (2.0% - 3.2%), October 1998 - February 1999 (2.2% - 2.9%) and from October through December 1999 (2.2% - 3.1%). All the GSI values lower than 4.4% were not significantly different. In 1997, the GSI increased from April to June and from March to June in both, 1998 and 1999. The highest GSI values were recorded in June 1997 (11.9%), April – July 1998 (11–10.4%) and May – July 1999 (10.7–10. 9%). GSI values decreased progressively after those periods, until December, when the lowest values (< 2.0%) were recorded in all the three years.

Relationships between indices, gonadal stages and environmental factors

    No significant correlations were found between temperature and GSI ($R = 0.23$, $P > 0.05$) (Fig. 4), or between temperature and the proportion

of ripe individuals ($R = -0.02$, $P > 0.05$) (Fig. 5). However, temperature was significantly correlated with the proportion of spawning individuals ($R = 0.58$, $P < 0.01$) (Fig 5). GSI values were significantly correlated with the proportion of both, spawning ($R = 0.72$, $P < 0.01$) and ripe individuals ($R = 0.83$, $P < 0.01$) (Fig. 5), and negatively correlated with chlorophyll *a* concentration ($R = -0.61$, $P < 0.01$) (Fig. 4). In turn, the concentration of chlorophyll *a* was significantly correlated with the proportion of undifferentiated individuals ($R = 0.71$, $P < 0.01$) (Fig. 6).

Discussion

    Results from both, the GSI and histological analyses, demonstrate that reproduction in *Hyotissa hyotis* is a markedly seasonal process, in which the undifferentiation stage occurs during the winter and spawning in the summer. However, the reproduction is affected accordingly with changes of temperature as is discussed forward.

    Physiological responses of many organisms are regulated by both internal and external cues,

such as temperature and food availability, which directly or indirectly act to restart or maintain internal clock mechanisms (Lawrence & Soame 2004) that influence metabolism and affect growth and reproductive patterns. It has been shown that high temperature reduces ingestion rate and increases respiration rate and ammonia excretion, thus having a negative impact on growth (Albentosa *et al*. 1994). On the other hand, it has been reported that temperature variations can trigger and synchronize the timing of some gonadal development stages (Lubet 1983), lead to variations

in the onset and intensity of spawning, and even inhibit the release of oocytes (Rose *et al*. 1990) or, alternatively, lead to different modes of gonadal recovery and to spawning patterns associated with environmental changes. Moreover, those physiological processes, being influenced by environment, might also be affected by large-scale environmental changes such as ENSO. Thus, the increase or decrease in temperature caused by these weather phenomena can either benefit or affect negatively the organisms' reproductive processes (Riascos 2006).
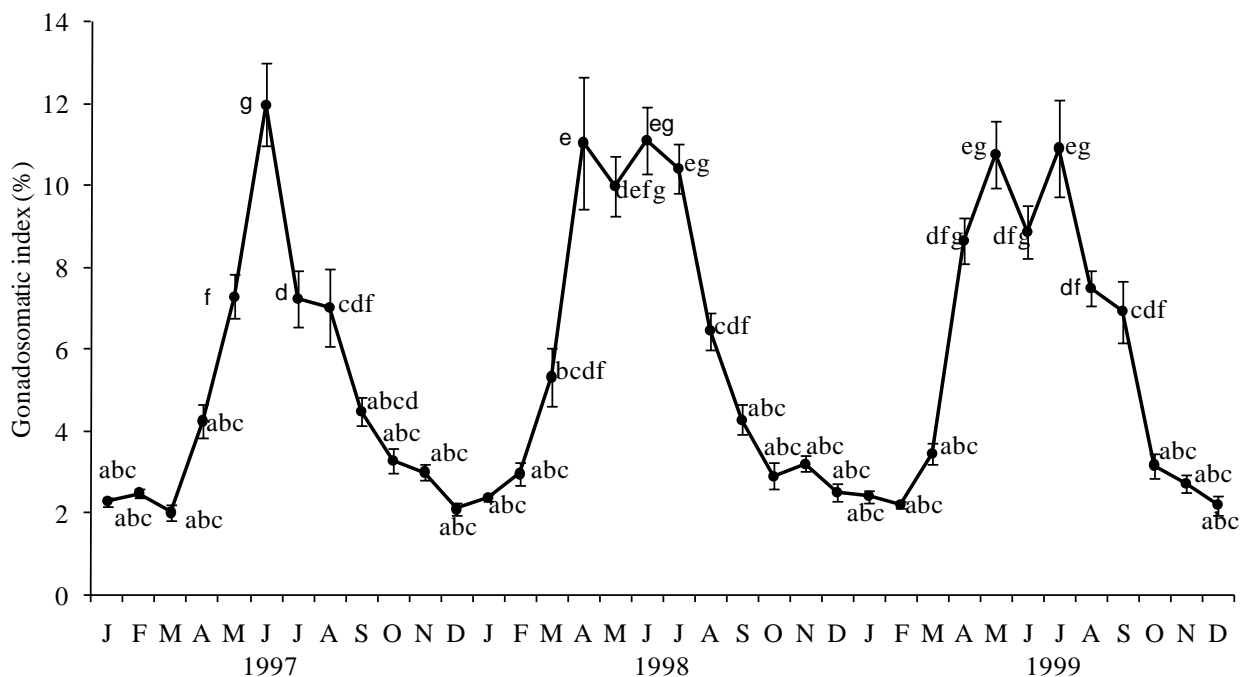

Figure 3. Temporal variation in the gonadosomatic index of *Hyotissa hyotis* at La Ballena Island, Gulf of California, Mexico. GSI values bearing different superscript are significantly different (ANOVA, $P < 0.05$). Vertical bars denote standard errors.

In this study, variations in the gonadal cycle related to El Niño and La Niña events were observed. During the spawning periods (as determined by histological analyses) of 1997 and 1998, under the influence of a El Niño event, the percent of individuals in spawn stage increase (related to the spawning frequency in the population) and was higher than that observed in the 1999 spawning period, under the influence of a La Niña event. However, the spawning period was equally long (in 1998) or even longer (in 1997) under the influence of La Niña than under El Niño events. Similar phenomena have been reported in other species of

marine bivalves whose reproductive patterns under the influence of El Niño and La Niña events have been studied. For example, in *Pinctada mazatlanica*, García-Cuellar *et al*. (2004) observed longer and more intense spawning periods during El Niño than during La Niña events, similar pattern was observed by Cantillanez *et al*. (2005) in *Argopecten purpuratus*.

Studies on some bivalve species from the Latin American Pacific were conducted during the El Niño event of 1992-93. In *Gari solida*, spawning occurred earlier in 1992 than in 1990 and extra events of spawning were observed in 1993.

However, the authors concluded that the El Niño event of 1992 had a negative impact on reproduction as the higher temperatures reduced the individuals' gonadic production, while in 1993 had a positive effect as the lower temperatures induced additional spawning events (Urban & Tarazona 1996). In *Tagelus dombeii* production of ripe individuals and spawning both increased as a result of the increase in sea surface temperature (Ishiyama & Shiga 1998). In *Argopecten purpuratus* spawning intensity was especially high (Wolff 1988).
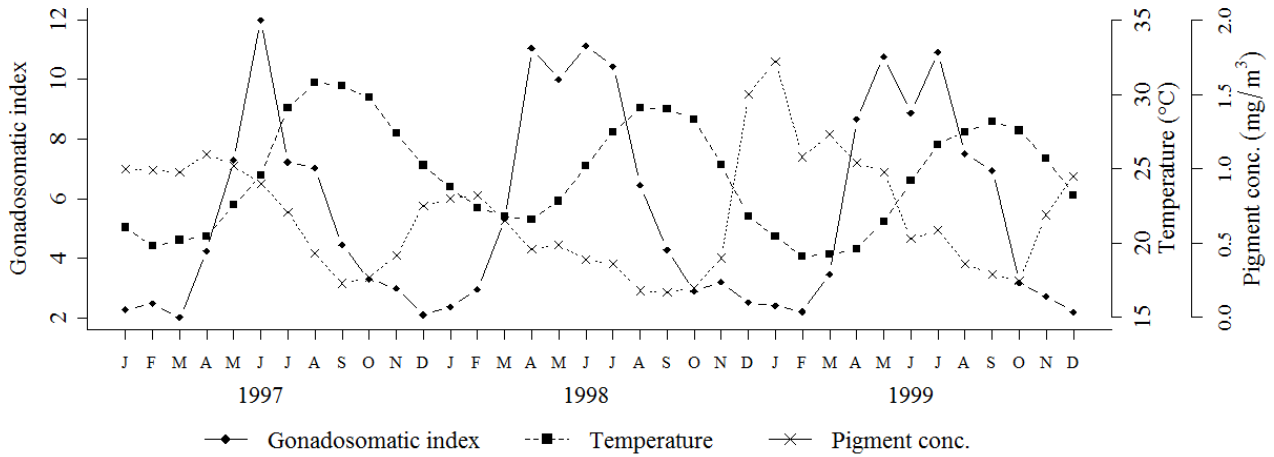

Figure 4. Relationship between sea surface temperature and chlorophyll *a* concentration with the gonadosomatic index of *Hyotissa hyotis* from January 1997 through December 1999 at La Ballena Island, Gulf of California, Mexico.
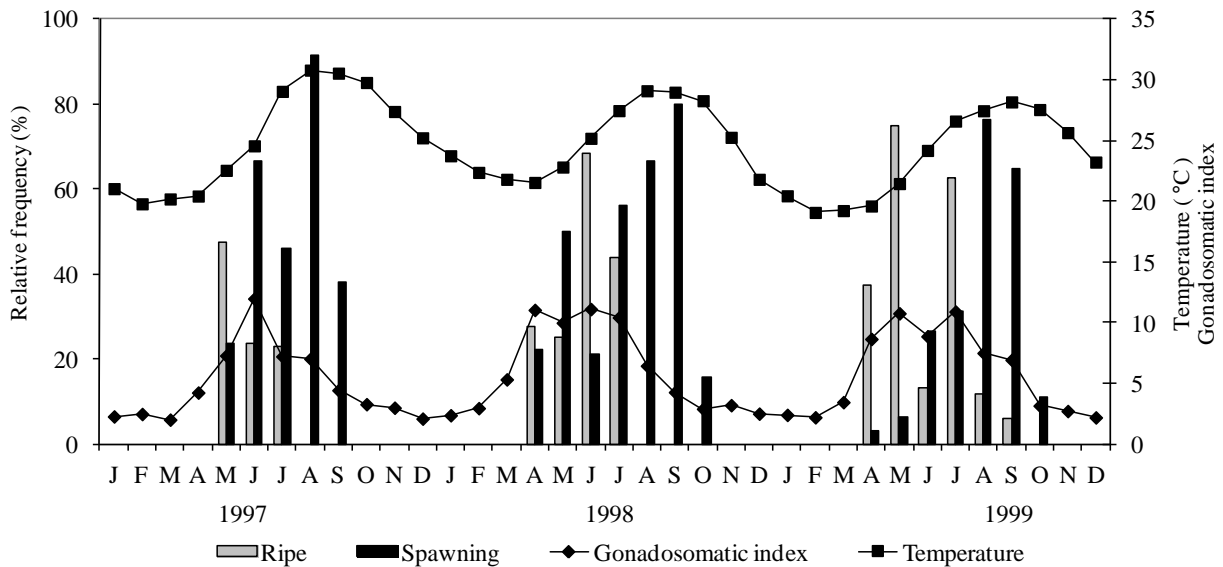

Figure 5. Relationship between the proportion of ripe and spawning *Hyotissa hyotis* individuals with the gonadosomatic index and sea surface temperature from January 1997 through December 1999 at La Ballena Island, Gulf of California, Mexico.

In *H. hyotis*, Duprat-Bertazzi & García-Domínguez (2005) found that spawning occurred almost throughout the study period, from August 1995 to December 1996, except for January and February; a pattern similar to the one observed by Cantillanez *et al*. (2005) in *Argopecten purpuratus* in 1996. That year has been considered as normal, except for the months January to March, when the last part of a weak La Niña event spanning from September/October 1995 through February/March

1996 (Wolter & Timlin 1998, Climate Prediction Center 2008) occurred. By comparing the results here obtained for the years 1997, 1998 (under the influence of an El Niño event) and 1999 (influenced by a La Niña event) with Duprat-Bertazzi & García-Domínguez (2005)'s results for the year 1996, it can be seen that in both cases spawning is significantly correlated with high temperatures. Duprat-Bertazzi & García-Domínguez (2005) found that, in 1996 (a "normal" year), the peak of spawning, with a part spawning frequency of 85%, occurred in August when temperature was 28.5°C.
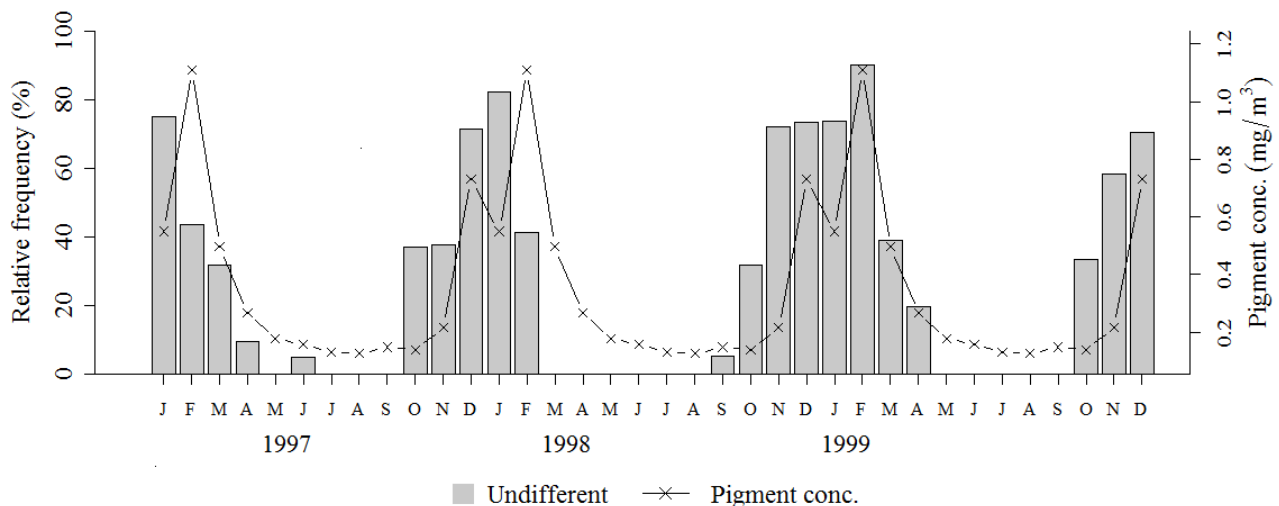

Figure 6. Relationship between the proportion of undifferentiated *Hyotissa hyotis* individuals and chlorophyll *a* concentration at La Ballena Island, Gulf of California, Mexico. This correlation was statistically significant (Spearman, P < 0.01).

In our study, spawning peaks during El Niño years were 91.7% in August 1997, with a temperature of 30.8°C, and 80% in September 1998, with 29°C. The spawning peak in 1999 (a La Niña year) was only 77% at 27.5°C. These results indicate that the percentage of spawning of *H. hyotis* increases during El Niño events and decreases during La Niña events, in comparison to "normal" years.

García-Cuellar *et al.* (2004) studied *Pinctada mazatlanica* at a locality near La Ballena Island during El Niño 1997-98 and La Niña 1999 events and found similar results to those obtained in our study. They concluded that the different patterns observed in *P. mazatlanica* compared to those observed by other authors in different years (Arizmendi-Castillo 1996, García-Domínguez *et al.* 1996, Solano-López *et al.* 1997) prove that those climatic events had a real impact on reproductive stages and suggest that, during El Niño event, environmental conditions were more favourable causing the intervals between reproductive stages to shorten and the gonads to recover rapidly, thus accelerating the onset of the ripe stage.

In this study, the reproductive cycle of *H. hyotis* during El Niño or La Niña years showed a clearly seasonal pattern in relation to water temperature. This was also noticed in the significant positive correlation between the proportion of spawning individuals and temperature and in the lack of correlation between the proportion of ripe individuals and temperature, as most individuals were ripe when temperature was higher and, when this starts decreasing, most spawning occurs. Duprat-Bertazzi & García-Domínguez (2005) found similar results for this same species in "normal" years. This explains why no significant correlation was found between GSI and temperature.

On the other hand, chlorophyll *a* concentration showed a different pattern during El Niño and La Niña years. The mean, maximum and minimum pigment concentrations were lower during El Niño years than during La Niña event. However, we found a significant correlation between chlorophyll *a* concentration and the proportion of undifferentiated individuals in the two El Niño years as well as during the La Niña event. A similar result was obtained by Duprat-Bertazzi & García-Domínguez (2005) for the same species in a "normal" year. This suggests that in those periods when more food is available, *H. hyotis* builds up reserve substances that are later used for gonadal development, as suggested by Rodríguez-Astudillo

et al. (2005) who found that *H. hyotis* stores glycogen in the adductor muscle during the periods of reproductive inactivity, which is then used when the population engages in reproductive activity. However, García-Cuellar *et al.* (2004) observed that, in *P. mazatlanica,* the gametogenic production stage began in the winter, coincident with the highest concentration of photosynthetic pigments.

Finally, we can conclude that the spawning intensity of *H. hyotis* increases during El Niño events but decreases during La Niña events and temperature is the main factor regulating spawning activity in both cases. In addition, we conclude that the gonadosomatic index is an indicator of gametogenic activity and that food availability is related to gonadal development.

Acknowledgments

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