

Growth Assessment of the Pink Queen Conch *Strombus gigas* by Direct Methods in Two Nursery Grounds of a Natural Protected Area of the Mexican Caribbean

Evaluación del Crecimiento del Caracol Rosa *Strombus gigas* por Métodos Directos en Dos Sitios de Reclutamiento de un Área Natural Protegida del Caribe Mexicano

Détermination de la Croissance du Lambi, *Strombus gigas* par Méthodes Directs dans Deux Sites de Recrutement dans une Aire Marine Protégée dans la Caraïbe Mexicaine

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ABSTRACT

The queen conch is an important fishery resource in the Caribbean, and high fishing pressure has led to its depletion. The Xel-Ha Inlet is a park used for ecotourism, representing a sanctuary for the conch. Most knowledge about its growth was generated in enclosures or derived from population dynamics, but has been studied little by direct methods. Growth appears to be higher under natural conditions than in enclosures or hatcheries. In this study, we compared the growth rates of 1,242 *Strombus gigas* in two protected nurseries (BN and CU), each with an area of 6,000 m² and average densities of 0.20 ± 0.0981 and 0.16 ± 0.0651 ind./m², respectively. The particularity of the sanctuary is the freshwater input from underground caves surrounding it. BN is characterized by fine sand/mud, while the bottom of CU is composed of coarser coralline algae rubble. Both sites present dense macroalgae patches. A capture-mark-recapture method was employed during the period from April 2009 to May 2011. Population size and relative density were estimated using Schnabel's method. Growth was highest in juveniles with an initial shell length of 100 - 149 mm and < 100 mm, increasing 0.29 ± 0.09 mm/day and 0.27 ± 0.07 mm/day, respectively being statistically equivalent. Growth decreased significantly in size classes 150 - 199 mm (0.19 ± 0.09 mm/day) and ≥ 200 mm (0.08 ± 0.08 mm/day). No differences could be detected between the two sites, except for the class of < 100 mm, with an average growth of 0.32 ± 0.09 mm/day at BN and 0.26 ± 0.06 mm/day at CU. Growth showed seasonal differences. The ecological significance of growth rates is discussed.

KEY WORDS: *Strombus gigas*, Marine Protected Area, population density, growth, mark-recapture

INTRODUCTION

The pink queen conch (*Strombus gigas* Linnaeus 1758) is a large herbivorous gastropod which represents one of the most important fishery resources in the Caribbean (Brownell and Stevely 1981, Chakalall and Cochrane 1996) together with the spiny lobster (Theile 2001). The increasing fishing pressure caused populations to decline in the 1980's and led to the inclusion of this mollusk in the Convention on International Trade of Endangered Species (CITES) and the list of commercially threatened species. This has led on one hand to the implementation of different management programs to protect the conch (Appeldorn 1994, Aldana Aranda et al. 2003, INP-SAGARPA 2008) and on the other hand, to the development of its aquaculture (Berg 1976, Brownell 1977, Brownell and Stevely 1981, Rathier 1987, Glazer et al. 1997, Davis 2000, Moreno de la Torre and Aldana Aranda 2007).

The inlet of Xel-Ha is a natural marine protected area under private administration, which has been used since 1995 as a park for ecotourism. The main attraction is the observation of marine fauna in its natural environment; hence the removal of any flora or fauna is prohibited by the park's administration. Xel-Ha is considered a sanctuary for the conservation of the queen conch in the Mexican Riviera Maya, hosting an important number of juvenile conchs (Peel et al. 2010, Peel and Aldana Aranda 2011).

Sound management of a resource such as *S. gigas*, as well as its rehabilitation, protection, and the development of aquaculture techniques require biological and ecological knowledge of the species, including growth rate, density, and population structure. Growth rates have been studied extensively, either by deriving them from population dynamics (Berg 1976, Appeldorn et al. 1987, Iversen et al. 1987, Strasdine 1988, Glazer and Berg 1992, De Jesús-Navarette et al. 1994, Aldana Aranda et al. 2005) or by direct methods (Randall 1964, Alcolado 1976, Brownell 1977, Gibson et al. 1983, Weil and Laughlin 1984, Ray and Stoner 1994, De Jesus-Navarrete and Oliva-Rivera 1997, De Jesus-Navarrete 2001, Peel and Aldana 2011). The comparison of growth rates from different areas has shown that growth may be markedly variable (Appeldorn 2005). Furthermore, comparing growth obtained by direct methods (Peel and Aldana 2011), growth of the queen conch appears to be higher under natural mark-recapture conditions (Gibson et al. 1983, Weil and Laughlin 1984, De Jesus-Navarrete and Oliva-Rivera 1997, Peel and Aldana 2011) than in enclosures (Randall 1964, Alcolado 1976, Brownell 1977, Ray and Stoner 1994, De Jesus-Navarrete 2001) or in hatcheries (Moreno de la Torre and Aldana Aranda 2007). The great variability often has been attributed to local environmental factors (Alcolado 1976), but little work has been focused on the ecological importance of growth rates (Ray and Stoner 1994, Stoner, 2003).

Body size is one of the most important attributes of an organism from an ecological point of view. Size has predominant influence on an animal's energetic requirements, its potential for resource exploitation, and its susceptibility to

predation (Werner and Gilliam 1984).

In this study we determined and compared the rate of growth of juvenile *S. gigas* by direct methods in two different nurseries of a natural protected area without fishing pressure and analyzed them in the context of population dynamics. Data was obtained through capture-mark-recapture methods, allowing the natural foraging behavior, resource selection, biotic interactions, and dispersal of the animals.

Study Site

Xel-Ha is located on the east coast of the Yucatan Peninsula ($20^{\circ}19'15''$ - $20^{\circ}18'50''$ N and $87^{\circ}21'41''$ - $87^{\circ}21'15''$ W) (Figure 1). The main oceanic current is the Caribbean Current. The area is characterized by medium wave energy and input of freshwater by underground rivers due to karstic conditions in the Peninsula. Xel-Ha is a creek that consists of a mix of fresh groundwater with seawater. The Inlet is connected to the Caribbean Sea by a 100 m wide channel and has a total surface of 14 ha with a center area and three appendices: Bocana, North Arm and South Arm. Its depth ranges from 0.5 - 4.5 m. The weather in the region is warm and sub-humid, with rains during summer and winter. The average annual temperature is 26° C. Average annual rainfall is 1079 mm (Organismo de Cuenca Peninsula de Yucatán Dirección Técnica, 2008). The sampling site CU ($6,000\text{ m}^2$) is located in the south-arm of the Inlet (Figure 1) and includes a small bay surrounded by mangroves (*Rhizophora mangle*) and several underground caves with upwelling of cold freshwater, forming a permanent thermo- and halocline at 1.25 m depth, with salinities ranging from 35 ‰ at the bottom and 10 ‰ at the surface. The site has a depth 1.5 - 3.5 m. The

bottom is composed of fine mud and sand formed of fragments of calcareous algae, mixed with rocks and dense isolated patches of macroalgae (e.g. *Padina* sp., *Halimeda* sp. *Penicillus* sp. *Amphiroa* sp. *Acanthophora* sp., *Caulerpa* sp., *Dictyota* sp.), decaying mangrove leaves and inverted jellyfish (*Cassiopea* sp.) may be found.

The second sampling site BN is located in the North arm of the Inlet (Figure 1). The sampled surface area was $6,000\text{ m}^2$. Depth ranges from 0.5 - 3.4 m. The bottom is composed of fine mud, big boulders, forming several channels and presents very dense macroalgae coverage (see above) and many inverted jellyfish (*Cassiopea* sp.). The water column is less stratified than in CU, but also presents a halo- and thermocline at 1.25 m depth with salinities ranging from 15 ‰ at the surface to 30 ‰ at the bottom.

Population Parameters

Between April 2009 and May 2011, eleven surveys were conducted, sampling a total area of $6,000\text{ m}^2$ at each site. The number of surveys carried out varied among years: three in 2009, five in 2010 and three in 2011. All organisms were collected in free-dive by three divers during three hours. We used mark-recapture method, marking all individuals with a plastic Dymo® tag, bearing a consecutive number, which was fixed to the spire of the conch with a plastic cable binder. At CU a total of 1,824 individuals were tagged. At BN 1,317 conch were tagged in the same period. In order to evaluate the size distribution and growth rate, shell length (SL) and lip thickness were determined for each individual, using a precision vernier caliper accurate to $\pm 1\text{ mm}$. We obtained shell length measurements of 3,936 individuals at CU and 3,128 at BN. All animals were released at the same location they were found.

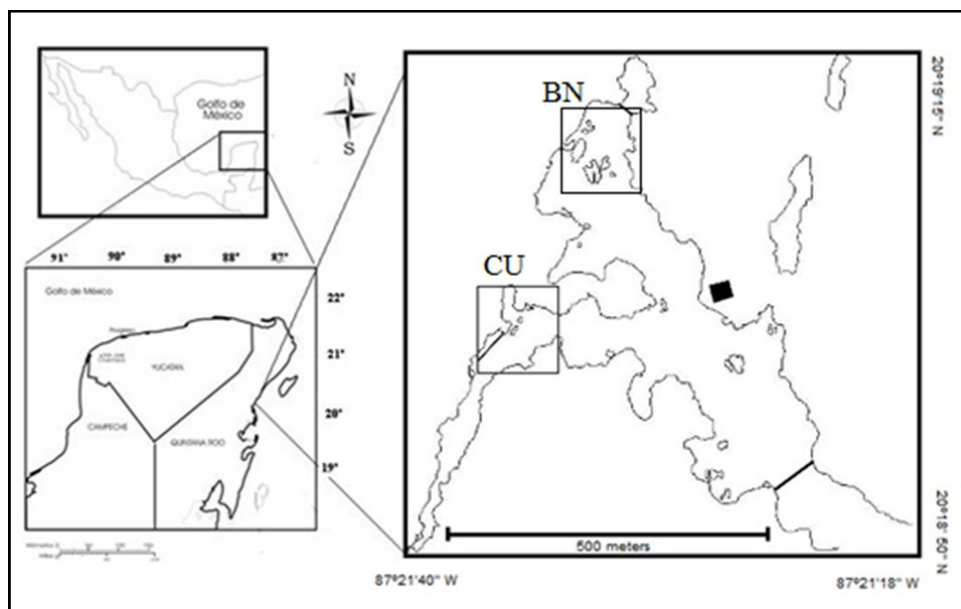


Figure 1. Location of marine protected area Xel-Ha Park, Quintana Roo, Mexico and sampling sites: CU and BN.

Statistical Analysis

With the abundance data of recaptured and unmarked individuals, we estimated population size using Schnabel's method (Schnabel 1938). Relative density of conch at each site was derived from population size.

In order to determine population structure and recruitment, the relative abundance of individuals per size class over time was calculated. An area chart was employed to visualize results.

To determine the growth rates of conch per day, we only used the measurements of individuals which were recaptured for the first time after being marked in the previous sample. In CU we estimated growth rates for 704 individuals, while at BN growth could be estimated for 538 individuals. Using the program Infostat/S, we calculated the mean daily growth and standard deviation per size class (< 100 mm, 100 - 149 mm, 150 - 199 mm and \geq 200 mm). Growth data was subjected to Analysis of Variance (ANOVA), using 95% confidence level, to detect significant differences in growth rates between the two sites and among size classes at the two sites. We used dot-plots showing mean and standard deviation. Growth data was pooled and mean growth and SD per size class were recalculated for the Xel-Ha Inlet. In order to detect seasonal differences in the conchs' growth, the mean growth per day in each size class over time was calculated and subjected to ANOVA ($\alpha = 0.05$) followed by Tuckey comparison ($\alpha = 0.05$). Pearson correlation was used to detect an association between growth and density per size class.

RESULTS

Population size was estimated using Schnabel method for both sites and relative densities were derived from population size (Tables 1 & 2). No significant differences could be found between population densities at both sites ($F_{0.05[1;19]} = 0.65$; $p = 0.4311$).

The dominant size class at both nurseries was 150 - 199 mm, representing on average $50.9\% \pm 17.5\%$ of the population at CU and $56.7\% \pm 13.6\%$ at BN. At both sites, a change in population structure could be observed over time (Figure 2). At the beginning of the study abundance of conch smaller than 149 mm was low, but increased dramatically between June 2009 and February 2010. Another smaller peak in the relative abundance of small juvenile conch was observed between September and November 2010. Conchs slowly incorporated into higher size classes and in May 2011 32.9% of the animals at CU and 39.7% of the individuals at BN had already developed a flaring lip.

Growth rates at both sites were similar, and no significant difference could be found ($F_{0.05[1;1249]} = 0.88$; $p = 0.3474$) (Figure 3). Nevertheless, significant differences in growth rates were detected between the < 100 mm class from both sites ($n_{BN} = 29$; $n_{CU} = 98$; $F_{0.05[1;125]} = 16.18$; $p < 0.0001$), with a value of 0.32 ± 0.09 mm/day at BN and

0.26 ± 0.06 mm/day at CU. At CU growth was highest in conch with an initial size of 100 - 149 mm ($n = 266$) with an increment of 0.29 ± 0.09 mm/day and decreased in the classes of conch with a SL of 150 - 199 mm ($n = 295$) to 0.19 ± 0.08 mm/day. Growth tended towards null in the ≥ 200 mm class ($n = 45$) with 0.07 ± 0.06 mm/day (Figure 3). At BN growth was highest for the conch with an initial SL of < 100 mm (0.32 ± 0.09 mm/day; $n = 29$) and decreased in the following size classes with an increment of 0.28 ± 0.09 mm/day in conch with a size of 100 - 149 mm ($n = 177$), 0.20 ± 0.09 mm/day in the class 150 - 199 mm ($n = 288$), and 0.09 ± 0.07 mm/day in individuals ≥ 200 mm ($n = 44$).

Growth rates from both sites were pooled in order to estimate an average growth of juvenile conchs in the Xel-Ha Inlet. The resulting growth curve is shown in Figure 4 and growth parameters are specified in Table 3. Growth had the highest variation in conch in the size class 100 - 149 mm, ranging from 0.01 - 0.63 mm/day.

Growth rates showed significant differences over time ($F_{0.05 [9; 1232]} = 44.89$; $p < 0.0001$) and where highest (Tuckey_{0.05}) in May 2010 and January 2011 in all size classes (Figure 5).

A very low negative association between growth rates and density ($R = -0.09$; $p = 0.0011$) was detected using Pearson Correlation. Furthermore, when the association was examined per size class, we found that it was only significant for the classes 100 - 149 mm and 150 - 199 mm, but not in the remainder ones (Table 4). Nevertheless, the growth of conch with an initial SL of 100 - 149 mm showed a positive association with density ($R = 0.11$, $p = 0.02$), while the association between growth and density in conch with an SL of 150 - 199 mm was negative ($R = -0.12$; $p = 0.0034$).

DISCUSSION

Conch population in Xel-Ha has been monitored since October 2001 (Aldana Aranda et al. 2003, Aldana Aranda et al. 2005), but BN was not included into sampling efforts before 2009, since conch were believed to be absent at this site. Aldana Aranda et al. (2005) estimated a population size of 632 ± 49.4 individuals in the period from 2001 to 2003 for the site CU, using Schnabel's method. In the present study, the population was initially small; however, we observed recruitment of juveniles being highest in October 2009 for conch in the < 100 mm size class at both sites, while recruitment of organisms in the 100 - 149 mm class peaked in February 2010. Recruitment can be inferred from the size frequency distribution (Figure 2) and the appearance of conch in the inferior size classes.

Recruitment was observed throughout most of the year but was of a higher magnitude from June 2009 to February 2010 and from July 2010 to January 2011. Aldana Aranda et al. (2003) observed through monthly mark-recapture samplings, that recruitment occurs in June - September and November - February, which coincides with our findings.

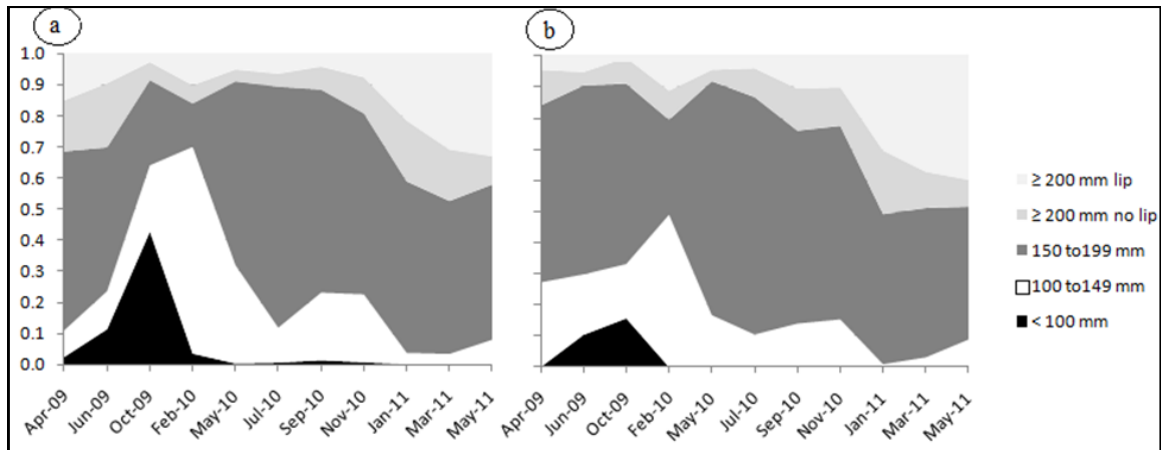


Figure 2. Relative abundance of *S. gigas* per size class, between April 2009 and May 2011 at (a) CU and (b) BN, in the Inlet of Xel-Ha Park, Mexico.

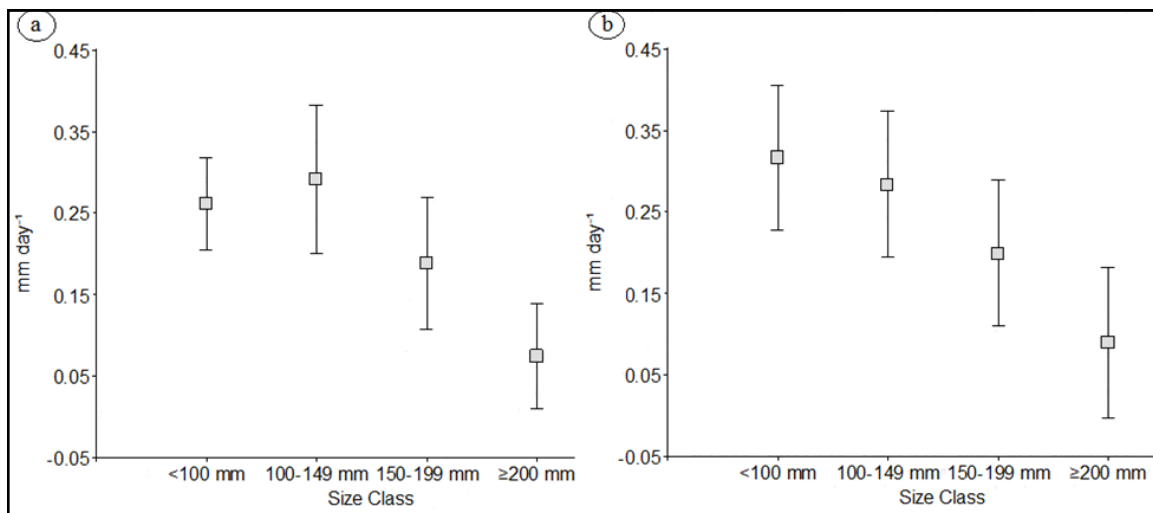


Figure 3. Mean growth rates and standard deviation of *S. gigas* at CU (a) and BN (b) per size class, in the Inlet of Xel-Ha Park, Mexico.

Table 1. Population size estimates of *S.gigas* using Schnabel method and relative densities at CU, in the Inlet of Xel-Ha Park, Mexico.

Sample	Ct	Rt	% Rt	Ut	Mt	Nt	Density (Ind/m ²)
Apr-09	127	0		127	0		
Jun-09	106	68	64.15094	38	127	198	0.0330
Oct-09	306	61	19.93464	245	165	496	0.0826
Feb-10	406	193	47.53695	213	410	716	0.1193
May-10	382	200	52.35602	187	623	897	0.1496
Jul-10	566	311	54.947	261	810	1113	0.1854
Sep-10	545	319	58.53211	226	1071	1820	0.3033
Nov-10	479	235	49.06054	244	1297	1537	0.2562
Jan-11	335	264	78.80597	71	1514	1598	0.2664
Mar-11	354	255	72.0339	99	1612	1684	0.2807
May-11	325	212	65.23077	113	1711	1830	0.3051

¹ Ct= Number of *S. gigas* caught in each sampling; ² Rt = Number of recaptures in each sample; ³ % Rt = Percentage of recapture per sample; ⁴ Ut = Number of untagged conch in each sample; ⁵ Mt = Total of marked animals at time; ⁶ Nt = Estimated population size using the Schnabel method.

The density at CU and BN is high, compared to other areas in the Caribbean (Table 5) and is higher than densities reported for Alacranes Reef, where conch fishery was banned in 1988 (Perez-Perez and Aldana Aranda 1998, Ríos-Lara *et al.* 1998, Perez-Perez and Aldana Aranda 2000, Perez-Perez and Aldana Aranda 2003), ranging from 0.0047 to 0.018 ind./m². They were also higher than the densities reported for the two most important commercial queen conch fishery grounds in Quintana Roo, Banco Chinchorro (0.0211 ± 0.035 ind./m²) and Banco Cozumel (0.0079 ± 0.01653 ind./m²) (INP-SAGARPA 2008). In Punta Gavilanes, a coastal area without commercial fishing, densities range from 0.003 to 0.0052 ind./m² (De Jesus-Navarrete *et al.* 1992, De Jesus-Navarrete and Oliva-Riviera 1997). Berg and Glazer (1994) reported in the Florida Keys, USA, densities between 0.000109 ind./m² and 0.000298 ind./m², where a permanent fishing ban has been implemented since 1985 and sanctuaries with surveillance have been created due to the rapid depletion of stocks of queen conch. The densities found in Xel-Ha are similar to the relatively natural populations in the Exuma Cays (Table 5) (Stoner and Ray

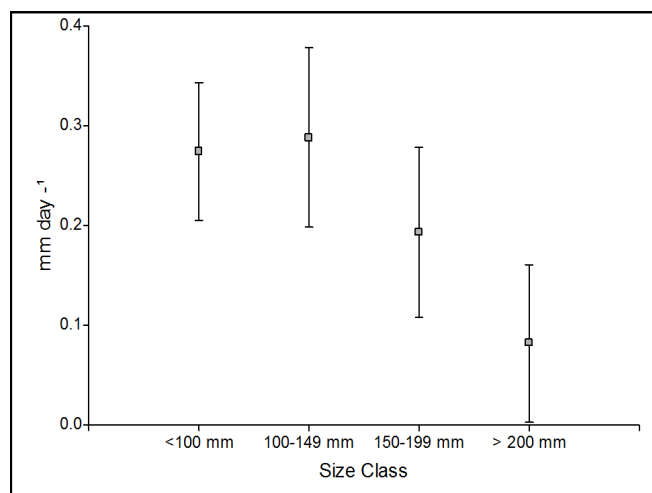


Figure 4. Mean growth rates and standard deviation of *S. gigas* per size class in the Inlet of Xel-Ha Park, Mexico.

Table 2. Population size estimates of *S. gigas* using Schnabel method and relative densities at BN, in the Inlet of Xel-Ha Park, Mexico.

Sample	Ct	Rt	% Rt	Ut	Mt	Nt	Density (Ind/m ²)
Apr-09	70	0		70	0		
Jun-09	259	31	11.96911	228	70	585	0.0975
Oct-09	254	120	47.24409	134	298	621	0.1036
Feb-10	300	141	47	159	432	765	0.1275
May-10	278	158	56.83453	120	591	862	0.1436
Jul-10	369	189	51.21951	180	711	1017	0.1696
Sep-10	289	219	75.77855	70	891	1603	0.2672
Nov-10	323	248	76.78019	75	961	1101	0.1835
Jan-11	297	224	75.42088	73	1036	1147	0.1912
Mar-11	343	268	78.13411	75	1109	1193	0.1988
May-11	346	213	61.56069	133	1184	1291	0.2151

¹ Ct = Number of *S. gigas* caught in each sampling; ² Rt = Number of recaptures in each sample;

³ % Rt = Percentage of recapture per sample; ⁴ Ut = Number of untagged conch in each sample;

⁵ Mt = Total of marked animals at time; ⁶ Nt = Estimated population size using the Schnabel method.

Table 3. *S. gigas* growth parameters per size class in the Inlet of Xel-Ha Park, Mexico.

Size Class	n	Mean	S.D.	Minimum	Maximum	Median
<100 mm	127	0.27	0.07	0.11	0.55	0.27
100-149 mm	443	0.29	0.09	0.01	0.63	0.29
150-199 mm	583	0.19	0.09	0	0.54	0.2
≥200 mm	89	0.08	0.08	0	0.44	0.07

¹n = sample size; ²S.D. = Standard Deviation

Table 4. Pearson Correlation between *S. gigas* growth and relative density at Xel-Ha Park, Mexico.

Size Class	R	p
<100 mm	-0.08	0.4000
100-149 mm	0.11	0.0200
150-199 mm	-0.12	0.0034
≥ 200 mm	-0.08	0.4500

¹R = Pearson Correlation coefficient; ²p=p-value.

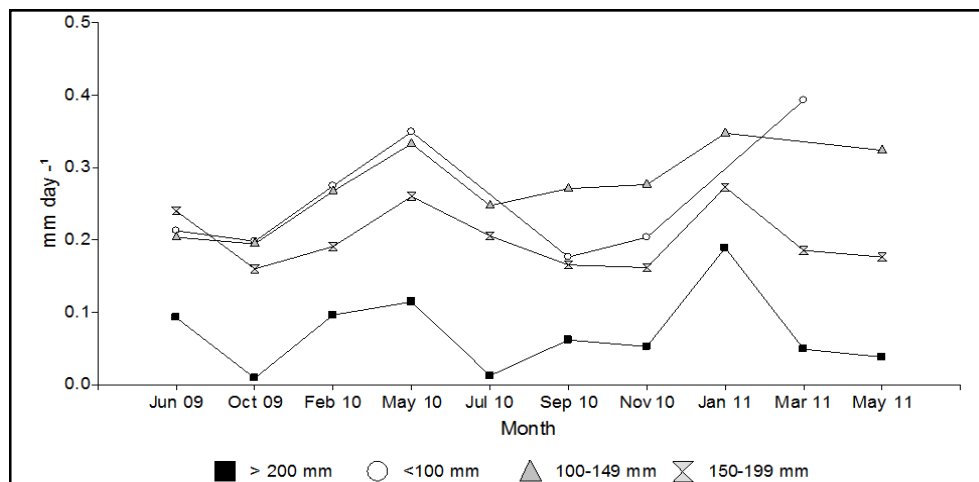


Figure 5. Mean growth rates of *S. gigas* per size class between April 2009 and May 2011, in the Inlet of Xel-Ha Park, Mexico.

1993, Stoner 1996) and can be compared to the high-density aggregation nursery grounds (Stoner and Ray 1993, Stoner and Lally 1994) in terms of density and population structure. In the case of Xel-Ha, density has probably increased due to favorable environmental conditions, not fully understood yet, as well as to active protection of the animals and banning fishing (Peel et al. 2010). The comparison of growth rates between sites showed that growth within the Inlet is similar, despite of local environmental differences between them.

The growth rate of juvenile conch in Xel-Ha was consistently higher in comparison with growth rates obtained in enclosures (Table 6). De Jesus-Navarrete (2001) estimated an average increase of 3.21 mm/month (~0.1052 mm/day) in Punta Gavilan and 2.30 mm/month (~0.075 mm/day) in Banco Chinchorro, maintaining conch in enclosures at a density of 0.4 ind./m². In other areas of the Caribbean similar increases were observed (Randall 1964, Alcolado 1976, Brownell 1977, Ray and Stoner 1994). Growth rates measured during this study were comparable to other studies conducted under natural conditions using mark-recapture methods. Gibson et al. (1983) determined a rate of 7.2 mm/month (~ 0.236 mm/day) in Belize, while in Venezuela an increase of 15 mm/month (~ 0.492 mm/day) was measured (Weil and Laughlin 1984) and in Punta Gavilan, juveniles grew an average of 10 mm/month (~ 0.327 mm/day) (De Jesus-Navarrete Oliva-Rivera 1997).

Nevertheless, growth rates of queen conch showed large individual variations, especially in animals of the class of 100 - 149 mm. Alcolado (1976) showed that growth may vary according to environmental variability between sites; however, the studied areas are relatively small, making it more likely that the organisms have been exposed to similar conditions within sites. Environmental conditions may be responsible for the variations in growth observed over time. No seasonal pattern was evident, but

high growth rates coincided with ceasing recruitment. Growth rates were significantly different for the size class < 100 mm between sites, but were attributed to sample size.

Several authors (Iversen et al. 1986, Ray and Stoner 1994, Ray et al. 1994, Stoner and Lally 1994, Ray and Stoner 1995) point out the vulnerability of juvenile conch to predation. Conch find refuge from predation either in size or by forming dense aggregations. Predation seems to be one of the most important factors in habitat choice and may lead to choose lower quality habitat in terms of resources, compromising maximum ingestion and growth, by aggregating or sheltering in dense vegetation. High density aggregation may lead to competition, having negative effects on growth, while increasing survival probabilities (Ray and Stoner 1995). Ray and Stoner (1995) demonstrated that growth rates and mortality were density-dependent and related to food limitation. In this study, we detected that growth was affected negatively in the 150 - 199 mm size class by increasing density, but we also detected the opposite effect in the 100 - 149 mm class. Smaller conch might benefit from aggregating, while in bigger conch it may lead to competition.

In a previous study, no density dependent effect could be detected (Peel and Aldana Aranda 2011), but conch density kept increasing in Xel-Ha and could have become an important factor regulating resource acquisition and intra-specific interactions.

CONCLUSION

Population size in the Xel-Ha Inlet has increased and conch density is higher than most of the populations reported throughout the Caribbean. The population growth can be attributed to recruitment of juvenile conch.

Growth rates were similar at the two sites, despite of some environmental differences between them. It was found that growth is highly variable within individuals of

the 100-149 mm size class and that density had a positive effect, while density affected growth negatively in bigger conch.

Comparison of our results with growth rates obtained in enclosures showed that growth is higher under mark-recapture conditions.

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Table 5. Average densities of *S. gigas* in the Caribbean.

Author, Year	Location	Density (ind./m ²)
Ríos-Lara et al. 1998	Alacranes Reef, Yucatan, Mexico	0.0047
Perez-Perez and Aldana Aranda 1998	Alacranes Reef, Yucatan, Mexico	0.0072
Perez-Perez and Aldana Aranda 2000	Alacranes Reef, Yucatan, Mexico	0.0084
Perez-Perez and Aldana Aranda 2003	Alacranes Reef, Yucatan, Mexico	0.018
De Jesus-Navarrete et al. 1992	Punta Gavilanes, Quintana Roo, Mexico	0.003
De Jesus-Navarrete and Oliva-Riviera 1997	Punta Gavilanes, Quintana Roo, Mexico	0.0052 ± 0.0023
INP-SAGARPA 2008	Banco Chinchorro, Quintana Roo, Mexico	0.0211 ± 0.035
INP-SAGARPA 2008	Banco Cozumel, Quintana Roo, Mexico	0.0079 ± 0.01653
Berg and Glazer 1991	Florida Keys, Florida, USA	0.000109-0.000298
Friedlander et al. 1994	Virgin Islands, USA	0.00171
Stoner and Ray 1993	Exuma Cays, Bahamas	0.2
Stoner and Schwarte 1994	Lee Stocking Island, Bahamas	0.0018-0.0088
Stoner 1996	Exuma Cays (unfished zones), Bahamas	0.0034-0.0147
Stoner 1996	Exuma Cays (fished zones), Bahamas	0.00022-0.0088
Stoner and Ray 1996	Exuma Park, Exuma Cays, Bahamas	0.027
Posada et al. 1999	Jaragua National Park, Dominican Republic	0.0004-0.01142

Table 6. Comparative Table of mean growth rates of *S. gigas* in the Caribbean.

Author, Year	Location	Method	Growth rate
Randall 1964	Virgin Islands, USA	Enclosure	4.16 mm/month ~0.136 mm/day
Alcolado 1976	Cuba	Enclosure, different environments	3.3 mm/month ~0.108/mm day
Brownell 1977	Florida Keys, USA	Enclosure	4.5 mm/month ~0.147 mm/day
Gibson et al. 1983	Belize	Mark-Recapture	7.2 mm/month ~0.236 mm/day
Weil and Laughlin 1984	Venezuela	Mark-Recapture	15 mm/month ~0.492 mm/day
Ray and Stoner 1994	Exuma Cays, Bahamas	Enclosure	0.058 mm/day to 0.139 mm/day
De Jesus-Navarrete and Oliva-Rivera 1997	Punta Gavilan, Mexico	Mark-Recapture	10 mm/month ~0.327 mm/day
De Jesus-Navarrete 2001	Banco Chinchorro, Mexico	Enclosure, different environments	3.21 mm/month ~0.1052 mm/day
De Jesus-Navarrete 2002	Punta Gavilan, Mexico	Enclosure, different environments	2.30 mm/month ~0.075 mm/day
Moreno de la Torre and Aldana Aranda 2005	Mexico	Laboratory conditions, artificial diet	0.16-0.23 mm/day

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