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Research Article

Mobility and Spatial Connectivity Between Nursery and Adult Populations of the Queen Conch (*Lobatus gigas*) In A Natural Protected Area of the Mexican Caribbean

Dalila Aldana Aranda[1*], Joanne Rebecca Peel[2]

[1]Research and Advanced Studies Center of the National Polytechnic Institute, Laboratory of Conservation, Aquaculture and Biology of Mollusk, Merida, Yucatan, Mexico

[2]Autonomous Metropolitan University, Department of Man and Its Environment, Mexico

[*]**Corresponding author:** Dalila Aldana Aranda, Research and Advanced Studies Center of the National Polytechnic Institute, Laboratory of Conservation, Aquaculture and Biology of Mollusk, Km 6 Old Road to Progreso, Merida, Yucatan, Mexico. Tel: +7877665927; Fax: +7877666239; Email: daldana@cinvestav.mx

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Abstract

The queen conch *Lobatus gigas* represents one of the most important fishery resources of the Caribbean. The conch's life cycle is highly complex, implying various ontogenic habitat shifts and migrations. The distribution of juveniles is generally restricted to certain areas and the failure to recognize this, may have caused bias in previous studies, either towards aspects of juvenile ecology or adult ecology. Few studies have addressed connectivity between nurseries and reproductive aggregations. Xel-Ha's inlet is a natural protected area under private administration, hosting a population of *L. gigas*. In the present study, we assessed size distribution and mobility throughout the inlet using a stratified mark-recapture scheme at four sites (Cueva, Centro, Bocana and Brazo Norte) in order to determine how *L. gigas* uses its habitat throughout its life and how the different stages of its life cycle connect. A total of 8,292 conchs were tagged between 2005 and 2011. The population was composed of 70% juveniles. At Cueva, Centro and Brazo Norte mainly juveniles were captured, while at Bocana mostly adults were encountered. Mobility increased in adult and sub adult conch and during summer months. Spatial distribution and mobility were associated with length and lip thickness, suggesting that conch might undergo an ontogenetic niche shift as they reach sexual maturity, which explains these gregated size distribution.

Summary

The Pink Snail, Lobatus gigas is one of the most important fishery resources in the Caribbean. The life cycle of this gastropod is complex, implying several changes in ontogenic habitat and migrations in its life cycle. The distribution of juveniles is generally restricted to certain areas and the error in their characterization may be caused by bias in previous studies, either towards aspects of juvenile ecology or adult ecology. Few studies have addressed the connectivity between breeding areas and areas of reproductive aggregation. The Caleta de Xel-Ha is a protected natural area, being a park under private administration, that houses a natural population of L. gigas. In the present study, the size distribution and the mobility of this organism along the cove were evaluated using a stratified tag-recapture scheme at four sampling sites (Cueva, Centro, Bocana and Brazo Norte) to determine how L. Gigas uses their habitat throughout their life and how different stages of their life cycle are connected. A total of 8,292 snails were marked between 2005 and 2011. The population consisted of 70% of juveniles. In Cueva, Centro and Brazo Norte mainly juveniles were captured, while in Bocana they were mostly adults. Mobility was greater in adult and sub-adult organisms and during the summer months. Spatial distribution and mobility were associated with lip length and thickness, suggesting that snails may exhibit an ontogenetic niche change as they reach sexual maturity, which explains this distribution of well-structured sizes.

Keywords: Breeding; Habitat Change; Mobility; Ontogenic Niche; Population Connectivity; Pink Snail

Introduction

The queen conch (*Lobatus gigas*) is a large gastropod which used to represent an important food and economic resource in the Caribbean [1]. The life cycle of the conch is complex, presenting an extensive pelagic larval stage, an in faunal stage and an epibenthic stage, which complicates the assessment of stocks by traditional methods used in fishery biology [2,3]. Furthermore, each stage of its life cycle is subject to a variety of factors which influence the abundance and distribution of this species (CFMC 1999) [4]. The queen conch performs several migrations throughout its life and at least two have been documented in the literature. The first systematic observations on conch mobility were made by Hesse (1979) [5] who documented that habitat use increased with body size. Furthermore, this author documented seasonal adult movements, which have also been documented by other authors and are thought to be associated with reproductive behavior [6-9]. The second type of migration reported in the literature consists of the mass movement of small juveniles, which is hypothesized to represent the dispersal of newly emerged classes (>1 year) classes from the centres of larval recruitment [10]. Ddescription of migrations of even smaller juveniles with shell lengths between 50-100 mm, believed to represent shifts from post-settlement habitats to nurseries have been studied [11,12]. Juveniles are predominantly found in certain areas characterized by soft sediments [5], Appeldoorn & Ballantine 1983) [13], while larger juveniles and adults are much more mobile and are found across a large variety of habitats [14]. Nevertheless, the characteristics of the benthic environment such as sea grass density, depth and sediment type are not good predictors for suitable habitats for this species [15]. Sampling of *L. gigas* populations is often biased either towards or against juveniles [14]. Most studies solely address ecologic aspects of juveniles [10,16,17] or adults [18,19] and rarely asses' complete life cycles or the connectivity between both stages. This is probably due to the spatial segregation of life stages, which is rarely considered in experimental designs.

The body size of an organism is a key aspect of its ecology, determining its ability to exploit resources and its susceptibility to predation [20]. Many species undergo extensive ontogenetic shifts in food or habitat use as they increase in size, known as ontogenic niche shifts, a phenomena especially well documented in aquatic communities [20].

Nurseries are habitats where juvenile fish or invertebrate species occur at higher densities, suffer lower rates of predation or have higher rates of growth in comparison with other habitats where juveniles are found [21]. However, these criteria cannot predict whether these juvenile habitats successfully transfer juvenile biomass to adult populations [21]. Hence, it is vital that studies assess take into account movements from juvenile to adult habitats, a link which is currently missing in our understanding of nurseries. *L. gigas* nursery locations provide for high juvenile growth, as a resulting of high macro algal production and low mortality. The nurseries persist where competent larvae are concentrated by tidal circulation and where settlement occurs selectively [15]; hence they depend directly on adult distribution and are determined by the intersection of habitat features and ecological processes which combine to yield high rates of recruitment and survivorship [15].

The Xel-Ha inlet is an enclosed coastal lagoon, which has been used since 1995 as a park for ecotourism. It has a persistent population of queen conch, composed of juveniles, sub adults, reproductive and old adults [22], as well as pelagic larvae [23,24]. Furthermore, the occurrence of mating and spawning activity in the lagoon [25], suggests that the conch completes its whole lifecycle within the limits of the inlet. In terms of growth and survival, Xel-Ha presents several features of a nursery [26].

The aims of this study were to describe habitat shifts of *L. gigas* related to size and determine the seasonality of these shifts. This work demonstrates the effects of body size on habitat use and may be of great interest for management, since it documents that different life stages have different habitat requirements. Furthermore, this work demonstrates that behavior may be used as a non-invasive assessment tool to determine sexual maturation, an aspect of fundamental importance for fishery management.

Materials and Methods

The Xel-Ha inlet is a coastal lagoon located on the east coast of the Yucatan Peninsula (20˚19’15’’-20˚18’50’’N and 87˚21’41’’-87˚21’15’’W) which consists of a mix of fresh ground water, supplied by underground rivers, and seawater. The inlet is connected to the Caribbean Sea by a100 m wide and 170 m long channel and has a total surface of 14 ha with a central area and three appendices: Mouth/channel, north-arm and south-arm. Its depth ranges from 0.5-4.5 m. Tidal variations may range from 36 cm at the mouth and up to 53 cm at the south-arm. Four sites were surveyed within the inlet: Cueva, Centro, Bocana and Brazo Norte.

Cueva (6,000 m²) is located in the south-arm of the inlet and includes a small bay surrounded by mangroves (*Rhizophora mangle*) and several underground caves with up welling of cold freshwater, forming a stable thermo-and halocline at about 1.25 m depth, with salinities ranging from 35 at the bottom to 10 at the surface. The site has a depth of 1-3 m. The bottom is composed of fine muddy sediment, sand, fragments of calcareous algae, small rocks, and dense isolated patches of macro algae (e.g. *Padina* sp, *Calimesa* sp, *Penicillus* sp, *Amphiroa* sp, *Acanthophora* sp, *Caulerpa* sp, *Dictyota* sp) Decaying mangrove leaves and inverted jelly fish (*Cassiopea sp*.) may also be found. *Centro* is located in the center area of the inlet and was the most extensive sampling site with a total area of 23,000 m². The site consists of an extensive coarse sand plain, parts of which are covered with sea grass (*Halodule sp*). Close to the shore, the bottom is rocky with macro algae growing on it. As in the case of Cueva, the water column is highly stratified. The sampling site Bocana includes part of the channel that connects the inlet with the Caribbean Sea and the adjacent zone in the interior of the inlet. The bottom is composed of coarse sand, coral fragments and small rocks. Isolated patches of sea grass (*Thalassia* sp) and coral may be found. Brazo Norte is located in the north-arm of the inlet. The sampled surface area was 6,000 m². The bottom is composed of fine muddy sediment, large rocks which form several channels, and has very dense macro algae coverage (see Cueva), as well as many inverted jellyfish (*Cassiopea* sp). The water column is less stratified than in Cueva, but also presents a halo and thermocline at a depth of about 1.25 m with salinities ranging from 15 at the surface to 30 at the bottom.

Between January 2005 and September 2011, a total of 26 surveys were conducted at Cueva, Centro and Bocana, sampling a total area of 39,000 m². In 2009, Brazo Norte was included in the sampling efforts, expanding the surveyed area to 45,000 m². In 2005 surveys were carried out monthly, and from 2006 to 2011 samples were collected taken every two months. At each of the four sampling sites all possible as many organisms as possible were collected by free-diving by three divers during three hours. We used the capture-mark-recapture method, tagging all individuals with a consecutively numbered plastic Dymo® tag, which allowed the identification of each individual. The tag was fixed to the spire of the conch with a plastic zip tie. Shell length and lip thickness were determined for each individual, using a precision caliper accurate to ±1 mm. All animals were released in the location where they were found.

For each site, the number of juveniles, sub adults and adults was determined. Since shell length is not a good indicator of age [27,28], lip thickness was used to establish size classes. A juvenile was defined as a conch with not lip, while conches with a formed lip, but thinner than 5 mm were classified as sub adults, and an adult was defined as a conch with a lip thickness≥5 mm, based on histological evidence proposed by Appeldoorn (1988) and Aldana-Aranda & Frenkiel (2007) [27,28].

In order to detect dispersal and movement, tag recovery was analyzed, counting and classifying all conch that were recaptured at a site different from the one they were initially tagged at, using the same classification criteria as explained before. In order to determine if whether were any significant differences between the source population and the population of emigrant conch, a Chi-square test with a 95% confidence level was carried out using R [29].

Analysis of variance (ANOVA) with a confidence level of 95% was used to determine if whether there were significant differences in the shell length and lip thickness, and the redistribution of conch throughout the inlet. Finally, the direction and seasonality of movements was evaluated, counting the total number of conch that moved in the dry-+rainy- and winter season. Frequency and goodness of fit test were used to determine frequency of these movements from the original site to a destination site showed significant differences between seasons.

Results

Figure 1 shows the population structure (number of juveniles, sub adults and adults) at each of the four source sites (site where the conchs were originally tagged), the number of juveniles, sub adults and adults which leave each source site, and the redistribution of conch in the inlet according to their life stage (juvenile, sub adult and adult).

At Cueva a total of 2,558 individuals were tagged throughout the duration of this study (Figure. 1), 85% were juveniles (2184), 6% (149 individuals) were sub adults and 9% (225 individuals) were adult conchs. The emigration of 366 individuals from Cueva was detected. More than half (212 individuals) of the emigrants were adults. The emigrant conch population composition was significantly different from the source population ($\chi^2_{calc}=725.0544>\chi^2_{[0.95;2]}=5.991$; $P<0.001$), which suggests that dispersal was not random. Juveniles and sub adults were mainly reencountered in *Centro*, while the most of the adults (112 individuals) were found at Bocana, the site where the inlet connects to the ocean.

At Centro a total of 2,846 animals were tagged, of which 73% (2,089 individuals) were juveniles, 15% (430 individuals) were sub adults and 12% (327 individuals) adult conchs (Figure 1). Emigration of 1,064 conchs was registered. Despite the fact that the source population consisted mainly of juveniles, 72% (762 individuals) of the emigrant conchs were adults, and significant differences between the source- and emigrant population were found ($\chi^2_{calc}=1393.756>\chi^2_{[0.95;2]}=5.991$; $P<0.001$), suggesting non-random dispersal. The majority of the movements (87%) were directed towards Bocana, where 979 individuals from Centro were recaptured. At Bocana a total of 1,292 conchs were tagged, of which 666 were adults (Figure 1).

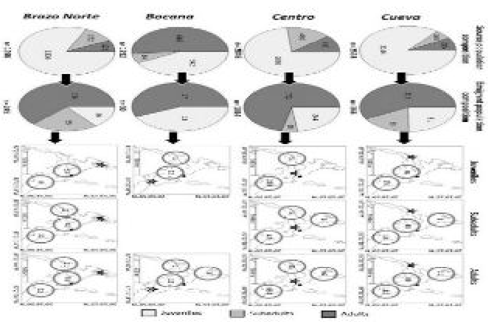

Figure 1: Number of animals tagged at each study site (N), source population composition (number of juveniles, sub adults and adults), number of animals that emigrated, emigrant population composition (number of juveniles, sub adults and adults) and redistribution of emigrants by life stage throughout the inlet of Xel-Ha.

Nevertheless, only 30 (2.3%) conchs were found to move towards the interior of the inlet and 83% of them were recaptured at the adjacent sampling site Centro.

At Brazo Norte 1,598 conchs were tagged (Figure 1). As in the case of Cueva and Centro, the source population was mainly composed of juveniles (81%). A total of 245 conchs were recaptured at other sites within the inlet. The majority (63%) of the emigrant conch were adults. The composition of the emigrant conch was significantly different from the composition of the population at the source site ($\chi^2_{calc}=586.9287>\chi^2_{[0.95;2]}=5.991$; P< 0.001), suggesting non-random dispersal. Most of the juveniles (33 out of 41 individuals) and sub adults (42 out of 44 individuals) were recaptured at Centro, while 92 (60%) of the adults were found at Bocana.

Figure 2 shows the average shell length and lip thickness of emigrant conch and the respective destination of migrations in the inlet. In the case of conch emigrating from Cueva, Brazo Norte and Centro, the average size ranged from 205 to 215 mm. There were no significant differences between shell length and final destination of the conch. In the case of conchs emigrating from Bocana, shell length was much more variable. Nevertheless, we detected significant differences (P> 0.001) in lip thickness, depending on the destination of migrations; conch reencountered at Bocana generally had thicker lips.

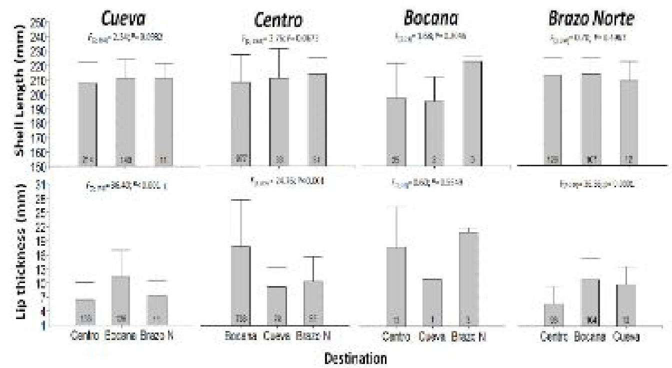

Figure 2: Average shell length, lip thickness and standard deviation of emigrant conch from Cueva, Centro, Bocana and Brazo Norte and relocation (destination) of conch in the inlet of Xel-Ha, Mexico; p values > 0.05 indicate significant differences, F: Fisher test value.

The animals' movements also showed seasonality (Figure 3) with conch emigrating from Cueva, Centro and Brazo Norte. Significant differences were observed between seasons (P< 0.001), and the animals presented higher mobility during the rainy season, with lower mobility during winter (corresponding to November-February). In the case of animals emigrating from *Bocana*, no significant differences between the frequencies of movements were detected among seasons (P = 0.219).

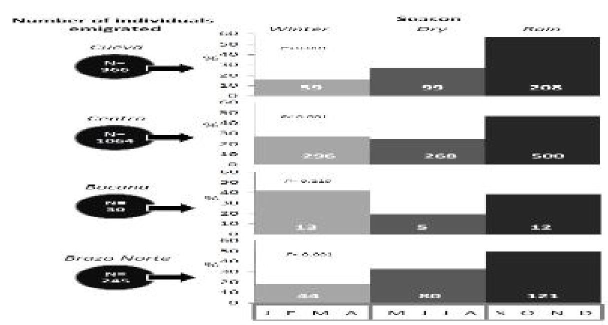

Figure 3: Total number of animals that emigrated (N) from source site (Cueva, Centro, Bocana, Brazo Norte), absolute and relative frequency (%) of movements per season (Winter= J: January, F: February, M: March and A: April; Dry = M: May, J: June, J: July and A: August; Rainy = S: September, O: October, N: November and D: December. P indicates significance level.

Discussion

The conch population at Xel-Ha was mainly composed of juveniles. Furthermore, we detected a biased distribution of juveniles and adults throughout the inlet, observing mainly adults at Bocana and juveniles or sub adults in the rest of the inlet. These results were consistent with previous observations made by Aldana-Aranda, et al. (2005) [30], who reported 79.2% juveniles and sub adults at this study site in the period from 2001-2003. Moreover, the authors reported 76% juveniles in Cueva and 82% adults in Bocana during 2001-2003. The impact of fishing causes a decrease in the population adult [31,32]. On the other hand, [5] described populations with a juvenile-adult ratio of 3:1, which could be explained by increased mobility of adults. Fishing is prohibited in Xel-Ha, suggesting that the population composition found in this study is natural and can be described to other factors, such as habitat shift, as this study suggests.

Mobility and redistribution of conch in the inlet appeared to be related to size, explaining the size segregated population distribution. Our finding seems to be consistent with observations made by Hesse (1979), reporting that mobility increases in conch > 170 mm. In the case of Xel-Ha, the average size of mobile conch was ~210 mm, although redistribution in the inlet was mostly related to lip thickness, with mainly reproductive adult conch (lip thickness ≥ 5 mm) in Bocana.

Alcolado (1979) [7] and Stoner & Ray (1996) [33] determined that nurseries are usually restricted to certain sites with special environmental features. Corporal size of an organism is a key aspect of its ecology, determining its ability to exploit resources and its susceptibility to predation [20]. Organisms that undergo large changes in body size typically display pronounced changes in resource use between birth and maturation, known as ontogenetic niche shifts, which often manifest as shifts in habitat use or diet with increasing body size [20,34,35]. This can generate complex interactions and dynamics within communities [20]. One of the key features of an ontogenic niche is segregation of the population by size. This phenomenon is especially well documented in aquatic communities [20], as for example in the Caribbean spiny lobster *Panulirus argus* [36] or *Archaster typicus*, a common sea star of the Indo Pacific regions [37]. Ontogenetic niche shifts are particularly important for organisms for which resource use, growth rates, and predation risk are strongly related to body size [20,38], as in the case of *S. gigas*, given that juveniles are highly vulnerable to predation and that mortality decreases dramatically with size [39-42]. Lobsters for example, attain partial refuge from predation in size, allowing the ontogenetic niche shift from full-time algal dwelling to diurnal crevice sheltering and nocturnal foraging [36]. The common Indo Pacific sea star *A. typicus,* is found to be associated with intertidal mangrove prop roots, sea grass meadows, sandy beaches, and shoals. Small specimens occur with higher densities in intertidal mangrove prop roots. High organic matter in sediment and a relatively low predation rate seems to support juvenile life among mangroves. Size and density analyses provide evidence that individuals gradually move to seagrass, sandy habitats, and shoals as they age, allowing an ontogenetic habitat shifts for sea stars to be documented, providing new biological information as a basis for management of harvested *A. typicus* populations [37]. On the other hand, spatial aggregations by age and sex have been described for *S. luhuanus*, a close relative of *L. gigas* from the Indo-pacific. Four types of discrete aggregations have been identified for this species: mixed age-class, juveniles, mating and cluster [42], which also indicates that population aggregation or segregation may be a common social feature of *Strombus* species.

The ecological processes operating in nursery habitats, compared to other habitats, must support greater contributions to adult recruitment from any combination of four factors: (1) density, (2) growth, (3) survival of juveniles, and (4) movement to adult habitats [21]. In the case of Xel-Ha, the first three aspects have already been identified successfully [44], while the present study supports evidence for the migration of juveniles to adult habitats. This suggests that the sites in the interior of the inlet probably function as nurseries, whereas Bocana may be associated with reproductive activity, where spawning aggregations have been observed from June to October [45].

Mobility of *L. gigas* in the Xel-Ha inlet increased during the rainy season, corresponding to the summer months. This has previously been reported by. Furthermore, the conch reproductive season has been associated with increasing temperatures [5,18,45-47], and as mentioned before, spawning conch have been observed in the inlet from June to October.

Our study provides evidence of spatial segregation of life stages, and coupled with previous studies on growth, survival and density [26], we conclude that the Xel-Ha inlet can be considered a true nursery, successfully transferring individuals from juvenile habitats to adult populations. Furthermore, we propose that the queen conch *S. gigas* performs ontogenic niche shifts related to size. The seasonality of the habitat shift from juvenile to adult habitats, strongly suggests that these are related to reproductive activity, hence conch mobility could be used as an indicator for sexual maturity.

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