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SCALY PEARL OYSTER, *PINCATADA LONGISQUAMOSA*, POPULATION DYNAMICS IN INLAND PONDS ON SAN SALVADOR ISLAND, BAHAMAS

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ABSTRACT

Only recently recognized as a distinct species, little is known about the lifecycle of the scaly pearl oyster (*Pinctada longisquamosa*). The purpose of this research was to compare oyster populations in differing habitats and develop a characteristic growth curve for the species. Data was collected from oyster populations in three inland ponds on San Salvador Island in the Bahamas, with hinge length measurements collected periodically over six years. Comparison between the habitats, using two sample t-tests and other methods, showed significant differences in size distributions. A von Bertalanffy growth curve fitted by identifying age cohorts provided evidence of rapid early growth that slows considerably after the first year. In addition, the increasing average hinge length of oysters in Oyster Pond provides evidence of a senescing population.

INTRODUCTION

The scaly pearl oyster, *Pinctada longisquamosa*, was first discovered by Dunker in 1852. However, it has been routinely misidentified for more than a century and a half afterwards (Mikkelsen, Tëmkin et al. 2004). In 2004, Mikkelsen, Tëmkin et al. once again identified it as a distinct species. Nevertheless, much remains unknown about the scaly pearl oyster.

In this study, we investigate the population dynamics of the scaly pearl oyster, focusing on its breeding patterns and growth rates. The study populations came from three inland ponds on San Salvador Island in the Bahamas: Little Granny

Pond, Oyster Pond, and Mermaid Pond. Using size measurements collected periodically between January 2001 and January 2007, we compare the populations of the ponds and model a growth curve for one of them.

Each pond presents a different environment. Since Little Granny Pond lacks conduits connecting it to the ocean, “evaporation outpaces rainfall, and its waters are hypersaline and variable” (Cole, Hoft et al. 2006). In contrast, Oyster Pond is fully marine due to underground conduits connecting it to the sea. Mermaid Pond is also fully marine and served by conduits (Button, Lanterman et al. 2007).

The ponds’ vegetation differ as well. Mangrove trees surround all three ponds, but the roots only enter the water in Oyster and Mermaid Ponds. The submerged roots are approximately 1 meter in length and are colonized by scaly pearl oysters in both Mermaid and Oyster Ponds. In Oyster Pond, the oysters also colonize carbonate outcroppings on the bottom of the middle of the pond. As for Little Granny Pond, mangrove roots are unavailable, and the oysters inhabit fronds of *Bataphora* algae growing in the shallows.

In this paper, the scaly pearl oyster populations of all three ponds are compared, in order to explore the relationship between habitat and lifecycle. In addition, we model growth curves and breeding patterns for this organism.

METHODS

The first data set was collected in January 2001 from Little Granny and Oyster Ponds. Re-

searchers returned to these two ponds in January 2003, January 2005, January 2006, and June 2006. In January 2006, Mermaid Pond was added to the study. In January 2007, all three ponds were sampled with more information recorded on the location and depth of each oyster. Oyster size was initially assessed by measuring hinge length, an easy value to obtain in that the hinge is straight and reasonably well defined. Later, heel depth was also recorded in order to evaluate the reliability of hinge length. Heel depth has been reported as a more accurate measure of age (Tranter 1958).

Sampling in Little Granny Pond was conducted in two main areas of the pond. One area was in shallow water (0.5-1.0m in depth), while the other was in deeper water (1.0-1.5m in depth). The shallow water was 10-15 feet from shore, while the deep water was 25-30 feet from shore.

In Mermaid Pond, researchers sampled oysters from the mangrove roots, the only habitat where oysters were found. Sampling took place along approximately 20 meters of the shoreline. The approximately meter long roots were divided in half, with oysters sampled from the top half meter recorded as "shallow water", and with oysters residing in the bottom half meter recorded as "deep water". For every sampled root, all the oysters on the root were recorded. Researchers sampled unsystematically from the approximately 85% of roots that had oysters.

In Oyster Pond, researchers sampled from both carbonate outcroppings and mangrove roots. The mangrove root sampling was consistent with the sampling done in Mermaid Pond and took place along approximately 20 meters of shoreline. Approximately one percent of roots harbored oysters. Researchers sampled carbonate outcroppings by collecting all the oysters on a given outcropping. Carbonate outcroppings were not chosen randomly; researchers sampled from as many as possible.

In 2006, oysters in Little Granny, Oyster, and Mermaid Ponds were tagged in order to allow for the collection of mark-recapture data. This data was used to determine actual growth rates. For oysters attached to mangrove roots, researchers placed numbered plastic tags around the prop-root immediately adjacent to the measured oyster

on the root. It was assumed that adult oysters were sessile, and would remain attached to the same location. Oysters from the algae beds were marked with nail polish on their shells. Different colors of nail polish corresponded to different size classes. In June 2006, researchers marked 21 oysters in Oyster Pond, 21 in Mermaid Pond, and 71 in Little Granny Pond. Then, in January 2007, of the 113 marked oysters, 8 were recovered from Oyster Pond, none from Mermaid Pond, and 4 from Little Granny Pond. Growth among recaptured oysters was calculated by subtracting the 2006 hinge length from the 2007 hinge length. In the 2007 study, additional oysters were marked in Little Granny Pond, using flagged rocks to denote areas containing marked oysters.

Our analysis of this data had four main objectives. First, we sought to use heel depth to evaluate whether or not hinge length was a valid measure of size. We analyzed the relationship between hinge length and heel depth by examining scatter plots and correlation values for the January 2007 data. Second, we examined the difference in size distributions between ponds and between habitats graphically and with two-sample t-tests. Third, we compared oyster size distributions by year sampled and examined possible time-series trends. Fourth, we fit a von Bertalanffy growth curve using a least squares criterion (Urban 2002). Finally, we simulated oyster growth in Little Granny Pond using our fitted growth curves and mixed distributions. The analyses were conducted with the statistical software Minitab, Stata, and R.

RESULTS

Measures of Size

Table 1 shows the sample size for every pond at each sampling period. Each oyster sampled was measured to assess its size, with an oyster's size used as a proxy age, which is vital for modeling growth curves and breeding cycles. Before January 2007, size measurements were based exclusively on hinge length. However, after reading that heel depth is considered a more valid measure of age (Tranter 1958), we collected both heel depth and hinge length for each oyster sam-

pled in January 2007. Finding the relationship between these two measures helped determine the

	01 Jan	03 Jan.	05 Jan.	05 June	06 Jan.	07 Jan
Oyster	99	200	325	485	389	274
Little Granny	114	455	6 199 dead	351	347	419
Mermaid	-	-	-	-	373	405

Table 1: Sample size by pond and sampling month

suitability of hinge length as a proxy for age. The scatterplot in Figure 1, created using pooled hinge length and heel depth data from all ponds, shows a strong, positive correlation between the two measures ($r=0.91$). The strength of this relationship varied between ponds. One can see average hinge lengths and heel depths in each pond in Figure 2. As Table 2 shows, the correlation between hinge length and heel depth was as high as 0.95 in the shallow water of Mermaid Pond, but as low as 0.56 in the carbonate habitat of Oyster Pond. The best fit line of the pooled data using a least squares criterion was hinge length = $4.40 + 1.54 \times \text{heel depth}$.

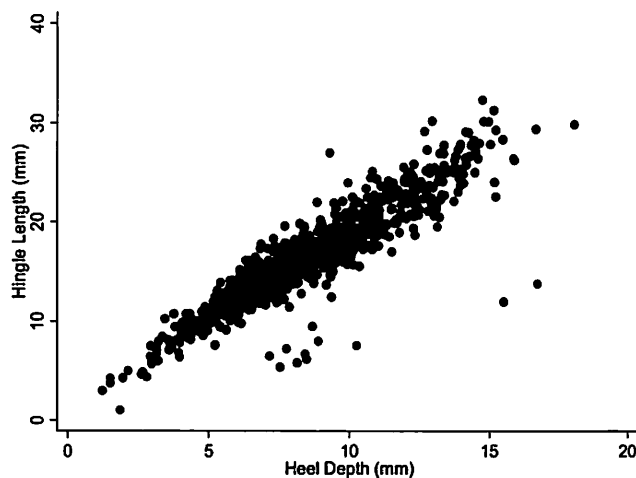


Figure 1. Hinge length versus heel depth for all oysters collected from all ponds and habitats in January 2007.

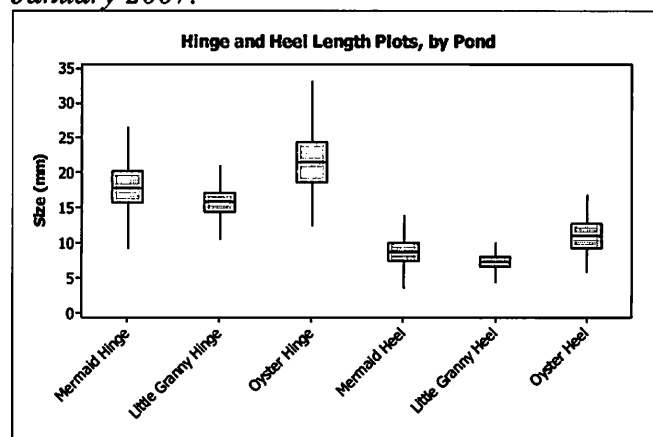


Figure 2. Hinge length (left) and heel depth (right) by pond. Data collected January 2007.

Table 2. Hinge lengths, heel depths, and their relationship by pond and habitat (January 2007 data).

Pond	Habitat	Sample Size	Mean Hinge Length (mm)	Hinge St. Dev. (mm)	Mean Heel Depth (mm)	Heel St. Dev. (mm)	Best Fit Line (x = heel depth)	r
Mermaid Pond	Shallow	183	18.05	4.18	8.86	2.53	$1.58x+4.06$	0.95
	Deep	215	17.62	3.80	8.68	2.24	$1.40x+5.47$	0.82
Little Granny	Shallow	199	14.94	2.53	7.00	1.37	$1.55x+5.07$	0.84
	Deep	214	16.31	2.31	7.66	1.22	$1.50x+4.81$	0.90
Oyster Pond	Mangrove	75	24.33	3.47	12.43	1.88	$1.61x+3.69$	0.87
	Carbonate	193	20.72	3.73	10.59	2.24	$1.06x+8.21$	0.56

Habitat

We also examined the effect of habitat on oyster size. Table 3 shows the mean and range of hinge lengths for each habitat in January 2007, and it also shows t-test results examining the mean difference between habitats in the three different ponds. Figure 3 shows the variation in hinge lengths between habitats and ponds. We see that the difference in oyster size between habitats is statistically significant in Oyster Pond (mean hinge lengths in mangrove 24.3 vs. carbonate 20.7mm, $t=7.24$, $p<0.001$) and Little Granny Pond (shallow 14.94 vs. deep 16.31mm, $t=-5.73$, $p<0.001$), but not in Mermaid Pond (shallow 18.05 vs. deep 17.62mm, $t=1.10$, $p=0.14$). Moreover, the difference in oyster size is statistically significant among all three ponds ($F=245.8$, $p<0.001$). Oyster Pond had the largest oysters on average, partially because its smallest oyster was fairly large at 12.5 cm. Little Granny had the smallest oysters and also displayed the least size variation.

A few differences among the three ponds were highlighted in water chemistry testing conducted in January 2007 (Table 4). As noted before, Little Granny Pond has the highest salinity of all three ponds (47.0g/L TDS).

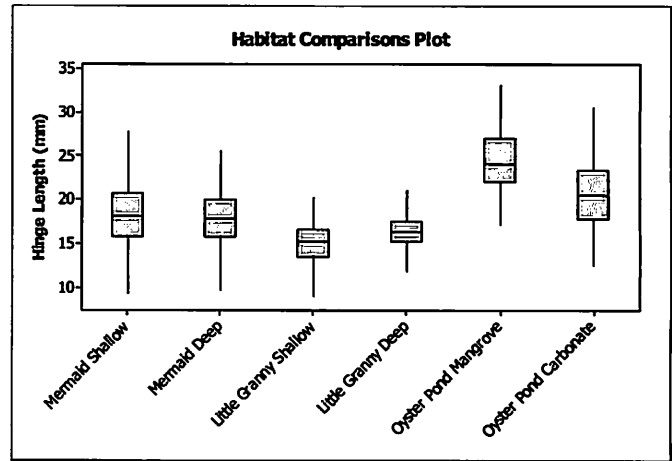


Figure 3. Comparisons of oyster sizes in different habitats within ponds. Data collected January 2007.

Pond	Mermaid	Oyster	Little Granny
Total Dissolved Solute (grams per liter)	34.1	34.8	47.0
pH	7.73	7.39	8.67
Temperature (C)	25.7	25.5	24.7

Table 4: Results from water chemistry testing conducted in January 2007.

Table 3: Mean, range, and test statistics of hinge lengths in each pond habitat from data collected January 2007.

Pond	Habitat	Sample Size	Mean Hinge Length (mm)	Hinge Length Range (mm)	Test statistic and p-value	95% CI of mean difference between habitats
Mermaid Pond	Shallow	183	18.05	4.2-28.8	7.24($p<0.001$)	(-0.35, 1.23)
	Deep	215	17.62	1.3-27.6		
Little Granny Pond	Shallow	199	14.94	8.1-22.0	-5.73 ($p<0.001$)	(-1.83, -0.90)
	Deep	214	16.31	6.8-28.6		
Oyster Pond	Mangrove	75	24.33	17.1-33.2	1.10	(2.63, 4.59)
	Carbonate	193	20.72	12.5-30.6	($p=0.14$)	

Growth Dynamics

Not only did the individual populations display different size distributions, they also displayed dissimilar demographic trajectories over time. As shown in Figure 4, the Mermaid Pond oyster population had approximately the same size distribution in January 2007 as it did in January 2006. However, the distribution for Oyster Pond shifted to the right with not only a higher mean hinge length, but also a higher minimum observed hinge length.

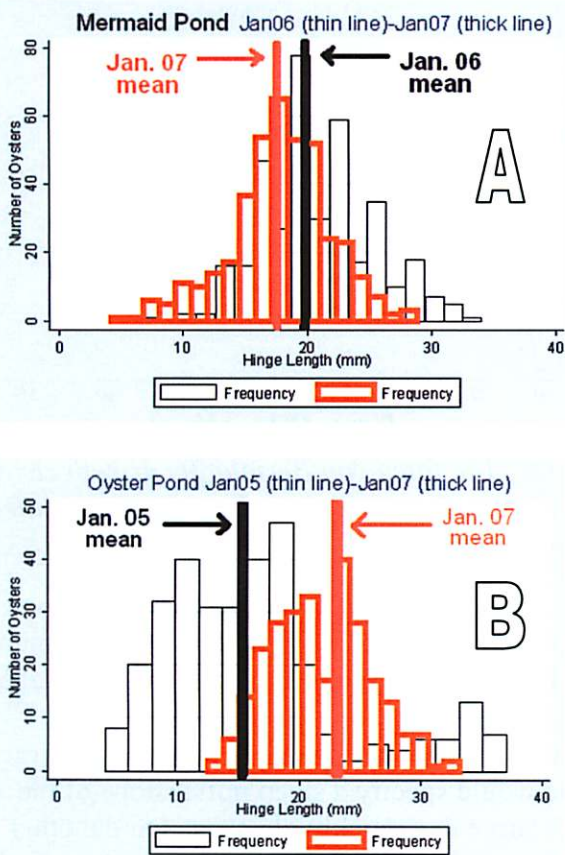


Figure 4. Hinge length distributions over time for a) Mermaid Pond and b) Oyster Pond.

So the Mermaid Pond oyster population appears stable over time, and there are juvenile replacements each year (oysters with hinge lengths less than 10 mm). On the other hand, Oyster Pond appears to lack juvenile replacement, and no oys-

ters with hinge lengths under 10 mm were observed in 2007.

Little Granny Pond’s oyster population dynamics are distinct from the other two populations in their response to the hurricanes that strike the island. Little Granny’s population appeared decimated after a September 2004 hurricane struck the island, with only 6 live oysters recovered the following January (Table 1). However, Oyster Pond did not appear similarly affected, with a normal sample size recovered in January 2005 (Cole, Hoft et al. 2006). We can see this January 2005 sample in black, thin line bars in Figure 4b. Despite the devastating hurricane, the oyster population in Little Granny Pond rebounded the following year with a cohort spawned presumably as the result of the hurricane (Table 1). This new generation appears to be growing larger with each successive year, and there appears to be juvenile replacement (researchers observed oysters with hinge lengths less than 5mm in subsequent years, Figure 5).

Growth Curve Parameter Estimation

We estimated the growth of oysters in Little Granny Pond by examining the change in average hinge length of an age cohort over time. Cohorts were identified by locating clusters in the data – groups of oysters having similar hinge lengths, implying that they have similar ages. Little Granny Pond was ideal for growth rate estimation because the 2004 hurricane had decimated the population, thereby making subsequent oyster age-cohorts clearly defined. Similar to Figure 4, in Figure 5 we examine demographic trajectories in Little Granny Pond. However, whereas in Figure 4 a unimodal distribution of oyster hinge lengths includes many different oyster cohorts, a unimodal distribution in Little Granny Pond results from just a single cohort of oysters because of hurricane decimation of oysters in that pond. Therefore, a growth curve can be calculated in Little Granny Pond, but not the other two ponds.

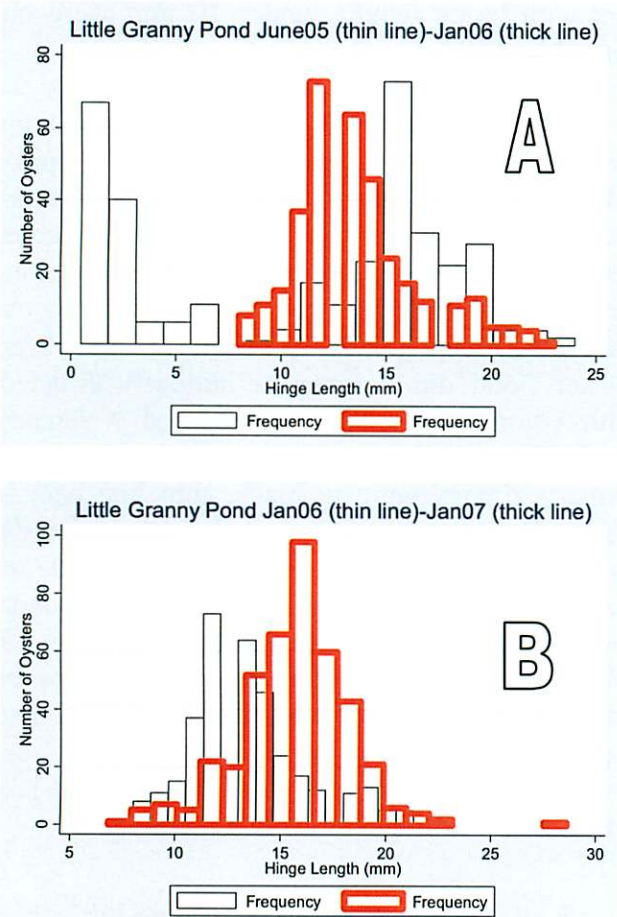


Figure 5 Hinge-length progression of oyster cohorts in Little Granny Pond in years following the 2004 hurricane.

Our estimated growth curve for Little Granny Pond was based on four reliable points relating average size to age. First, we estimated that an oyster had approximately no length (approximately 0.1 mm) at settlement, an estimate supported by field researchers' observations. To estimate the first segment of our growth curve, we examined the change in average hinge length of the one cluster of Little Granny Pond oysters from June 2005 to January 2006 (Figure 5a). The June 2005 dataset contained by far the smallest oysters the researchers had ever found, indicating the presence of very young oysters and leading researchers to hypothesize a hurricane-triggered breeding event following the 2004 hurricane. For the next segment of the growth curve, we measured the change in the average hinge length of the oyster cohort from January 2006 to January 2007

using peaks of the two histograms in Figure 5b. Finally, we examined the mark-recapture data for the three 14 mm oysters recovered in Little Granny Pond to estimate the last segment of the growth curve (one year growth of 1.1, 1.2, & 1.3 mm). After reaching 14 mm, the marked oysters grew on average 1.23 mm in the next year.

Although we do not have a large number of points for our growth curve, each point reflects a large accumulation of oysters. We then fit a von Bertalanffy curve to these estimated data points using a least square criterion (Urban 2002). This growth curve is shown in Figure 6.

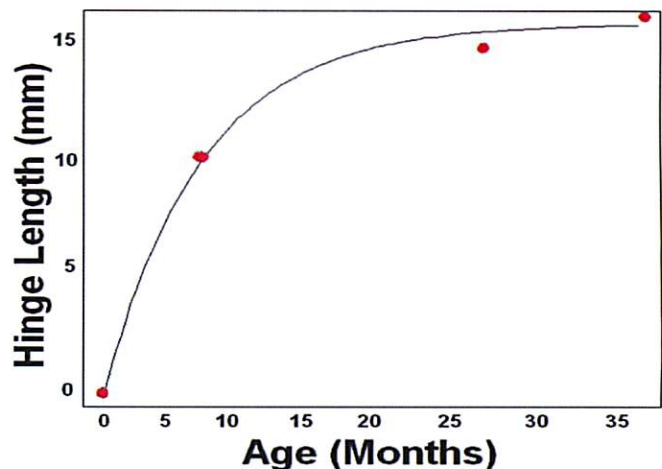


Figure 6. The fitted von Bertalanffy growth curve for scaly pearl oysters based on four estimated data points.

The equation of a von Bertalanffy growth curve is given below. L_{∞} represents the maximum hinge length of an oyster. L_0 represents the hinge length of the oyster at birth. The k parameter represents the shape of the growth curve. A large k value would specify a steep initial slope of the growth curve that quickly plateaus. On the other hand, a small k value would specify more gradual growth; initial growth would be relatively slow, but growth would last longer than it would in an organism with a high k value.

$$Length = L_{\infty} - (L_{\infty} - L_0)e^{k*age}$$

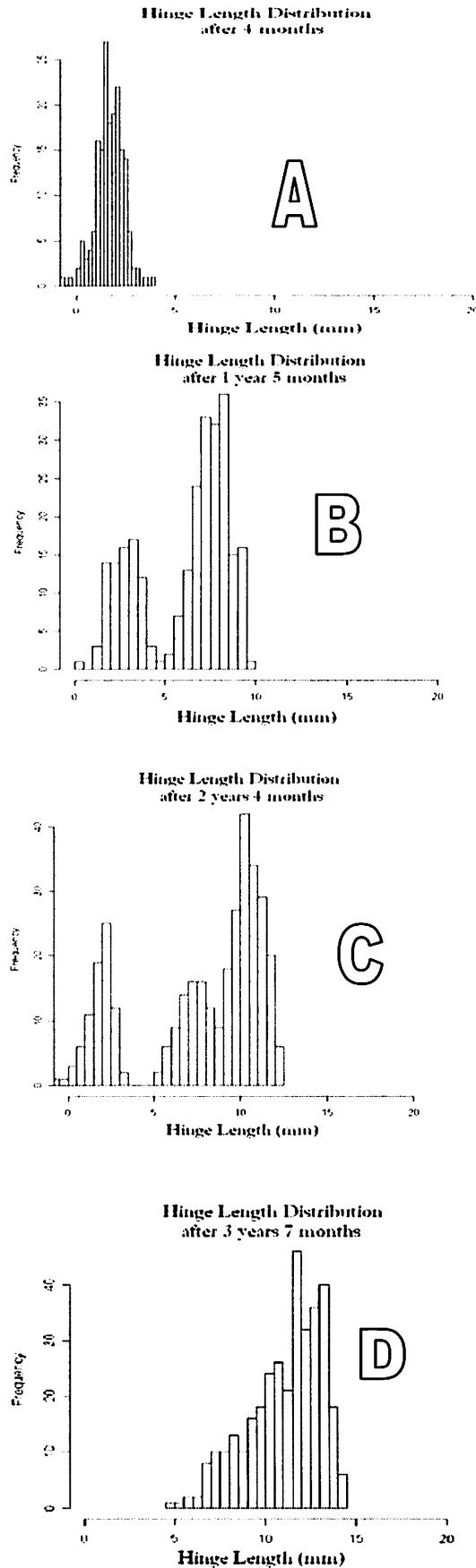
For scaly pearl oysters, we estimated $L_{\infty}=18.33\text{mm}$, $L_0=1.67\text{mm}$, and $k=0.90/\text{yr}$ using a least squares criterion with code written in R. We

calculated these values by searching a large parameter space and finding parameters that minimized the squared difference between our data points and the growth curve estimates based on specified parameters.

Simulation

Researchers observed much smaller oysters in the single June collection than were ever seen in the January data, implying a late-fall to mid-winter breeding event, possibly triggered by that year's September hurricane. Since oysters of similar age are also of similar size, one would expect to find multiple clusters of oysters in our hinge length distributions. With the exception of the post-hurricane populations in Little Granny Pond, no such clusters were observed; distributions of hinge lengths in all three ponds were generally normal with a single mode. To further investigate the puzzling lack of clustering in our hinge length distributions, we simulated the growth of oysters in Little Granny Pond using the open source statistical software R. In the simulation, three generations of virtual oysters grew according to our estimated von Bertalanffy growth curve over a period of four years (Figure 7). The growth dynamics of the simulated oyster generations showed that annual breeding patterns could indeed be consistent with the observed unclustered, unimodal hinge length distributions. Since the estimated parameters for our von Bertalanffy growth curve specify rapid initial growth that slows after the first year, younger cohorts of oysters quickly become nearly as large as older oysters. Therefore, the hinge length distributions of multiple cohorts overlap considerably, resulting in a combined distribution that appears normal.

Figure 7: The simulated progression of hinge lengths for 3 different generations of oysters. In 7a, the 1st generation has been born. In 7b, the first generation grows, but at a slower rate, 2nd generation grows quickly. 7c, the quicker growth rate of the second generation causes the two distributions to merge. 3rd generation is distinctively smaller, but growing the quickest. In 7d, all three generations have merged; no new fourth generation is shown in this plot.



DISCUSSION

Our estimated growth curve for the *Pinctada longisquamosa* population in Little Granny Pond is the first known empirically based growth model for this species. The model has certain limitations which must be acknowledged. Although our von Bertalanffy growth curve is suggestive for the species overall, it is limited in scope to Little Granny Pond, which possesses definitive characteristics such as its hypersalinity, its lack of oysters on mangrove roots, and its susceptibility to hurricanes. One point used in curve fitting was based on recapture data, which had a very small sample size, and we did collect some oysters in Little Granny Pond with hinge lengths greater than 18.33mm, indicating that a more refined growth model would likely have a higher L_{∞} . Moreover, some sampling bias may exist in the larger samples, especially in initial years, but in later years, sampling procedures were refined to ensure a representative sample. Despite these caveats, we believe that our model yields important new information.

The parameters of our growth curve are significantly different than those of other *Pinctada* species. The estimated k-values include 0.34-0.56 for *Pinctada radiata* (Yassien and Abdel-Razek 2000; Mohammed and Yassien 2003) and 0.35-0.75 for *Pinctada margaritifera* (Pouvreau, Tiapari et al. 2000). Our k-value of 0.90 is larger than those of these other species, possibly due to the smaller size of the *Pinctada longisquamosa*; a larger k-value indicates faster initial growth, and smaller organisms tend to mature more quickly than larger ones.

The differences in average oyster size between the three ponds imply that the growth curve parameters may likely differ among ponds. The cause of the disparate average sizes is unknown, although the differing habitats and water chemistry provide two possible explanations. Oyster Pond's habitat contains mangrove roots and carbonate outcropping, while Mermaid Pond has only mangrove roots and Little Granny Pond only *Bataphora* stalks. The pH levels were in the normal range and comparable for all three ponds, but salinity levels were not. Little Granny Pond is

modestly hypersaline, whereas the other two ponds are not. An additional possible explanation is the greater nutrient availability in Little Granny because of a lack of conduits connecting to the ocean.

A growth curve for Oyster Pond might differ even more than habitat alone could explain. Oyster Pond had the largest average oyster size, partially due to the high minimum observed size of 12.5mm, whereas the smallest oysters in Little Granny and Mermaid Ponds had hinge lengths of 6.8mm and 1.3mm respectively. The absence of small oysters suggests a lack of recent breeding. The average hinge length of Oyster Pond has been steadily increasing over the study period, unlike those of the other ponds. Researchers noted that most oysters in Oyster Pond looked abnormally old and unhealthy. Histology revealed that gonads were almost universally lacking in eggs and sperm (Cole, et al., this volume). Therefore, we hypothesize that the population of Oyster Pond is senescing. There is no evidence of senescence in either Little Granny or Mermaid Pond.

We plan to test our hypothesis about overall growth patterns and environmental effects on these patterns by developing growth curves for the other ponds. Further sampling is planned to assist in the development of new models and refinement of the existing growth model for Little Granny Pond. This research will allow for a deeper understanding of *Pinctada longisquamosa*, especially its growth and development.

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