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THE EFFECT OF HURRICANE ACTIVITY ON SCALY PEARL OYSTERS, *PINCTADA LONGISQUAMOSA*, IN TWO DISSIMILAR INLAND MARINE PONDS ON SAN SALVADOR ISLAND, BAHAMAS

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ABSTRACT

Since 1996, we have explored a remarkable set of inland marine habitats on the Bahamian island of San Salvador in the Caribbean. These ponds represent natural experiments in which such gross ecological features as salinity, tidal flux, exclusion of marine predators, and the presence or absence of mangrove prop-root habitat have been manipulated by natural causes. Our studies have focused specifically on two ponds, one of which (Oyster Pond) is fully marine, tidal due to a system of subterranean caverns and conduits connecting Oyster Pond to the sea, and in possession of a rich mangrove prop-root habitat. The other (Little Granny Pond) is hyper-saline, non-tidal, and devoid of a prop-root habitat. Each pond supports a distinctive marine invertebrate community including the Scaly Pearl Oyster, *Pinctada longisquamosa*.

In September of 1999, hurricane Floyd struck the island. When we visited in January 2001, the adult oyster population of Little Granny pond had been decimated, whereas the population in Oyster Pond was relatively unaffected. Furthermore, the few surviving oysters in Little Granny Pond had spawned and a uniform juvenile cohort could now be observed. Oyster Pond appeared to be populated by five to six reproductive cohorts recognizable by their shell dimensions. Over the next five years, we followed growth dynamics of oysters in these two dissimilar ponds. We were able to estimate annual rates of growth, and annual spawning periods.

In September of 2004, hurricane Frances struck the island. In February 2005, we discovered that, once again, the oyster population of Little Granny Pond had been decimated (less than 0.1% survival), whereas the population in Oyster Pond was relatively intact. A follow-up visit in June of 2005 revealed that, again, spawning had occurred in Little Granny Pond and it would be possible to follow this juvenile cohort much more closely over time. Such differing responses of two breeding populations of oysters to hurricane activity may have had evolutionary consequences. We offer predictions regarding changes in life-history characteristics, and propose future study.

INTRODUCTION

Geography and Geologic History of the Study Sites

San Salvador Island is an outlier in the Bahamian Archipelago. The island itself lies in deep water, yet its structure is the result of a long depositional history of shallow marine sediments. The entire Bahamian platform appears to be the result of shallow-water sedimentation occurring since at least the Cretaceous, over 65 Myrs ago, (Carew & Mylroie, 1994) and drilling reveals shallow-water sediments extending over 5.4 km down without encountering crustal materials (Meyerhoff & Hatten, 1974). It appears that carbonate deposition has kept pace with

subsidence at a pace of 1 m/40,000 years (Mullier & Lynts, 1977). More recent geologic history has been much influenced by the Pleistocene glaciation and concomitant fluctuations in sea level. Indeed, the Bahamas have been periodically exposed during periods of intense glaciation and submerged during the intervening interglacial periods. Consequently, the terrestrial geology of San Salvador Island can be attributed to forces acting during inundation (deposition of calcium carbonate and erosion by wave action) and during exposure (wind-driven dune formation, rainwater dissolution, and lithification of sand grains into various forms of limestone). The last interglacial period (the Sangamon) elevated sea level 6 m higher than it currently stands, whereas the last glacial episode (the Wisconsin) dropped sea level over 140 m compared with today's shoreline. Currently, sea level is rising at the rate of 3 mm per year, producing noticeable changes in coastal flora and fauna.

The island's profile appears as a series of lithified dune ridges and intervening swales. Many of the swales harbor inland ponds or lakes ranging from fully marine to hypersaline conditions, or marine with a freshwater halocline lying over a salty bottom layer. These marine ponds are frequently connected to the open ocean via terrestrial "blue holes": subterranean conduits and caverns that interconnect within the island's interior and extend miles underground. Such ponds can be far from shore, yet the under-ground conduits can create tidal influences and produce significant water exchange over the course of a day.

Our two study sites represent two extremes in this salt-water continuum. Oyster Pond (Figure 1), is tidal, fully marine (35 ppt), and supports a littoral red mangrove (*Rhizophora mangle*) prop-root community. Its shores are flanked by a carbonate platform rich in shell fossils from the Sangamon interglacial period, suggesting that it formed a lagoon environment 150,000 years ago that connected Oyster Pond with the sea.

Little Granny Pond (Figure 2) is deep within the island's interior. It has no measurable

tide, and no discernible conduits. Consequently, evaporation outpaces rainfall, and its waters are hypersaline and variable (typically 45 ppt). Red mangroves grow along its shores, yet at some distance so that their prop-roots never enter the water (Figure 2). This is strange, in that mangroves are found in far saltier standing waters on the island. Freshwater drains from surrounding

Figure 1. Oyster pond. Note *Rhizophora community bordering pond, roots submerged.*

hillsides, and enters the pond along its margins as shallow water seeps. The rocky shore has been characterized and its composition includes the Grotto Beach carbonate formation (125,000 years old) overlying the older Owl's Hole formation (220,000 and/or 320,000 years old). These deposits represent relics of the last interglacial periods (Carew & Mylroi, 1995; Sparkman-Johnson et al., 2000), and again suggest historic
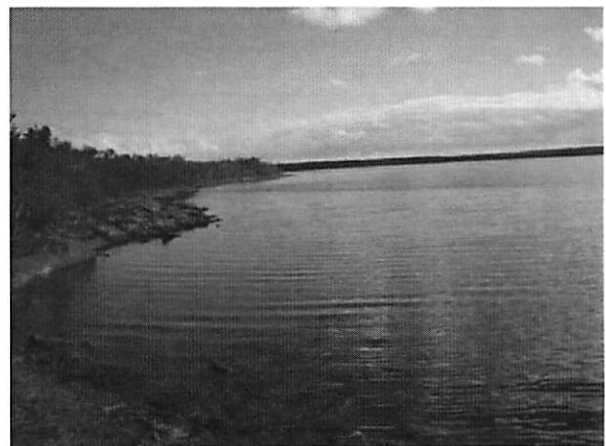

Figure 2. Little Granny Pond. Note rocky shore devoid of emergent vegetation.

contact between Little Granny Pond and the sea. Curiously, carbonate of biological origins was only found in the older, Owl's Hole formations (Panuska *et al.*, 2001).

MATERIALS & METHODS

Water chemistry was determined using a hand-held Quanta Probe from Hydrolabs. Oyster shell dimensions were calculated by measuring hinge lengths.

RESULTS

Ecology of the Study Sites and Their Community Structure

<u>The Oyster Pond Community</u>

Oyster pond supports three distinctive habitats: the "floc" bottom (a deep flocculent organic sediment covering the carbonate bottom to a depth of 1.5 m); carbonate outcroppings that rise above the floc-line; and aquatic *Rhizophora mangle* prop-roots. The floc bottom habitat is a rich microbial community that becomes anaerobic within 10 cm of its surface (Figure 3). The floc appears to be slightly less saline than the overlying water column, has a lower pH, and a reducing environment with a redox potential of -13 mV compared to +100mV at the surface (Table 1). Silver jewelry submerged for 30 sec in the flocculent sediment emerges completely tarnished. As a consequence of these harsh
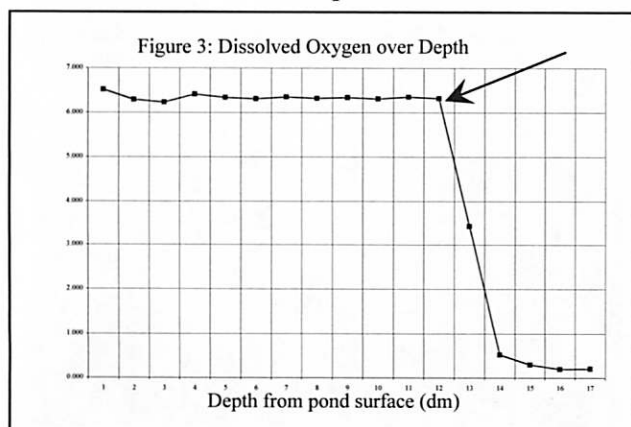
Table 1. Physical parameters of Oyster Pond and Floc measured with Quanta^{TM} Probe.

Depth (cm)	pH	TDS (g/L)	DO%	ORP (mV)
10.0	7.740	34.80	98.20	99.0
20.0	7.740	34.80	96.40	99.0
30.0	7.740	34.80	95.00	100.0
40.0	7.740	34.80	96.50	100.0
50.0	7.740	34.80	97.50	100.0
60.0	7.740	34.80	96.90	100.0
70.0	7.740	34.80	95.90	100.0
80.0	7.740	34.80	97.00	100.0
90.0	7.740	34.80	96.50	100.0
100.0	7.740	34.80	96.00	100.0
110.0	7.750	34.80	96.70	100.0
120.0	7.740	34.80	97.30	101.0
130.0	**7.600**	**34.60**	**25.40**	**73.0**
140.0	7.310	32.80	6.00	16.0
150.0	7.350	32.40	3.70	6.0
160.0	7.230	32.30	4.00	-5.0
170.0	7.180	32.30	3.40	-13.0

* Note: 130 cm denotes the uppermost layer of floc

conditions, macro-invertebrates tend to be scarce. We do find an abundance of Atlantic lugworms (*Arenicola cristata*; Figure 4) that survive in this habitat by ventilating burrows with peristaltic pumping. At the surface of the floc, small bivalves (*Anomalocardia auberiana*) are

Figure 3. Dissolved O$_2$ in Oyster Pond measured in mg/L. Decimeter 12 marks the floc interface (arrow).

Figure 4. Arenicola cristata (Atlantic Lugworm) exposed on floc surface.

submerged with only their siphons exposed. These are typically capped by single-celled algae of the genus *Acetabularia*. A delicate anemone is also abundant, attached to leaves or other bits of emergent substrate. Carbonate out-croppings (Figure 5) support rich communities of green alga (*Valonia oscellata, Anadyomene stellata,* and *Acetabularia crenulata*).
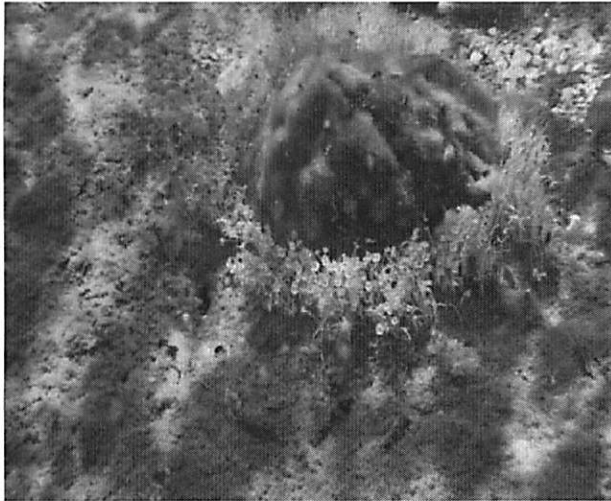

Figure 6. Rhizophora prop-root colonized by algae and invertebrates. Note Pinctada longisquamosa *(scaly pearl oyster) at arrow.*

1995 and made formal surveys of the prop-root invertebrates in 1996, 1998, 2001, and 2003. Figure 7 shows a sample of our invertebrate survey from the Oyster Pond prop-root community, indicating both species diversity and abundance. As one can see, pearl oysters are far out-numbered by other bivalves, including burnt mussels and black mangrove oysters. Less common organisms include sipunculids

Figure 5. Floc bottom and algal-covered carbonate outcropping.

Embedded within these algal gardens are a variety of sponges, "naked" sea cucumbers (*Synaptula* sp.), polychaetes, and brittle stars. All three of the lake's larger bivalves find purchase on these outcrops: the black mangrove (tree) oyster (*Isognomen alatus*), the burnt mussel (*Brachiodontes exustus*), and the scaly pearl oyster (*Pinctada longisquamosa*). Prop-root habitat is the most productive, supporting a great number of invertebrates, including the pearl oysters (Figure 6). We began investigating invertebrate diversity of Oyster Pond in
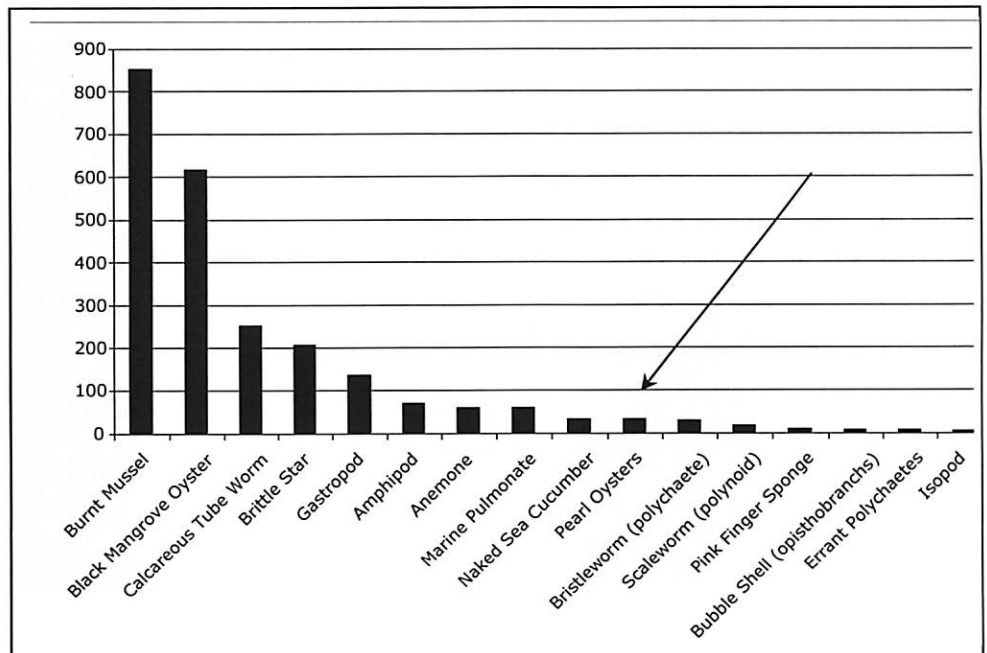

Figure 7. Total invertebrates tallied from four mangrove prop-roots harvested from Oyster Pond, January 2001. Pearl oysters (arrow) are not the most abundant species.

(imbedded in sponge-algal aggregates near the prop-root habitat) and a small, shell-less marine pulmonate seen in only one of our surveys.

Conduits support a number of other species not typically seen in the other habitats, including silverside minnows and the red shrimp (*Barbouria cubensis*), and may be considered a fourth habitat. It is worth noting that neither in this pond, nor any others we have visited, have we found tunicates (which have been reported elsewhere). We believe they are truly absent.

The Little Granny Pond Community

We began a similar invertebrate survey for Little Granny Pond in 1996, continuing in 1998, 2001, and 2003. This pond is marked by an impoverished species diversity and rich abundance of the species that are present. Little Granny Pond can be divided into 3 zones (Figure 8). The interior is 3-4 m deep and covered in a uniform deep floc layer with few conspicuous invertebrates.

Close to shore, the floc-bottom rises to a depth of 1-3 m. In the shallows, floc gives way to a hard carbonate, shelly-sand bottom that is covered in a dense monoculture of "finger"-algae (*Batophora oerstedi*) (Figure 9A). The algae itself serves as a substrate on which a tiny, highly mobile "sea grass" anemone anchors (Figure 9B). *Batophora* also serves as the primary substrate for
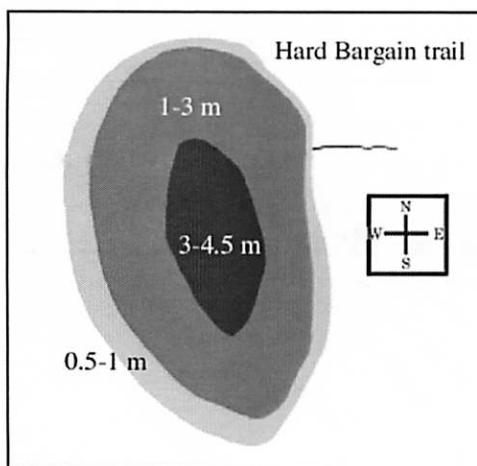

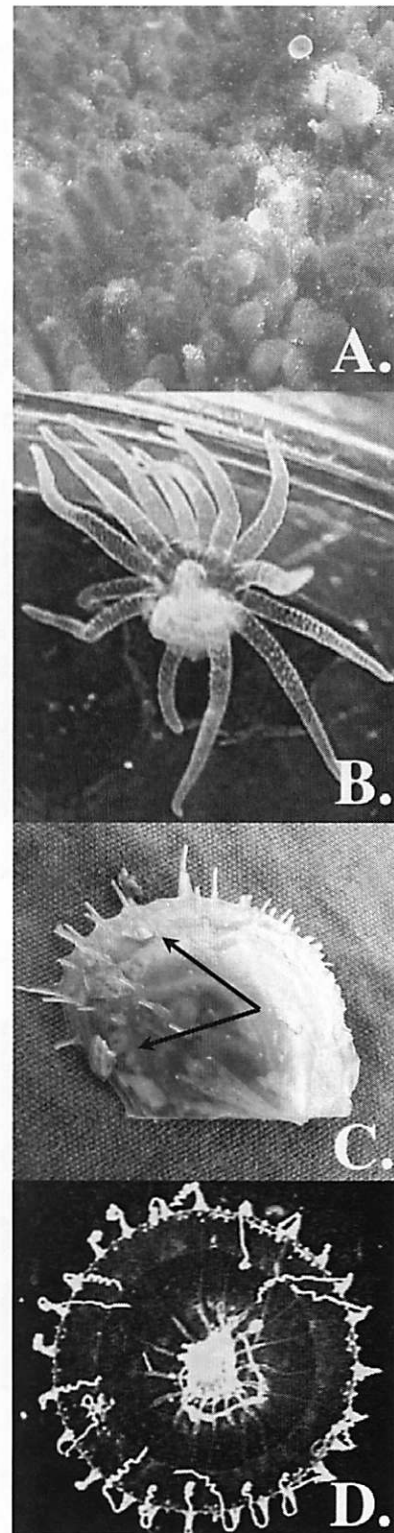Figure 8. Depth zonation of Little Granny Pond (0-1 m, 1-3m, 3-4.5m).

Figure 9. Little Granny Pond organisms. A. Batophora, B. Sea-grass anemone. C. Pinctada; arrows indicate juveniles. D. Aquoreid hydromedusan.

Pinctada longisquamosa (Figure 9C). *Acetabularia* was also abundant. The water column supports a population of hydromedusans of the family *Aqueoridae* (Figure 9D). It seems that species normally associated with sea grass habitat are using *Batophora* in its place.

These substrates are rich in micro-invertebrates, including a tiny isopod, copepods, ostracods, and numerous protists. Several species of polychaete annelids are also abundant. Even closer to shore, and clustered around freshwater seeps, we found the black mangrove oysters and burnt mussels anchored to the carbonate substrate. We also found abundant *Anomalocardia*. Four gastropods were abundant as well: *Battalaria minimus*, *Polymesodea maratima*, *Cerithium lutosum*, and *Crithidia costata*. The same two tiny fish species were found in both Oyster Pond and Little Granny Pond: *Cyprinodon variegatus* and *Gambusia* (sp.). Overall, in comparison with Oyster Pond, Little Granny Pond can be characterized as species poor, but population dense.

Natural History of the Pearl Oyster

The Atlantic Pearl Oyster.

We recently learned that the pearl oyster, common to the inland ponds of San Salvador, has been consistently mis-identified as *Pinctada imbricata* (the Atlantic pearl oyster) when, in fact, it appears to be the Scaly Pearl Oyster: *Pinctada longisquamosa* (Mikkelsen *et al.*, 2005). Both oysters are sessile bivalves (family Pterriidae), more closely related to a mussel than to the edible oysters of the family Ostreidae. Adults attach themselves to substrate using byssal threads rather than cement. Pearl oysters filter feed on algal phytoplankton. In the Atlantic pearl oysters (for which there is an abundant literature), breeding can occur throughout the year (in open ocean environments), though in one Caribbean study peak breeding occurred during the colder parts of the year (Urban, 2000). Arntz & Farnbach (1991) and Urban & Tarazona (1996) suggested that cold-water upwelling causes an increase in nutrient availability that may support gonad development,

and this subsequently drives reproductive conditioning to peak during the colder months. Coastal populations of Atlantic pearl oysters tend to have a broad period of reproductive readiness, with two annual peaks in spawning, as evidenced by individuals with "spent" gonads. Open ocean oysters grow rapidly, following a modified von Bertalanffy growth curve (Urban, 2002). In these conditions (temperature 23-27°C), oysters grow to 50 mm shell diameter in less than a year.

Atlantic pearl oysters breed by releasing gametes through their excurrent siphons. Fertilization occurs in the water column and embryos develop into veliger larvae commonly known as "spat". After approximately one month as free-swimming members of the plankton community, veliger larvae settle, attaching to an appropriate hard substrate, and metamorphose into 0.2 mm juveniles (Ruffini, 1984). During their first year of growth, juveniles attain sexual maturity as males. Following further growth and development, two years in open ocean species, genetic females that begin life as males undergo a sexual trans-formation into females. The sex ratio of Pacific populations of *Pinctada* typically favors males 8:1 (Saucedo & Monteforte, 1997). This is likely due to age-dependent mortality favoring small, young oysters that are most likely to be phenotypic males, whereas older, larger oysters are more likely to be females.

The Scaly Pearl Oyster.

After our initial studies characterizing the invertebrate diversity of these ponds, we turned our attention to the pearl oysters. We noted that pearl oysters of the inland marine ponds on San Salvador Island (*P. longisquamosa*) were atypical when compared with coastal populations of *Pinctada imbricata*. A recent publication by Mikkelsen *et al.* (2005), and correspondence with its co-author, Ilya Temkin (AMNH), helped clarify matters, and we were able to properly identify our species as the scaly pearl oyster (*P. longisquamosa*), for whom all these odd characteristics were normal. (It should be noted that very little has been published on this frequently mis-identified organism.) We

documented growth rates by following the dimensions of reproductive cohorts through time. Shell diameters grew approximately 6 mm in each of the first two years of growth (almost 10 times slower than *P. imbricata* colonies), though water temperatures were 25-26°C in each pond even during the coldest months. The largest adults (estimated at 6-7 years of age) were rarely over 40 mm. These organisms were also far more delicate in appearance than specimens of *P. imbricata*, being translucent and ornamented with long, fragile protrusions on the tips of their shells (Figure 9C).

Oysters of Little Granny Pond.

Though our invertebrate survey began in 1996 (see data from Figure 7), we did not notice differences in the oysters from these two ponds until January 2001, 16 months following Hurricane Floyd. The hinge-length data from oysters collected that year in Little Granny Pond appear in Figure 10. Little Granny Pond was conspicuous in 2001 for having an abundance of oysters, all of a very similar and diminutive size

(compare these numbers to those collected from Oyster Pond; Figure 13).

It seemed clear to us that something extraordinary had happened in Little Granny Pond. We hypothesized that Hurricane Floyd (9/99) had eliminated most of the larger oysters in Little Granny Pond, and possibly provoked a massive spawning event from the surviving adults. Dramatic changes in both salinity and temperature have been shown to provoke spawning in marine bivalves (Taylor, 2004). Alternatively, Little Granny Pond may support a population that is stunted by the rather harsh, hyper-saline conditions. In 2003, we were able to test these possibilities. Hinge-length data clearly showed that the oysters were not merely stunted. Maximum oyster hinge lengths grew from 1.2 cm in 2001 to 2.4 cm in 2003. Furthermore, we could distinguish three conspicuous size classes. Statistical analysis supported the view that these represented three super-imposed normal distributions. It was compelling to model these data as three reproductive cohorts suggesting that breeding activity exhibits relatively discrete (though broad) annual peaks, and we were
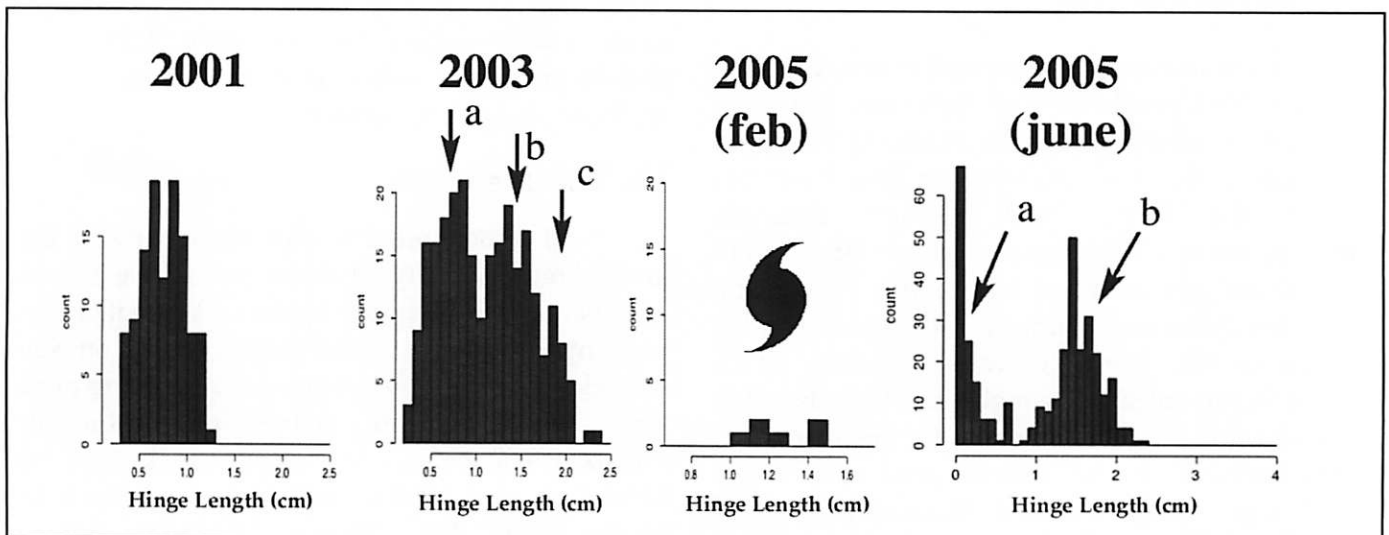

Figure 10. _Pinctada longisquamosa *shell dimensions from Little Granny Pond. Arrows in 2003 indicate three reproductive cohorts representing spawning events from a) '01-'02, b) '00-'01, and c) '99-'00, the year of Hurricane Floyd and presumably the same cohort depicted in the 2001 graph. Oysters from the current year were never seen in January collections probably because they breed in midwinter and are too tiny to detect. Data from 2005 were collected in February, five months after Hurricane Frances struck (9/13/04). The June 2005 data show two populations. We interpret population "a" as a fresh, '04-'05 cohort, spawned in February 2005, after Hurricane Frances struck. Population "b" we interpret as a partially recovered parental stock that has re-established attachment in the* Batophora *beds.*
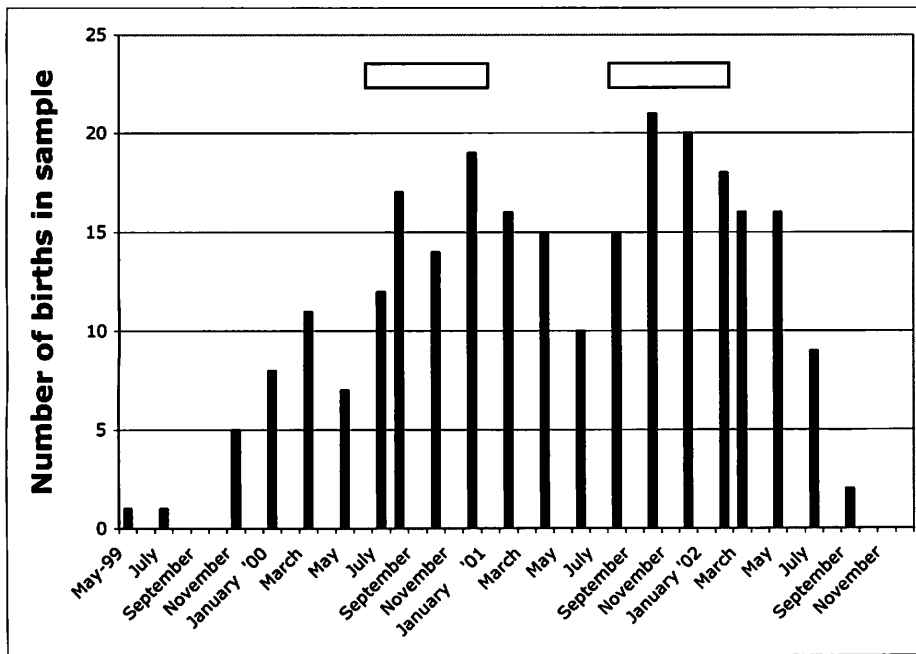
Figure 11. Predicted calendar dates of breeding in Little Granny Pond 1999-2002.

witnessing the reproductive output from the three years following the 9/99 Hurricane event. More precise analysis, especially from the 2001 data, suggests a bimodal pulse of breeding activity with each breeding season. The 2003 data also allowed us to estimate growth rates. Average growth rates for the first three years were 6.3 mm per year, in contrast with up to 50 mm/yr in the first year of *P. imbricata* (Urban, 2000). Using this estimate, it would appear that *Pinctada longisquamosa* reaches peak breeding activity in the months from September through March (Figure 11, see boxes). This corresponds roughly with the rainy season on San Salvador Island (Figure 12). This analysis also suggested that the 1999 hurricane did not trigger a spawning event as we initially supposed. The abundance of juvenile oysters seen in 2001 seems to have come from a breeding period lasting from January 1999 to late June.

Hurricane Frances (September 2004) allowed us to witness the impact of such a storm on our two ponds (and thwarted our continued monitoring of the 1999 cohort). Following Frances, we discovered that over 99.99% of the mature oysters in Little Granny Pond had been either destroyed or dislodged to places where we

could not find them for census purposes. The shoreline was littered with their shells. In June, 2005, we discovered that a number of predominantly small adults had survived and recovered their attachments to the *Batophora* beds, and their shells, in turn, were colonized by juveniles of a size class we had never seen before (see arrows in Figure 9C and right panel in Figure 10). This was the first time we had visited Little Granny Pond during the summer months, and since breeding appears to occur predominantly in winter, the most recent juveniles may have always escaped our winter census.

In summary, oysters of Little Granny Pond grow remarkably slowly during the best of times, and are uniquely sensitive to hurricane impact. There appears to be age-dependent mortality, and this is accentuated during hurricane incidents. The largest oysters appear to be the most severely affected. Population decimation could have several causes: wave action may strip the oysters from the shallow water and from their weakly anchored *Batophora* beds, and a large drop in salinity or temperature could further affect mortality or detachment.

Oysters of Oyster Pond.

For comparison with the hyper-saline population in Little Granny Pond, we also surveyed scaly pearl oysters in the more benign, Oyster Pond (Figure 13). After sampling oysters from both the *Rhizophora* prop-roots and carbonate out-croppings, we determined that there was no significant difference in shell dimensions between habitats, so samples from these two populations were pooled. In January 2001, 16 months after Hurricane Floyd, there was still a robust population of *Pinctada longisquamosa* in

Figure 12. Average monthly rainfall on San Salvador Island (from Shaklee, 1996).
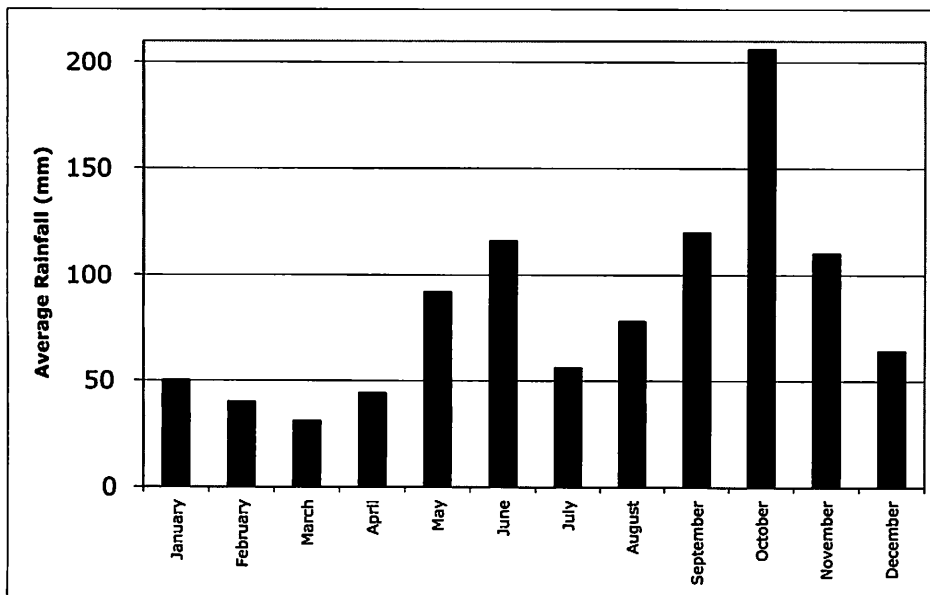
suspect food resources are limiting in both ponds. Oyster Pond is flushed thoroughly with daily tides acting through its conduits, and it maintains a salinity no different than open ocean at 35 ppt. Using statistical analysis, we identified 4-6 cohort peaks in each year of this study. Curiously, Oyster Pond was relatively unaffected by the 1999 Hurricane, and also survived the 2004 Hurricane Frances (compare hinge length data from 2003 and 2005 in Figure 13.) Though there appears to be a loss of larger oysters in 2005, this tailing had already occurred in 2003 and may be attributed to a steady state, age-dependent mortality. What is remarkable is the abundance of oysters, including large (>3 cm) oysters, even after a direct hit from Hurricane Frances as it passed over the island. Clearly, something about Oyster Pond protects its oyster population from the impact seen in Little Granny Pond. Possibilities include factors affecting wave
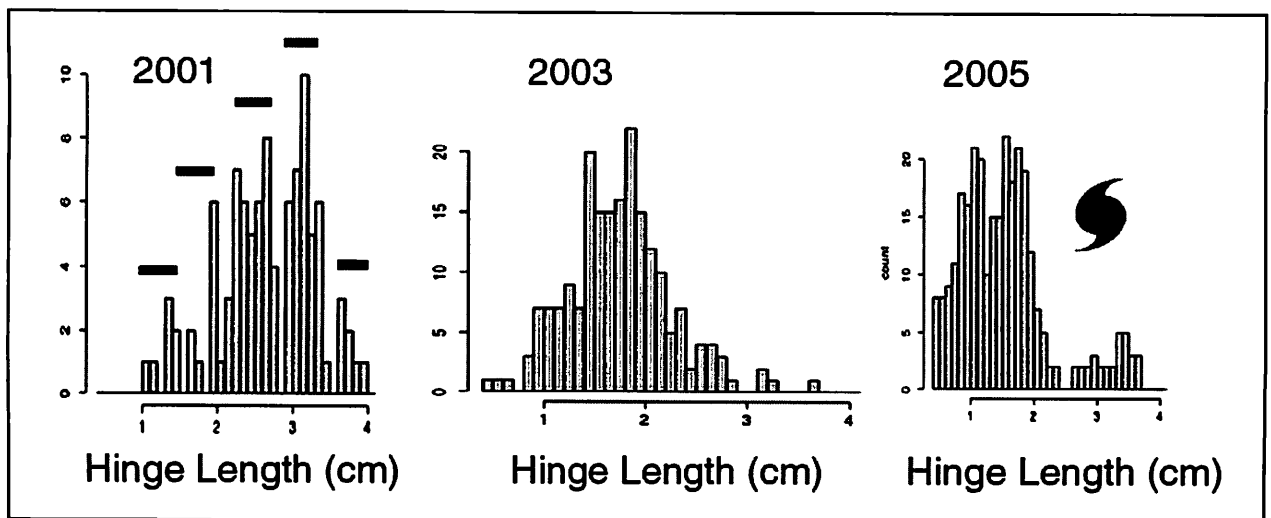
Oyster Pond showing a wide range of size classes. There appear to be five reproductive cohorts (see bars in Figure 13, first panel), and the largest oysters are over 4.0 cm. From the 2001 data, we estimated growth at 5.8 mm/yr (not statistically different from Little Granny population at 6.3 mm/yr). This strongly suggests that the poor growth of our hypersaline inland pond oyster populations is not due to high salinity, and we

Figure 13. Hinge length data for Pinctada longisquamosa collected from Oyster Pond. Bars over 2001 data suggest the presence of at least five age-group cohorts (size classes are consistent with growth data). Size distribution for 2003 and 2005 were nearly identical despite occurrence of 2004 Hurricane Frances, and size classes were more obscure.

propagation (both the mangrove prop-root habitat and Oyster Pond's smaller dimensions), or the tidal flushing that would buffer Oyster Pond against dramatic changes in salinity during a deluge.

Predictions

The physical characteristics of these two ponds, one vulnerable to periodic hurricane impact, the other relatively buffered against storm activity, have produced a unique natural experiment. We might predict that individuals that are fast to mature would have a selective advantage in a population where reproductive adults are periodically eliminated. If the scaly pearl oyster, *Pinctada longisquamosa*, proves to be a protandrous hermaphrodite like its cousin, the Atlantic pearl oyster (*P. imbricata*), then periodic devastation of its population might also lead to selection favoring survivors whose offspring become female on an accelerated schedule. Against a background of all-male juveniles and rare adult females, juveniles that mature fast and differentiate quickly into females should have a selective advantage. We have initiated a histological analysis of oysters by size class to determine at what age/size sexual maturation occurs, and to determine the dynamics of male/female differentiation between these various populations.

ACKNOWLEDGMENTS

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