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The potential of marginal coastal nursery habitats for the conservation of a culturally important Caribbean marine species

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Abstract

Aim: Identifying the potential of marginal habitats for species conservation is of key importance when their core high-quality habitats are under substantial disturbances and threats. However, there is currently a knowledge gap on how useful marine marginal habitats may be for conserving endangered marine species. Here, we investigate the potential of groundwater-fed coastal areas for the conservation of the queen conch, an economically and culturally important marine gastropod.

Location: The inlet of Xel-Há, typical of groundwater-fed coastal areas widely distributed along the Yucatan Peninsula coast in Mexico and partially protected by a network of marine protected areas.

Methods: We tracked 66 queen conchs (*Lobatus gigas*) using acoustic telemetry over a period of 3.5 years. We investigated for ontogenetic niche shift using a network analysis and by modelling their growth.

Results: The queen conchs exhibited the same ontogenetic niche shift required to complete their life cycle in this marginal habitat as they do in offshore core habitats. A total of 33 individuals departed the inlet and migrated from shallow groundwater-affected nursery grounds to deeper marine habitats more suitable for breeding aggregation.

Main conclusions: As the broad-scale movement behaviour of queen conch in this inlet is similar to that observed on the overfished core habitats, our findings suggest that groundwater-fed coastal areas should be included in conservation planning for an effective management of this species within a network of marine protected areas.

KEYWORDS
connectivity, dispersal, fisheries, marine protected area, movement ecology, sub-optimal habitats

1 | INTRODUCTION

Identifying key habitats for commercially exploited species is highly important for their conservation as large populations usually thrive in high-quality habitats (Kawecki, 2008; Pulliam, 2000). Those highly productive areas are often overexploited to the point that their populations of many species are close to collapse (Ceballos et al., 2000; Halpern et al., 2008; Imhoff et al., 2004; Jackson et al., 2001). In contrast, marginal habitats are of lower quality and often characterized by a lower density of individuals due to the environmental conditions being near the boundaries of the species' ecological niche (Kawecki, 2008; Pulliam, 2000). Despite being of lower quality, marginal habitats can play a role in the persistence of species in situations where the core habitat is under substantial disturbance and where most of the individuals inhabiting this key area are under threat of disappearing (Wintle et al., 2019). Such marginal habitats can offer protection against threats such as dramatic stochastic environmental variations (e.g., floods for birds, Jankowiak & Ławicki, 2014 and lagomorphs, Crawford, Nielsen, & Schauber, 2018; groundwater seeps during drought conditions for freshwater fishes, Vrdoljak & Hart, 2007) but also habitat degradation by human activities (e.g., roadside grassland for native bees, Hopwood, 2008). However, this type of protection is only efficient on the long term if the individuals are able to emigrate from marginal habitats to repopulate the core habitats (Kawecki, 2008; Kerley, Kowalczyk, & Cromsigt, 2012). It is, therefore, important to gain an understanding of the movement and dispersal abilities of threatened species to evaluate the potential of a marginal habitat for species conservation.

Similar to terrestrial ecosystems, high productivity marine areas are often overexploited by fisheries to unsustainable levels (Halpern et al., 2008; Jackson et al., 2001). Compared with terrestrial ecosystems, our knowledge of marine marginal habitats remains limited and is often only documented in the context of predator–prey interactions (e.g., for sea turtles, Heithaus et al., 2007; dolphins, Heithaus & Dill, 2002), interindividual competition (e.g., for shrimps, Duarte, Flores, Vinagre, & Leal, 2017; rockfishes, Larson, 1980) or in an evolutionary perspective (e.g. seaweed of genus *Fucus*, Coyer et al., 2006; microconchid tubeworms, Zatoń, Vinn, & Tomescu, 2012). Overall, a knowledge gap remains on how marine marginal habitats could contribute to the conservation of endangered marine species, for example by allowing the repopulation of disturbed core habitats by individuals migrating from protected marginal habitats.

The queen conch (*Lobatus gigas*) is a prominent example of a commercially and culturally important species that has been overexploited over most of its geographical distribution area (Acosta, 2006). The queen conch is one of the most important fishery resources in the Caribbean region, but populations have been in decline for more than two decades (Theile, 2001). Protection measures for the queen conch are currently unable to compensate for exploitation by fisheries in the core areas (Acosta, 2006). The queen conch life cycle includes a 3–5 weeks larval stage, followed by recruitment in a shallow (1–3 m depth) nursery habitat (often associated with seagrass beds, Stoner, 2003). Maturing individuals exhibit an ontogenetic niche shift, tending to segregate from the juveniles and to migrate from shallow nurseries grounds to a range of deeper habitats types (e.g. coarse-sand and rubble/coarse-sand habitats, Doerr & Hill, 2013; Glazer & Kidney, 2004; Stoner & Schwarte, 1994). The queen conch is also observed outside its optimal niche in habitats such as groundwater-fed coastal areas which are characterized by large variations in salinity and dissolved oxygen concentration (i.e. stressful for stenohaline species) and which are considered to be marginal for species typically
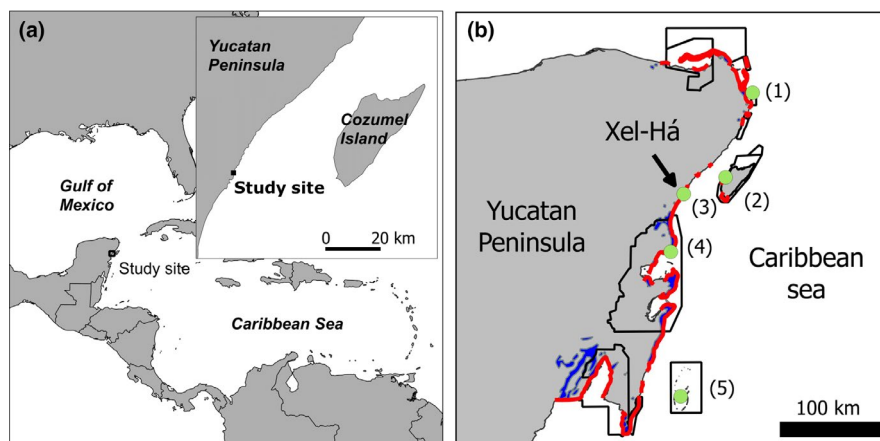

FIGURE 1 (a) Location of Xel-Há inlet (Yucatan peninsula, Mexico) in the Caribbean Sea, (b) Geographical distribution of the groundwater-fed coastal habitats (in red) along the north-eastern coast of the Yucatan Peninsula. The black polygons indicate the marine protected areas, the blue polygons the presence of freshwater, brackish lakes or lagoons located less than 20 km from the coastline and the green dots the locations in which the presence of queen conch has been documented with from North to South: (1) Isla Mujeres (Tello-Cetina, Rodríguez-Gil, & Rodríguez-Romero, 2005), (2) Cozumel Island (Lozano-Álvarez & Briones-Fourzán, 2007), (3) Xel-Há inlet (Stieglitz & Dujon, 2017, this study), (4) Sian Ka'an Biosphere Reserve (Mazzotti et al., 2005) and (5) Banco Chinchorro (Tello-Cetina et al., 2005). The location of lakes and lagoons was obtained from Gondwe et al. (2010)

found in fully marine habitats (Dujon, Stieglitz, Amice, & Webber, 2019; Stieglitz & Dujon, 2017; Stoner, 2003). Along the Yucatan Peninsula coastline (Mexico), an extensive underground cavern system channels water to coastal lakes, lagoons and submarine springs over the majority of the north-west Yucatan coast (Figure 1) and which accounts for >99% of the freshwater input in the area (Back, Hanshaw, Pyle, Plummer, & Weidie, 1979; Beddows, Smart, Whitaker, & Smith, 2007; Perry, Velazquez-Oliman, & Marin, 2002). This coastline, mainly composed of groundwater-fed habitats, is inhabited by a population of queen conchs commercially exploited since 1950s (Posada et al., 2006) and is locally protected by a network of marine protected areas (Figure 1b). Yet relatively little is known on how groundwater-fed habitats along this coast impact the ecology of this species in terms of habitat usage and connectivity. Specifically, while groundwater-affected areas can be suitable for the growth of juveniles, with a foraging behaviour adapted to the marginal conditions (Dujon et al., 2019; Stieglitz & Dujon, 2017), it is to date not documented if adult individuals emigrate from those marginal habitat to marine areas more suitable for breeding aggregations a prerequisite to adult and larval spillover in the core habitats (Kough et al., 2019; Stoner & Ray-Culp, 2000). This information is of key importance as ecological spillover from strongly enforced marine protected areas has been shown, in certain cases, to be efficient in repopulating habitat depleted by fisheries (Grüss, Kaplan, Guénette, Roberts, & Botsford, 2011; Kough et al., 2019). Here, we investigate whether queen conchs

inhabiting groundwater-fed marginal habitats exhibit an ontogenetic niche shift similar to what is observed in the core habitat, and if these populations are connected to offshore core habitats. Using acoustic telemetry, over a period of 3.5 years we tracked queen conchs in the inlet of Xel-Há, a representative site of groundwater-fed coastal habitats in the region (Gondwe et al., 2010; Perry et al., 2002; Figure 1b). We hypothesize that the queen conchs either remain resident in the inlet, which would suggest this type of marginal habitat is a population sink for this species (Kawecki, 2008), or alternatively depart from the inlet to reach habitats favourable for breeding. We then illustrate the potential utility of groundwater-fed marginal habitats for the conservation of this species. Our results have large-scale implications for its conservation, considering that groundwater-fed coastal habitats and associated queen conch nursery grounds are widely distributed along the north-eastern coast of the Yucatan Peninsula, some of which are currently included in a network of marine protected areas.

2 | METHODS

2.1 | Study site

The study was carried out in the small coastal inlet Xel-Há, on the northeast coast of Mexico's Yucatan Peninsula, which is part of the Mesoamerican reef system (20.32°N, 87.36°W; Figure 1a). Typical
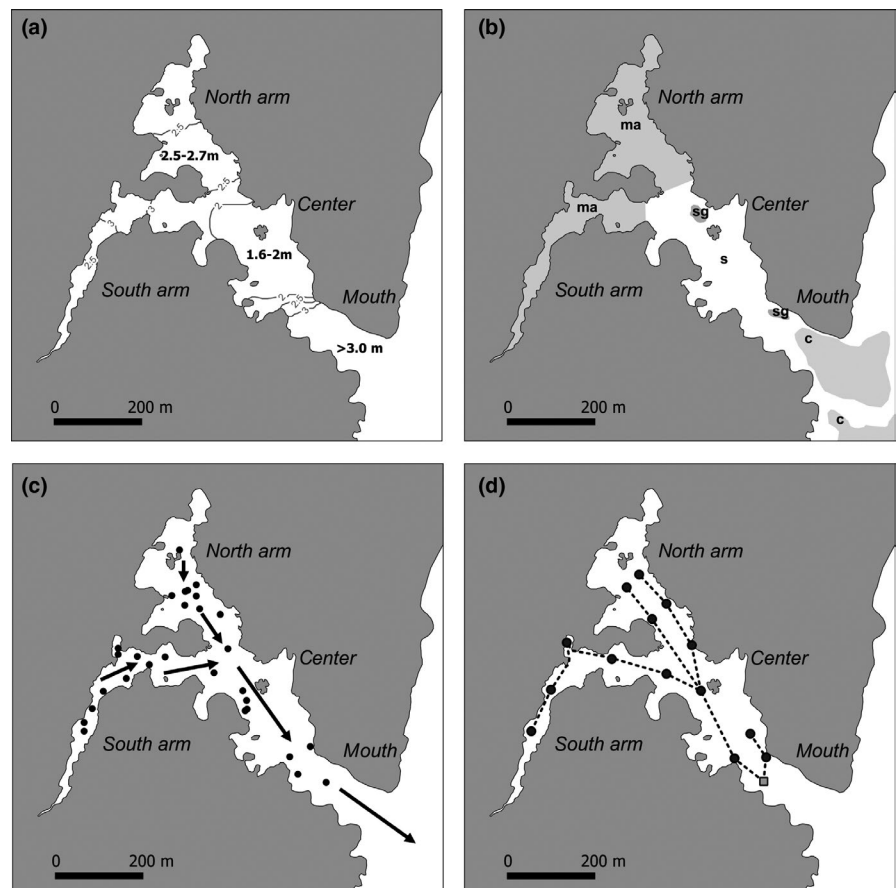

FIGURE 2 (a,b) Bathymetry and simplified habitat maps of the study site (ma, macroalgae; sg, seagrass; c, coral reef; s, bare sand). (c) Release locations of the tagged queen conchs (black dots) and general direction of the queen conch migration towards the mouth of the inlet and the offshore habitats. (d) Receiver network in the inlet. Black dashed lines represent the vertices of the minimum cost tree connecting the receivers (dark grey dots). The grey square represents the receiver defined as the root of the tree. Figure modified from Stieglitz and Dujon (2017)

for this coastline, this inlet was formed by groundwater carbonate dissolution (Back et al., 1979; Perry et al., 2002; Stoessell, Ward, Ford, & Schuffert, 1989; Figure 1). Connected to the Caribbean Sea by a 100 m wide channel, the inlet is ~1 km long, covers an area of ca. 110 000 m^2 and has a maximum depth of 3.5 m (Stieglitz & Dujon, 2017, Figure 2a). A persistent inflow of low-salinity groundwater maintains a permanent thermohaline stratification throughout the year, with salinity on the bottom ranging from 10 to 35 (Back et al., 1979; Stieglitz & Dujon, 2017). The bottom substrate is mostly sandy, with small and large isolated rocks, bare sand, extended macroalgal mats (*Padina* sp., *Halimeda* sp., *Penicillus* sp., *Amphiroa* sp., *Acanthophora* sp., *Caulerpa* sp. and *Dictyota* sp.; Peel & Aldana Aranda, 2012a, 2012b), and isolated *Thallasia testudinum* seagrass beds. While bottom cover is patchy, generalized broad-scale habitats can be defined (Figure 3b). The inlet is inhabited by a population of mostly juvenile queen conchs with new individuals recruiting mainly between March and April at comparable levels to the other nursery grounds in the Caribbean sea (Peel & Aldana Aranda, 2012b, 2012a; Valle-Esquivel, 1998). The habitat is considered to be marginal for this stenohaline species, principally due to persistent substantial input of fresh groundwater, resulting in considerable stratification and oxygen stress in bottom layers (Dujon et al., 2019; Stieglitz & Dujon, 2017; Stoner, Mueller, Brown-Peterson, Davis, & Booker, 2012). One of the main consequences of dissolved oxygen variations is a near-complete cessation of grazing activity during the early day of the hours and thus an alteration of the foraging behaviour (Dujon et al., 2019). There is no fishing of queen conchs in the inlet, which is part of an eco-tourism park, fenced, and patrolled by security guards. In addition,

the immediate surroundings of the inlet are difficult and dangerous to access from the sea because of the presence of emerging coral reefs and almost permanent strong waves, ensuring a high level of protection of the site.

2.2 | Animal tagging

Queen conch specimens were collected by diving or free diving from four locations (one in each of the four regions of the inlet, Figure 2c). Sites were randomly predetermined on a map to avoid bias due to, for example, to accessibility or variation in conch density. Individuals were searched for in a circular pattern around these locations (Stieglitz & Dujon, 2017). A total of 66 animals (see Data S1) were tagged with an individually coded VEMCO V7 (*n* = 26, battery life expectancy of ca 630 days) or V9 (*n* = 40, battery life expectancy of ca 830 days) transmitter (see Stieglitz & Dujon, 2017, for the full attachment protocol). Over the study duration, six tagged individuals were recaptured, and the tags redeployed on a different individual (see Data S1). Each tagged animal was released within a few tens of metres from where it was caught. In addition, the syphonal length of each conch was measured from the apex of the spire to the end of the syphonal canal, and shell lip thickness was determined following methods described by Peel and Aldana Aranda (2012b). The size distribution of tagged animals (70 – 235 mm syphonal length) reflects well the size distribution in the entire population (Peel & Aldana Aranda, 2012a, 2012b). Here, we separate individuals with a lip thickness <l mm from individuals with a shell lip thickness ≥1 mm to test for the potential effect of early lip development.
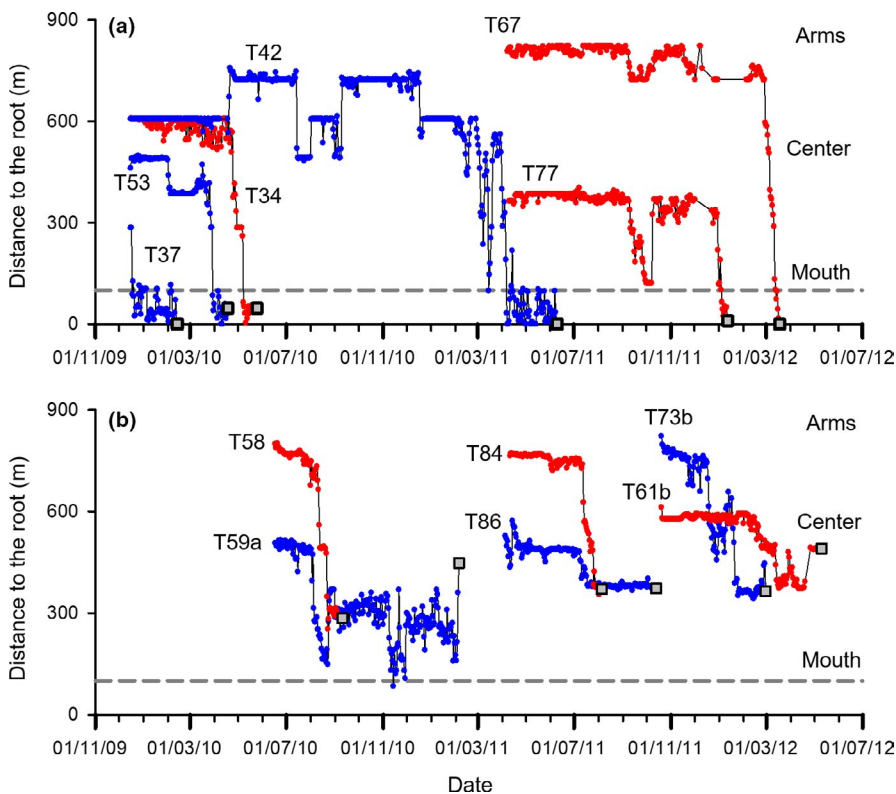

FIGURE 3 (a) Daily average distance to the root for six queen conchs out of 33 that departed the inlet over the study duration. (b) Daily average distance to the root for six queen conchs that remained resident to the inlet up over their tracking duration. A rapid decrease in the distance to the root indicates the animal is migrating towards the mouth of the inlet. On both plots, the grey horizontal dashed line represents the 100-m threshold used as criterion to determine departure. The grey squares represent the day each animal was detected for the last time. On a, animals were last detected just before their departure from the inlet, and on b, animals were last detected at the end of the tag battery life

An array of 15 acoustic receivers (VEMCO VR2W) installed throughout the northern, central and southern (mouth) sections of the inlet recorded the transmissions (Figure 2d). The permanent moorings consisted of steel rods and concrete blocks sunk into the sediment. Receivers were located in 1.5 to 3.5 m water depth, deployed approximately 0.5 m above the bottom. Receiver locations were optimized for coverage (large overlap), to avoid topographic shading from rocks where possible, but were constrained by tourism operations in this dive ecotourism park (Stieglitz & Dujon, 2017).

2.3 | Quantification of animal movement

We used a network analysis to quantify the movement of queen conchs in the inlet (see Minor & Urban, 2008). We first computed the minimum cost tree connecting all receivers to a root. We defined the root as the receiver located the closest to the mouth of the inlet (Figure 2d), whereby we ensured that a link connecting two receivers did not cross the shoreline (Figure 2d). This approach allows to take in account the morphological specificities of the study site and the presence of multiple nonlinear arms in the inlet in order to have a more accurate estimate of the distances travelled by the queen conchs. After building the tree we subsequently computed, for each receiver, the distance D as the shortest cumulative length of the links connecting it to the root. Then, for each queen conch we calculated a daily average distance to the root as

$$\text{Daily average distance to the root (m)} = \frac{\sum_1^k (D_i * N_i)}{\sum_1^k N_i} \qquad (1)$$

with k the number of receivers in the network which detected the queen conch during a given day, D_i the distance to the root for the ith receiver in this subset of k receivers, and N_i the number of detections recorded for that ith receiver on that given day. The average daily distance to the root ranged between 0 m when the animal was only detected by the root receiver and 823 m when the queen conch was only detected by the receiver located in the extremity of the southern arm (Figure 2d). In addition, for each individual, we recorded the initial daily average distance to the root on the day they were released in the inlet and on the day they were detected last.

2.4 | Determination of departure from the inlet and status classification

Using the daily average distance to the root, we determined whether each queen conch departed from the inlet over the study duration. A decrease in the average daily distance to the root indicated that an individual was moving closer to the mouth of the inlet. Departure from the inlet was characterized by a sharp decrease in the daily average distance to the root to <100 m followed by a complete lack of detections that lasted up to the end of the study (Figure 3a). For each

queen conch that departed the inlet, we calculated the time elapsed between the day the individual was tagged and the date it departed the inlet. Queen conchs exhibiting no variation in the daily average distance to the root over long period of time followed by a complete loss of detections were assumed to have died (Appendix S1). The status of living individuals (i.e. still detected as moving) for which the detection was lost inside the inlet was classified as "unknown". All other living queen conchs that did not leave the inlet and were still detected at the end of the study or at the time the individual was collected were considered to be resident over the tracking duration (Figure 3b).

2.5 | Growth model

To account for the growth of the animals over the study duration, we used a von Bertalanffy equation ($L\infty$ = 278.73 mm and K = 0.71 year^{-1}) established for Xel-Há to estimate the shell size on the day of the last detection (Peel & Aldana Aranda, 2012b). The calculations were based on the syphonal length measured on the day the queen conchs were tagged.

2.6 | Statistical analyses

Mean values throughout this manuscript are reported as Mean ± SD, and the range as minimum and maximum. Means between two groups were compared using a nonparametric Wilcoxon test, as were mean siphonal lengths between two periods of time. Correlations between variables were tested using the Pearson correlation test. A Watson's goodness-of-fit test was performed to determine whether the distribution of monthly departure was deviating from a uniform circular distribution. All statistical analyses were performed using R software version 3.3.2. (R Development Core Team, 2013).

3 | RESULTS

The network recorded a total of 3,925,868 queen conch detections. The average tracking duration was 311.0 ± 209.0 days (range: 53–757). On average, queen conchs were detected on 93.8 ± 10.2% (range: 63.9–100) of days during their tracking duration. The overall average number of detections per day for the 66 queen conchs was 182.5 ± 218.9. A total of three individuals were assumed dead and excluded from the subsequent analyses (see Appendix S1). Detailed statistics for each queen conch are provided in Data S1.

3.1 | Movement patterns

A total of 33 queen conchs departed from the inlet between February 2010 and May 2013 (14 conchs tagged as juveniles, 19 tagged as sub-adults). Thirty animals remained resident (24 conchs tagged as juveniles,
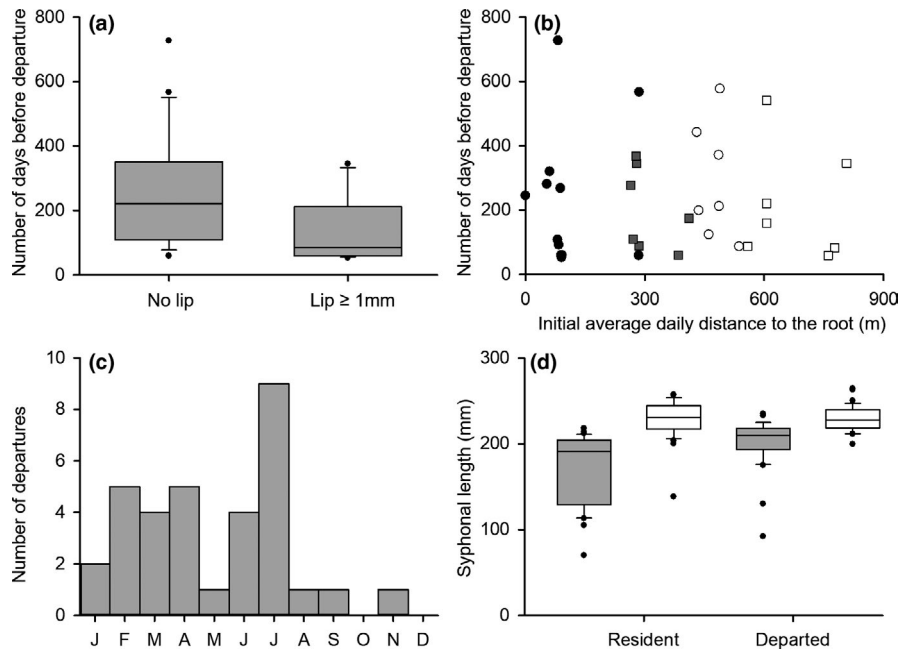
FIGURE 4 (a) Time to departure from the inlet for the queen conchs tagged as juveniles or subadults at the start of the study. Overall, subadults departed from the inlet faster than the juveniles. (b) Time to departure as a function of the daily average distance to the root on the day of release in the inlet (white squares: individuals released in the southern arm; grey squares: individuals released in the northern arm; white circles: individuals released in the centre of the inlet; and grey circles: individuals released at the mouth of the inlet). No relationship is observed. (c) Histogram of the monthly number of departures. Most queen conchs (91%) depart between January and July. (d) Syphonal length of the tagged queen conch on the day of release (grey box plots) and on the day their last detection was recorded (white box plots). Individuals were split into two groups, those which were resident to the inlet (on the left) and those that departed (on the right)

eight as subadult and one of undetermined life stage). It took up to two weeks for queen conchs to exit the inlet when they started their migration from the extremity of the inlet arms. This corresponds to a minimum straight-line distance of at least 60 m covered per day. On average, individuals tagged with a lip ≥ 1 mm departed from the inlet earlier compared to those tagged with no lip (Wilcoxon's test, $p < .001$, Figure 4a). Individuals tagged without a lip remained in the inlet for an average of 320.1 ± 161.6 days (range: 89–577) while individual tagged with a lip ≥ 1mm remained for an average 173.1 ± 169.1 days (range: 53–727, Figure 4a). We found no evidence that the release location in the inlet (i.e., the initial average daily distance to the root) influenced the time to departure (Pearson correlation test, $r = -.01$, $p = .94$, Figure 4b) suggesting the departure pattern is not random. All conch departures from the inlet were observed all year round except October and December, with nine individuals departing in July (Figure 4c), with further evidence that this pattern was not random (Watson's goodness-of-fit test, $p < .01$). Over the study duration, an overall unidirectional movement from the head of the inlet towards the mouth was almost consistently observed, and more importantly, none of the individuals who departed the inlet returned at a later stage as evidenced by the total lack of detections once they departed (Figures 2a and 3).

3.2 | Estimated size at departures

The syphonal length of the queen conchs which departed the inlet increased significantly from an average of 202 ± 29 mm (range:92–235)

on the day they were tagged to a predicted average of 230 ± 15 mm (range: 200–264) on the day they departed the inlet (Wilcoxon's paired test, $p < .001$, Figure 4d). This suggests that all the individuals that departed the inlet were at least subadults. Similarly, the syphonal length of the resident individuals increased from an average of 174 ± 41 mm (range: 70–218) to a predicted average of 227 ± 24 mm (range: 138–257) on the last day of the study (Wilcoxon's paired test, $p < .001$, Figure 4d). At the end of the study there was no significant difference between the average syphonal length of the tagged queen conch that departed the inlet and those that remained inside (Wilcoxon's test, $p = .99$). A total 10 out of 11 subadult individuals with a lip > 5 mm at the time of tagging departed the inlet over the study duration with the 11th individual being located close to the mouth of the inlet.

4 | DISCUSSION

4.1 | Main findings

We found that the queen conchs where able to complete the same ontogenetic niche shift in groundwater-fed reduced-salinity habitats as in their optimal and fully marine habitat. Over the study period, slightly more than half (52%) of the tagged queen conchs departed the inlet and migrated from this habitat suitable for juvenile growth to marine habitats more suitable for breeding. Based on our no-movement criteria, mortality rate was relatively low among the

tagged queen conchs indicating the inlet is efficient at protecting the individuals and is likely not a sink for the population.

4.2 | Performance of the minimum cost tree approach

Our approach using the average daily distance to the root as main metric succeeded in capturing the overall movement of these slow-moving animals. Overall, the movement of queen conchs departing the inlet was directed from the bottom of the inlet towards the mouth (often associated with a rapid decrease in the daily average distance to the root). Some local small-scale variations (typically < 10 m per day) within the network are consistent with the queen conchs' foraging movement over a period of time of a few days (compared to the minimum of 60 m covered per day while migrating, see Dujon et al., 2019; Stieglitz & Dujon, 2017). A total of 12 individuals were classified as "unknown" because the detection for those individuals was lost from the detection array while still being detected as moving indicating they have not deceased. It is likely those individuals moved outside the optimal detection coverage of the network, as the whole inlet was not completely covered because of acoustic shading due to rocks (Huveneers et al., 2016). The temporary loss of detection during a day or two may be due to burying (Hesse, 1979). Our approach succeeded at capturing the queen conchs migratory movement pattern, though does not aim to resolve fine scale movement during foraging (Dujon et al., 2019; Stieglitz & Dujon, 2017). The daily detection rate of >90% for most individuals represents a large number of detections per day which ensured the daily average distance to the root was accurate and appropriate for the purpose of this study. Our approach can be applied to a range of different acoustic networks (e.g., in lakes or in riverine ecosystems) and species, as long as a minimum cost tree can be built from it. It is especially well adapted to systems with curvy arms.

4.3 | Queen conch movement and ontogeny of departure

All queen conchs who departed the inlet had a predicted syphonal length between 200 and 264 mm, indicating significant growth during the period the individuals remained in the inlet. This is consistent with observations in marine nursery grounds (Boman et al., 2018; Stoner, Davis, Davis, & Booker, 2012; Tewfik, Babcock, Appeldoorn, & Gibson, 2019). The majority of individuals with a lip thickness >5 mm at the time of tagging departed the inlet. Siphonal length does not allow for the determination of sexual maturity, which is largely based on lip thickness (Boman et al., 2018; Tewfik et al., 2019). However, there is currently no reliable lip thickness growth model available for queen conchs so we were unable to determine whether the individuals who departed the inlet were sexually mature. There was no relationship between the initial release location and the time of departure, which excludes an explanation based on the geographical distance to the mouth of the inlet. Importantly, the rapid movement towards the mouth that immediately precedes almost every departure from the inlet indicates a change in the animal behaviour to a migratory state. Those results are consistent with the expected ontogenetic niche change observed in offshore core areas. Spatial segregation between juveniles and older individuals is commonly observed in queen conchs. Juveniles show a preference for moderate to dense seagrass beds and for habitats possessing the characteristics to settle and survive natural predators (Stoner, 2003). This type of seabed is mostly observed in the northern, the southern arm and the central part of Xel-Há inlet where most of the juvenile conch remains (Peel & Aldana Aranda, 2012b; Stieglitz & Dujon, 2017). The bottom of the inlet may also act as a barrier to fully marine predators, therefore enhancing the protection of the juveniles. In comparison, adults prefer coarser sediment with sparser seagrass bed to form breeding aggregations (Berg, Ward, Luckhurst, Nisbet, & Couper, 1992; Glazer & Kidney, 2004). This type of habitat is located at the mouth and outside the inlet where the adults migrated to. The extent of the queen conch breeding season varies along its distribution range, but in most locations (including Mexico), it falls into the summer months, and little reproductive activity is observed during winter (Aldana Aranda et al., 2014; Boman et al., 2018). The peak of departures observed in July, and the lower occurrence of departures during November and December is consistent with those documented seasons (Aldana Aranda et al., 2014; Boman et al., 2018). Some of the animals that remained resident over the tracking duration were close to maturity and can be expected to depart later.

4.4 | Implications of a network of marine protected areas for conservation of the queen conch and other marine species

The departure of a significant fraction of tagged queen conchs from this groundwater-fed marginal habitat suggests that this habitat is not a sink for this species (Kawecki, 2008). This suggests that groundwater-fed marginal habitats could play an important role in conserving the species and that they should be more broadly considered for inclusion in conservation planning. Modelling studies estimate that single reserves must be at least as large as the average dispersal distance for a species without contributions of individuals from elsewhere (Gaines, White, Carr, & Palumbi, 2010; Grüss et al., 2011). While completely protecting large, high-quality areas would be efficient to conserve queen conch populations (and more broadly a range of marine species), it is rarely an economically viable option as those areas also concentrate much of the economical human activities (Halpern et al., 2008). In some cases, rather than protecting a single large area, it has been advocated that a network of smaller protected areas targeting key habitats (or part of the life cycle, such as nursery grounds) and relying on spillover effects would be as efficient for conserving a species (Gaines et al., 2010; Kough et al., 2019). While it is not known exactly how far queen conchs disperse

along the Yucatan coast, a significant relationship between genetic and geographical distances exist for this species, suggesting that dispersal mostly occurs locally (Truelove et al., 2017). Therefore, a network of well-enforced reserves locally connected by adult and larval spillover is likely to be a valuable alternative to larger reserves (Gaines et al., 2010; Kough et al., 2019). This management approach was for example recommended for improving the sustainability of the Bahamian queen conch fisheries (Kough et al., 2019). There is currently a network of marine protected areas (including our study site Xel-Há, see Figure 1) encompassing groundwater-fed marginal habitats along the eastern Yucatan Peninsula coast. Since 2018, in the southern part of the peninsula, along approximately 450 km of coastline, the removal of queen conchs is prohibited during February and from May to November in designated areas (Diario Oficial de la Federación, 2017). This encompasses the period when most of sthe adult queen conchs are departing from their marginal nursery habitat. Similar to Xel-Há, the Sian Ka'an Biosphere Reserve (6,510 km^2) receives important amounts of groundwater (Lagomasino et al., 2015) and has several core zones designed to reduce the pressure on the main marine resources (Mazzotti et al., 2005). Overall, we suggest that the base for a network of protected marine habitats already exists. If the level of protection is maintained or expanded (i.e., by preventing the removal of juveniles, subadults and adults that have yet to breed) this network, while encompassing large area of marginal habitats, might efficiently contribute to the conservation of this species in the region through adult and larval spillover. However, further work on the quantification of population exchange will be required to fully assess the efficiency of those marine protected areas (see for example, Kough et al., 2019), or if additional protected marine habitats would be required along the coast. Further, this network of marine protected areas would likely also contribute to the conservation of a range of other commercially or culturally important species, for example fish populations (Gaines et al., 2010), hence contributing to the larger-scale management of sustainable resources to support the local population.

In conclusion, our results demonstrate that adult queen conch is able to depart from groundwater-fed marginal habitats suitable for juvenile growth and to migrate to habitats suitable for reproduction. It is therefore unlikely this habitat is a sink for this species. Overall, this study suggests that this type of groundwater-fed marginal habitat has considerable potential to significantly contribute to the recovery of this species, and therefore should be considered in conservation planning.

DATA AVAILABILITY STATEMENT
The raw data are provided as Data S1.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.