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Newly discovered deep-water nursery and spawning habitats of the queen conch *Aliger gigas* in Puerto Rico

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ABSTRACT: The queen conch *Aliger gigas* is a large marine gastropod and sustains one of the most important fisheries in the Caribbean. Overfishing of queen conch has led to shifts in the distribution and abundance of this species in some Caribbean countries; as a result, fishing effort has been redirected to deeper waters (>25 m), where fishers have largely switched from harvesting conch by snorkeling to using SCUBA. Advances in technology such as camera sleds have been used to identify, measure, and study queen conch in shallow habitats, but only sparingly in deeper habitats that may serve as refugia. To define deep-water habitat use and composition, we used a camera sled to quantify siphonal length, life stage, and environmental characteristics of the queen conch on the west coast of Puerto Rico. We conducted multiple 2 h transect surveys at 25–45 m depths during summer 2018. Queen conch densities ranged from 2.6 to ~3000 ind. ha^{-1}, with relative abundance highest at the 27 m depth interval. A novel finding was the discovery of deep-water nurseries and aggregations of juvenile queen conch in association with deep-water spawning grounds at the 27 m depth interval. Densities in deep-water habitats rivaled those in shallower habitats and indicate that deep-water nursery and spawning habitats warrant management measures for sustainable exploitation as well as integration of these habitats into metapopulation dynamics.

KEY WORDS: Deep-water nursery · Spawning ground · Camera surveys · Queen conch

1. INTRODUCTION

The queen conch *Aliger gigas* is a large marine gastropod that supports important fisheries in the Caribbean, where it is valued for its meat and as a collectible shell (Davis 2005). Queen conch inhabit waters down to 60 m deep (Randall 1964) but are commonly found in habitats less than 30 m depth (Stoner & Schwarte 1994, SEDAR 2007) dominated by seagrass beds (turtle grass *Thallassia testudinum*, manatee grass *Syringodium filiforme*, and shoal grass *Halodule wrightii*), coral rubble, algae, and sand (Appeldoorn 1991, Davis 2003, Marshak et al. 2006, SEDAR 2007, CFMC & NOAA 2013). Overfishing has significantly reduced shallow-water populations, some of which have been closed to fishing by moratorium (Davis 2005, SEDAR 2007, Ehrhardt & Valle-Esquivel 2008).

Queen conch occur in waters deeper than 25 m in various Caribbean locations such as the Bahamas, Belize, Jamaica, Martinique, Turks and Caicos, and Puerto Rico (Berg & Olsen 1989, Stoner & Sandt 1991, Garcia-Sais et al. 2012, Boman et al. 2021, Vaz et al. 2022). These deeper habitats have been hypothesized to act as spatial refugia for adults, which may sustain the heavily fished shallow-water populations (the deep reef refuge hypothesis) (Appeldoorn 1997, Theile 2001, Riegl & Piller 2003, Bongaerts et al. 2010, NMFS 2014, Stefanoudis et al. 2019, Boman et al. 2021).

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Recently, fishing pressure has increased due to the demand for queen conch in the Caribbean and in international trade (NMFS 2014). Consequently, fishing effort has been redirected to deeper areas (Ballantine & Appeldoorn 1983, FAO 1993, CFMC & NOAA 2013). In the past 5 yr, hurricanes have also contributed to changes in the patterns of queen conch fishing. In previous years, fishers captured queen conch from 15–20 m depths, whereas after Hurricane Maria (2017), fishers began to fish for conch in deeper waters at 30–60 m depths (Agar et al. 2020). The recent transition of fishing to deeper areas could be limiting the potential contributions from these deep-water queen conch populations to shallow-water populations.

Deep-water queen conch in the western Puerto Rico shelf are mostly located within the US Exclusive Economic Zone (EEZ), defined as waters extending 9 nautical miles (16.7 km) from the coast, a region where fishing is prohibited. When diving to depths below 25 m, fishers often utilize 2 or more tanks, which gives them more time in the water to fish for deeper conch (confidential pers. comm. to W.C.M.). Although this practice puts fishers at high risk of decompression sickness and other diving-related illnesses (Nord et al. 2019), the economic benefits of conch fishing often outweigh the risks.

Investigating deep-water habitats has been difficult due to the depth limitations of air-based SCUBA surveys (>30 m) (Appeldoorn & Baker 2013, Boman et al. 2016). Closed-circuit rebreathers, mixed-gas SCUBA surveys, and tools such as remotely operated vehicles have recently been used to characterize the physical and biological characteristics of deep reefs (Armstrong & Singh 2012, Ballantine et al. 2016), including fish, coral (Sherman et al. 2010), and sponge assemblages (Garcia-Hernandez et al. 2018). Moreover, emerging technologies such as multibeam sonar and underwater camera systems have promoted the study of deeper habitats (Boman et al. 2016, 2021, Cruz-Marrero et al. 2020).

Underwater image systems provide a relatively new methodology to estimate queen conch density and size (Boman et al. 2016, 2021, Cruz-Marrero et al. 2020). This method eliminates the risks of SCUBA surveys, creates a permanent record, and provides more bottom time than SCUBA surveys. Given the recent expansion of fishing to deeper habitats, the potential of deep-water populations as larval sources (i.e. metapopulation source–sink dynamics; Lipcius & Ralph 2011) for shallow-water populations and emerging technologies for investigating deep habitats, we sought to quantify queen conch abundance and size structure in deep habitats. Specifically, the goal of this study was to use an underwater camera-sled system to estimate the density and size structure of queen conch in habitats at depths > 25 m of the western Puerto Rico shelf and test 2 hypotheses. The first is that deep-water habitats in Puerto Rico harbor significant populations of adult queen conch that may serve as sources for the metapopulation, and the second is that deep-water habitats serve as nurseries for juvenile queen conch, which has never been documented but has been anecdotally reported (pers. comm. to R.N.L.).

2. MATERIALS AND METHODS

2.1. Surveys

Six 2 h transects were conducted in waters southwest of Puerto Rico using an underwater camera-sled system (camera sled) during July and August 2018 (Fig. 1). The camera sled (approximately 2 m long × 1 m wide × 1.5 m high) was composed of a downward facing camera (Point Grey Research, Zebra2 5.0 MP 2448 × 2048 at 5 frames per second with a high-definition serial digital interface; Sony ICX625 CCD) with 3 synchronized strobes (Bridgelux BXRA-C2002 LED; Fisheries Research Instrumentation) attached to an aluminum frame that transmitted live video through an ethernet connection to a topside computer, which allowed topside control of camera operation (Cruz-Marrero et al. 2019, 2020). The sled was towed using the 13 m R/V 'La Sultana' at an average speed of 2–3 knots (2.5–5.5 km h^{-1}). The camera sled covered a field of view of 0.7 m^2 (Cruz-Marrero et al. 2020). Images were collected at a rate of 5 images s^{-1}. Each image recorded the GPS position of the boat, and laser dots were spaced at 10 cm for reference measurements.

Transects were selected at depths ranging from 24–45 m within the EEZ and non-protected fishing areas (Fig. 2). To avoid collisions with hard structures, we utilized a haphazard selection process: potential sled transects within the desired depth range were surveyed with a Garmin 420 sonar before deploying the camera sled. If the sonar showed the desired bottom characteristics (level surface, no obvious reefs or rocks) then we deployed the camera sled. If no desirable bottom was found, then we moved to another location until a desirable depth and bottom type were found.

Images were automatically assigned to consecutive folders spanning 5 min intervals. Each folder could hold up to 1500 images (5 min × 60 s min^{-1} × 5 images s^{-1}). Each folder with its images was treated as a 'sub-

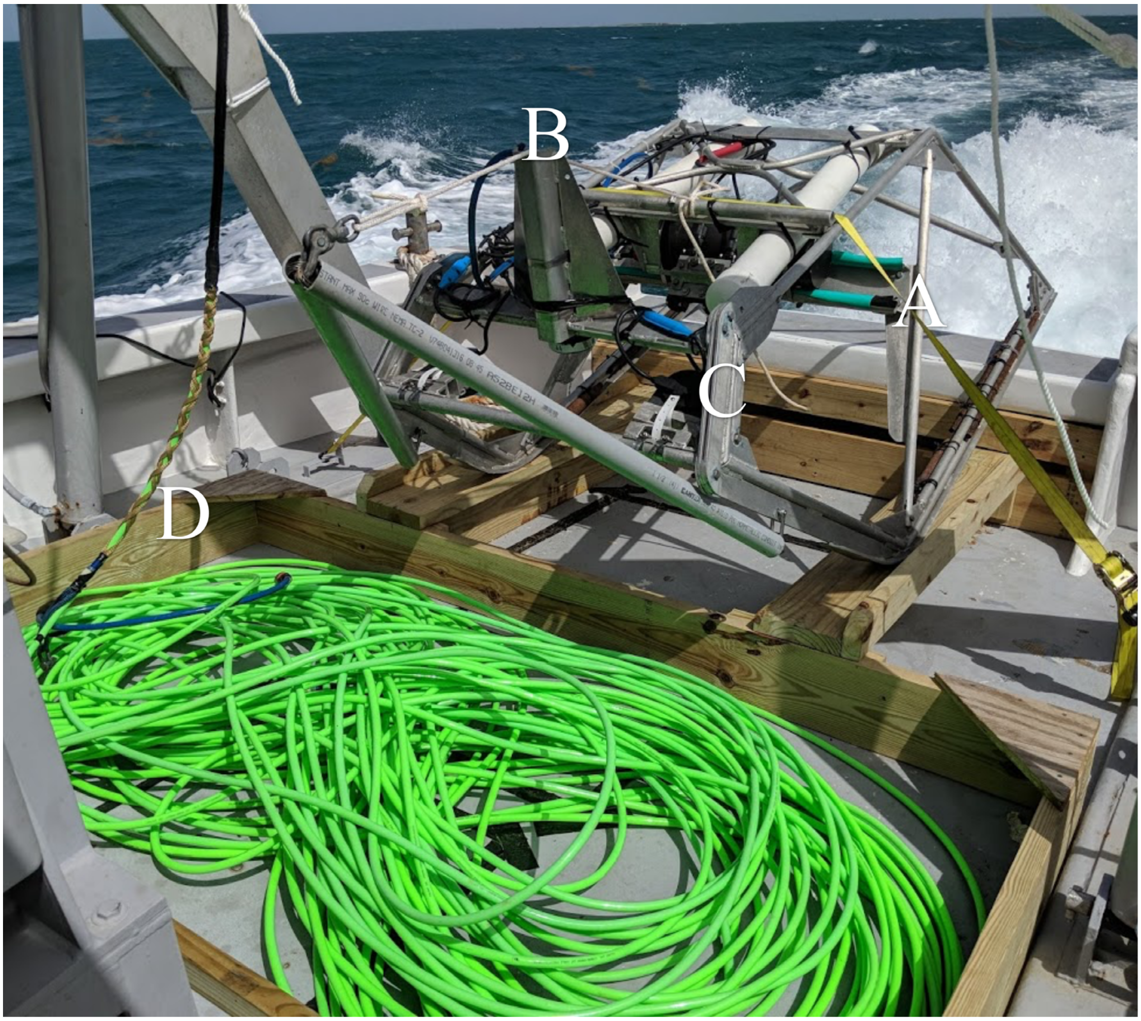

Fig. 1. Image of the camera sled, which consists of an aluminum frame (A), camera (B), strobe lights (C), and Ethernet towing cable (D)

transect' within each transect. The actual number of images in each sub-transect was occasionally <1500 due to variations in camera start and stop times, power surges, and electronic malfunctions.

2.2. Image annotation

Two experienced viewers annotated a total of 209 474 images. Viewers were previously trained to identify conch species, including dead and live animals, and to use shell measuring tools (Cruz-Marrero et al. 2020). Viewers followed Cruz-Marrero et al. (2020) and Boman et al. (2016) to distinguish between dead and live conch using shell coloration, track marks, shell damage, and position of the shell. Only conch in images that included the spire were counted as live conch; these were included as the variable count. Once a conch was considered alive, annotators measured the siphonal length of the conch with ImageJ software, using the 10 cm lasers as a reference (Cruz-Marrero et al. 2020). Not all images included the laser points due to sediment color, sled position, or poor image quality. Observed conch were characterized following previous Puerto Rico queen conch visual surveys into 2 categories: juveniles and adults. We characterized juvenile conch as those having a tan and clean to patchy periostracum with no obvious or thin flared lip; these were usually small individuals with prominent pointed spines. Adult conch had a flared lip, had lost the periostracum, had low to severe erosion of the outer shell and spines, and had shells colonized by epifauna (Appeldoorn et al. 2003, Baker et al. 2016, Cruz-Marrero et al. 2020).

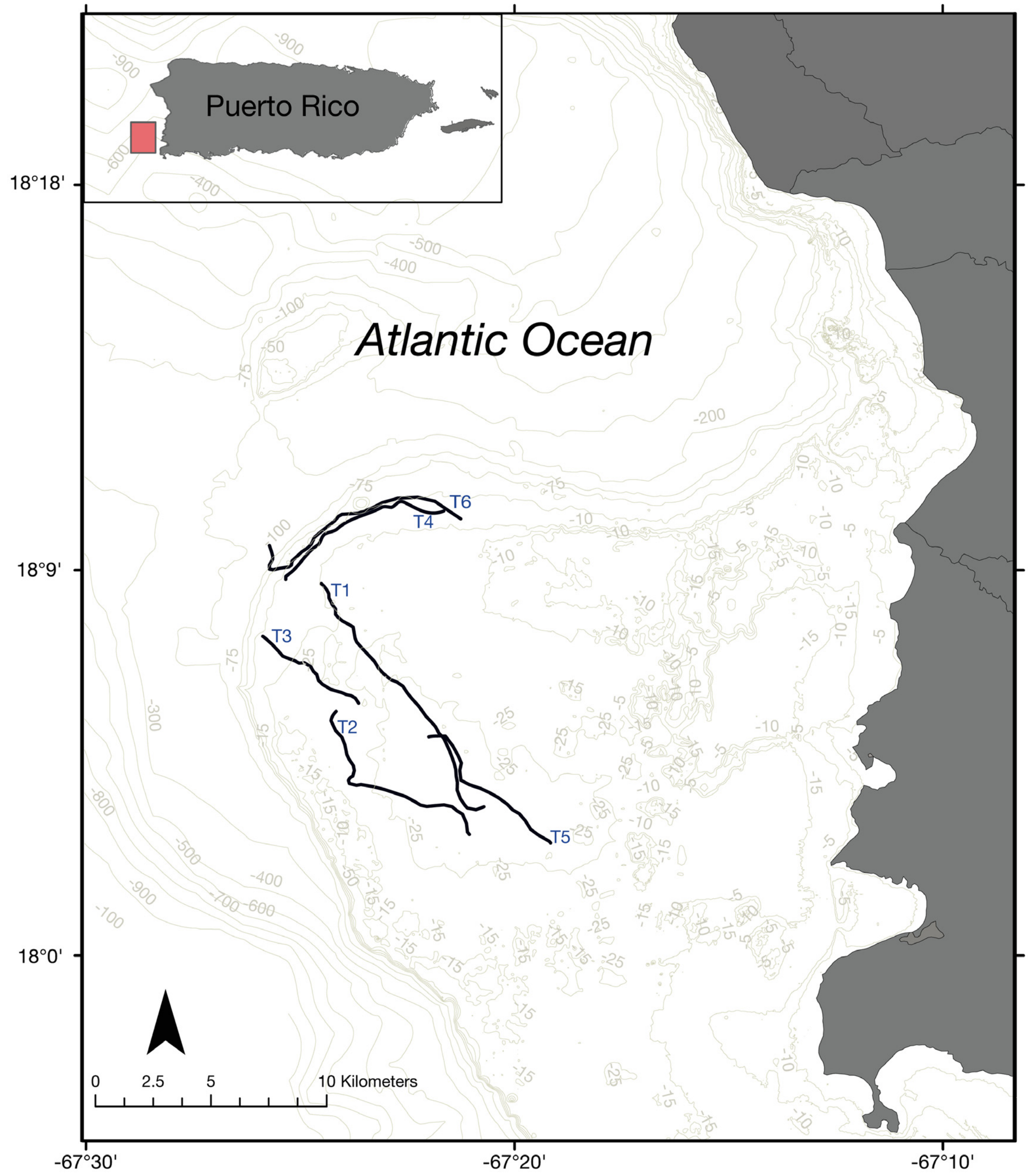

Fig. 2. Sampling area on the west coast of Puerto Rico. Sampling occurred during July and August 2018. Black lines: camera sled tracks; T1–T6: transects 1–6. Depths are shown in m

Annotators visually identified the 2 major substrate types (Hab1 and Hab2) in each image from the following alternatives: sand, rubble (a collection of small round rocks), seagrass (sediment harboring seagrass species), coral (any area covered with hard or soft structure of any species from the class Anthozoa), algae (any algal species coverage or algal filaments), shell (any type of mollusk shell), and rhodolith as indicated by circular red algae.

2.3. Data analysis

Conch counts were grouped into transects, and each transect observation was paired with the mean depth (27, 36, 41 m). The distribution of conch by mean depth was estimated by considering each image frame as a unit of effort. Depth preference was determined by dividing the proportion of images with live conch observed in that mean depth by the proportion of frames captured in that mean depth to compute a depth-specific relative abundance. Counts of queen conch were not normally distributed (Shapiro test, $p < 0.0001$), and variances of counts were not homogeneous between depth or age groups (Levene's test, $p < 0.0001$). For these reasons, we used generalized linear models (GLM) with a Poisson distribution to test the associations between count, depth, and stage. We compared models using the Akaike information criterion to find the model that best fit the data. Five models were tested, including a null model (intercept only) and models with depth, stage, depth + stage (without interaction), and depth × stage (with interaction) as treatment levels of the 2 factors, depth and stage. Tukey's tests based on the GLM-Poisson models were used to compare abundance (expressed as mean number per sub-transect) between mean depth within each conch stage.

The numbers of queen conch in each of the primary and secondary habitat groups were plotted with a heatmap, which visualized the hierarchical clustering of the combinations where conch were most common. Transect length was calculated utilizing the planar measurement tool in ArcGIS version 10.2.2, which allowed us to measure the boat tracks (Cruz-Marrero et al. 2020). The area surveyed on each transect was calculated by multiplying the transect length by the frame width of the camera sled (1.0 m) (Cruz-Marrero et al. 2020). Overall density (conch ha^{-1}) was calculated using total queen conch count divided by transect length.

2.4. Shell analysis to identify juvenile queen conch in aggregations

Juvenile conch in the deep-water aggregations (Fig. 3) could not be easily differentiated between milk conch *Macrostrombus costatus* or queen conch *Aliger gigas*. Consequently, we developed a method using allometry of the shell to differentiate the 2 species based on the relative ratio of spire length to shell length (SL) (Fig. 4). SL was measured as the distance from the tip of the spire to the base of the shell and standardized to 20 units on a grid (Fig. 4). Spire length was measured as the length in units from the tip of the spire to the crown of the anterior-most tubercle (Fig. 4).

To achieve references for each species, we used some of our own photos and those available through a Google search to gather 10 estimates of spire length for each species. Next, we selected 14 images of conch from the aggregations and analyzed spire length with a general linear model using a Gaussian

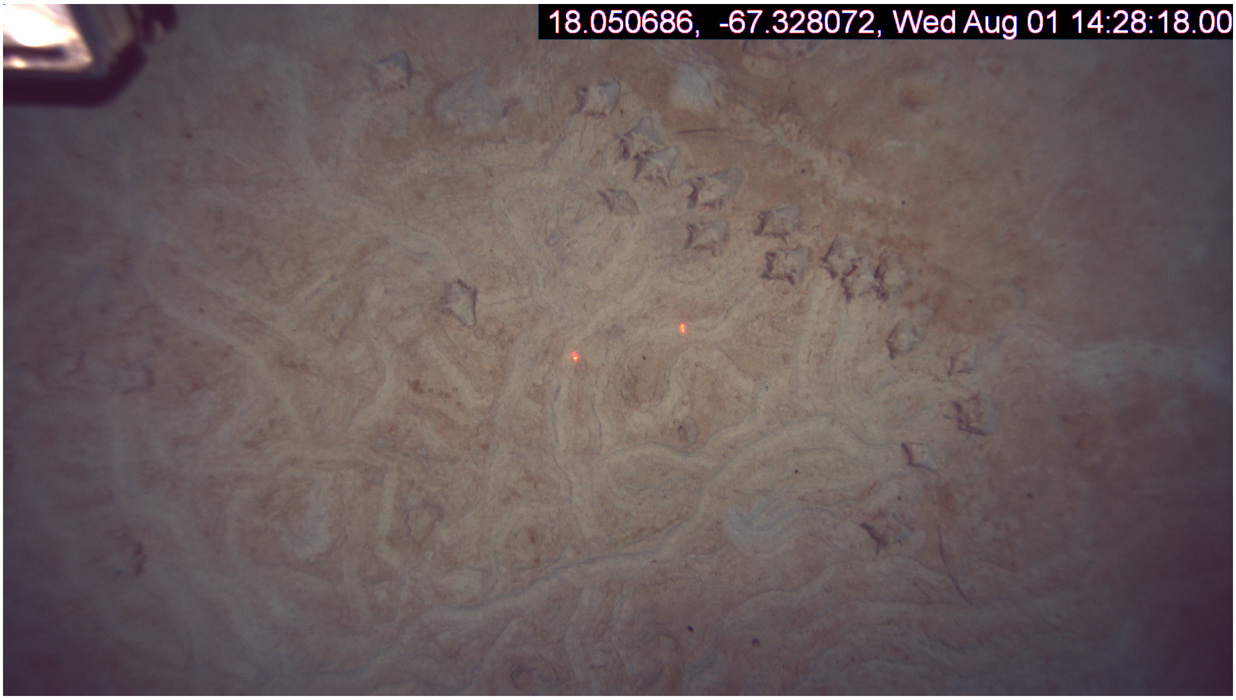

Fig. 3. Still-frame example of juvenile queen conch. The aggregation is similar to waves of juveniles moving in a shallow seagrass bed while feeding in Exuma Sound, Bahamas (Stoner et al. 1988). Distance between red laser dots: 10 cm

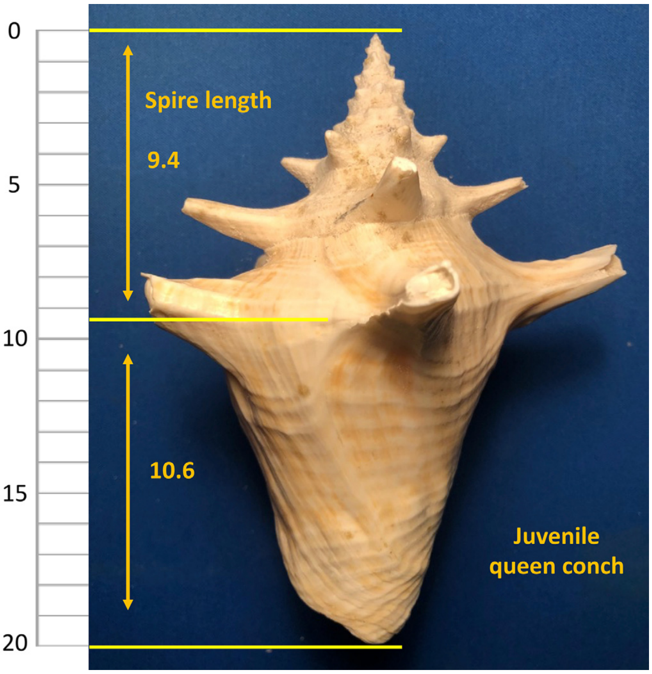

Fig. 4. Measurements of juvenile conch, with a juvenile queen conch as an example, used to distinguish juvenile queen conch and milk conch. The measurements are relative and unitless

link with conch species (milk, queen, unknown from aggregations) as a factor and spire length as the response variable. Spire length was approximately normally distributed and variances in spire length as a function of the factor were not heterogeneous (Levene's test, p = 0.780).

3. RESULTS

3.1. Observations

A total of 209 474 images were captured over 6 transects, and all were examined. Queen conch observations were concentrated in each transect at mean depths of 26.6 m (n = 5077), 36.2 m (n = 110), and 40.6 m (n = 44), including numerous egg masses at deeper depths (Table 1). We also observed Pacific red lionfish *Pterois volitans*, milk conch *Macrostrombus costatus*, Caribbean spiny lobster *Panulirus argus*, sea stars, tunicates, hermit crabs, sea urchins, sea cucumbers, and various species of soft corals.

3.2. Shell analysis to identify juvenile queen conch in aggregations

Spire length was significantly shorter for reference milk conch than for reference queen conch and juvenile in aggregations (Fig. 5, Table 2). In contrast, the spire length of aggregation juveniles did not differ significantly from that of reference queen conch (Fig. 5, Table 2). Consequently, we conclude that the juveniles were those of the queen conch.

3.3. Queen conch size

We observed 426 queen conch, including 264 live and 162 apparently dead individuals, plus 17 milk conch and 4969 juvenile conch (Fig. 3). Of the 264 live queen conch, 208 were measured in reference to the laser dots. Maximum SL ranged from 3.2 to 29.7 cm. Few identifiable queen conch of <5 cm SL were observed or measured. The size distribution between 5 and 25 cm SL was relatively flat and dropped dramatically above 25 cm SL, with no conch >30 cm SL (Fig. 6). All conch <15 cm were identified as juveniles, whereas adult conch comprised 35% of those in the 15–20 cm range, 87% in the 20–25 cm range, and all conch >25 cm (Fig. 6).

The mean size of measured conch (Fig. 7) did not differ significantly between the 27 m mean depth (mean ± SE: 15.0 ± 1.64 cm SL, n = 82) and the 36 m mean depth (16.2 ± 1.36 cm SL, n = 98) (Tukey's test,

Table 1. Summary of conch observations on Transects 1–6 collected southwest of Puerto Rico (Fig. 2) using an underwater camera-sled system during July and August 2018

Transect	All queen conch (number)	Density (ha^{-1})	Mean shell length (cm)	Egg masses (number)	Mean depth (m)	Area (ha)
1	66	56.3	16.0	1	26.6	1.17
2	32	36.6	16.4	6	26.0	0.88
3	9	14.70	19.9	5	27.6	0.61
4	110	127.91	16.5	19	36.2	0.86
5	2271	2988.1	15.3	2	28.7	0.76
6	44	62.0	20.9	17	40.4	0.71

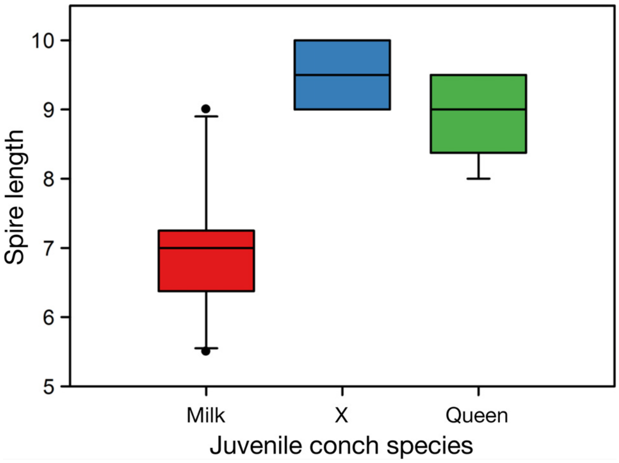

Fig. 5. Relative spire lengths of reference juvenile milk conch (Milk), reference juvenile queen conch (Queen), and juvenile conch from the field transects (X). Each box contains the interquartile range and the median (horizontal line). Vertical lines with 'whiskers' bound the minimum and maximum values; points outside the whiskers are outliers (>1.5× interquartile range). Spire length is described in Fig. 4. Measurements are relative and unitless

Table 2. Parameter values from general linear model analysis of spire length as a function of juvenile conch species (queen: reference queen conch; milk: reference milk conch; X: juvenile conch from video transects). Spire length estimates for queen and X did not differ significantly (Tukey's test, $p = 0.510$), whereas both queen and X estimates were significantly longer than that of milk (Tukey test, $p < 0.001$)

Parameter	Estimate	SE	*t*	p
Intercept (milk)	6.95	0.23	31.65	<0.001
Queen	2.00	0.31	6.44	<0.001
X conch	2.55	0.29	8.87	<0.001

$p > 0.2$), but both groups were significantly smaller than conch in the deepest area (41 m) (20.8 ± 1.26 cm SL, $n = 28$) (Tukey test, $p < 0.005$).

3.4. Depth and habitat association

For relative density, the best-fitting model (weighted probability: 0.958) was Model 5, with depth, stage, and depth × stage interaction (Table 3). All other models had weighted probabilities of <0.001. Model 5 produced a significantly better fit than other models, including the null model (likelihood ratio test, $p < 0.001$). Because of the interaction effect, comparisons of counts between depth strata were made separately for adults and juveniles.

Adult queen conch were at greatest relative density (0.0035) at the 36 m mean depth (Tukey's test, $p < 0.0005$) and at lower density in the 27 and 41 m depths (0.0008 and 0.0011, respectively; Fig. 8). In contrast, the density of juveniles was highest in the shallowest depth, 27 m (Tukey test, $p < 0.005$; Fig. 8). Relative abundance of all conch was greatest in the 27 m mean depth when juveniles ($n = 5076$) were included (Fig. 8).

The heatmap of habitat preference (Fig. 9) shows that sand–sand was the most common habitat, followed by sand–rubble, algae–rubble, algae–sand, and sand–seagrass. Less preferred habitats included coral–sand, algae–coral, coral–sand, and rubble–coral. Queen conch were rarely observed in any other habitat combinations. Still images showed queen conch mating as well as depositing eggs, and 50 queen conch egg masses (Fig. 10).

3.5. Distribution along transects

Numbers of conch observed on Transects 1–6 ranged from 2 to 2271 (Table 1, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m750p065_supp.pdf). Density estimates among transects ranged from 14.7 to ~3000 ha^{-1} with a mean of 51.4 ha^{-1} (Table 1). The numbers of conch within individual sub-transects varied greatly along each transect (Fig. S1). A total of 4971 juveniles were observed on Transect 5 (Fig. S2). Peaks in abundance reflected aggregations between patches of low density in Transects 2 (mostly adults) and 3 (mostly larger conch). At a boat speed of 2–3 knots (1–1.5 m s^{-1}), these conch 'aggregations' were separated by about 1500–2250 m. This is a crude approximation, however, due to variations in boat speed and assignment of images to sub-transects.

4. DISCUSSION

Our data represent one of the first surveys of queen conch at (mesophotic) deeper depths in the Caribbean. Our major findings included the discovery of queen conch nursery habitats as well as spawning grounds at depths ranging from 24 to 45 m. Average queen conch densities of 51.4 ind. ha^{-1} were higher than the threshold for an Allee effect (Stoner & Ray-Culp 2000, Gascoigne & Lipcius 2004), although lower than the mean density (210.7 ind. ha^{-1}) that we observed using the same methods in shallower water (Cruz-Marrero et al. 2020). Conch in the deepest (41 m) mean depth were significantly larger than those in shallower depths

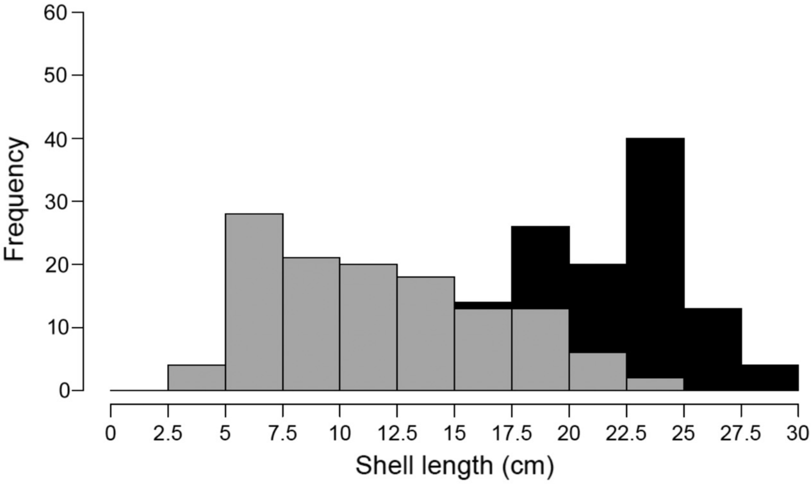

Fig. 6. Shell length of measured queen conch observed on Transects 1–6, grouped into juveniles (gray) and adults (black)

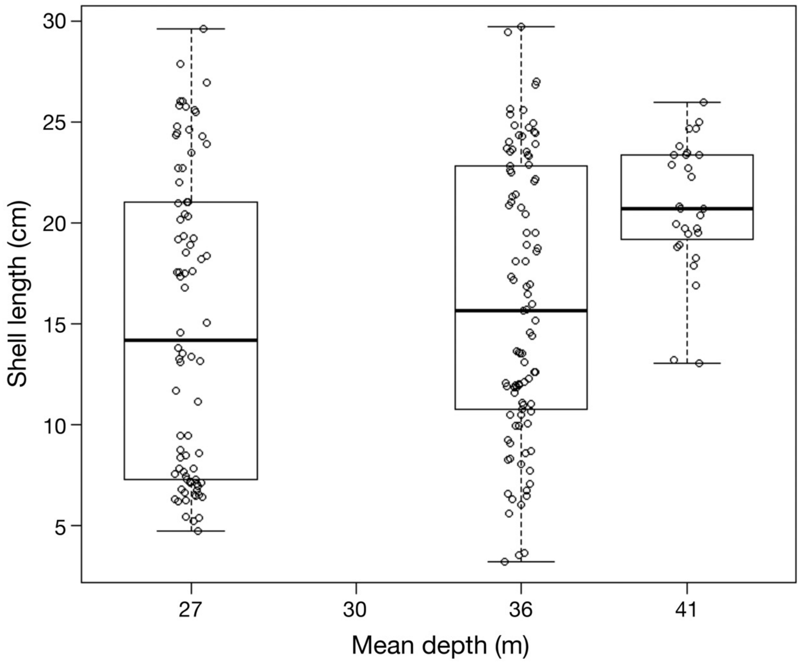

Fig. 7. Queen conch shell length by mean depth. Circles represent individual queen conch values (jittered for clarity). Dark horizontal line: median; upper whisker: maximum value; lower whisker: minimum value

Table 3. Information theory analysis of queen conch counts. AIC: Akaike's information criterion; AICc: corrected AIC; dAICc: difference in AICc from the best model (Model 5); weight: weighted probability of each model being the best fit to the data

Model	Factors	df	AIC	AICc	dAICc	Weight
1	Intercept only	1	1377.444	1377.517	215.9516	0.0000
2	Depth	2	1320.892	589.465	159.474	0.0000
3	Stage	3	1224.576	601.551	63.2577	0.0000
4	Depth + stage	3	1167.590	561.461	6.2723	0.0416
5	Depth × stage	4	1161.565	540.793	0	0.9584

(Baker et al. 2016, Cruz-Marrero et al. 2020). The relative abundance of juvenile queen conch was highest at the shallowest (27 m) mean depth, whereas the proportion and number of newly mature and adult queen conch were highest at the 36 m mean depth. Conch were most commonly observed in the sand–rubble–algae habitat combinations, which differed from previous mesophotic surveys where conch were most common in rhodolith reef habitat (Garcia-Sais et al. 2012).

The deep-water (mesophotic) zone of the west Puerto Rico Shelf is topographically variable and subject to strong currents and wind conditions. The deep-water (mesophotic) habitat in Puerto Rico has been previously characterized by Garcia-Sais et al. (2012), who described its primary habitats (sand, patch reefs with sand, colonized pavement, rhodolith reef, and rocky wall). Our research was focused on areas with mainly soft sediments due to our equipment specifications and cable limitations. The habitat categories that we used differed from those of previous studies, as sand, sand–rubble, algae–rubble, and sand–seagrass combinations were more prevalent in our study. We observed queen conch mating and egg deposition, including 50 queen conch egg masses similar to those found by Garcia-Sais et al. (2012). More importantly, we observed an aggregation of queen conch juveniles on Transect 5 that were apparently moving en masse while grazing in a fine layer of algae in soft sediment, similar to those observed in shallower depths (Stoner et al. 1988). These observations indicate that juvenile queen conch nursery habitats occur at depth, not just in shallow areas, and that these juveniles also form aggregations, similar to 'waves' in shallow habitats of the Bahamas (Stoner et al. 1988, Stoner & Lally 1994).

The size structure of deep-water conch differed from conch observed in the photic zone. Baker et al. (2016) and

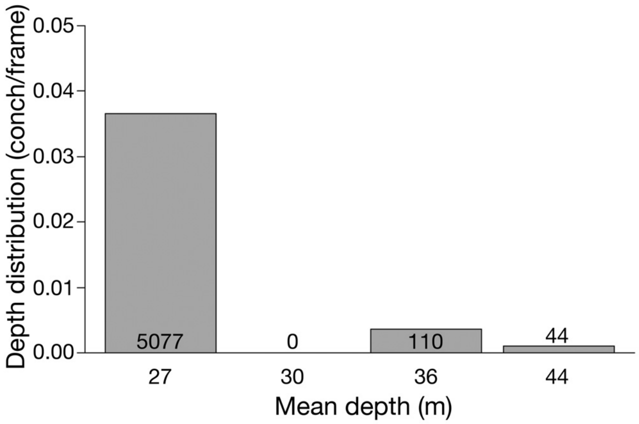

Fig. 8. Queen conch observations by mean depth. Bar height represents relative proportion of conch versus images counted. Numbers in bars: sample size. No queen conch were observed at the 30 m depth

Cruz-Marrero et al. (2020) observed similar composition in size classes of conch in the photic zone, with immature conch being the most abundant in both of those surveys. Similarly, juvenile conch were most abundant in the deep-water region, with densities up to 300 ind. ha^{-1}. Deep-water conch observed by Garcia-Sais et al. (2012) were adults with length ranging from 20 to 28 cm. Previously, juvenile conch were only observed inhabiting shallow settlement and nursery habitats before migrating to deeper spawning grounds (Appeldoorn & Baker 2013, Stoner et al. 2018).

Deep-water habitats previously acted as refugia from fishing and physical disturbances for various species that are typically abundant in shallower habitats (Semmler et al. 2017, Garcia-Hernandez et al. 2018, Rocha et al. 2018). Though these deeper locations were once considered pristine, deep zones are also currently exposed to fishing, habitat loss, invasive species, and climate change (Loya et al. 2016, Semmler et al. 2017, Vaz et al. 2022). Unfortunately, our observations showed signs of fishing activity, as evidenced by multiple observations of adult conch with the typical shell damage when fishers remove the conch from its shell (Fig. 11). Further research is necessary to understand the contribution of deep-water conch to Puerto Rico's metapopulation and fishable stocks.

Our observations of queen conch fishing were apparent across all transects within the open Puerto Rico and EEZ zones. On multiple occasions, we had to change our transect location to avoid encounters with divers and their boats, even though fishing for queen conch using SCUBA at depths greater than 30 m constitutes a potential health risk for divers (Nord et al. 2019). Our project results provide unique information about queen conch population densities in deeper areas and habitat preferences. The observations of this project could be used in future projects to help understand the connectivity of deeper queen conch with shallow-water populations (Stoner & Appeldoorn 2021, Vaz et al. 2022). This project presents evidence of reproductive behavior in deep areas, including egg masses and juvenile aggregations (Garcia-Sais et al. 2012, Boman et al. 2021, Vaz et al. 2022). A change in the management of fishing practices for queen conch stocks in deep areas is urgently needed.

The camera sled provided important new information about queen conch in deep areas. Working with heavy equipment in deep water and strong seas presented challenges, including equipment malfunction, collision of the camera sled with the seafloor, and

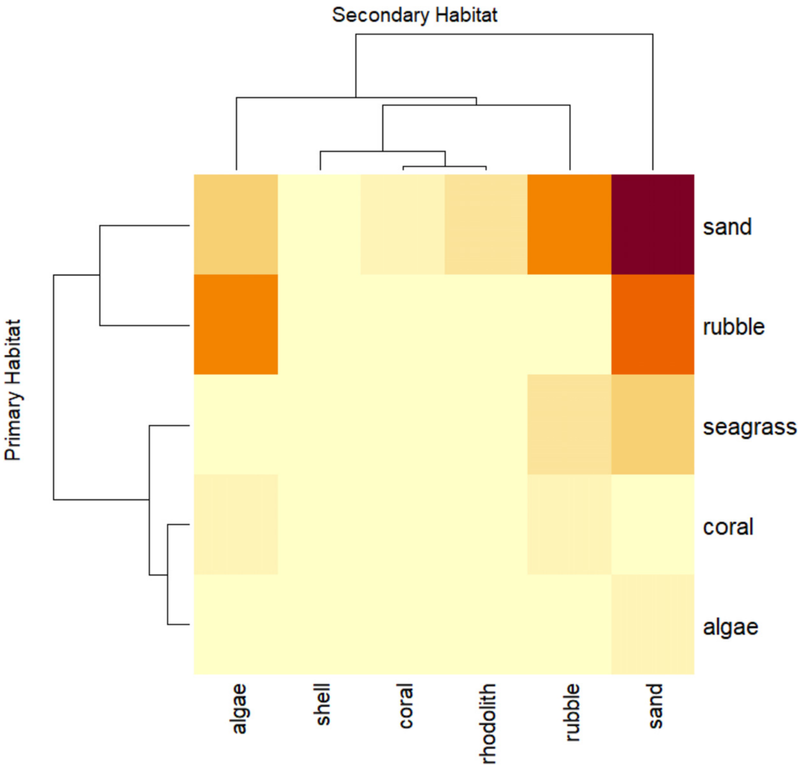

Fig. 9. Hierarchical cluster of queen conch juvenile abundance by combinations of primary and secondary habitat types. Dark colors: high values where conch were most commonly found; light colors: low values

Fig. 10. Queen conch depositing egg mass. Red dots: 10 cm lasers

Fig. 11. Evidence of queen conch fishing activity in the deeper area. The circle indicates shell damage done by a fisher when extracting the animal's soft tissue. Red dots: 10 cm lasers

entanglement as well as occasionally towing the sled over a steep dropoff. Density estimates were approximations due to variations in boat speed and GPS malfunctions affecting the assignment of images to subtransects. Equipment modifications were needed to survey depth zones deeper than 45 m.

We observed conch behavior and multiple juvenile queen conch aggregations at average depths of 30 m, which are unique to this study. Moreover, the still images are a permanent record that can be useful for other types of research, such as documenting the abundance of giant barrel sponges and other sessile or sedentary species. At present, the results of this study provide the only available information concerning the deep-water queen conch stocks in Puerto Rico and enhance our understanding of this species. We recommend that the management of queen conch consider both the presence and role of deeper subpopulations and the impacts of fishing on these potential refugia.

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