



NOAA Technical Memorandum NMFS-SEFSC-756
doi:10.25923/4ykr-1m56

ENDANGERED SPECIES ACT STATUS REVIEW REPORT: QUEEN CONCH (*ALIGER GIGAS*)

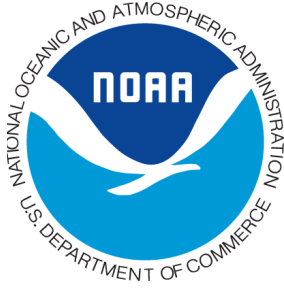
BY

CALUSA HORN, MANDY KARNAUSKAS, JENNIFER C. DOERR, MARGARET H.
MILLER, MELISSA NEUMAN, RON HILL, AND KEVIN J. MCCARTHY



U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southeast Fisheries Science Center
75 Virginia Beach Drive
Miami, FL 33149

May 2022



Endangered species act status review report:
Queen conch (*Aliger gigas*)

By

Calusa Horn, Mandy Karnauskas, Jennifer C. Doerr, Margaret H. Miller, Melissa Neuman, Ron Hill, and Kevin J. McCarthy

National Marine Fisheries Service
Southeast Fisheries Science Center
75 Virginia Beach Drive
Miami, FL 33149

U.S. DEPARTMENT OF COMMERCE
Dr. Gina M. Raimondo, Secretary

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
Dr. Richard W. Spinrad, Under Secretary for Oceans and Atmosphere

NATIONAL MARINE FISHERIES SERVICE
Janet L. Coit, Assistant Administrator for Fisheries

May 2022

This Technical Memorandum series is used for documentation and timely communication of preliminary results, interim reports, or similar special-purpose information. Although the memoranda are not subject to complete formal review, editorial control, or detailed editing, they are expected to reflect sound professional work.

NOTICE

The National Marine Fisheries Service (NMFS) does not approve, recommend, or endorse any proprietary product or material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends, or endorses any proprietary product or proprietary material herein or which has as its purpose any intent to cause directly or indirectly the advertised product to be used or purchased because of NMFS publication.

Authors and Affiliations:

Calusa Horn. NMFS, Southeast Regional Office, 263 13th Avenue South, St. Petersburg, FL 33701

Mandy Karnauskas, Kevin J. McCarthy. NMFS, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149

Jennifer C. Doerr. NMFS, Southeast Fisheries Science Center, 4700 Avenue U, Galveston, TX 77551

Margaret H. Miller. NMFS, Office of Protected Resources, 1315 East West Hwy, Silver Spring, MD 20910

Melissa Neuman. NMFS, West Coast Region, 501 West Ocean Blvd, Long Beach, CA 90802

Ron Hill. NMFS, Southeast Fisheries Science Center, 3500 Delwood Beach Road, Panama City, FL 32408

This report should be cited as follows:

Horn, C., M. Karnauskas, J. C. Doerr, M. H. Miller, M. Neuman, R. Hill, and K. J. McCarthy. 2022. Endangered species act status review report: Queen conch (*Aliger gigas*). NOAA Technical Memorandum NMFS-SEFSC-756. 138 pp. <https://doi:10.25923/4ykr-1m56>

Copies may be obtained by writing:
National Marine Fisheries Service
263 13th Avenue South
St. Petersburg, FL 33701

Supplemental Materials:
Supplemental materials are available upon request to Calusa.Horn@noaa.gov

PDF version available at www.sefsc.noaa.gov

Executive Summary

This is the status review report for queen conch (*Aliger gigas*) under the Endangered Species Act (ESA). Information and data were reviewed for approximately 40 jurisdictions through July 1, 2021. This report summarizes the best available scientific and commercial information on the species and presents an evaluation of the queen conch's status and extinction risk. Where available, we provide literature citations to review articles that provide more extensive citations for each topic.

The queen conch is a slow moving, benthic herbivore that primarily occurs in seagrass beds, sand plains, and coral reefs; their distribution is believed to be limited by the availability of algae and native seagrass detritus. The queen conch is harvested intensively throughout the Caribbean for its meat, shell, and pearls. This species is also a cultural symbol, being a significant local food source for hundreds of years. The species still occurs throughout the Caribbean, but while the total population size remains unknown, the majority of available density estimates suggest that conch populations are below minimum thresholds necessary for reproduction. Numerous lines of evidence suggest that the vast majority of conch populations have declined and are suffering recruitment failure or Allee effects¹, with evidence of ongoing declines in many populations.

The most significant threat to queen conch is overutilization (through commercial; artisanal; and illegal, unreported, or unregulated fishing) for commercial purposes. There is very little indication that regulatory mechanisms will be able to reverse this trend in the foreseeable future. Many jurisdictions have regulations that are inadequately enforced or implement regulations that use inappropriate metrics for managing the queen conch fisheries – often allowing for the legal harvest of juvenile conch. Despite current regulations, queen conch populations continue to decline and the few jurisdictions with sustainable management protocols do not yet report substantial stock recovery. The species currently suffers from low population densities and poor recruitment throughout a vast majority of its range and experiences limited larval dispersal and interrupted population connectivity. Therefore, the viability of the species is currently reliant on a handful of populations located in Cuba, Colombia (Serrana Bank), Jamaica (Pedro Bank), Nicaragua, The Bahamas (Cay Sal and Jumento/Ragged Cays), and Turks and Caicos. The higher densities recorded within these locations suggest that reproduction and recruitment is still occurring. While these jurisdictions have queen conch populations that are not experiencing Allee effects (based on adult density estimates), they operate significant queen conch fisheries, which are likely to become unsustainable within the foreseeable future (30 years). The SRT concluded that it is likely that queen conch fisheries will continue to close as populations become more depleted, poaching will likely continue or increase, and without adequate enforcement to halt illegal harvest of conch, the species will continue a downward trajectory, placing it at a moderate risk of extinction over the next 30 years.

Furthermore, the Caribbean region is likely to be impacted by climate change, and those adverse impacts, while not yet fully realized, could have devastating implications for queen conch over the next century (2100), specifically in combination with the threat of overutilization.

¹ Negative rates of per capita growth (depensation) that occur below a critical population size or density (Stoner and Ray-Culp 2000).

Table of Contents

List of Tables	vi
List of Figures	vii
Life History	1
Taxonomy.....	1
Distinctive Characteristics.....	1
Range, Distribution, and Habitat Use.....	2
Early Life Stages.....	2
Adults.....	4
Diet.....	5
Age and Growth.....	5
Reproduction	6
Fecundity.....	8
Spawning Season and Length.....	10
Spawning Density.....	14
Population Structure	16
Conch Habitat Estimate	18
Density Estimates	20
Population Abundance Estimates	29
Population Connectivity	35
Analysis of the ESA Section 4(a)(1) Factors	38
Present or Threatened Destruction, Modification, or Curtailment of Habitat or Range.....	38
Overutilization for Commercial, Recreational, Scientific, or Educational Purposes.....	45
Disease and Predation.....	60
Inadequacy of Existing Regulatory Mechanisms.....	63
Other Natural and Manmade Factors Affecting its Continued Existence.....	82
Extinction Risk Analysis	86
Foreseeable Future.....	86
Methods.....	87
Threats Assessment.....	87
Overall Extinction Risk Analysis.....	88
Extinction Risk Results and Conclusions.....	89
Threats Assessment.....	94
Determination of Status Throughout a Significant Portion of its Range (SPR).....	103
Acknowledgements	109
Supplemental Files	109
References	110

List of Tables

Table 1. Reproductive cycle of queen conch through the species range arranged in order of decreasing latitude.	12
Table 2. Median value of the distribution of adult conch densities from the set of available surveys for each jurisdiction or bank	22
Table 3. Apicomplexan parasite locations reported in the literature.	61
Table 4. Overall extinction risk likelihood point distribution.....	100

List of Figures

Figure 1. Queen conch shell morphology	1
Figure 2. Map of the geographic distribution of queen conch.....	2
Figure 3. Life cycle of the queen conch.....	3
Figure 4. Queen conch size and growth.....	6
Figure 5. Estimates of areal habitat coverage by jurisdiction.....	20
Figure 6. Estimated adult conch densities for jurisdiction within the species range.	27
Figure 7. Adult queen conch per hectare by jurisdiction.	29
Figure 8. Histograms showing distributions of reported adult conch densities.....	31
Figure 9. The estimated adult population size (individuals) by jurisdiction.....	32
Figure 10. Estimated conch abundance by jurisdiction.	33
Figure 11. Estimated conch habitat by jurisdiction.	34
Figure 12. Connectivity networks for queen conch.	36
Figure 13. Relative betweenness centrality for each jurisdiction in the queen conch network. ...	38
Figure 14. CARICOMP seagrass sites, ordered according to latitude.....	41
Figure 15. Reconstructed landings (SAU) converted to numbers of individual conch (vertical axis) compared with FAO reported landings in a stacked bar graph.....	50
Figure 16. Reconstructed landings (metric tons) data for queen conch by SAU by jurisdiction compared to FAO data, from 2000 – 2018.	51
Figure 17. SAU reported mean annual landings (black bars) from 1950 – 2016	52
Figure 18. Estimated average annual exploitation rates for the period 2010 – 2018.....	54
Figure 19. Estimated densities in adult conch per hectare are plotted against the annual average landings in metric tons.	55
Figure 20. Time series of density estimates, landings, and imports.	56
Figure 21. Ocean acidification and shell calcification.....	84
Figure 22. Demographic risk analysis results.....	90
Figure 23. Threats assessment results.....	94
Figure 24. Boxplot of overall extinction risk results	101
Figure 25. Relative Betweenness Centrality for each jurisdiction within the queen conch’s range.	108

Life History

Taxonomy

There have been taxonomic changes proposed within Strombidae that affect *Strombus gigas*. Simone (2005) separated the members of the *Strombus* genus into three different genera based on morphology where *S. pugilis*, *S. alatus*, and *S. gracilior* are retained in *Strombus*, and *S. goliath* and *S. gigas* were moved to the genus *Eustrombus* (previously a subgenus). Furthermore, *S. costatus* and *S. gallus* were moved to the genus *Aliger*. Latiolais et al. (2006) recommended a similar phylogeny and classification using molecular techniques, but did not propose generic name changes. Direct comparison between these two studies proves difficult as Latiolais et al. (2006) did not include *S. goliath* and Simone (2005) did not include *S. raninus*. More recently, Landau et al. (2009) proposed that the genera *Eustrombus* and *Aliger* be combined into the genus *Lobatus* and Latiolais et al. (2006) proposed similar phylogeny changes. Notably, these changes in nomenclature affect higher taxonomic classification and do not combine or split the classification of *S. gigas*, or call into question its status as a recognized full species.

For the purpose of this review, the SRT used the classification *Strombus gigas* (Linnaeus 1758), but acknowledge taxonomy is evolving. The most recent classification places queen conch under the genus *Aliger gigas* (Maxwell et al. 2020) in the Class Gastropoda, Order Neotaenioglossa, and Family Strombidae. Other accepted synonyms include: *Strombus gigas* (Linnaeus 1758); *Lobatus gigas* (Linnaeus 1758); *Strombus lucifer* (Linnaeus 1758); *Eustrombus gigas* (Linnaeus 1758); *Pyramea lucifer* (Linnaeus 1758); *Strombus samba* (Clench 1937); *Strombus horridus* (Smith 1940); *Strombus verrilli* (McGinty 1946); *Strombus canaliculatus* (Burry 1949); and *Strombus pahayokee* (Petuch 1994), as cited in (Landau et al. 2009).

Distinctive Characteristics

Adult queen conch have a heavy shell (5 pounds, 2.3 kg) with spines on each whorl of the spire and a glossy, deep pink, flared aperture (Figure 1). The outside of the shell becomes covered by an organic periostracum (“around the shell”) layer as the queen conch matures that can be much darker than the natural color of the shell. Characteristics used to distinguish queen conch from other family members include: (1) large, heavy shell; (2) short, sharp spires; (3) brown and horny operculum and; (4) bright pink interior of the shell (Prada et al. 2009).



Figure 1. Queen conch shell morphology image by Jennifer Doerr, SEFSC.

Range, Distribution, and Habitat Use

The queen conch occurs throughout the Caribbean Sea, the Gulf of Mexico, and around Bermuda (Figure 2) and includes the following jurisdictions: Anguilla, Antigua and Barbuda, Aruba, Barbados, Bahamas, Belize, Bermuda, Caribbean Netherlands, Colombia, Costa Rica, Cuba, Curaçao, Dominican Republic, French West Indies, Grenada, Haiti, Honduras, Jamaica, Mexico, Montserrat, Nicaragua, Panama, Puerto Rico, St. Kitts and Nevis, St. Lucia, St. Vincent and the Grenadines, Trinidad and Tobago, the Turks and Caicos, the United States (Florida, Puerto Rico, U.S. Virgin Islands, Flower Garden Banks National Marine Sanctuary), British Virgin Islands, and Venezuela (Theile 2001).

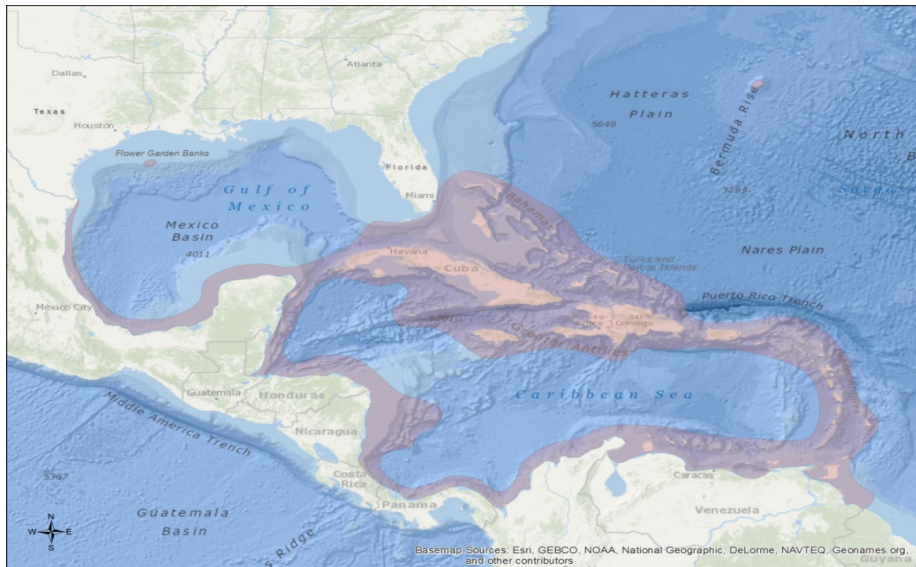


Figure 2. Map of the geographic distribution of queen conch.

Queen conch inhabit a range of habitat types during their life cycle. As discussed in the following sections, as conch develop they use different habitat types including seagrass beds, sand flats, algal beds, and rubble areas from a few centimeters deep to approximately 30 meters (Brownell and Stevely 1981).

Early Life Stages

After the eggs hatch, the veligers (larvae) drift in the water column up to 30 days depending on phytoplankton concentration, temperature, and the proximity of settlement habitat. These veligers are found primarily in the upper few meters of the water column (Paris et al. 2008; Posada and Appeldoorn 1994; Stoner 2003; Stoner and Davis 1997) where they feed on phytoplankton. When the veligers are morphologically and physiologically ready, they metamorphose into benthic animals in response to trophic cues from their seagrass habitat (Davis 2005; Figure 3). The key trophic cues shown to induce metamorphosis are epiphytes associated with macroalgae and sediment (Davis and Stoner 1994). Settlement locations are usually areas that have sufficient tidal circulation and high macroalgae production.

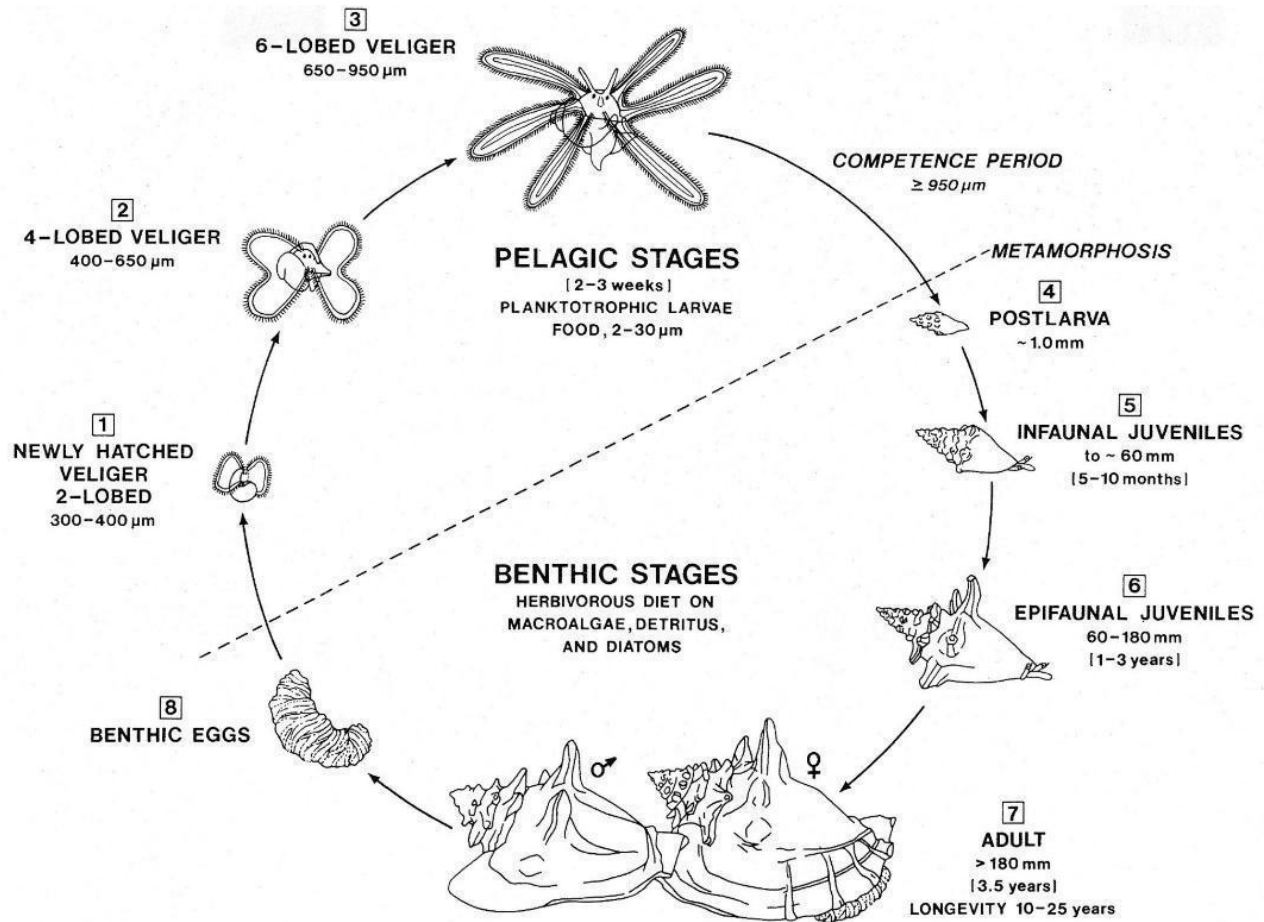


Figure 3. Life cycle of the queen conch by Bonnie Bower-Dennis.

Juvenile queen conch are primarily associated with native seagrass, such as *Thalassia testudinum*, in large parts of their range in the Caribbean and the southern Gulf of Mexico (Boman et al. 2019). However, juvenile queen conch can occur in a variety of habitat types. Randall (1964) reported that juvenile conch in the U.S. Virgin Islands were most abundant in shallow coral-rubble environments, with lower densities on bare sand and in seagrass beds. A similar association was reported from Puerto Rico, with high numbers in coral rubble compared with sand, seagrass, and hard bottom (Torres Rosado 1987). In Florida, juveniles are found in a variety of habitats, including reef rubble, algae-covered hard bottom, and secondarily in mixed beds of algae and seagrass, depending upon general location (Glazer and Berg Jr. 1994). In Cuba (Alcolado 1976), the Turks and Caicos Islands (Hesse 1979), Venezuela (Weil and Laughlin 1984), and The Bahamas, juvenile conch are associated primarily with native seagrass (Stoner 2003; Stoner et al. 1996; Stoner et al. 1994). In St. Croix, U.S. Virgin Islands, densities of juvenile and adult queen conch were the highest in habitats characterized as 50-90% and 10-50% patchy seagrass, respectively (Doerr and Hill 2018).

After the veligers settle on the bottom, they bury into the sediment. This submerged life phase makes it difficult to survey and therefore they are often under-sampled (Appeldoorn 1987; Hesse 1979). They emerge about a year later (Stoner 1989a) as juveniles at around 60 mm shell length.

Most conch nursery areas occur primarily in back reef areas (i.e., shallow sheltered areas, lagoons, behind emergent reefs or cays) of medium seagrass density, depths between 2 to 4 m, with strong tidal currents (at least 50 cm/s; Stoner 1989b), and frequent tidal water exchanges (Stoner et al. 1996; Stoner and Waite 1991). Seagrass is thought to provide both nutrition and protection from predators (Ray and Stoner 1995; Stoner and Davis 2010). The structure of the seagrass beds decreases the risk of predation (Ray and Stoner 1995), which is very high for juveniles (Appeldoorn 1988a; Stoner and Glazer 1998; Stoner et al. 2019a). Posada et al. (1997) observed that the most productive nurseries for queen conch tended to occur in shallow (<5-6 m deep) seagrass meadows. Jones and Stoner (1997) found that optimal nursery habitat occurred in areas of medium density seagrass, particularly along the seagrass gradient. Boman et al. (2019) observed a significantly higher probability of positive growth in juvenile conch in native seagrass compared to invasive seagrass (i.e., *Halophila stipulacea*). In The Bahamas, juveniles were only found in areas within 5 km from the Exuma Sound inlet, emphasizing the importance of currents and frequent tidal water exchange that affects both larval supply and growth of their algal food (Jones and Stoner 1997). However, there are certain exceptions, such as in Florida, where many juveniles are found on shallow algal flats, or in Jamaica, where they can be found on deep banks such as Pedro Bank.

When juvenile conch first emerge from the sediment and move to nearby seagrass beds, densities can be as high as 200-2000 conch/ha (Stoner 1989a; Stoner and Lally 1994; Stoner 2003). Stoner and Ray (1993) showed decreased predation mortality and higher survivorship in juvenile queen conch within dense aggregations, but at a cost of lower growth rates. The slow growth rate of juvenile conch in the presence of predators was subsequently confirmed in a laboratory study (Delgado et al. 2002).

Adults

Adult conch can be found in a wide range of environmental conditions (Stoner et al. 1994) such as in sand and algal or coral rubble (Acosta 2001; Stoner and Davis 2010). Adult queen conch are rarely, if ever, found on soft bottoms composed of silt and/or mud, or in areas with high coral cover (Acosta 2006). Adult conch are found in shallow, clear water of oceanic or near-oceanic salinities at depths generally less than 75 m, and are most often found in waters less than 30 m (McCarthy 2007). It is believed that depth limitation is based mostly on light attenuation limiting their photosynthetic food source (McCarthy 2007; Randall 1964).

The movements of adult conch are associated with factors like changes in temperature, food availability, and predation. The average home range size for an individual queen conch is variable and has been measured at 5.98 ha in Florida (Glazer et al. 2003), 0.6 to 1.2 ha in Barbados (Phillips et al. 2010), and 0.15 to 0.5 ha in the Turks and Caicos Islands (Hesse 1979). Glazer et al. (2003) found that there were no significant differences in movement rate, site fidelity, or size of home range between adult males and females. There was a statistically significant difference in mean speed of the conch among the four seasons (winter, spring, summer, and fall) of the year. Specifically, queen conch move at a greater speed during the summer. This increase in speed may be due to the increased metabolic activity associated with warmer waters and increased movement related to their reproductive season (i.e., males searching for mates and females moving into egg-laying habitat; Glazer et al. 2003). Studies have suggested that adult conch move to different habitat types during their reproductive season, but afterwards return to feeding grounds (Glazer et al. 2003; Hesse 1979; Stoner and Sandt

1992). In general, adult conch do not move very far from their feeding grounds during their reproductive season (Stoner and Sandt 1992).

Diet

The primary diet of juvenile conch consists of native seagrass detritus and red and green macroalgae, primarily *Laurencia* spp. and *Batophora oerstedii* (Randall 1964; Serviere-Zaragoza et al. 2009; Stoner and Sandt 1992; Stoner and Waite 1991). The production of red and green algae, which can be highly variable, has been shown to directly affect the growth of juvenile conch (Stoner 2003; Stoner et al. 1994; Stoner et al. 1995). Organic material in the sediment (benthic diatoms and particulate organic matter and cyanobacteria) has also been suggested to be sources of nutrition to juvenile conch (Serviere-Zaragoza et al. 2009; Stoner et al. 1995; Stoner and Waite 1991). Although several studies have indicated that seagrass detritus is a food source for juvenile queen conch, in particular detritus of *T. testudinum* (Stoner 1989a; Stoner and Waite 1991), its importance in the diet is less than previously thought. A recent study conducted by Boman et al. (2019) suggests that organic material in the sediment (i.e., benthic diatoms and particulate organic matter) may be the most important source of nutrition for juvenile conch. The importance of the organic material in the sediment for juvenile queen conch was already suggested by Stoner and Waite (1991), who found large amounts of sediment in the stomachs of juvenile conch. Stoner and Waite (1991) also showed that macroalgae were the most likely food source of juvenile conch (shell length 120-140 mm) in native seagrass beds in The Bahamas. The epiphytes that live on seagrass also provide nutrition for juveniles (Stoner 1989b). In sand habitats, juveniles can also feed on diatoms and cyanobacteria that are found in the benthos (Creswell 1994; Ray and Stoner 1995). Adults feed on different types of filamentous algae (Creswell 1994; Ray and Stoner 1995). The presence of the green algae, *B. oerstedii*, in The Bahamas even caused an aggregation to change direction (Stoner and Ray 1993) and is also correlated to areas of higher conch densities (Stoner et al. 1994).

Age and Growth

Queen conch are estimated to have a life span of 25-30 years (Davis 2005; McCarthy 2007). Growth rate and shell morphology of queen conch can vary depending on sex, depth, latitude, food availability, age class, and habitat type. Small outplanted hatchery-raised juveniles grew 0.21 mm/day at 17 m depth off southwest Puerto Rico (Appeldoorn 1985), while juveniles in hatcheries grew 0.3 mm/day (Ballantine and Appeldoorn 1983; Brownell 1977). Queen conch in Exuma grew an average of 0.12 mm/day in Exuma (Wicklund et al. 1991) and 0.3 mm/day in Barbados (Phillips et al. 2010). In a protected area of Mexico, juveniles grew an average of 0.28 mm/day, conch 150 to 199 mm grew 0.19 mm/day and those greater than 200 mm grew 0.08 mm/day (Peel and Aldana Aranda 2012). On average, female queen conch grow more quickly than males (Alcolado 1976), to a bigger size (Randall 1964), and have a greater tissue weight, although overlap does occur. This species also exhibits periods of seasonal growth associated with water temperature and food availability. Summer growth rates are greater than winter growth rates (Stoner and Ray 1993). Juvenile growth rates were 4.4 to 16.3 mm/month in the summer and 1.8 to 3 mm/month for the rest of the year in The Bahamas (Iversen et al. 1987). Size at maturity can vary depending on local environmental conditions that promote or slow growth. Shell length continues to increase until the onset of sexual maturity (Figure 4).



Figure 4. Queen conch size and growth image by Jennifer Doerr, SEFSC.

The queen conch reaches maturity at around 3.5 to 4 years, at which time the edge of the shell lip turns outward to form the flared lip (Stoner et al. 2012a). Once the shell lip is formed, the shell does not increase in length (Appeldoorn 1996; Tewfik et al. 1998). Future shell growth is limited to thickening of the shell, in particular the thickening of the flared lip (Appeldoorn 1988b). Studies indicate that shell thickness is a better indicator of sexual maturity than the formation of the flared lip (Appeldoorn 1994a; Clerveaux et al. 2005; Stoner et al. 2012a). However, lip thickness can vary by region. For example, lip thickness in reproducing adult queen conch was greater in The Bahamas as compared to Colombia (Stoner et al. 2012a).

With the onset of sexual maturity, tissue growth decreases and switches from primarily thickening of the meat to increasing the weight of the gonads. Once the conch is around ten years of age, the shell volume starts to decrease, as layers of the shell mantle are laid down from the inside (Randall 1964). Eventually, the room inside the shell can no longer accommodate the tissue and the conch will start to decrease their tissue weight (CFMC and CFRAMP 1999). Stoner et al. (2012a) found that after shell lip thickness reached 22 to 25 mm, both soft tissue and gonad weight decreased.

Reproduction

Queen conch are dioecious with sexual dimorphism and reproduce via internal fertilization. Males and females are distinguished by either a verge (penis) or egg groove. During copulation, the male aligns his shell behind and slightly on top of the posterior portion of the flared lip of the female (Tewfik et al. 1998). The verge extends forward from the male under the female's shell and is inserted into the egg groove. Approximately three weeks after copulation the female lays a demersal egg mass on coarse sand of low organic content, completing deposition within 24-36 hours (D'Asaro 1965; Randall 1964). The egg mass consists of a long continuous egg-filled tube

that folds and sticks together in a compact crescent shape, adhering to sand grains that provide camouflage and discourage predation. After an incubation period of approximately five days, the larvae emerge and assume a pelagic lifestyle (D'Asaro 1965; Weil and Laughlin 1984). The minimum pelagic duration is reported from four field studies to be 16 days (Brownell 1977; Davis 1994, 1996; Salley 1986), but can range from 21 days to 30 days (Brownell 1977; D'Asaro 1965; Davis 1994; Paris et al. 2008; Salley 1986) with a mean of approximately 25 days. However, larval growth and development can be delayed if the appropriate food supply is not available (Brownell 1977). Modeling of natural mortality during the larval planktonic stage shows it to be quite high (Chávez and Arreguín-Sánchez 1994), but we were unable to find any information on natural larval mortality rates in the literature. Upon metamorphosis, veligers settle to the bottom and bury completely into the sediment where they spend much of their first year of life.

Depensatory mechanisms have been implicated as a major factor limiting the recovery of overharvested queen conch populations (Appeldoorn 1995; Stoner et al. 2012b). Reproductive potential is primarily reduced by the removal of spawners from the population (Appeldoorn 1995). Empirical observations have suggested mating and egg-laying in queen conch are directly related to the density of mature adults (Stoner et al. 2011; Stoner et al. 2012c; Stoner and Ray-Culp 2000). In animals that aggregate to reproduce, low population densities can make it difficult or impossible to find a mate (Appeldoorn 1995; Erisman et al. 2017; Rossetto et al. 2015; Stephens et al. 1999; Stoner and Ray-Culp 2000). Challenges associated with mate finding are likely exacerbated for slow-moving animals such as conch (Doerr and Hill 2013; Farmer and Doerr 2022; Glazer et al. 2003). This limitation translates directly into limited recovery because increased “search time” depletes energy and time resources, reducing the rate of gametogenesis and the overall reproductive potential of the population. Simulations by Farmer and Doerr (2022) confirm that limitations on mate finding associated with density are the primary driver behind observed patterns in mating and spawning activity, but similar to field observations by Gascoigne and Lipcius (2004), it cannot be the only explanation for lack of reproductive activity at low densities.

An additional postulated depensatory mechanism is the breakdown of a positive feedback loop between contact with males and the rate of gametogenesis and spawning in females, where copulation stimulates oocyte development and maturation, leading to more frequent spawning (Appeldoorn 1995). Copulation in conch is more likely in spawning than non-spawning females, providing an additional positive feedback mechanism that amplifies the effect at high densities (Appeldoorn 1988c). Evidence supporting this idea has been provided by several studies that reported a consistent lag at the start of the reproductive season between first observations of copulation and first spawning (Brownell 1977; Hesse 1976; Randall 1964; Weil and Laughlin 1984). This lag period, averaging three weeks, may represent the time required to achieve oocyte maturation after first copulation. Farmer and Doerr (2022) considered differences in adult density, movement speeds, scent tracking, barriers to movement, interbreeding rest periods, perception distance, and sexual facilitation. Sexual facilitation was the only mechanism explaining the lack of empirical observations of mating at relatively low population densities, providing statistical confirmation that the reductions of densities caused by overharvesting of spawning aggregations increases the probability of recruitment failure beyond what would be anticipated from delays in mate finding alone. This is consistent with field experiment findings from Gascoigne and Lipcius (2004), which indicate that in addition to depensatory mechanisms

associated with mate finding, delayed functional maturity at low density sites can explain declines in reproductive activity.

Fecundity

Assessments of fecundity require knowledge of the population sex ratio, spawning season duration, rate of spawning during the season, number of eggs per egg mass, and the relationship between body mass and age (Appeldoorn 1988c). Few studies have investigated these factors concurrently, and the variability reported in these metrics is high. For example, estimates of the number of eggs contained within each egg mass produced range from 150,000 to 1,649,000 eggs per mass (Appeldoorn 1993; Appeldoorn 2020; Berg Jr. and Olsen 1989; D'Asaro 1965; Delgado and Glazer 2020; Mianmanus 1988; Randall 1964; Robertson 1959; Weil and Laughlin 1984). Additionally, females are capable of storing eggs for several weeks before laying an egg mass, so it is possible that multiple males have fertilized the same eggs (Medley 2008). The ability to store sperm is advantageous for conch populations since females are still capable of laying egg masses without encountering another male. The number of egg masses produced per female is also highly variable and ranges between 1 and 25 per female per season for experiments performed in different areas throughout the queen conch range (Appeldoorn 1993; Berg Jr. and Olsen 1989; Davis and Hesse 1983; Davis et al. 1984; Weil and Laughlin 1984).

The number of masses produced as well as the number of eggs per mass may decrease toward the end of the reproductive season (Weil and Laughlin 1984) but individual variability may also be influenced by spawning frequency and the size and number of egg masses produced during the season (Appeldoorn 2020). Differences in spawning rates have been attributed to spawning site selection, population densities, and food selection and availability, among other factors. Previous experimental studies of fecundity showed that female conch laid an average of 13.6 egg masses containing about 750,000 eggs each in low density treatments that were not food limited, while in high density populations experiencing food limitation females laid only 6.7 egg masses containing 500,000 eggs (Appeldoorn 1993). Appeldoorn (2020) recently reexamined fecundity and mating frequencies in field enclosures with both low and high densities of male and female conch and reported that conch in low-density enclosures produced more and larger egg masses and demonstrated a longer spawning season than conch in high-density enclosures. Variability in spawning activity may also be correlated to water temperature and weather conditions. Reproductive activity decreased with increasing water turbulence (Davis et al. 1984) and reproduction peaked with longer days, warmer water temperatures, and relatively stable circulation patterns (Stoner et al. 1992). Appeldoorn (1993) modeled the relationship between female age based on lip thickness and total fecundity, which resulted in the following equation:

$$\text{Log}_{10}(\text{Fecundity}) = 4.157 + 2.012 \text{Log}_{10}(\text{Age}) \quad r^2 = 0.672, N = 10$$

However, this equation is applicable only during the first years following maturation when tissue weight is still increasing and lip thickness reflects age. To further define this relationship Appeldoorn (1993) then included the assumption that fecundity was proportional to wet weight and utilized the Gompertz equation given in Appeldoorn (1992) to predict weight from age for the average adult in the La Parguera, Puerto Rico, population. This resulted in the following predictive equation,

$$E_t = E_{\max} (1 - e^{-k(t-3.2)})$$

where E_t is fecundity at age t , E_{max} is the average maximum fecundity for an individual, k is the instantaneous growth constant, and 3.2 is the age in years at the onset of maturation. Appeldoorn (1993) applied this equation to the La Parguera, Puerto Rico, conch population and determined that 95% of adult growth occurs by age 6, or 2.8 years after the onset of maturation.

Queen conch exhibit determinate shell growth, wherein growth in shell length ceases followed by the formation and continuous thickening of the shell lip upon the onset of maturity. Conch are often considered to be mature when the lip is flared, however Appeldoorn (1988c) observed that the verge of thin-lipped males in Puerto Rico was not yet functional, and true reproductive maturity did not occur until at least two months after the lip flared outward at about 3.6 years of age. The result is that thin-lipped individuals probably do not mate or spawn in the first reproductive season after the shell lip flares and are at least 4 years old before first mating. This growth pattern makes it difficult to estimate age at maturity, and therefore to determine age structure of the population. Further complicating the accurate assessment of maturity status is plasticity in shell morphology and growth influenced by environmental conditions, habitat, geographic nuances, and genetics (Martín-Mora et al. 1995; McCarthy 2007).

Lip thickness measurements used to determine age at sexual maturity are highly variable and growth in lip thickness is dependent on sex, depth, latitude, temperature, food availability, and shelter (Appeldoorn 1988b; Appeldoorn and Baker 2013; Stoner and Sandt 1992). Recent verification studies assessing the relationship between lip thickness and onset of maturity have established several metrics to identify maturity stages of the population including LT_{min} (lip thickness at first maturity) and LT_{50} (lip thickness at 50% population maturity). Boman et al. (2018) sampled seven representative locations in the wider Caribbean and identified an LT_{min} for females between 2-12 mm and for males between 3-9 mm. They also found that the LT_{50} of both females (7-14 mm) and males (4-11.5 mm) varied between their sampling locations, was not dependent on variations in water temperature, and that females had a larger LT_{50} than males, indicating sexual dimorphism (Boman et al. 2018). Similarly, Foley and Takahashi (2017) reported an LT_{min} for females and males of 12 mm and 4 mm, respectively, and an LT_{50} of 15.51 mm for females and 12.33 mm for male conch in Belize. Queen conch in The Bahamas mature at slightly larger lip thicknesses, with females and males reaching LT_{min} at 12 mm and 9 mm, respectively, and achieving LT_{50} for the population at 26 mm for females and 24 mm for males (Stoner et al. 2012a). Aldana Aranda and Frenkiel (2007) showed the correlation between the lip thicknesses of *S. gigas* versus the reproductive cycle. They studied 700 organisms sorted in three groups: a) 100-170 mm shell total length, without lip; b) shell total length ≥ 170 mm and lip thickness < 5 mm; and c) shell total length ≥ 170 mm and lip thickness > 5 mm. Only undifferentiated stages were observed for organisms of 100-170 mm of shell length, without lip. The group of shell length ≥ 170 mm and lip thickness > 5 mm exhibited gametogenic activity. These and other studies (Avila-Poveda and Baqueiro-Cárdenas 2006) consistently report maturation of females at larger sizes and lip thicknesses, confirming sexual dimorphism in this species. The hypothesis of sexual selection, where increase in size corresponds with increased fecundity for females, may explain dimorphism between the sexes (Boman et al. 2018; Ilano et al. 2004; Shine 1989). Further supporting this hypothesis, Stoner et al. (2012a) found that gonad weight increases in female queen conch up to 22 mm LT, suggesting a continued increase in fecundity with lip thickness, and therefore age. At $LT > 22$ mm, the gonadosomatic index of females decreased slightly, although histological data indicated no loss of reproductive capability (Stoner et al. 2012a). Delgado and Glazer (2020) examined individual egg masses from females

of varying lip thicknesses and observed that older individuals had the same frequency of reproductive activities and there was no significant relationship between lip thickness and the number of eggs in an egg mass. In aging female there is no direct evidence of senescence in histological or behavioral observations of conch; however, Stoner et al. (2012a) and Foley and Takahashi (2017) suggest the possibility for decreased fecundity given declining shell volume associated with older individuals and the limited internal space available for ovary development.

Spawning Season and Length

Seasonal movements, usually associated with the initiation of the reproductive season, are widely known for queen conch. Weil and Laughlin (1984) reported that adult conch at Los Roques, Venezuela, moved from offshore feeding areas in the winter to summer spawning grounds in shallow, inshore sand habitats. In the Turks and Caicos, adult conch moved from seagrass to sand-algal flats with the onset of winter (Hesse 1979). Movements to shallower habitats have also been reported for deep-water populations at St. Croix (Coulston et al. 1987). Increasing water temperature and photoperiod are believed to trigger large-scale migrations and the subsequent initiation of mating. In locations where adult conch are abundant, these migrations culminate in the formation of reproductive aggregations. These aggregations generally form in the same locations each year (Glazer and Kidney 2004; Marshak et al. 2006; Posada et al. 1997) and are dominated by older individuals that produce large, viable egg masses (Berg Jr. et al. 1992).

However, in some areas large-scale movements do not occur. For example, in the Florida Keys, adult aggregations are relatively persistent throughout the year, although reproductive activity does not occur year-round (Glazer et al. 2003; Glazer and Kidney 2004). Queen conch found in the deep waters near Puerto Rico are geographically isolated from nearshore, shallow habitats and remain offshore during the spawning season (García-Sais et al. 2012). The distribution of feeding and spawning habitats may also be an important factor in the timing and extent of adult movements. In deeper water populations near Lee Stocking Island in The Bahamas, Stoner and Sandt (1992) reported that adult queen conch moved from a hard bottom mound in the winter to a nearby sand plain during the spawning season. They also noted that small foraging trips between the hard substrata and the sandy spawning grounds continued throughout the reproductive season and that the close proximity of feeding and reproductive habitats may be an important characteristic of optimal spawning sites (Stoner and Sandt 1992). Similarly, Glazer and Kidney (2004) reported that movement of queen conch at two sites in Florida was minimal, but individuals were found in coarse sand during the spawning season versus rubble in the non-spawning months of the year.

Multiple studies comprising visual surveys of mating and spawning events in the field and histological examinations of gonadic activity show that the duration and intensity of the spawning season varies extensively throughout the queen conch's range (Table 1). External variables such as temperature, photoperiod, and weather events interact to mediate seasonality in reproductive and spawning behaviors. Generally, reproductive activity begins earlier and extends later into the year with decreasing latitude. Visual surveys of reproductive activity occurring in the field have reported the reproductive season to extend from May to September in Florida (D'Asaro 1965), May to November in Puerto Rico (Appeldoorn 1985), March to September in the Turks and Caicos (Davis et al. 1984; Hesse 1976), and February through November in the U.S. Virgin Islands (Coulston et al. 1987; Randall 1964). In warmer regions such as Cuba and

Banco Chinchorro, Mexico, reproductive activity can occur throughout the year (Cala et al. 2013; Corral and Ogawa 1987; Cruz S. 1986); however, there is a seasonal peak in activity in most areas during the warmest months, usually from July to September (Aldana Aranda et al. 2014).

The gonadic cycle of conch may vary in its seasonality, duration, and intensity of rest and post spawn, as well as the duration and intensity of the gametogenic, maturation, and spawning periods. Aldana Aranda et al. (2003a) conducted histological studies and identified different reproductive strategies of queen conch at two locations in Mexico, Chinchorro Bank in the Caribbean and Alacranes Reef in the Gulf of Mexico. They found that conch in Chinchorro Bank exhibited fast gametogenesis followed by one short spawning pulse and little post spawn or rest stages, while conch in Alacranes Reef exhibited low intensity gametogenesis throughout the year, experienced limited gonad recovery, but spawned constantly (Aldana Aranda et al. 2003a). Conch in Colombia, Mexico, and Belize demonstrated similar pulsed strategies (Avila-Poveda and Baqueiro-Cárdenas 2009). However, gametogenic development is not necessarily an indication of successful mating and spawning, thus regional seasonality and individual reproductive capability should be interpreted cautiously in terms of reproductive success and positive recruitment to the population

Table 1. Reproductive cycle of queen conch through the species range arranged in order of decreasing latitude. First section illustrates the results of visual surveys conducted in the field and the second section is based on histological examinations of sampled gonads. Colors indicate relative activity of reproductive activity (white = none, light gray = low, medium gray = medium, dark gray = high or peak activity). Compiled from Avila-Poveda and Baqueiro-Cárdenas (2009), Appeldoorn and Baker (2013), Boman et al. (2018), and original literature sources.

Time of Year												Duration (month)	Geographic Area	Original Source
J	F	M	A	M	J	J	A	S	O	N	D			
												4.5	Bermuda	Berg Jr. et al. (1992)
												4.5	Florida	D'Asaro (1965)
												7	Florida	Davis et al. (1984)
												6	Florida	Delgado and Glazer (2020)
												6.5	The Bahamas	Stoner et al. (1992)
												5.5	The Bahamas	Wicklund et al. (1991)
												12	Cuba	Cala et al. (2013)
												7	Turks & Caicos	Hesse (1976)
												6	Turks & Caicos	Davis et al. (1984)
												8	Alacranes Reef, Mexico	Pérez-Pérez and Aldana-Aranda (2003)
												8	Yucatan, Mexico	Paris et al. (2008)
												4	Quintana Roo, Mexico	Santana Flores and Aldana-Aranda (2013)
												5	Quintana Roo, Mexico	Sánchez et al. (2019)
												6	Jamaica	Salley (1986)
												6	Puerto Rico	Appeldoorn (1988b)
												5	Puerto Rico	Appeldoorn (1993)
												9	St. John (USVI)	Randall (1964)
												9	St. Croix (USVI)	Coulston et al. (1987)
												4	Saba Bank	de Graaf et al. (2014)
												4	Saba Bank	Boman et al. (2018)
												6	St. Eustatius	Meijer zu Schlochtern (2014)
												9	St. Eustatius	Boman et al. (2018)
												5.5	St. Kitts/Nevis	Wilkins et al. (1987)
												8	Barbados	Bissada (2011)
												6	Venezuela	Brownell (1977)
												8	Venezuela	Weil and Laughlin (1984)

Time of Year												Duration (month)	Geographic Area	Original Source
J	F	M	A	M	J	J	A	S	O	N	D			
												4.5	San Andrés, Colombia	García E. et al. (1992)
												6	San Andrés, Colombia	Márquez-Pretel et al. (1994)
												4	Santa Marta, Colombia	Botero (1984)
												8	San Bernardo, Colombia	Lagos-Bayona et al. (1996)

Histological Surveys:

												3	Alacranes Reef, Mexico	Aldana Aranda et al. (2003a; 2003b)
												3	Chinchorro Bank, Mexico	Gordillo-Morales (1996)
												3	Chinchorro Bank, Mexico	Aldana Aranda et al. (2003a; 2003b; 2003c)
												7	Belize	Foley and Takahashi (2017)
												12	Belize	Egan (1985)
												6	St. Kitts/Nevis	Buckland (1989)
												5	St. Kitts/Nevis	Tiley et al. (2018b)
												3	Colombia	Avila-Poveda and Baqueiro-Cárdenas (2009)

Spawning Density

Because direct physical contact is necessary for copulation and queen conch are slow moving, the density of mature adults within localized queen conch populations is a critical and complex factor governing mating success and population sustainability. Although many surveys of conch populations have been completed over the last half century, few studies have simultaneously investigated the relationship between adult density and reproductive rates. Of these, the reported rates of reproductive activity associated with surveys of adult populations have varied extensively across multiple territories as density is dependent on the scale of measurement and the targeted area surveyed. For example, in adult populations in The Bahamas at densities near 200 adults per hectare (/ha), Stoner and Ray-Culp (2000) reported mating and spawning rates of approximately 13% and 10%, respectively. During continued surveys in fished areas (Berry and Andros Islands) and a no-take reserve (Exuma Cays Land and Sea Park [ECLSP]) of The Bahamas, Stoner et al. (2012c) observed that, at a mean density of 60 adults/ha within the ECLSP, 9.8% of adults were mating, while at 118 adults/ha at Andros Island approximately 2.4% were mating, and at 131 adults/ha at the Berry Islands, only 5.9% were involved in mating activity. Doerr and Hill (2018) reported reproductive activity in 2.4% of adult conch located across the shelf of St. Croix, USVI, and the lowest mean density of adults at survey sites where reproductive activity occurred was 63.7 adults/ha. Of these studies, the highest densities were reported from Cuba, where at one protected site with densities of 223 adults/ha only 0.3% of adults were mating, while at another site with a reported density of 497 adults/ha, 3.7% of conch were mating and 2.5% were involved in spawning (Cala et al. 2013). In Colombia, however, reproductive activity demonstrated by the presence of egg masses was reported in areas with population densities as low as 24 and 11 conch/ha (Gómez-Campo et al. 2010). The scale over which these observations were recorded and subsequent interpretation of the spatial dispersion of queen conch is critical to understanding differences among study conclusions. In addition, it is difficult to demonstrate a causal relationship between reproductive output and density in observational studies such as these when there may be alternative explanations for the correlations observed (Gascoigne and Lipcius 2004).

Life history traits of queen conch make them vulnerable to depensatory mechanisms resulting in reduced per capita population growth rates and poor recovery of the stock. The principle of inverse density dependence at low densities is referred to as an Allee effect, which potentially impacts queen conch populations through depressed reproductive activity due to low encounter rates of adults (Stoner and Ray-Culp 2000) or delayed functional maturity in young adults (Gascoigne and Lipcius 2004). When reproductive fitness declines such that the per capita population growth rate becomes negative, localized extinction may result (Allee 1931; Courchamp et al. 1999). Appeldoorn (1988a) initially suggested that queen conch may have a critical density for egg production, and Stoner and Ray-Culp (2000) provided evidence for demographic Allee effects in queen conch populations, reporting a complete absence of mating and spawning in population densities less than 56 and 48 conch/ha, respectively. They concluded that the absence of reproduction in low-density populations was primarily related to encounter rate and noted that reproductive activity reached an asymptotic level near 200 adults/ha (Stoner and Ray-Culp 2000). Based on these landmark studies 50 adult conch/ha is generally accepted as the minimum threshold required to achieve some level of reproductive activity within a given conch population (Appeldoorn 1995; Gascoigne and Lipcius 2004; Stephens et al. 1999; Stoner and Ray-Culp 2000). Conversely, Delgado and Glazer (2020) reported the highest threshold densities below which no reproduction was observed, with no mating occurring at aggregation

densities below 204 adults/ha and no spawning at aggregation densities less than 90 adults/ha. However, population densities estimated from randomized shelf-wide transect methodologies versus directed intra-aggregation approaches very likely result in vastly different conclusions regarding minimum reproductive threshold densities. The density values reported in these studies represent the absolute minimum values and additional research should be conducted to identify reproductive density thresholds throughout the queen conch's range. Nevertheless, whatever the population survey approach, it is clear that the occurrence and frequency of mating behavior is density dependent. Simulations suggest population density, coupled with sexual facilitation, are the primary drivers of reproduction at low densities (Farmer and Doerr 2022). For management purposes, a critical consideration is demographic consequences resulting from reduced mating frequency. If queen conch, particularly females, do not have the opportunity to mate and spawn to their full potential, the fewer offspring produced per individual is likely to lead to a decrease in the per capita population growth rate (Gascoigne et al. 2009). For this reason, although observed minimum reproductive thresholds are highly variable, the United Nations Environment Programme (UNEP) has recommended a minimum reference point of 100 adult conch/ha to avoid significant impacts to recruitment (UNEP 2012). This reference point is derived from cross shelf data from unfished areas in The Bahamas that show that mating and spawning plateau at approximately 100 adult conch/ha and yield no further benefits to reproductive activity at higher densities (Stoner and Ray-Culp 2000; Stoner et al. 2012b). However, given the highly aggregated nature of queen conch (Glazer et al. 2003; Glazer and Kidney 2004), managing for minimum cross-shelf densities does not specifically protect the high-density spawning aggregations where most reproduction occurs (Delgado and Glazer 2020).

The relationship between adult densities and the probability of reproductive activity is also dependent on levels of fishing pressure. For example, in the ECLSP, a no-take marine reserve in The Bahamas, no mating was observed where adult densities were less than 74 adults/ha (Stoner et al. 2012b). In historically fished sites of the Berry Islands and Andros Island, mating was observed at minimum densities of 47 and 64 adults/ha, respectively (Stoner et al. 2012b). Although reproductive activity was observed at these densities, mating frequency was highly variable resulting in a much higher estimated 50% probability of mating at the fished sites, with estimates of 70 (ECLSP), 180 (Andros Island), and 300 (Berry Islands) adults/ha required (Stoner et al. 2012b). Stoner et al. (2012b) concluded that differences in size, age, or phenotype of adult conch provided the most likely explanation for the differences in mating frequencies and probabilities among the study sites, particularly the contrast between ECLSP and the two fished areas. Specifically, adults in the ECLSP population had larger shell lengths (32-40% larger) and mean shell lip thicknesses nearly twice as thick as conch in the fishing areas (Stoner et al. 2012b), indicating that the ECLSP population was older.

The persistent formation of adult aggregations may help to sustain some populations since long-term intra-aggregation surveys conducted by Delgado and Glazer (2020) in Florida show that, as aggregation densities increase, both mating and spawning increase correspondingly. They observed an increase in mating activity, peaking at 71% of the aggregation at densities greater than 800 adults/ha, and spawning reached a maximum just over 84% when densities exceeded 600 adults/ha (Delgado and Glazer 2020). Similarly, Stoner et al. (2012b) reported that mating frequency increased at higher densities of adults in The Bahamas, with a maximum of 34% of the population mating at a high density of ~2500 adults/ha. Nevertheless, species such as the queen conch, which are susceptible to Allee effects, might be more vulnerable to population collapses with only slight increases in either fishing or natural mortality rates (Courchamp et al.

1999). Repeat visual surveys in the same sites in The Bahamas have provided evidence of this susceptibility, revealing that adult densities in the ECLSP have declined significantly over 22 years due to lack of recruitment (Stoner et al. 2019a). Stoner et al. (2019a) further concluded that most conch populations in The Bahamas are currently at or below critical densities for successful mating and reproduction and that significant management measures are needed to preserve the stock. Similar long-term declines of reproductively active adult conch have been reported within the Port Honduras Marine Reserve in southern Belize. Densities of conch in this no-take zone have been continuously declining since 2009 and fell below 88 conch/ha by 2013, decreasing further to <56 conch/ha in 2014 (Foley 2016, unpubl., cited in Foley and Takahashi 2017).

For the purposes of further analysis and summarization, the SRT defined the following thresholds, which are based on the aforementioned best available information, to determine the status of queen conch populations throughout the greater Caribbean:

- Populations with densities above 100 adult conch/ha are considered to be at a density that supports reproductive activity resulting in population growth.
- Populations with densities between 50-99 adult conch/ha are considered to have reduced reproductive activity resulting in minimal population growth.
- Populations with densities below the 50 adult conch/ha threshold are considered to be not reproductively active due to low adult encounter rates or mate finding. This threshold is largely recognized as an absolute minimum required to support mate-finding and thus reproduction.

Population Structure

Early studies using allozymes to examine the genetic structure of queen conch implied high levels of gene flow but showed isolated genetic structure for populations either at isolated sites or at the microscale level. Mitton et al. (1989) collected samples from nine locations across the Caribbean including Bermuda, Turks and Caicos Islands, St. Kitts, Nevis, St. Lucia, the Grenadines, Bequia, Barbados, and Belize and reported high gene flow as well as genetic differentiation at all spatial scales. They also suggested that conch populations were not panmictic and that conch in Bermuda and Barbados were isolated from Caribbean populations, while populations north and south of St. Lucia were significantly different (Mitton et al. 1989). Conch sampled in the Florida Keys also demonstrated significant spatial and temporal genetic variation, although genetic similarity among populations was high (Campton et al. 1992). Tello-Cetina et al. (2005) sampled conch from four sites along the Yucatan Peninsula and reported relatively high levels of intrapopulation diversity and little geographic differentiation, with the population from the Alacranes Reef having the furthest genetic distance from the other three sites.

Although allozyme studies have limited utility in discerning fine-scale population structure since allozymes are typically slow to evolve and possess low levels of polymorphism, recent studies using microsatellites and single nucleotide polymorphism (SNPs) have found similar levels of connectivity and genetic differentiation. Morales (2004) compared partial sequences from 13 sites in the Caribbean and found evidence of connectivity among distant locations throughout the region. Kitson-Walters et al. (2018) focused their sampling in the EEZ of Jamaica and found a weak but significant population structure suggesting that mainland Jamaica acts as a slight divide between the northern and southern populations. Similarly, Blythe-Mallett et al. (2021) sampled

multiple zones across Pedro Bank and identified two possible subpopulations, one on the heavily exploited eastern end of the bank and another on the central and western end. Pedro Bank, an important commercial fishing ground southwest of Jamaica, is geographically isolated and receives limited gene flow from mainland Jamaica and other historically important offshore populations within the EEZ (Kitson-Walters et al. 2018). The high degree of genetic relatedness within conch sampled from Pedro Bank likely indicates that the populations are sufficiently self-sustaining (Kitson-Walters et al. 2018) but still receive larvae from upstream sources that contribute to the population on the eastern end of the bank (Blythe-Mallett et al. 2021).

Many studies conducted in the Mexican Caribbean have detected a spatial genetic structure for queen conch populations in their territorial waters. Pérez-Enriquez et al. (2011) identified a genetic cline along the southern Mexican Caribbean to north of the Yucatan Peninsula with a reduced gene flow observed between the two most distant sites, representing an increase in genetic differences as geographic distance increased. These authors further suggested that since the overall genetic diversity varied from medium to high values, the queen conch had not reached genetically threatened levels indicative of a population bottleneck (Pérez-Enriquez et al. 2011). Machkour-M'Rabet et al. (2017) used updated molecular markers to analyze conch from seven sites within the same area and observed similar results with the exception of the apparent genetic isolation of conch collected on Isla Cozumel, which was not detected by Pérez-Enriquez et al. (2011). The results of this study also led Machkour-M'Rabet et al. (2017) to conclude that populations of conch along the Mesoamerican Reef are not panmictic and demonstrate genetic patchiness indicative of homogeneity among sample areas, providing further evidence for the pattern of isolation by distance.

Márquez-Pretel et al. (2013) found four genetic stocks reflecting heterogeneous spatial mosaics of marine dispersion between the San Andres archipelago and the Colombian coastal areas. Queen conch in these areas exhibited an overall deficit of heterozygosity related to assortative mating or inbreeding, potentially leading to a loss in genetic variation (Márquez-Pretel et al. 2013). Similarly, Zamora-Bustillos et al. (2011) observed significant genetic deviation in two populations in Mexico (Alacranes Reef and Chinchorro Bank) due to a deficit in heterozygotes but attributed it to inbreeding as a consequence of overfishing. However, Zamora-Bustillos et al. (2011) reported significant levels of gene flow between both populations and concluded that these were part of a single panmictic population in the Yucatan Peninsula.

Truelove et al. (2017) used nine microsatellites to genetically characterize 643 individuals from 19 locations including Florida, The Bahamas, Anguilla, the Caribbean Netherlands, Jamaica, Honduras, Belize, and Mexico and determined that queen conch do not form a single panmictic population in the greater Caribbean. The authors reported significant differentiation between and within jurisdictions and among sites irrespective of geographic location. Gene flow was constrained by oceanic distance and local populations tended to be genetically isolated. Most recently, genetic investigations using SNPs have shown both low and high levels of genetic differentiation within the Caribbean basin. Douglas et al. (2021) identified distinct populations on the south side of Grand Bahama Island and the west side of Eleuthera Island potentially due to larval separation by the Great Bahama Canyon. Despite extensive spatial separation of sampled populations around Puerto Rico, Beltrán (2019) concluded that there was little genetic structure in the conch population. However, genetic analyses of four visually characterized phenotypes showed that one morph (designated as Flin) was slightly differentiated from the other phenotypes sampled. Further research into this aspect of queen conch biology is needed to

examine the degree of differentiation between phenotypes and if they share the same distribution across the Caribbean region. The results presented in all of these studies provide evidence that variation in marine currents, surface winds, and meteorological events can either promote larval dispersal or act as barriers enhancing larval retention.

Conch Habitat Estimate

The SRT estimated the total area of conch habitat and prepared a spatially explicit map for the greater Caribbean region. This spatially explicit conch habitat estimate was necessary in order for the SRT to estimate total abundance and conduct the population connectivity analysis. To develop an estimate of habitat area, the SRT conducted an extensive search for the best available habitat information, contacting researchers and institutions involved in various mapping efforts. Available estimates to satisfy the SRT's requirements were limited, given that the SRT required a defensible estimate of habitat area that was available and comparable across the entire range of the species. The most comprehensive and suitable publicly-available habitat map that could be found was the Millennium Coral Mapping Project (Andréfouët 2008; IMaRS-USF 2005; IMaRS-USF and IRD 2005; Spalding et al. 2001; UNEP-WCMC 2021), which specifies 1,359 8-km by 8-km polygons (Holstein et al. 2014; Staaterman et al. 2013) based on coral reef locations. The polygons included seagrass and coral reef locations where conch occur (Kough et al. 2019; Souza Jr. and Kough 2020). From this data source, only polygons with centroid depth between 0 and 20 m were considered as conch habitat, as the majority of conch and spawning habitat occurs in waters less than 20 m depth. The SRT determined that 0-20 m habitat area would represent a best estimate given the available information indicates that conch are found in shallow waters generally less than 20 m depth (Berg Jr. et al. 1992; Boidron-Metairon 1992; Delgado and Glazer 2020; Salley 1986; Stoner and Sandt 1992; Stoner and Schwarte 1994). In addition, the SRT noted that primary conch habitat is likely limited to that depth range by seagrass and algae cover, which are their preferred habitats. The jurisdiction-specific (or in some cases, bank-specific) areal estimates were calculated by summing the area of the polygons, within the 0-20 m depth range, and are reported in Table 2.

The SRT validated the habitat map with a list of published spawning sites (Berg Jr. et al. 1992; Boidron-Metairon 1992; Brownell 1977; Cala et al. 2013; Coulston et al. 1987; D'Asaro 1965; Davis et al. 1984; de Graaf et al. 2014; García E. et al. 1992; Lagos-Bayona et al. 1996; Márquez-Pretel et al. 1994; Meijer zu Schlochtern 2014; Pérez-Pérez and Aldana Aranda 2003; Randall 1964; Stoner et al. 1992; Stoner and Schwarte 1994; Truelove et al. 2017; Weil and Laughlin 1984; Wicklund et al. 1991; Wilkins et al. 1987; Wynne et al. 2016). This step was carried out to ensure the habitat map was covering these notable areas of high conch densities. Following this review, the SRT incorporated 13 shallow polygons not initially present in our habitat layer in St. Eustatius, USVI, Colombia, Florida, Mexico, Jamaica, Saba, Bonaire, and The Bahamas (Meijer zu Schlochtern 2014; Randall 1964; Coulston et al. 1987; Garcia E. et al. 1992; Márquez-Pretel et al. 1994; Truelove et al. 2017). The SRT also included 13 additional deep spawning sites located outside of our polygons for Venezuela, Cuba, The Bahamas, USVI, Turks and Caicos, Saba, Colombia, Belize, Honduras, and Jamaica (Brownell 1977; Cala et al. 2013; Davis et al. 1984; de Graaf et al. 2014; Lagos-Bayona et al. 1996; Randall 1964; Stoner et al. 1992; Truelove et al. 2017; Weil and Laughlin 1984; Wicklund et al. 1991).

To confirm habitat areas were generally at the correct magnitude, the SRT compared the selected habitat estimates with alternative habitat area estimates (e.g., those that were available

for only parts of the species range) by compiling estimates of seagrass habitat cover and conch fishing areas from the literature (Figure 5). Other available estimates of seagrass that were considered included compilations of global geomorphic zones (UNEP-WCMC and Short 2021; Allen Coral Atlas 2020; McKenzie et al. 2020; Schill et al. 2021), and studies focused on jurisdictions or regional levels (Colete et al. 2008; Leon-Perez et al. 2019; Tewfik et al. 2017). These studies use different methodologies to estimate the aerial coverage of seagrass meadows, mostly a combination of high resolution satellite imagery, models, and corrections based on data collections. For example, The Nature Conservancy dataset incorporates high-resolution satellite images, aerial fly-over technology, drones, and divers to estimate benthic habitat classes, but are only available for the insular Caribbean (Schill et al. 2021). Fishing bank areas were derived from Prada et al. (2017) based on national reports presented at the First and Second meeting of the Western Central Atlantic Fishery Commission/Caribbean Fisheries Management Council/Caribbean Fisheries Regional Mechanism and the Organization del Sector Pesquero y Acuicola del Istmo Centroamericano Working Group. Of note, the fishing bank area estimates are not always directly comparable; in some cases the entire geographical area of a shelf or bank was reported (e.g., the total area from surface to a given depth), whereas in other cases, areal estimates were defined for specific areas over which the fisheries were known to operate (e.g., a specific region within a bank).

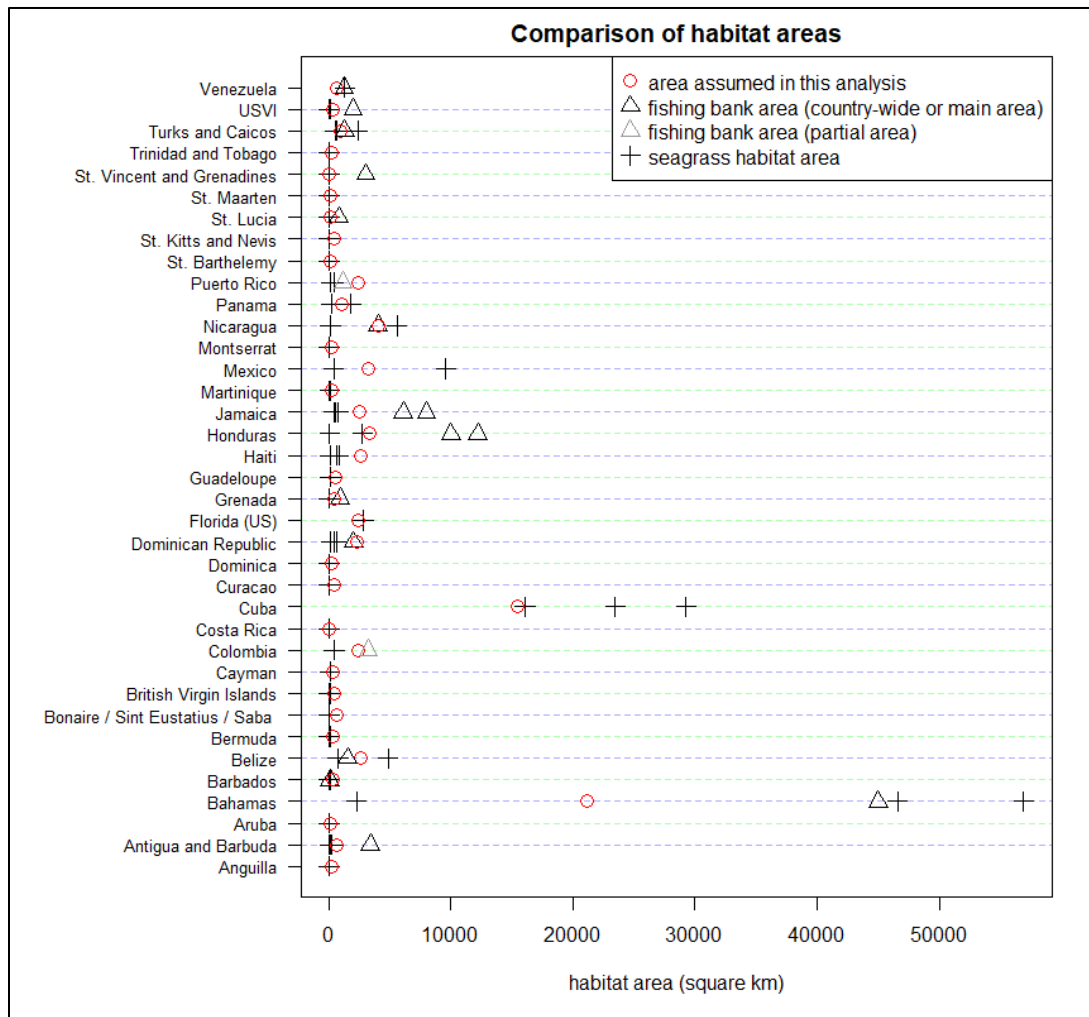


Figure 5. Estimates of areal habitat coverage by jurisdiction. Plus symbols (+) pertain to estimates of seagrass habitat coverage from various sources and triangles (Δ) represent estimated areas of conch fishing banks from the literature. Red circles show the estimated habitat areas from the data source selected for use in the present analysis. Figure used with permission from Vaz et al. (2022).

Estimates of seagrass area by jurisdiction were highly variable, and estimates of conch fishing areas are generally much lower than the highest estimates of seagrass cover (Figure 5). Overall, the habitat area estimates from the data source selected by the SRT were much lower than total seagrass area estimates, and generally range from ~30%-100% of the area of the fishing bank estimates (Figure 5). There is only one case (Belize) where the habitat estimate is significantly greater than the fishing bank area estimate; however, the fishing bank area estimate only includes offshore areas. Additionally, the habitat estimate for Belize is lower than one estimate of total seagrass cover (Schill et al. 2021). Thus, the SRT concluded that the habitat estimates were likely conservative but suitable for analysis of general connectivity patterns and estimation of minimum population abundance.

Density Estimates

In order to develop estimates of conch density, the SRT conducted a comprehensive, jurisdiction-by-jurisdiction search to identify literature pertaining to the status of queen conch throughout its range. The SRT reviewed the best scientific and commercial information

including all relevant published and grey literature, databases, and reports. The SRT organized this information and data by jurisdiction and searched systematically for information regarding estimated conch densities. The SRT also considered any relevant information provided during the public comment period (84 FR 66885, December 6, 2019). The goal was to compile robust, cross-shelf adult conch density estimates for each jurisdiction, and so, to the extent possible, the SRT focused on the most recent studies where randomized sampling was conducted across broad areas of the shelf, including a range of habitats and depths. For jurisdictions where such studies were not available, the SRT used any available density information; for example, in some cases the only available data were single point estimates from a study or workshop report. In the case of jurisdiction where no density data were available, the SRT used a nearest-neighbor approach to borrow density estimates from neighboring locations. In these cases, the SRT used any available qualitative information on the general population status (e.g., severely depleted, moderately fished, lightly exploited) to ensure that the nearest neighbor approach was reasonable.

From each study or report compiled, the SRT noted the location, year of the survey, total area surveyed, status (fished, unfished) of the area surveyed, and the survey methods used. The SRT extracted information on the overall density and/or the adult density of conch and recorded these in a spreadsheet and standardized to a per hectare unit (File S5). For jurisdiction with large shelf areas (e.g., Bahamas, Belize, Mexico) densities were recorded at the sub-jurisdiction level (e.g., as defined by region, bank, or cardinal direction from an island). For smaller jurisdiction (e.g., those within the Lesser Antilles) densities were typically reported for entire islands or island groups. Most studies reported a global average for a given region and year within the text, but in cases where more detailed depth-specific or habitat-specific densities were reported, they were averaged to produce a single estimate (weighted averages were used when areas surveyed were also reported). Many studies reported adult densities separately; however, the definition of “adult conch” was variable as it was sometimes defined as a function of shell length and other times as lip thickness. Occasionally the densities of different stages of adults (e.g., mature or older “stoned” conch) were reported separately; in these cases the densities of both mature and stoned conch were summed (subadults were not considered in the adult density estimates when they were reported separately). In some studies, overall density estimates were reported alongside estimates of the percentages of adults in the population and/or length frequency data; in these cases, percentages were multiplied by the overall densities to obtain the estimates of adult conch densities. In a few cases, no adult densities were reported, only overall densities. In these cases, the SRT used the global average percentage of adult/overall conch densities across all jurisdiction, where both metrics were reported (this value was 46.0%). Lastly, there were several cases where the densities were only reported graphically; in these cases, the SRT extracted the exact numbers using the *digitize* package in R.

The above literature search methods were translated to a database containing the suite of conch density estimates for each jurisdiction from all available studies over time, which was then further synthesized on a per-jurisdiction basis (File S5). For jurisdiction with large shelf areas and where data were available across multiple regions or distinct islands and banks (The Bahamas, Belize, Colombia, Honduras, Mexico), the SRT analyzed regional patterns to understand whether conch densities varied significantly across areas. Of these jurisdictions, only The Bahamas and Colombia appeared to have densities that varied significantly among regions (banks) and separate density estimates were created for these areas accordingly.

To quantify recent adult conch density for each jurisdiction, the SRT subset the data for all years including and after the year 2000. In the few cases where data were rare or absent within this timeframe (Bermuda, Dominican Republic), the SRT included data from the late 1990s. From this subset of data, the SRT took the available set of estimates of the adult conch mean densities by survey, and treated them as independent samples, fitting a univariate distribution to understand the dispersion and central tendency of the set of estimates. For each jurisdiction and set of data, the SRT fit normal, lognormal, and Weibull distributions using maximum likelihood estimation (via the *fitdistrplus* package in R) and compared the model fits using the Akaike information criterion. A best fitting model was determined by the lowest AIC value, and the resulting parameter estimates were recorded to specify a distribution representing the adult conch density estimates for each jurisdiction or bank. Because most of the distributions of the independent mean estimates were non normal, the SRT reported the summary median of the distribution of estimated mean conch densities. When only two estimates were available, a uniform distribution between the two points was assumed, and when a single estimate was available it was used as the density estimate, with its associated variance when reported. Table 2 summarizes the resulting adult conch density estimate values developed by the SRT for each jurisdiction, including the data sources and treatment used.

Table 2. Median value of the distribution of adult conch densities from the set of available surveys for each jurisdiction or bank, the estimated habitat area for each country or bank, and descriptions of the data sources used to support the density estimates.

Jurisdiction or bank	Latitude	Longitude	Estimated habitat area (km ²)	Adult conch density (/ha)	Nature of data sources used to support the estimate
Anguilla	18.2	-63.1	215.7	24.3	Two studies available from 2011 and 2015; means and standard deviations reported
Antigua and Barbuda	17.1	-61.8	593.1	29.0	Single point estimate available for 2013 study; mean and standard deviation reported
Aruba	12.5	-70	161.8	11.3	Point estimate from a single 2011 study
Bahamas - Western Great Bahama Bank			21135.4	47.3	Used all data from Stoner et al. 2019a which had comprehensive surveys from 2009 – 2017; high variability among regions warranted separation. However, many habitat cells were located well outside survey areas and there was risk in extrapolating very high or low density estimates into these areas. For the connectivity modeling, habitat cells were assigned densities based on subregional (bank specific) numbers. For the derivation of abundance estimates, a single density distribution (with a median of 47.3 conch/ha) was extrapolated across total habitat areas.
Bahamas - Western Great Bahama Bank	25.1	-77.8		6.2	
Bahamas - Little Bahama Bank	26.8	-77.8		16.1	
Bahamas - Cay Sal	23.5	-80		187.6	
Bahamas - Central Great Bahama Bank	23.9	-76.2		9.6	

Jurisdiction or bank	Latitude	Longitude	Estimated habitat area (km ²)	Adult conch density (/ha)	Nature of data sources used to support the estimate
Bahamas - Jumentos and Ragged	22.7	-75.7		137.1	
Barbados	13.2	-59.5	269.6	1.4	Single study from 2006 reported estimates for 2007 and 2008
Belize	17.2	-88.5	2588	17.4	Distribution derived from fished and unfished sampling points across jurisdiction reported 2003 – 2018; weighted average of unfished vs. fished densities based on ~15% total area protected (Dahlgren 2014)
Bermuda	32.3	-64.8	269.6	0.5	Single point estimate available from 1992 study; reported mean and standard deviation across shelf
Bonaire	12.2	-68.3	269.6	9.6	Single point estimate for study from 2010
British Virgin Islands	18.4	-64.6	431.3	24.7	Distribution derived from single 2003 study; only overall densities reported; average mean length reported was 14.4 cm which suggests that less than half are adults; used global conversion ratio of 0.46
Cayman Islands	19.3	-81.3	269.6	63.8	Jurisdiction-wide estimates available from 2000 – 2008; overall densities were reported; used global conversion factor of 0.46
Colombia - mainland	10.9	-75.2	1401.8	2.4	Distributions derived from sites sampled from numerous studies and reports from 2003 – 2019; high variability among banks warranted separation by region
Colombia - Quitasueño Bank	14.3	-81.2	485.3	8.0	
Colombia - Serrana Bank	14.4	-80.3	161.8	103.5	
Colombia - Serranilla Bank	15.9	-79.9	377.4	24.5	
Costa Rica	9.7	-83.8	53.9	207.3	No density information available - no commercial fishery and uncommon in local diet; unlikely to be heavily exploited so borrowed from Nicaragua which has relatively high densities

Jurisdiction or bank	Latitude	Longitude	Estimated habitat area (km ²)	Adult conch density (/ha)	Nature of data sources used to support the estimate
Cuba	21.5	-77.8	15420.2	285.1	Used average across 3 sites from only available study in unfished sites (2009); assume 26% of waters are unfished and that fished areas are depleted by 20% as per stated management targets
Curaçao	12.2	-69	377.4	9.6	No density information available - borrowed from nearest neighbor (Bonaire)
Dominica	15.4	-61.4	215.7	20	No density information available - borrowed from nearest neighbor (Martinique)
Dominican Republic	18.7	-70.2	2318.4	2.5	Distribution derived from 4 studies 1996 – 2000; earlier years used in estimate because only one estimate from 2000 available
Grenada	12.1	-61.7	377.4	26.9	No density information available - borrowed from nearest neighbor (Saint Vincent)
Guadeloupe	16.3	-61.6	485.3	9.6	Distribution derived from single comprehensive 2009 study reporting densities in regions across the jurisdiction; weighted by area
Haiti	19	-72.3	2641.9	4.7	Distribution derived from comprehensive 2010 study reporting densities in regions across the jurisdiction from 2007 – 2009 data collections
Honduras	15.2	-86.2	3342.9	61.9	Distribution derived from 3 banks sampled from 2009 – 2011; average densities by region weighted by survey area; only overall abundances reported; used global conversion ratio of 0.46
Jamaica	18.1	-77.3	2480.2	133.7	Distribution derived from numerous Pedro Bank studies from 2002 – 2018; only one study reported overall and adult densities; used reported ratio of 0.65 and applied to overall densities from all studies
Martinique	14.6	-61	215.7	20.0	Single point estimate available from FAO report in 2012

Jurisdiction or bank	Latitude	Longitude	Estimated habitat area (km ²)	Adult conch density (/ha)	Nature of data sources used to support the estimate
Mexico	19.9	-87.4	3181.1	33.8	Distribution derived from fished sites reported across jurisdiction from 2000 – 2013; high densities from tiny private marine park were excluded as negligible
Montserrat	16.7	-62.2	215.7	29.0	No density information available - was threatened in the 1980s and high local demand - borrowed from nearest neighbor (Antigua & Barbuda)
Nicaragua	12.9	-85.2	4097.7	207.1	Distribution derived from single study from 2009 reporting regional densities across three seasons
Panama	8.5	-80.8	1024.4	0.2	Point estimate from one CITES reference from 2000
Saba	17.6	-63.2	269.6	128.3	Two studies based on Saba Bank conducted from 2013 – 2015; reported bank-wide mean and standard deviation
Saint Kitts and Nevis	17.4	-62.8	377.4	96.4	No density information available - heavily managed and major exporter - borrowed from nearest neighbor (Sint-Eustatius)
Saint Lucia	13.9	-61	161.8	111.7	Single report from 2010 with island wide average; assumed to be overall density and converted to adult density with global conversion of 0.46
Saint Martin	18.1	-63.1	107.8	24.3	No density information available - borrowed from nearest neighbor (Anguilla)
Saint Vincent and the Grenadines	13	-61.3	53.9	26.9	Single study from 2016; offshore island averages reported for 2013 and 2016
Saint Barthelemy	17.9	-62.8	107.8	24.3	No density information available - borrowed from nearest neighbor (Anguilla)
Sint Eustatius	17.5	-63	53.9	96.4	Distribution derived from comprehensive studies conducted from 2013 – 2014 reporting island-wide densities

Jurisdiction or bank	Latitude	Longitude	Estimated habitat area (km ²)	Adult conch density (/ha)	Nature of data sources used to support the estimate
Trinidad and Tobago	10.7	-61.2	215.7	19.5	No density info but thought to be highly exploited - borrowed from nearest neighbor (Venezuela)
Turks and Caicos Islands	21.7	-71.8	970.5	180.9	Distribution derived from studies conducted in 2001 – 2015; used area-weighted average between fished and unfished areas when reported separately
United States - Florida	27.7	-81.5	2372.3	7.0	Average from studies of non-aggregation sites from 2012 – 2019; cross-shelf densities from Glazer 2020 were derived by dividing total abundance estimates by statistical sampling domain
United States - Puerto Rico	18.2	-66.6	2372.3	6.1	Derived distribution from sites in east, west, and south from 2001 – 2013; excluded unfished mesophotic site with higher density (reported separately)
United States - Puerto Rico mesophotic reef	18	-67.4	NA	54.6	Unfished mesophotic site is only location where densities are over 20 conch/ha; reported separately
United States Virgin Islands	18.3	-64.9	323.5	44.5	Derived from all estimates from 3 islands; surveys done 2001 – 2011; most data are from St. Croix
Venezuela	10.7	-66.2	593.1	19.5	Single study available from 2006; distribution derived from weighted average by area for 3 regions reported

The adult queen conch density estimates reported in Table 2 are plotted by their geographical location (Figure 6). Data points are color coded according to where the density estimates fall with respect to the important thresholds defined by the SRT (see *Spawning Density* section). Populations with green circles indicate densities greater than 100 adult conch/ha, a density considered to support reproductive activity and population growth (UNEP 2012). Those areas indicated in gold had estimated adult densities of 50-99.9 conch/ha, a density associated with reduced reproduction (Appeldoorn 1988c; Stoner and Ray-Culp 2000). Areas indicated by red circles had adult conch densities below 50 adult conch/ha, densities associated with likely Allee effects and limited viable reproduction (Stoner and Ray-Culp 2000; Stoner et al. 2012b; UNEP 2012). Jurisdictions located in the north-central to the southwestern Caribbean (Turks and Caicos, the southern Bahamas, and Cuba to Jamaica and Nicaragua) tended to have higher densities. The remainder of the region, with a few exceptions, had reported adult queen conch densities that were near or below the 50 conch/ha threshold.

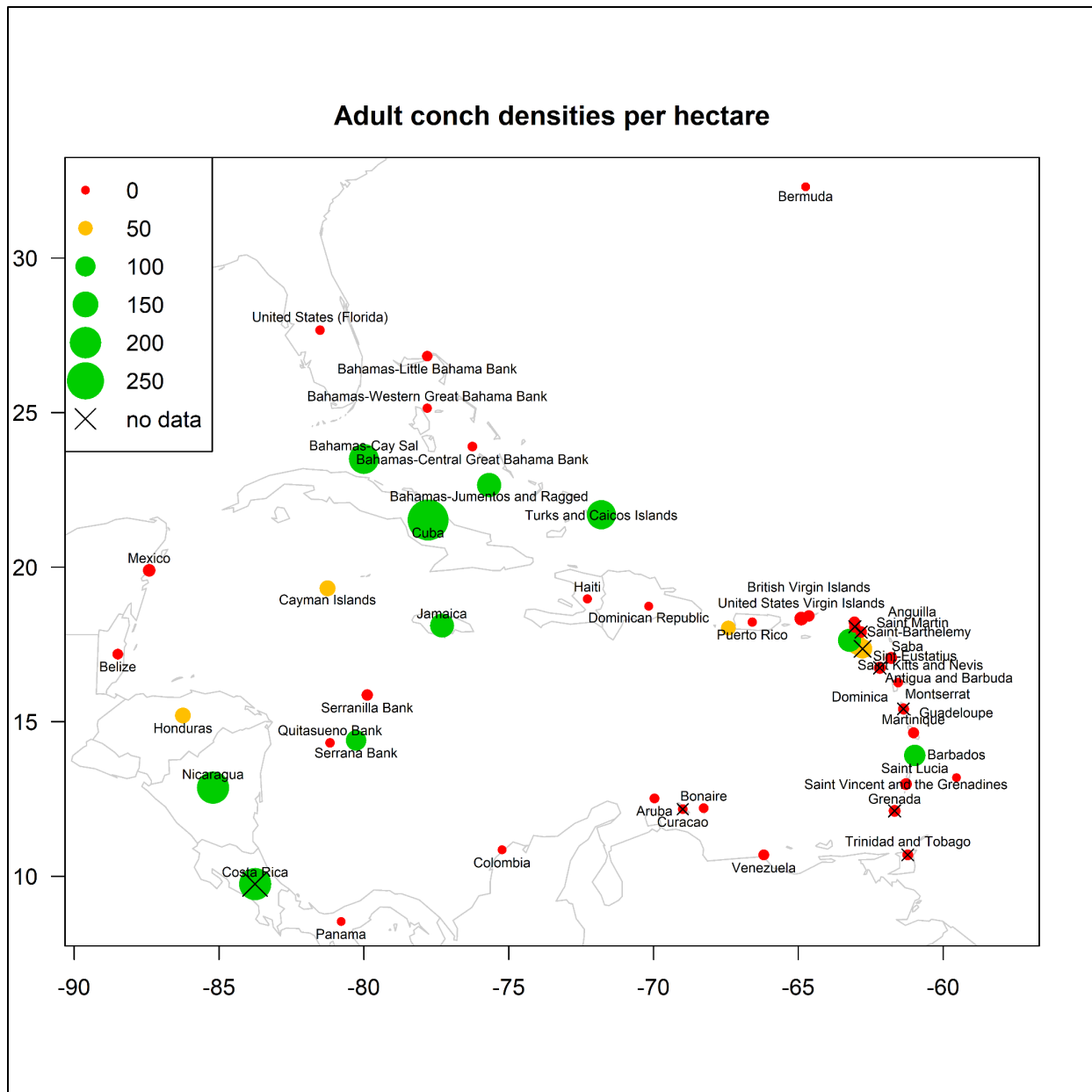


Figure 6. Estimated adult conch densities for jurisdiction within the species range. Data points are sized relative to densities; green symbols indicate conch populations with >100 adult conch/ha, gold symbols indicate 50-99.9 adult conch/ha, and red symbols indicate <50 adult conch/ha. Countries without density data and relying on borrowed values are indicated with an X. Where densities are summarized on a country level, the points appear at the approximate center point of the country; where densities are summarized on a sub regional level the points appear at the location of fishing banks or sub regions. Figure used with permission from Vaz et al. (2022).

The SRT plotted each jurisdiction’s compiled conch densities over time (Figure 7). Data were sufficient in some cases (e.g., Belize, Mexico, Puerto Rico, The Bahamas, and the U.S. Virgin Islands) to follow adult densities over several decades (~1980s – present). Estimates of adult density within each of those areas varied among reports for each year, but in recent years were generally below 100 adult conch/ha which is recognized as a critical threshold to support reproductive activity (UNEP 2012; see *Spawning Density* section). There is substantial heterogeneity in densities that exists due to depth or habitat factors, as can be seen in the

available confidence intervals that are plotted (where within-study variability measures were reported). The high within-year variability among density estimates may be due, in part, to surveys conducted in different areas within a jurisdiction. This is the case in Colombia, for example, where conch densities are reported for several banks and shoals distant from the mainland, and along mainland Colombia. Adult conch density estimates vary widely among those locations (estimated density at Serrana Bank was 103.5 conch/ha, but mainland Colombia estimated adult density was 2.4 conch/ha). Within the Bahamas, adult conch densities vary among locations with densities well above 100 conch/ha in the southern Bahamas and at Cay Sal Bank, but densities below 50 adults/ha occur in central and northern Bahamas (Table 2). In Puerto Rico, adult densities have increased over time (note the log scale, Figure 7), but remain below the minimum required critical threshold to support significant reproductive activity (i.e., 50 adult conch/ha; see *Spawning Density* section). In the U.S. Virgin Islands, adult conch densities have also increased, in some locations, with recent estimates near or exceeding 100 conch/ha (Doerr and Hill 2018). Adult densities in Florida were estimated to be much higher in recent years than densities in the late 1980s and early 1990s. That change, however, may be partially attributable to survey methodology changes; the early Florida surveys were random transects, but surveys that are more recent have targeted known conch aggregations (Delgado and Glazer 2020). For most jurisdiction, data were insufficient to provide density over time.

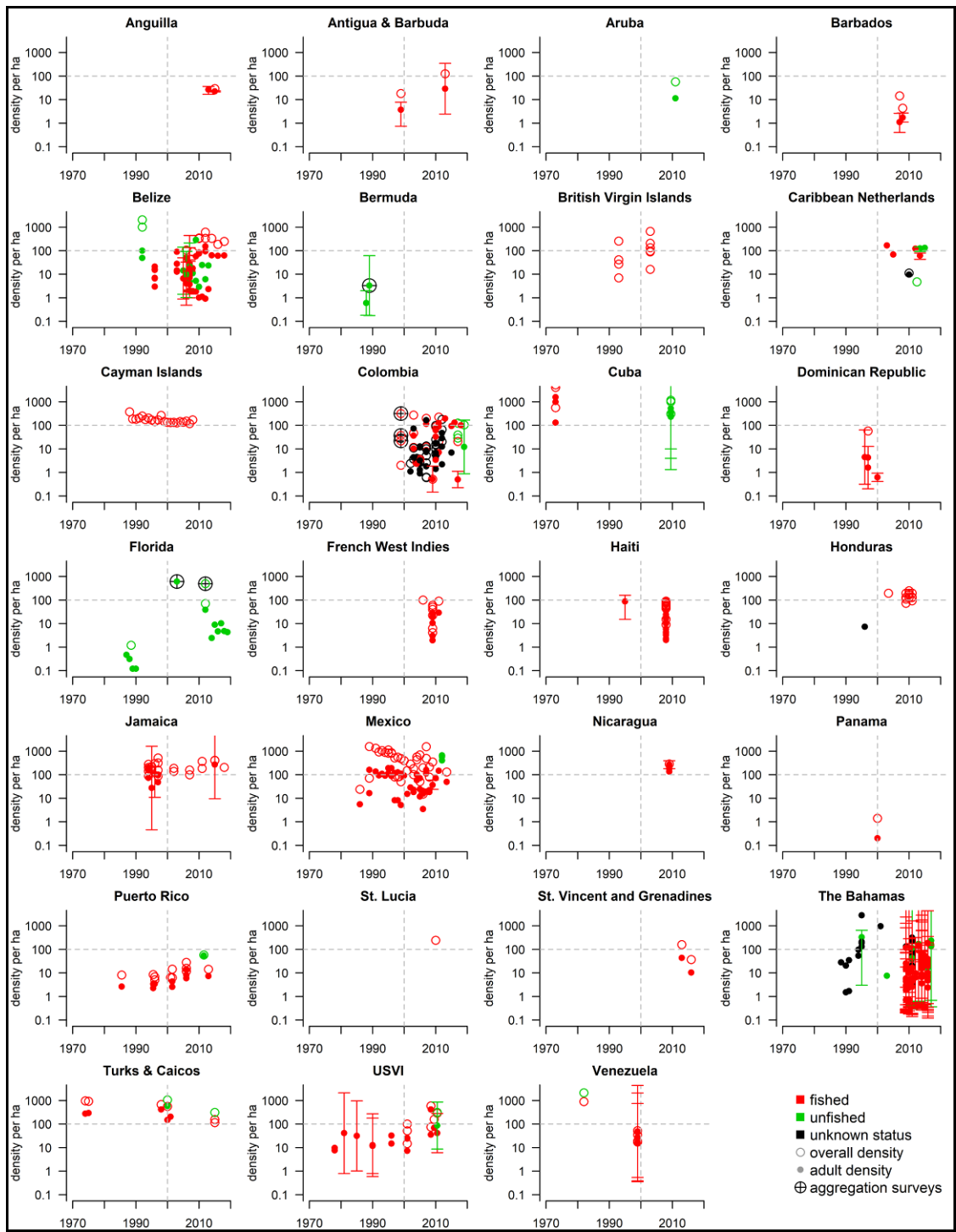


Figure 7. Adult queen conch per hectare by jurisdiction over time. Horizontal dashed line is 100 conch/ha; vertical dashed line is at the year 2000. Error bars represent reported range of estimates or 95% confidence intervals.

Population Abundance Estimates

The SRT reviewed approximately 40 jurisdictions and their major fishing banks, throughout the species range (See Supplement 4). The SRT developed total adult population abundance estimates for each jurisdiction, by extrapolating the conch density estimates across the estimated conch habitat areas, using the following equation:

$$N_c = D_c \times A_c$$

where N is the total adult conch population abundance estimate, D is a jurisdiction-specific density estimate in units of adult conch per hectare, sampled from the distribution of available data (Figure 8), and A is the estimated conch habitat area in hectares (taken from Table 2) for each jurisdiction c . This extrapolation implies an assumption that all estimated conch habitat areas in each jurisdiction support equal densities of conch. In jurisdictions where comprehensive surveys were carried out across all areas of the shelf, the mean estimates reported from each survey typically take into account any sub-jurisdiction level variability in conch densities; however, in cases where extrapolations were based on only a few reported estimates or sampling that was done over a limited area, this assumption may be violated. In most studies, conch densities were surveyed across various habitat types (including those types supporting few or no conch) and weighted averages were reported; thus those survey means account for areas of both high and low density. The SRT extrapolated abundances directly based on these estimates and thus the abundance estimates should be robust to potential bias from habitat variability. The SRT notes that these density estimates rely largely on surveys that are routinely used for such extrapolations to estimate total abundance of queen conch over a given region. Additionally, the SRT made efforts to quantify the uncertainty inherent in basing the abundance estimates on survey data reported over a wide time span and range of spatial scales. To carry the uncertainty in the set of reported mean density estimates through to the total population estimates, 100,000 random draws were made from each jurisdiction-specific distribution (Figure 8) and then multiplied by the estimated habitat area; the total population estimates are therefore reported as distributions (Figure 9).

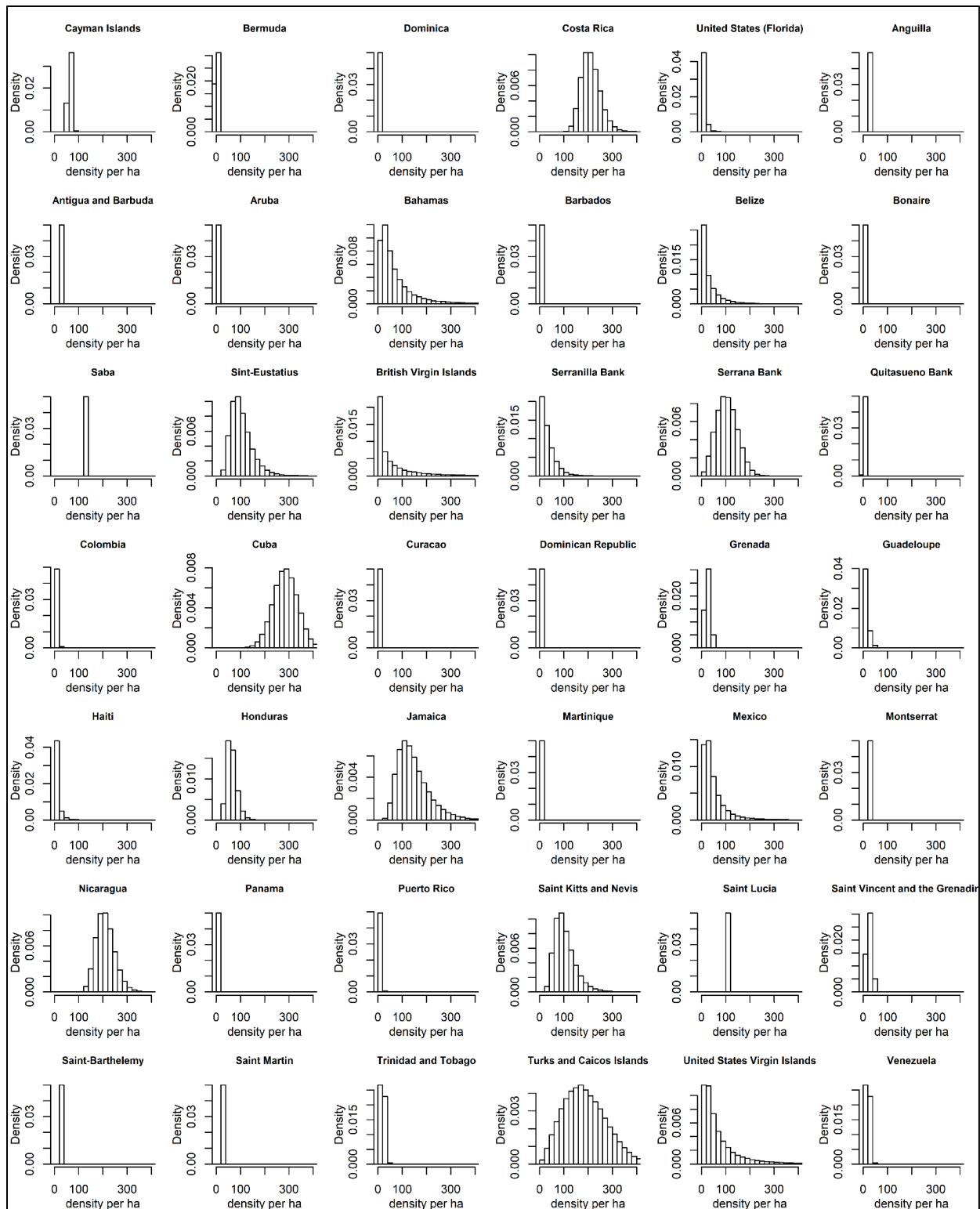


Figure 8. Histograms showing distributions of reported adult conch densities that were multiplied by the estimated habitat area to derive abundance estimates.

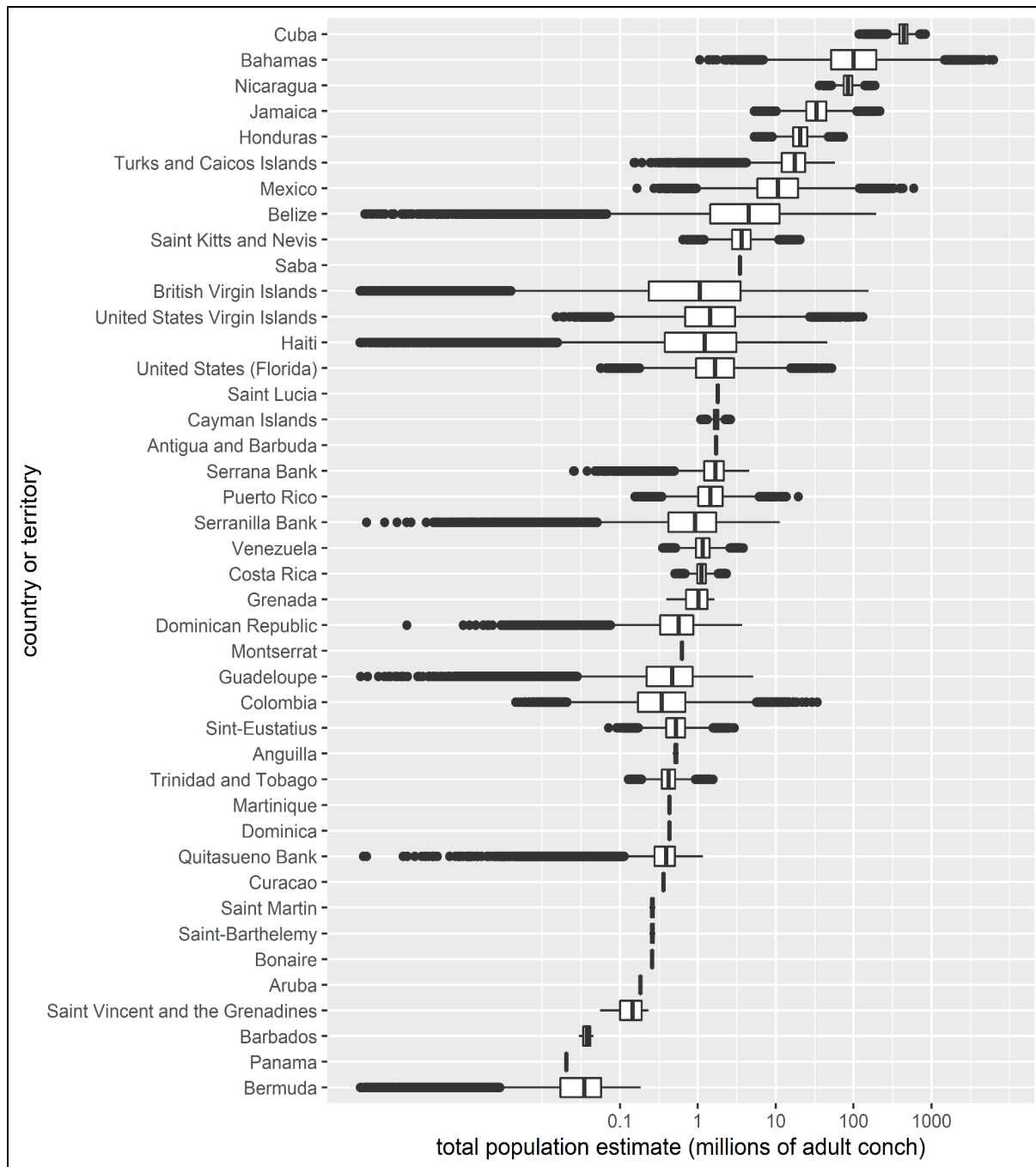


Figure 9. The estimated adult population size (individuals) by jurisdiction. Distributional estimates as box and whisker plots; boxes denote interquartile range and points denote the full range of possible estimates. Note log scale.

Estimates of adult queen conch population size are provided by jurisdiction in Figure 9. The median of the estimated population size in Cuba exceeded 400 million adult conch. Adult conch abundance was estimated to be between ten and 100 million individuals in six jurisdictions, and 15 jurisdictions had median estimated abundances between one and ten million adults. Estimated adult population size was less than one million adults in each of 20 jurisdictions, with three of those jurisdictions estimated to have populations of fewer than 100,000 adult queen conch. Total adult queen conch estimated abundance (i.e., the sum of median estimated abundance across all

jurisdictions) was 743 million individuals (90% confidence interval of 451 million to 1.49 billion). Seven jurisdictions (i.e., Cuba, Bahamas, Nicaragua, Jamaica, Honduras, the Turks and Caicos Islands, and Mexico) accounted for 95% of the population of adult queen conch (Figure 10). Note that these estimates are associated with substantial uncertainty as indicated by the spread in the boxplots, and should be treated with caution as they are based on data of varying quantity and quality by jurisdiction. Additionally, unpublished deeper water (>20 m) habitats are largely unaccounted for in these estimates and the estimates may be conservative in some jurisdictions.

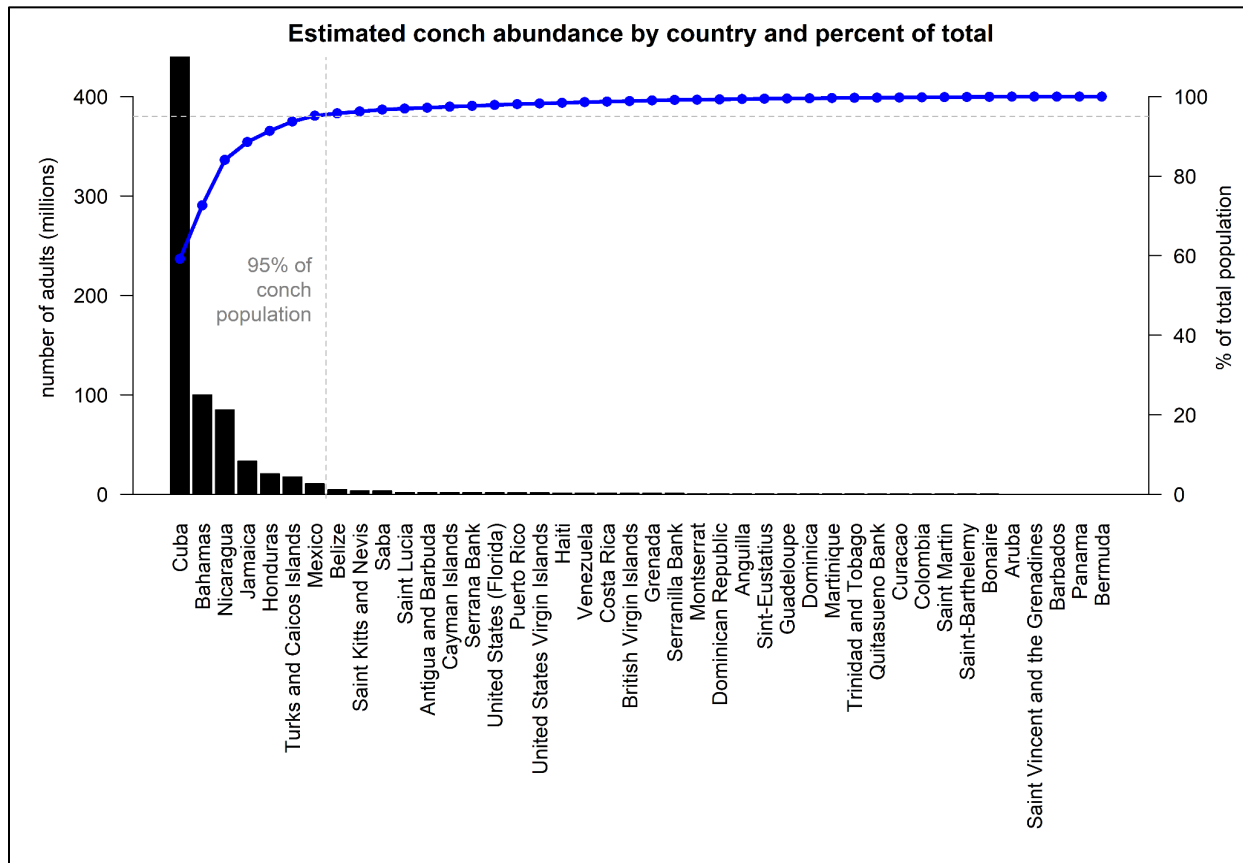


Figure 10. Estimated conch abundance by jurisdiction. Vertical dashed line indicates the jurisdictions that account for 95% of the total estimated population of adult queen conch.

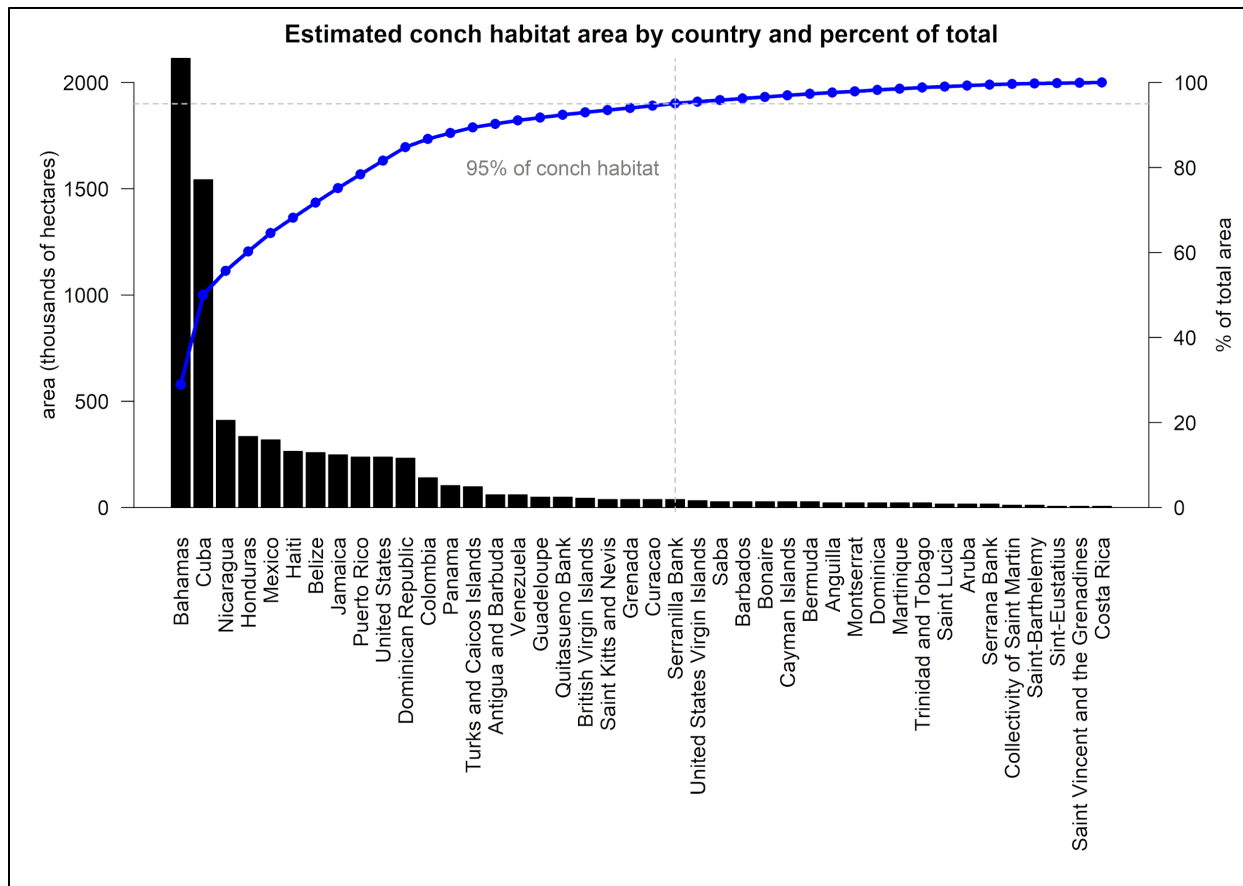


Figure 11. Estimated conch habitat by jurisdiction. Jurisdictions are ordered by amount of estimated conch habitat in descending order, left to right. Countries to the left of the vertical dashed line collectively account for 95% of the total amount of estimated conch habitat across all jurisdictions.

Three jurisdictions (i.e., Bahamas, Cuba, and Nicaragua) comprise about half of the estimated queen conch habitat (55.6%) and the majority of adult population abundance (84.1%). Jamaica, Honduras, Turks and Caicos, and Mexico are other major contributors in terms of both habitat area and conch abundance (Figures 10, 11). Twenty-three jurisdictions make up 95% of the total estimated conch area, while only seven jurisdictions make up 95% of the total estimated abundance. This indicates that conch are depleted in many of those jurisdictions with large habitat areas, and the remaining population is concentrated in just a few jurisdictions.

The SRT’s abundance estimates should be used with caution, given that the density estimates on which they are based are sometimes outdated or based on sparse data or surveys conducted in limited areas. The number of available surveys with adult queen conch densities was often low (e.g., Cuba). The very high estimated abundance from Cuba is particularly uncertain due to the low sample size of survey data and the large shelf area over which the survey density data were expanded. In some cases (i.e., Costa Rica, Curaçao, Dominica, Grenada, St. Kitts and Nevis, St. Barthelemy, Monserrat, St. Martin, and Trinidad and Tobago), density estimates were borrowed from neighboring jurisdictions and these abundance estimates are also highly uncertain. The estimated conch habitat areas also introduce some uncertainty in the estimates, and the resolution of our habitat map is coarse.

Population Connectivity

The SRT evaluated queen conch population connectivity based on a simulation of the entire pelagic phase of the conch early life cycle, from the hatching of eggs to the settlement of conch veligers in suitable habitats (Vaz et al. 2022). To elucidate the potential impacts of localized low adult conch densities on population-wide patterns, the SRT carried out two sets of simulations. First, the connectivity patterns were simulated for uniform egg releases over the entire domain; this represents an “unexploited” spawning scenario in which all jurisdictions and areas have the same potential for reproductive, on a per-area basis. Second, present-day “exploited” reproductive output levels were simulated by scaling the number of eggs released (on a per-area basis, by jurisdiction or region) by the observed adult conch densities that were compiled (see aforementioned *Density Estimates*) and also accounting for Allee effects at very low densities (<50 adults/ha). In the absence of detailed information on size composition by jurisdiction, the SRT was forced to assume that the per-capita fecundity was consistent across all regions. Comparison of the two sets of simulations then offers insights into how overall exchange of larvae across the entire population range has been impacted by depletion of adult conch in certain areas (Figure 12, left versus right panels). Two different oceanographic models were used as the basis of the biophysical model, so uncertainty in the oceanographic inputs could be quantified (Figure 12, top panels versus bottom panels).

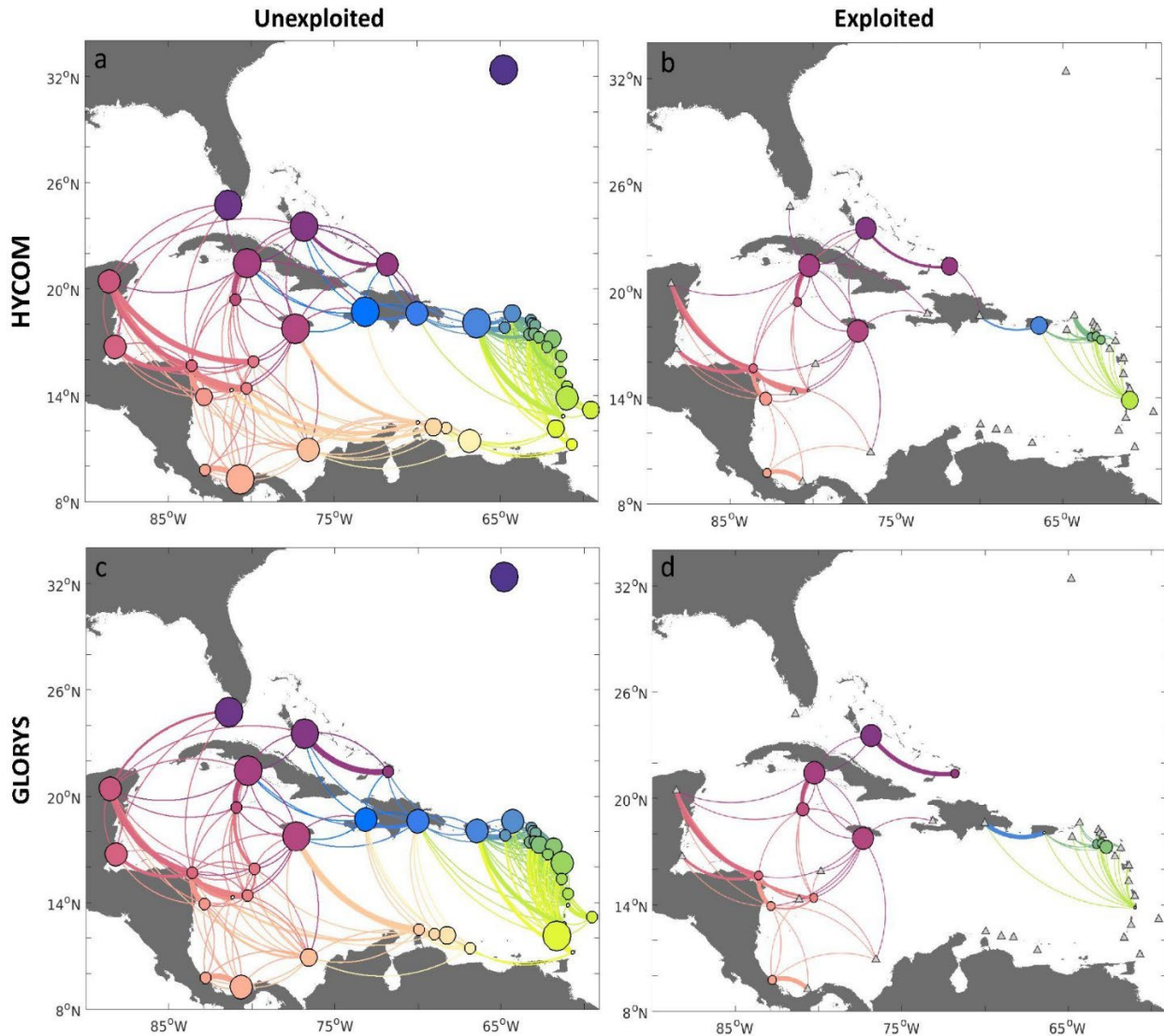


Figure 12. Connectivity networks for queen conch with a theoretical “unexploited” virgin stock with uniform spawning (a, c left column) and present day “exploited” stock reproductive output, i.e., spawning scaled by observed adult densities of conch on each jurisdiction and the Allee effect (b, d right column). Larvae are dispersed with a, b GIB-HyCOM velocities (top row), and c, d Mercator GLORYS12-V1 reanalysis (bottom row). To interpret the estimated direction of larval flow between countries, the arcs are followed in a clockwise direction and the thickness of the lines represents the strength of larval flow; node sizes represent the probability of self-settlement. For example, panel D indicates that Turks and Caicos Islands have relatively low self-settlement and export many of their larvae to The Bahamas, while The Bahamas has high-self-settlement and transports a smaller number of larvae to Turks and Caicos. Countries with no reproductive output on the present day scenario are marked with a triangle. Figure used with permission from Vaz et al. (2022).

Comparison of the two sets of simulations illustrates the population-level impact of heterogeneous patterns in densities of adult conch (Figure 12). The most apparent differences in the two sets of simulations emerge from the fact that many of the jurisdictions have conch densities well below the critical threshold for reproduction and are considered to be reproductively non-viable (Figure 6; see *Density Estimates* section). Within the present day “exploited stock” simulation, the SRT assumed no larvae are spawned from these jurisdictions; subsequently they can only act as sinks for larvae but are not sources for themselves or other

locations. Connectivity patterns emerging from present-day reproductive output simulations are thus drastically different (Figure 12). For example, due to their position up current and their small shelf areas, the Leeward and Windward Islands (i.e., Lesser Antilles) are estimated to be historically important for contributing larval input to other jurisdictions downstream (i.e., to the west). However, due to low adult conch densities in many of these jurisdictions, they no longer are expected to contribute larvae in the present-day exploited scenario, resulting in reduced larval input into the Greater Antilles and Colombia.

Other patterns in comparing the unexploited versus exploited simulations are more subtle, but would be locally significant. For example, historically the Turks and Caicos Islands is estimated to have received many larvae from the Dominican Republic and Haiti, which would have been important given its low local retention rate (Figure 12). However, due to low adult conch densities in these source jurisdictions, the present-day exploited scenario suggests that Turks and Caicos Islands are now entirely dependent on local production, and a substantial percentage of larvae are exported to The Bahamas. Likewise, the unexploited virgin stock simulation suggests that the United States (Florida) was dependent on relatively high local retention, with the most significant external source of larvae coming from Mexico (Figure 12, left column). Both Florida and Mexico are thought to now have very low adult densities (less than 50 conch/ha) unable to support reproductive activity; in other words, Florida currently has no significant upstream or local sources of larvae. This could explain why, despite a moratorium on fishing for several decades, Florida's conch population has been slow to recover (Glazer and Delgado 2020).

Some jurisdictions act as important “connectors” between different regions of the population as a whole, and could be important for maintaining genetic diversity. The importance of a jurisdiction in playing this role can be quantified mathematically as betweenness centrality (BC), which is a measure of the number of connections a jurisdiction has to other jurisdictions. Jurisdictions with high BC play critical roles in maintaining population connectivity. The unexploited simulation identified Jamaica, Cuba, and the Dominican Republic as having high BC, and to a lesser extent Puerto Rico and Colombia (Figure 13). This is not surprising given the relative central location of these jurisdictions and their shelves that are exposed to a diversity of ocean currents, which allows them to be “connectors” of larval flow. In contrast, jurisdictions located at the most up current (e.g., Leeward and Windward Islands or Lesser Antilles) or down current locations (e.g., Florida), or those located at the fringes of the region (e.g., Panama, Bermuda) are not important connectors of larval flow and, as expected, have low centrality measures (Figure 13).

The effects of localized areas of low adult conch densities that have been documented in recent years also influence the estimated connections between jurisdictions. One of the most significant changes is a result of the absence of reproductive output from Puerto Rico, Dominican Republic, and Haiti - these were jurisdictions with high centrality measures under the unexploited stock scenario, which, under the present-day exploited scenario, no longer function as important connectors (Figure 13). An almost complete break in the network is now apparent based on the present-day exploited scenario, with the Dominican Republic receiving limited larvae from Cuba, Turks and Caicos, and from a deep mesophotic reef off the west coast of Puerto Rico. While these three nodes have been removed from the chain of larval supply, Jamaica and Cuba remain important connectors in the western portion of the range, and some of the offshore banks in Colombia remain functional connectors (Figure 13). Although connections have been lost in other locations due to the existence of low adult conch densities in recent years, there are still

connection points, albeit reduced, that would allow some exchange of larvae and maintenance of some genetic diversity.

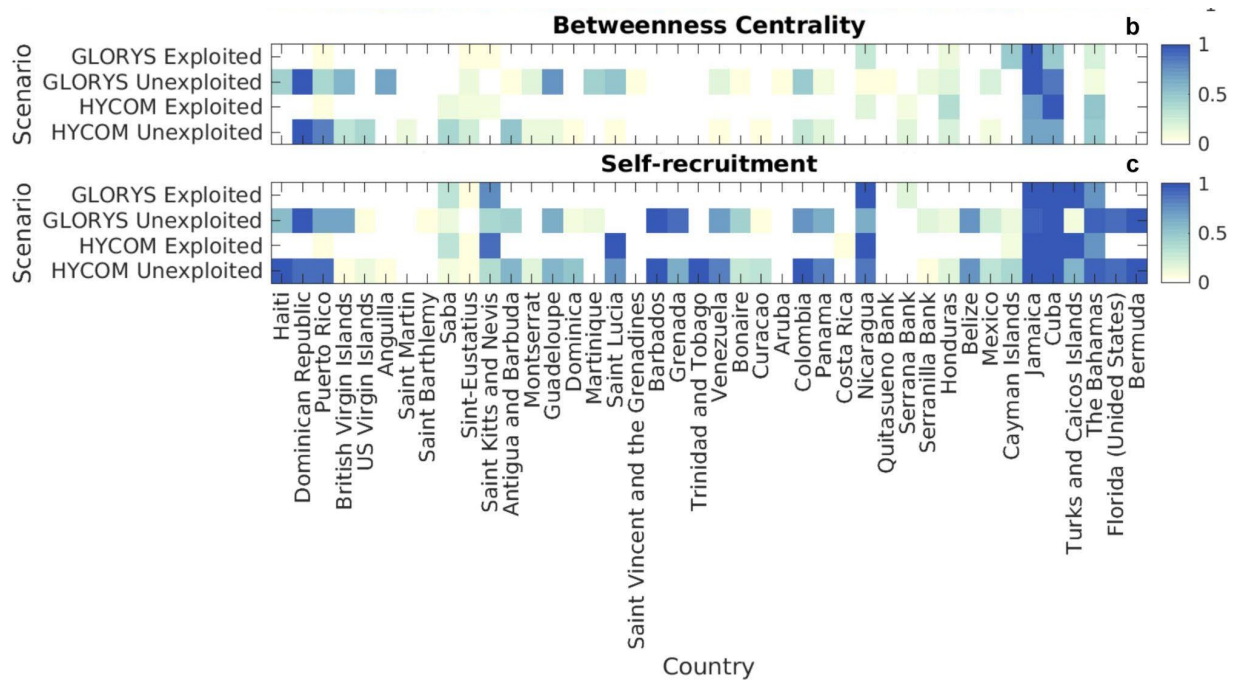


Figure 13. Relative Betweenness Centrality for each jurisdiction in the queen conch network. Panel (a) BC measures the fraction of shortest paths passing through a node (country) - higher values represent most central nodes (ecological corridors). Probability of self-recruitment for each country in the queen conch network (panel b) defined as the proportion of settlers spawned locally in a given country (local settlers over all settlers in a given country). Rows on each panel exhibit potential connections based on different hydrodynamic products (Mercator, GlbH), and reproductive output - “exploited” represent present-day reproductive output levels estimated from observed adult conch distributions, contrasted with a theoretical “unexploited” “virgin stock” spawning over all habitat units. Each node represents all polygons from individual countries along the Caribbean and Eastern Atlantic, organized in a clockwise direction from Haiti towards Bermuda. Figure used with permission from Vaz et al. (2022).

Analysis of the ESA Section 4(a)(1) Factors

Pursuant to the ESA and implementing regulations, NMFS determines whether species are threatened or endangered based on any one or a combination of the following Section 4(a)(1) factors: (1) the present or threatened destruction, modification, or curtailment of habitat or range; (2) overutilization for commercial, recreational, scientific, or educational purposes; (3) disease or predation; (4) inadequacy of existing regulatory mechanisms; and (5) other natural or man-made factors affecting the species’ existence. Below, the SRT provides information on threats from each of the five factors as they relate to queen conch.

Present or Threatened Destruction, Modification, or Curtailment of Habitat or Range

As discussed above, queen conch depend on seagrass meadows, algal plains, and/or sandy substrate associated with coral reef systems that encompass shallow (~0.3 m; Stoner and Lally 1994) to deeper depths (~35-50 m; García-Sais et al. 2012) over the course of their lives. Adult conch can be found in a wide range of environmental conditions (Stoner et al. 1994) such as in sand and algal or coral rubble (Acosta 2001; Stoner and Davis 2010); however, inshore movements to form summer spawning aggregations in shallower sand/seagrass meadows have been observed in a number of locations. Juvenile conch, on the other hand, appear to have more

specific habitat requirements (Stoner et al. 1994), and in large parts of their distribution range (e.g., The Bahamas) juvenile conch are associated primarily with native seagrass such as turtle grass (*Thalassia testudinum*) (Stoner 2003), which provides both nutrition and protection from predators (Ray and Stoner 1995; Stoner 2003; Stoner and Davis 2010).

The dietary needs of queen conch can help shed light on patterns of habitat use. The primary diet of juvenile conch consists of native seagrass detritus, and red and green macroalgae, primarily *Laurencia spp.* and *Batophora oerstedii* (Randall 1964; Serviere-Zaragoza et al. 2009; Stoner and Sandt 1992; Stoner and Waite 1991). The production of red and green algae, which can be highly variable, has been shown to directly affect the growth of juvenile conch (Stoner 2003; Stoner et al. 1994; Stoner et al. 1995). Organic material in the sediment (benthic diatoms and particulate organic matter) and cyanobacteria have also been suggested to be sources of nutrition to juvenile conch (Serviere-Zaragoza et al. 2009; Stoner et al. 1995; Stoner and Waite 1991). Given the wide variety of habitats occupied by different life stages throughout the range of queen conch, and a growing number of studies suggesting that the availability of a variety of habitat types may help to increase queen conch resilience over the long-term (Brownscombe et al. 2015; Doerr and Hill 2018; Dujon et al. 2019; Stieglitz et al. 2020), any activity that destroys, modifies or curtails seagrass meadows, algal plains, and/or sandy substrate associated with coral reef systems may pose a threat to queen conch.

Seagrass and Substrate

Agricultural, urban and industrial runoff from terrestrial sources, dredging, urban/port infrastructure development, trawling, oil spills, increasing severity of tropical storms, recreational boat damage, sea level rise, and competition with invasive vegetation are thought to have negative impacts on the survival and resilience of seagrass meadows (Boman et al. 2019; Cullen-Unsworth et al. 2014; Duarte 2002; Grech et al. 2012; Orth et al. 2006). The impacts can occur directly through physical destruction of seagrass (e.g., prop scarring from recreational or commercial boat traffic and boat groundings) or more indirectly through the depletion of oxygen and light or burial by fine sediments at the benthos due to anthropogenically induced algal blooms, competition with invasive species, or coastal/terrestrial run-off.

Synoptic studies to date have examined the distribution, status, and trends of seagrass habitat, and have clearly indicated that seagrasses are declining globally (Green and Short 2003; Orth et al. 2006; Waycott et al. 2009). Waycott et al. (2009) assessed 215 sites around the world and found that seagrass areas have declined at a rate of 110 km²/yr since 1980, with 29% of the known historical areal extent of seagrasses, or more than 51,000 km², having been lost over the past 127 years. The authors also found that the loss rate of seagrass meadows has increased from a median of 0.9% per year before 1940 to a disappearance rate of 7% per year since 1990 (Waycott et al. 2009). In the Caribbean region, however, the sites showed about equal rates of decrease and increase or no change. The two major causes for the loss of seagrass from the observed sites were coastal development and dredging activities (direct impacts) and declining water quality (indirect impacts) (Waycott et al. 2009). The recent occurrence and observed expansion of an invasive seagrass may mitigate widespread losses of native seagrass meadows. *Halophila stipulacea* is a tropical seagrass native to the Red Sea, Persian Gulf, and Indian Ocean. First reported in the Caribbean in Grenada in 2002, *H. stipulacea* has rapidly spread throughout the basin primarily via fragmentation caused by storms, nearshore fishing and boating activities, and inter-island vessel transit (Willette and Ambrose 2012; Willette et al. 2014). Studies have shown that *H. stipulacea* rapidly colonizes open substrates (e.g., sand halos, sand flats, and coral

reef margins) and is capable of physically displacing native Caribbean seagrasses (i.e., *Syringodium filiforme*, *Halophila decipiens*, and *Halodule wrightii*), changing the seagrass landscape and potentially diminishing their nursery function. Of the native seagrass species, *S. filiforme* and *Thalassia testudinum* are integral to the queen conch life cycle, particularly during the postlarval and juvenile stages. Displacement of these native seagrasses by *H. stipulacea* could negatively impact early survivorship, growth, and fitness of queen conch. Studies have found that a range of Caribbean algal species grow with *H. stipulacea*. Although it has been reported that *H. stipulacea* supports a higher abundance and composition of seagrass-associated organisms (Willette and Ambrose 2012), there is little information available regarding the composition of the epiphytic communities and their suitability as food resources for juvenile conch. Boman et al. (2019) found that growth of juvenile conch was higher in native seagrasses compared to the invasive and that *H. stipulacea* detritus is unlikely to be a replacement for native food sources such as *T. testudinum* detritus.

Queen conch's dependence on native seagrasses during multiple life stages makes the documented declines of seagrass meadows in the greater Caribbean a major concern for species persistence (CITES 2012; DEMA 2012; Vallés and Oxenford 2012). Early life stages of conch in particular depend on seagrass structure for cues to metamorphose and settle, nutrition, and shelter from predators. It is likely that these vulnerable life stages are particularly sensitive and are differentially impacted by seagrass destruction. For example, seagrass destruction was considered a cause for the initial decline in conch populations in Montserrat (Posada et al. 1997). There has also been a significant amount of seagrass loss on the west and south coast of Barbados (Vallés and Oxenford 2012) which could be contributing to low conch densities (Stoner 2003). In 2002, population declines observed in Saint Kitts and Nevis were attributed to general habitat degradation, dredging, and hurricanes (CITES 2012). Similarly, nearshore queen conch populations in the Turks and Caicos have declined as a result of habitat degradation and recent hurricanes (DEMA 2012). Adult conch aggregation habitats are characterized by non-vegetated flats composed of coarse, low organic content sand. These areas are important for conch mating and spawning and the expansion and colonization of the invasive *H. stipulacea* into these open areas has unknown consequences. A small study conducted in Lac Bay, Bonaire, found a nearly equal occurrence of conch in native and *H. stipulacea* seagrass meadows with no indication of seagrass preference or avoidance by conch (Becking et al. 2014). However, additional large-scale studies are needed to understand potential changes in the distribution and habitat use patterns of both juvenile and adult queen conch resulting from the expansion of this invasive seagrass. Adult spawning grounds could also be compromised by the deposition of fine sediment or sediment with high organic content (Appeldoorn and Baker 2013). For example, the main island of Trinidad does not have a significant queen conch population, likely due to low salinities and high turbidity associated with continental rivers and streams (CITES 2012). In addition, habitat loss (e.g., construction and heavy sedimentation from coastal erosion) was identified by Gore and Llewellyn (2005) as a possible factor that contributed to the species decline in the British Virgin Islands.

The Caribbean Coastal Marine Productivity (CARICOMP) monitoring network assessed 52 seagrass sampling stations at 22 sites (mostly *T. testudinum*-dominated beds in reef systems) across the Wider Caribbean, twice a year over the period 1993 to 2007 and in some cases up to 2012 (van Tussenbroek and van Dijk 2007). The CARICOMP monitoring program shows wide variation in seagrass productivity and biomass across the Caribbean, reflecting the different environmental settings among the sampling sites, although most were associated with coral reef

systems. This study included a broad spectrum of seagrass community types dominated by *T. testudinum*, from highly productive almost monospecific beds to multi-species communities with several seagrass species and benthic macro-algae. Wide variations in community total biomass and annual foliar productivity of the dominant seagrass *T. testudinum* were found among sites. Solar-cycle related intra-annual variations in *T. testudinum* leaf productivity were detected at latitudes. Hurricanes had little to no long-term effects on these well-developed seagrass communities, except for one station, where the vegetation was lost by burial below 1 m of sand. At two sites the seagrass beds collapsed due to excessive grazing by turtles or sea urchins (the latter in combination with human impact and storms). The regional-scale monitoring program was sufficient to detect long-term shifts in the communities, and fifteen (43%) out of 35 long-term monitoring stations showed trends in seagrass communities consistent with expected changes under environmental deterioration (Figure 14).

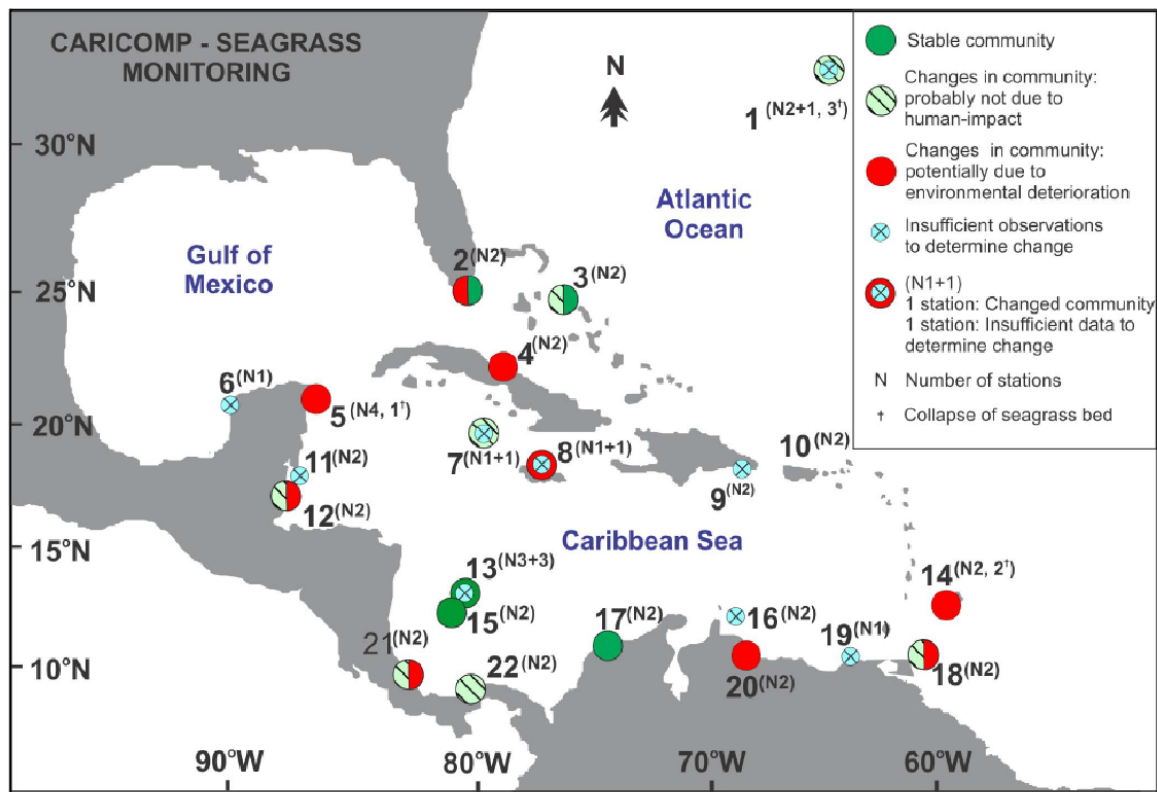


Figure 14. CARICOMP seagrass sites, ordered according to latitude. 1. Bermuda, 2. USA-Long Key, 3. Bahamas-San Salvador, 4. Cuba-Cayo Coco, 5. Mexico-Puerto Morelos, 6. Mexico-Celestun, 7. Cayman Islands-Grand Cayman, 8. Jamaica-Discovery Bay, 9. Dominican Republic-Parque Nacional Este, 10. Puerto Rico-La Parguera, 11. Belize-Turneffe Island, 12. Belize Twin Cays/Carrie Bow Cay, 13. Colombia-Isla Providencia, 14. Barbados-St. Lawrence, 15. Colombia-Isla San Andres, 16. Curaçao-Spaanse Water, 17. Colombia-Chengue Bay, 18. Tobago-Bon Accord Lagoon, 19. Venezuela-Isla de Margarita, 20. Venezuela-Morrocoy, 21. Costa Rica-Cahuita, 22. Panama-Isla de Colon. doi:10.1371/journal.pone.0090600.g00

These changes over a relatively short time-span (6-18 years) across many sites is a worrying trend, particularly because most of these sites were only moderately disturbed by humans at the outset of the study (Figure 14). Only two originally undisturbed sites, Colombia-Isla Providencia, and Colombia-Chengue Bay remained in ‘pristine’ condition up to the end of the monitoring period (2007 and 2005, respectively). Several sites, such as Bahamas-San Salvador, Colombia Isla San Andres, Tobago-Bon Accord Lagoon, Panama-Isla de Colon, have been

impacted by human development for decades or more than a century (van Tussenbroek and van Dijk 2007). However, van Tussenbroek et al. (2014) did not detect indications of further degradation during their study period.

The consequences of these changes in seagrass communities across the Caribbean are difficult to assess at this point because baseline information concerning the structure, processes, and drivers of Caribbean seagrass beds is deficient. However, it is likely that the ecosystem services offered by the seagrass communities will be compromised by changes in the productivity and composition of the seagrass community. For example, a community shift from *T. testudinum* (seagrass species primarily associated with juvenile conch), to faster-growing or invasive seagrass species will result in a change in the overall structure of the seagrass canopy and possibly a change in associated fauna (van Tussenbroek et al. 2014). Interpretation of the long-term shifts in the seagrass communities is not unequivocal, because responses of individual communities depend on local conditions and the state of the seagrass community when monitoring began. While overall seagrass coverage trends in the Caribbean are mixed (some increasing, some decreasing), if native seagrasses are being replaced by an invasive seagrass species, which constitutes suboptimal habitat for queen conch, then overall habitat quality in the Caribbean is likely declining and is likely to continue to decline in the future. However, the scope and severity of seagrass and substrate destruction depend on the spatial and temporal persistence of the threat and the ability of queen conch to adapt to changing environments. Threats such as coastal development, recreational access, and dredging may occur infrequently, have a narrow geographic scope, or have uncertain or indirect effects on queen conch. Recent studies have suggested queen conch have the ability to utilize a variety of habitats during its life history and this flexibility may give the species an advantage as the extent and boundaries of seagrass meadows and coarse sand patches are dynamic (Dujon et al. 2019; Stieglitz et al. 2020). Other threats, especially those associated with long-term climate change such as sea level rise and increased erosion, turbidity, siltation, and severity of tropical storms, have the potential to produce more widespread impacts, especially as they affect key ecological processes during early life such as larval delivery, growth, and predation. All in all, how particular threats or combinations of them will affect queen conch dynamics and long-term viability is highly uncertain at this time.

Environmental Contaminants

Environmental contaminants such as heavy metals, pesticides, and other pollutants have been shown to negatively impact queen conch habitats and consequently conch populations in many locations throughout the species range. Current and historical land use has the potential to impact the ecological health of marine ecosystems as land-based sources of contaminants can affect habitats, alter food webs, and directly impact the health of marine organisms (Laskowski and Hopkin 1996; Spade et al. 2010). Gastropod studies have related heavy metal exposure, particularly copper and zinc, to reduced fecundity measured in terms of egg-laying (Cœurdassier et al. 2005; Ducrot et al. 2007; Laskowski and Hopkin 1996; Snyman et al. 2004). The bioaccumulation of metal in conch can occur via exposure to dissolved metals through feeding as conch ingest considerable amounts of sediment particles while eating (Brownell and Stevely 1981). Juvenile conch exposed to sub-lethal concentrations of copper in the lab had reduced grazing rates, fecal pellet production, and slower “righting time” which is the time it takes for a conch to turn themselves over using a kicking motion of the operculum when overturned (Sanders 1984). High levels of copper, zinc, and lead have been observed in queen conch from

Guacanayabo Gulf, Cuba (Rizo et al. 2010). While the authors did not address potential effects to queen conch reproductive fitness, they determined that concentrations of copper and lead in some of the conch were above typical public health recommended limits (Rizo et al. 2010). The source for these heavy metals in the queen conch environment is likely from anthropogenic activity in the Guacanayabo Gulf. Such activities include dredging, agricultural use of metal-containing fertilizers and pesticides, the emission of untreated sewage, and also metal contaminated effluents from medical use and industrial units (Rizo et al. 2010). In addition, Spade et al. (2010) reported that copper and zinc concentrations in nearshore conch found in the Florida Keys were similar to those found in other gastropods where reproductive inhibition was detailed (Ducrot et al. 2007; Laskowski and Hopkin 1996). Given that heavy metals are documented to impair egg-laying in female gastropods, and point sources for metal contamination exist close to shore in the Florida Keys, Spade et al. (2010) postulated that heavy metals were likely contributing to the reproductive failure.

Apeti et al. (2014) assessed contaminant levels in queen conch around St. Thomas, U.S. Virgin Islands, specifically sampling conch within the St. Thomas East End Reserve (STEER). The assessment concluded that contaminant levels [mean polycyclic aromatic hydrocarbons (PAHs) and tributyltin (TBT) totals] within conch tissues were relatively low when compared to other mollusk studies in the region. Apeti et al. (2014) determined that contaminant levels in conch tissue were at background levels, given that levels were similar to other areas in the Caribbean and there were no ecotoxicity thresholds for conch. Similarly, in Vieques, Puerto Rico, Whitall et al. (2016) analyzed heavy metals, pesticides such as DDT, and energetic compounds (associated with munitions) within queen conch. The authors also concluded that while heavy metals and DDT were detected in the sampled queen conch, the concentrations were within the range or comparable to those reported elsewhere in the Caribbean (e.g., Florida, Cuba, and U.S. Virgin Islands). However, when comparing these two studies statistically (Wilcoxon test, $\alpha = 0.05$), copper, lead, tin, and zinc concentrations in the STEER exceeded those in Vieques, Puerto Rico, whereas concentrations of chromium, nickel, and selenium were higher in Vieques, Puerto Rico, than in the STEER.

TBT, a once popular biocide in antifouling paint, has been found in water and sediment samples in high concentrations in areas adjacent to boating activity such as shipyards, marinas (Titley-O'Neal et al. 2011), and shipping lanes (Chau et al. 1997). High TBT levels in queen conch around the British Virgin Islands (BVI) may be affecting the species based on records of imposex (Titley-O'Neal et al. 2011). Imposex is a condition in which male external genitalia are present in the female conch. Titley-O'Neal et al. (2011) found a strong relationship between females with external male sex organs and concentrations of TBT in the environment. These findings are consistent with earlier studies that show TBT to be a causative agent for imposex in gastropods (Phillip 2000). Within the BVI, concentrations of TBT were also found in the seagrass *Thalassia* and algae (two of the primary nutrition sources for queen conch; Titley-O'Neal et al. 2011).

Naled and permethrin (brand names Dibrom and Biomist 30-30, respectively) are pesticides commonly used to control mosquitos. Both are sprayed as an ultra-low volume mist with naled applied from aircraft and permethrin applied from a truck-mounted mister. Queen conch generally breed during the spring and summer months; consequently, their larvae are most abundant when pesticide usage is at its peak. Aerial drift and runoff can carry pesticides into non-targeted areas (Hennessey et al. 1992; Pierce et al. 2005). In addition, queen conch larvae

are associated with surface layers (Barile et al. 1994; Stoner and Davis 1997) where many contaminants, including pesticides, accumulate (Rumbold and Snedaker 1997). Several studies have indicated that pesticides have both direct and indirect impacts on queen conch early life stages. For example, McIntyre et al. (2006) recorded that permethrin and naled have significant toxicological effects on the development and survival of queen conch embryos in laboratory experiments. The abnormalities were observed during embryogenesis, with slow development seen in all pesticide treatments. Defects increased with increased pesticide concentrations, and in some cases, if the larvae hatched were so deformed as to be unviable (McIntyre et al. 2006). Similarly, Delgado et al. (2007) suggested that larvae exposed to these pesticides were slow growing, which would increase their chance of predation as larvae would remain adrift in the water column for an extended period of time before they reached competency (i.e., recruitment size) resulting in settlement in suboptimal habitat and decreasing survival.

In Florida, queen conch occur in two spatially distinct regions in the Florida Keys: nearshore in habitats immediately adjacent to the shoreline and offshore in habitats along the reef tract south of the islands. Queen conch located in the nearshore habitats do not reproduce and the direct cause(s) remain unknown, but studies have suggested that the cause may be anthropogenic (Delgado et al. 2004; Delgado et al. 2019; Delgado and Glazer 2020; Glazer et al. 2008; Spade et al. 2010). A study funded by the U.S. EPA sought to identify the specific causes of the reproductive failure (Glazer et al. 2008). This study looked at morphology, histology, neuropeptides, protein biomarkers, gene expression, and water, sediment, and tissue chemistry. Despite the breadth and thoroughness of the analyses, no causative contaminant could be definitively tied to the reproductive deficiencies of nearshore conch in Florida (Glazer et al. 2008; J. McCawley, letter addressed to C. Horn, February 4, 2020). While the nearshore waters of the Florida Keys are hardly pristine (Atkinson et al. 2003; Kruczynski 1999; Paul et al. 2000; Pierce et al. 2005), there is no conclusive evidence for an anthropogenic cause for the reproductive issues in nearshore queen conch (Glazer et al. 2008). FWCC most recent data suggests that temperature variability may be a major factor (J. McCawley, letter addressed to C. Horn, February 4, 2020). Where temperature variability is greatest, queen conch are under chronic physiological stress and there is insufficient time for proper gonadal development (J. McCawley, letter addressed to C. Horn, February 4, 2020). Delgado et al. (2019) hypothesized that the reproductive deficiencies seen in nearshore Florida queen conch involved the cerebral ganglia. The sexual development in gastropods is controlled by hormones secreted by the cerebral ganglia. Histological comparisons confirmed that gonadal maturity was delayed and that gamete production was reduced in nearshore conch compared to offshore animals. These gonadal deficiencies were associated with abnormal cerebral ganglion histology (i.e., significant hypertrophy of ganglion cells and significantly lower density of ganglion cells). But authors noted that research is needed to evaluate the hypothesis that the causative agent(s) are targeting the cerebral ganglia and interfering with hormone production

In summary, queen conch, particularly larvae, are vulnerable to contaminants and pesticides that degrade important habitats. Exposure of conch to contaminants and pesticides is likely highest in areas subject to coastal development, urbanization, agriculture, and other human activities on land. However, some conch range far from human activities on land (e.g., reefs, atolls, deep waters, etc.) which likely limits their exposure. Thus, exposure may be higher in some areas, but low to none in a large portion of the species range, resulting in low exposure overall. Nonetheless, those conch populations located close to shore in urbanized settings may experience impacts resulting from exposure to pesticides and contaminants. As discussed above,

exposed conch may experience reduced recruitment and higher mortality rates. Where populations are already recruitment limited, this will likely impact the exposed population's ability to recover. However, at this time, there is limited information on impacts to queen conch populations resulting from exposure to contaminants and pesticides throughout much of the species range, with only portions of populations located in Cuba, USVI, Florida, and Puerto Rico having documented high contaminant levels.

Oil Spills

Oil spills are also a concern for queen conch, for both the potential effects on habitat (substrate destruction or modification) and on the queen conch themselves. These effects would be of particular concern where the species occurs in shallower waters. The threat of an oil spill is greater in areas with higher ship traffic and human development. If a spill were to occur, acute effects could be very damaging in the localized area of the spill. There is some information available on the effects of oil spills on seagrass meadows (Nadeau and Bergquist 1977) and other marine gastropods (Blackburn et al. 2014), but little information available on the direct effects of oil on queen conch.

Microplastic Pollution

The occurrence of microplastics in the marine environment is increasing worldwide. These particles are now present in marine sediments and in the water column where they can be ingested by marine organisms. Aldana Aranda et al (2018) quantified and analyzed microplastics in the wider Caribbean using queen conch as an indicator species and a nondestructive method of sampling. This study showed the presence of microplastics in all conch sampled. Queen conch from Alacranes Reef, Mexico, and Florida, U.S., had a higher abundance of microplastics than conch from the Eastern Caribbean sites. The concern surrounding ingestion of microplastics in conch is that the plastics contain additives such as Polyphenol A (a carcinogenic compound) and can cause endocrinological inhibition in humans (FAO 2020). Aldana Aranda (as cited in FAO 2019) indicated that high levels of microplastics ingestion in conch can have a negative effect on reproduction.

In summary, habitat stability, quality, and resilience is decreasing in many parts of the Caribbean due to anthropogenic activities that have led to direct and indirect impacts to seagrass and substrate that are important to queen conch, and increased pollutants, contaminants, and microplastics are impacting conch via their habitats. The severity of these habitat related threats depend on the spatial scope and temporal persistence of the specific activities and the local demographics of queen conch populations. At this time, the best available information indicates that habitat loss and degradation alone are not threatening the species persistence.

Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

Description of the Fishery

Queen conch have been harvested for centuries and are an important fishery resource for many nations in the Caribbean and Central America. The most common product in trade is the conch meat, with recent regional annual production estimated at about 7800 mt. The majority of the queen conch meat is landed in the Bahamas, Honduras, Nicaragua, Belize, Turks and Caicos, and Jamaica. In the artisanal fishery, queen conch are landed alive or fresh, sometimes with the shell, but mostly as unclean meat with the majority of organs still attached. In some cases, the

subsistence and locally marketed catches are small, but they can be highly significant in others. Queen conch production shows a negative trend over time and the decrease can largely be attributed to overfishing. Some stocks have collapsed and have yet to recover (Appeldoorn 1994b; Theile 2005).

Queen conch shells are also used as curios and in jewelry, but are generally of secondary economic importance. It may simply be offered to tourists in its natural or polished form (Prada et al. 2017). The large and pinkish queen conch shells are brought to the landing sites only in a few places. In most cases, shells are discarded at sea, generating several underwater sites with piles of empty conch shells. According to Theile (2001) from 1992 to 1999 a total of 1,628,436 individual conch shells, plus 131,275 kg of shells were recorded in international trade. Assuming that each queen conch shell weighs between 700 and 1500 g, the total reported volume may have been equivalent to between 1,720,000 and 1,816,000 shells (Prada et al. 2017). In addition, queen conch pearls are valuable and rare, but their production and trade remain largely unknown across the region. In Colombia, one of the few jurisdictions with relevant data, exports of 4074 pearls, valued around USD 2.2 million, were reported between 2000 and 2003 (Prada et al. 2009). With the reduction of the fishing effort in Colombia, the number of exported queen conch pearls went from 732 units in 2000 to 123 units in 2010 (Castro-González et al. 2011). Japan, Switzerland, and the United States of America are the main queen conch pearl importers (Prada et al. 2017). In recent years operculum trade has developed, but similarly little is known about it. China is the major importer and it is believed opercula are used in traditional Chinese medicine. In 2020 the U.S. Fish and Wildlife Service (USFWS) confiscated a shipment in-transit from Miami, Florida, to China (weighing ~1 ton) of conch products, consisting largely of opercula. The shipment was confiscated by USFWS as both CITES and U.S. Lacey Act violations (GCFINET, June 10, 2020).

Indications of Overutilization

In broadest terms, a sustainable fishery is based on fishing “excess production” and supported by a stable standing stock or population. The abundance of the fished population is not diminished by fishing (i.e., new production replaces the proportion of the population being removed by fishing). Under ideal conditions, the age structure of a fished population is also stable, for example, without truncation of the largest most productive members of the population. Overfishing or overutilization of the resource can be demonstrated in a variety of ways. Declines in fishing catches or landings with the same amount of fishing effort (i.e., CPUE) can be indicative of a population that is being overfished. Changes in spatial distribution, e.g., depletions near fishing centers or depletions in more easily accessible shallow water habitats, are likely indicating overutilization. Reductions in distribution as well as overall population levels can be especially problematic for queen conch since they require a minimum local density for effective reproductive output. Reduction of genetic diversity or reduction in maximum size achieved can both be indications of severe overutilization. Drastic differences between population densities found in protected non-fishing reserves and those found in fishing areas can be indications of overfishing even though the reserve may serve to moderate the effects of overfishing to a certain extent. Several of these factors are considered in assessing overutilization of the queen conch resource.

Assessing the Landings Data

Managing queen conch fisheries presents a broad range of challenges, including accounting for the complex biology of the species, uncertainty of catch and effort data, illegal and/or unreported (IUU) fishing, weak surveillance and enforcement mechanisms, and unsustainable fishing practices.

National and regional efforts have continued to gain a better understanding of the impacts of fishing on conch populations. As with other small-scale tropical fisheries, it can be challenging to document the full extent of fishing pressures on particular populations or stocks. Individual jurisdictions vary in their capabilities to characterize all fishery sectors and international efforts to compile uniform data can only provide the data supplied to them. The SRT examined two international databases for the purpose of this review. The UN Food and Agriculture Organization (FAO) maintains data supplied by member nations in the FishStat database. These queen conch data cover the landings of commercial fisheries, generally artisanal and industrial, in the Western Tropical Atlantic. There are continuing discussions among scientific working groups regarding the inadequacy and inconsistency of reporting (FAO Western Central Atlantic Fishery Commission 2020). Data submitters have different capacities to collect data on commercial fisheries throughout their jurisdiction. While an accounting of the numbers and sizes of queen conch being harvested is most informative, many different measures have been provided depending on how much processing has been done (FAO Western Central Atlantic Fishery Commission 2020), including live weight which equates to whole animals, and various grades of cleaned weight, e.g., dirty conch (unprocessed, removed from shell), 50% (operculum and viscera removed), 65% [operculum, viscera, and “head (eyes, stalks, and proboscis)” removed], 85% (all of the above plus verge, mantle, and part of the skin removed), and 100% cleaned (fillet, i.e., only the pure white meat remains). The types of submitted landings have not always been clearly defined and a continuing effort is attempting to encourage conch fishing jurisdictions to submit consistent data and use standardized conversion factors so data can be more reliably compared (FAO Western Central Atlantic Fishery Commission 2020). Aside from interpreting the level of processing, some contributors apply conversion factors of unknown validity and improvement of jurisdiction-specific conversion factors is on-going (FAO Western Central Atlantic Fishery Commission 2020). Additional complications in interpreting FishStat data can relate to a lack of explanation of changes in local conditions or influences on the fisheries. Interannual changes in landings may be due to changes in availability of queen conch (i.e., lowered CPUE), but they may also be due to changes in regulations or enforcement or to unfavorable environmental conditions (e.g., hurricane disruptions of fishing). Without some concomitant data on fishing effort, it can be difficult to interpret changing landings.

The second international repository of conch data is maintained by the Convention of International Trade in Endangered Species (CITES). The CITES database records exports/imports of commercially marketed queen conch. The CITES data do not include commercial catches for local markets and can suffer from the same shortcomings as the UN Food and Agriculture Organization (FAO) FishStat data. Neither database includes spatial information that allows analysis of local effects on populations. In addition to providing data for international obligations, most jurisdictions have widely varying capabilities for collecting complete data that would adequately characterize all fishing sectors. They primarily have focused on commercial fishing, either industrial or artisanal. Jurisdictions have typically inadequately recorded data from the artisanal commercial fishing sector since landing sites can

be too numerous to effectively monitor with the limited number of fishing inspectors employed, and self-reporting is often incomplete. There is a general lack of information across the region on recreational or subsistence fishing, sectors that generally fish for personal consumption but may include minor sales or barter of catches. There can also be gaps in the data collected on catches destined for local consumption, either by family, neighbors, or restaurants. One additional complication with trying to interpret fishing data and compare its significance to ecological or fishery independent data is that different metrics tend to be used. Commercial landings are reported in weight (e.g., metric tons) and ecological surveys typically count numbers and estimate or measure lengths of queen conch. As mentioned above, conversion factors may be jurisdiction- or site-specific, so comparing reported landings to density surveys carries its own inherent difficulties and opportunities for miscalculation.

In an effort to fill the gaps in total landings, the Sea Around Us (SAU) Program (Fisheries Centre, Univ. of British Columbia, www.seaaroundus.org) developed a protocol to reconstruct landings histories for most of the jurisdictions where queen conch is fished. The SRT determined the SAU data was the best option for understanding the magnitude and impact of fishing pressure on local stocks. To reconstruct the catch data, SAU followed a seven-step approach (from Zeller et al. 2007):

1. *Identification, sourcing and comparison of baseline reported catch times series, i.e., a) FAO (or other international reporting entities) reported landings data by FAO statistical areas, taxon and year; and b) national data series by area, taxon and year;*
2. *Identification of sectors (e.g., subsistence, recreational), time periods, species, gears etc., not covered by (1), i.e., missing data components. This is conducted via extensive literature searches and consultations with local experts;*
3. *Sourcing of available alternative information sources on missing data identified in (2), via extensive searches of the literature (peer-reviewed and grey, both online and in hard copies) and consultations with local experts. Information sources include social science studies (anthropology, economics, etc.), reports, colonial archives, data sets and expert knowledge;*
4. *Development of data ‘anchor points’ in time for each missing data component, and expansion of anchor point data to country-wide catch estimates;*
5. *Interpolation for time periods between data anchor points, either linearly or assumption-based for commercial fisheries, and generally via per capita (or per-fisher) catch rates for non-commercial sectors; and*
6. *Estimation of total catch times series, combining reported catches (1) and interpolated, countrywide expanded missing data series (5).*
7. *Quantifying the uncertainty associated with each reconstruction.*

In some instances, interpolations, cautious extrapolation, and assumptions based on local expert opinion were made in lieu of quantitative data. This results in potentially higher uncertainty in some of the data provided here (Zeller et al. 2011), but is justifiable due to the unacceptable alternative: namely, catches for missing sectors, species and/or time periods are interpreted as zero catches (Pauly 1998).

The SRT compared the reconstructed landings from the SAU project (Pauly et al. 2020) to the reported FAO landings for queen conch in the western Caribbean to examine the magnitude of potential differences (Figure 14). As indicated in the various reports (Pauly et al. 2020), for each

jurisdiction, the SAU scientists assembled available data on landings and used additional sociological and fishing data plus expert information and opinion, to produce their best estimates of total landings from all fishing sectors. Generally, subsistence fishing, recreational fishing, and small-scale artisanal sectors are poorly documented in other reporting. For locations or years lacking SAU estimates, the SRT relied on reported landings from the FAO database. There are a few caveats with the data used. Barbados, Haiti, Trinidad and Tobago, and the U.S. Virgin Islands have FAO data but no SAU reconstructions. The FAO listed Netherlands Antilles but also includes separate entries for Curaçao and Sint Maarten. The FAO data also combines Bonaire and St. Eustatius/Saba, and the SRT combined the SAU data here to be equivalent. The SAU database also includes landings for Montserrat, Panama, St. Barthelemy, and St. Martin, not included in the FAO dataset. Based on the data available, early reports of FAO landings were greatly underestimated. From 1950-59, unreported landings averaged 93.8% of total reconstructed queen conch landings (Figure 14). For regional landings, this mean percent varied in each decade, 1960-69: 72.1%, 1970-79: 53.0%, 1980-89: 42.0%, 1990-99: 15.8%, 2000-09: 23.0%, 2010-16: 23.7%. Since about 1990 there were improvements in the correlation between FAO and the reconstructed landings (ranging from 15-25% unreported), but the FAO landings will never include all of the fishing sectors in each jurisdiction.

To provide a more meaningful comparison with population estimates, the reconstructed landings were converted to estimated abundance. For this region-wide comparison, a standard regional conversion factor was used (live weight: 1.283 kg/individual, Thiele 2001); subsequent analyses in jurisdictions used location-specific conversion factors where available. At the peak (Figure 14), regional landings translated into about 32-33 million conch per year and, after a slight dip in 2005 – 2006, landings stayed around 30-31 million conch landed per year from 2012 – 2016, the most recent years with complete data. Repeatedly in the reports of SAU, the landings are stated as conservative, underestimating the likely actual landings. The conversion factor that the SRT used is recommended as a standard for the region for an average adult conch when no jurisdiction or site-specific information is available. The information cited in Supplemental 1 (File S1) provides evidence that some jurisdictions are landing significant amounts of juvenile or sub-adult conch, thus, the converted figures should also be considered an underestimation.

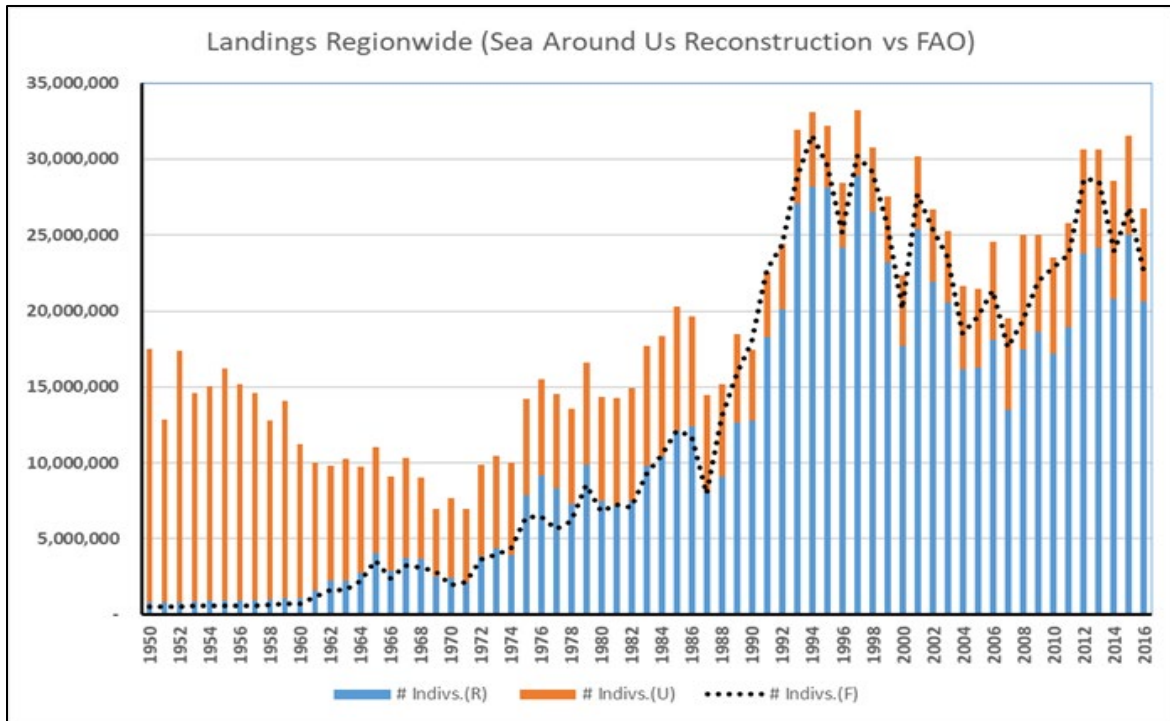


Figure 15. Reconstructed landings (SAU) converted to numbers of individual conch (vertical axis) compared with FAO reported landings in a stacked bar graph. Landings are converted from mt using a standard region wide conversion factor. Blue bars are reported (R) landings, from FAO reported data or national reports. Orange bars are estimated unreported (U) landings from SAU for undocumented fishing sectors. The dotted line represents the landings reported to FAO.

To understand the data better, they can also be displayed by jurisdiction (Figure 15). Some jurisdictions such as Anguilla show close adherence to the pattern described above for the regional compilation, with large discrepancies in early years but close correlation between FAO and reconstructed data in recent decades. Some jurisdictions like Aruba, St. Martin, and others do not have FAO data; Haiti and Barbados only have FAO data. Turks and Caicos and The Bahamas have large amounts of unreported landings throughout the time period displayed. In the Turks and Caicos, the reconstructed landings are more than double the reported FAO landings. Those estimated total landings are cited as being underestimated (Ulman et al. 2016), as is the case for all the reconstructed landings (Zeller et al. 2016) in the region. The SRT chose to use the SAU reconstructed landings, when available, as the best estimate of total landings and used them to compare exploitation rates (e.g., individuals removed) and stock size estimates. If SAU data were not available, FAO landings data were used for the comparisons.

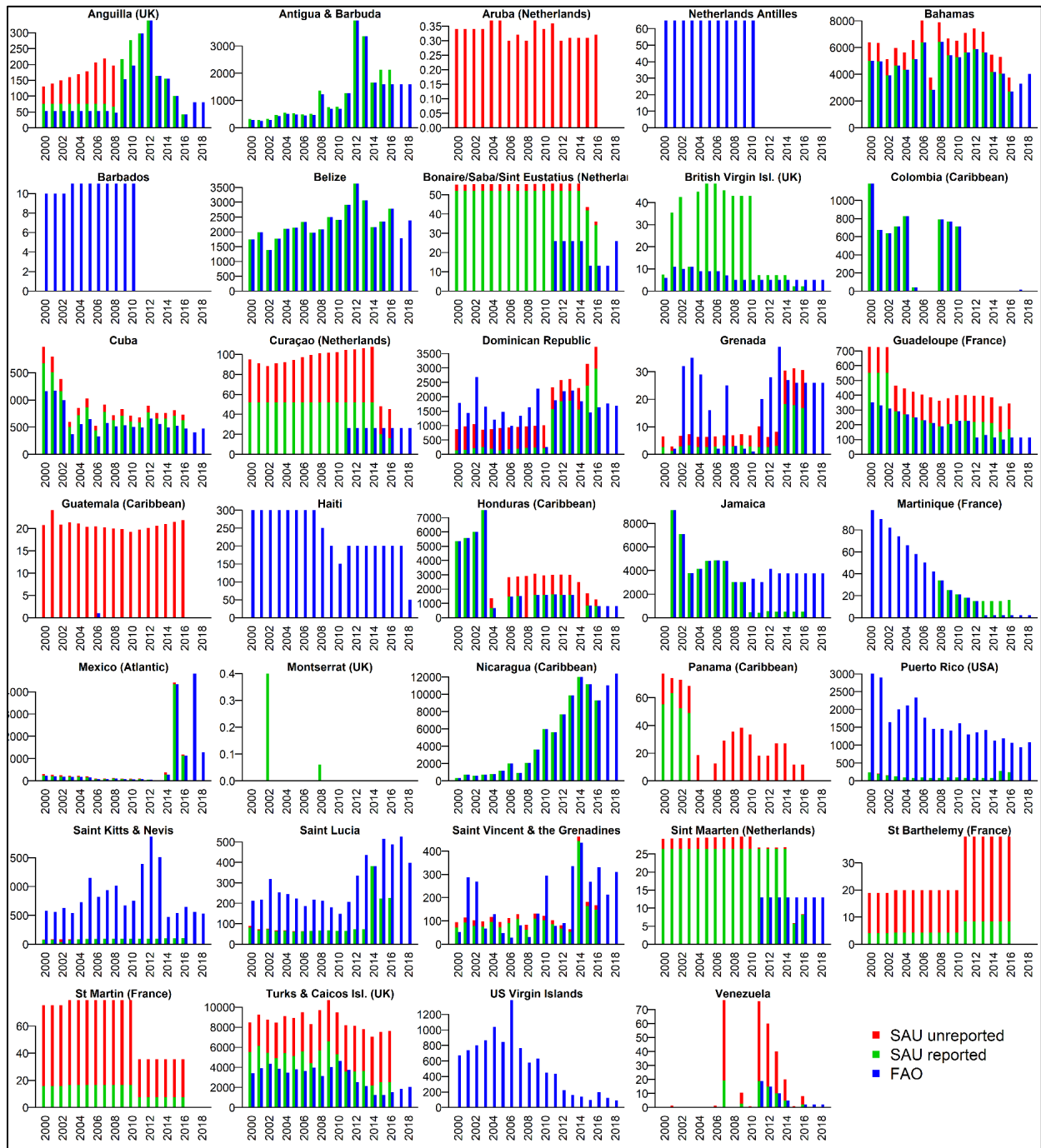


Figure 16. Reconstructed landings (metric tons) data for queen conch by SAU by jurisdiction compared to FAO data, from 2000 – 2018. Note: SAU landings were available only through 2016; FAO data were available through 2018.

These data give some indication of the full impact of fishing on queen conch across the range of the species. Most of the jurisdictions where queen conch occur are included in the analyses by the SAU project. The reconstruction of the data attempts to include estimates for all sectors, including those such as recreational and subsistence which are rarely tracked in national data

collections. Most of this fishing is dispersed and sporadic with no common landing sites or marketing channels to assess the magnitude of the effects on fished populations. As is now being found in dedicated recreational fishing studies (Ault et al. 2008; Coleman et al. 1996), the impact of recreational or subsistence fishing can be equal to or greater than the fishing pressure of commercial fisheries.

The regional SAU landings can be examined in detail for each jurisdiction across the time series (Figure 16) (Pauly et al. 2020). The mean landings per year from 1950 – 2016 show that the twelve highest producing jurisdictions have produced 95% of the landings across the region. The leaders, by far, are the Turks and Caicos Islands, The Bahamas, Honduras, and Jamaica, followed by Belize, Nicaragua, Dominican Republic, Mexico, Cuba, Antigua and Barbuda, Colombia, and Guadeloupe.

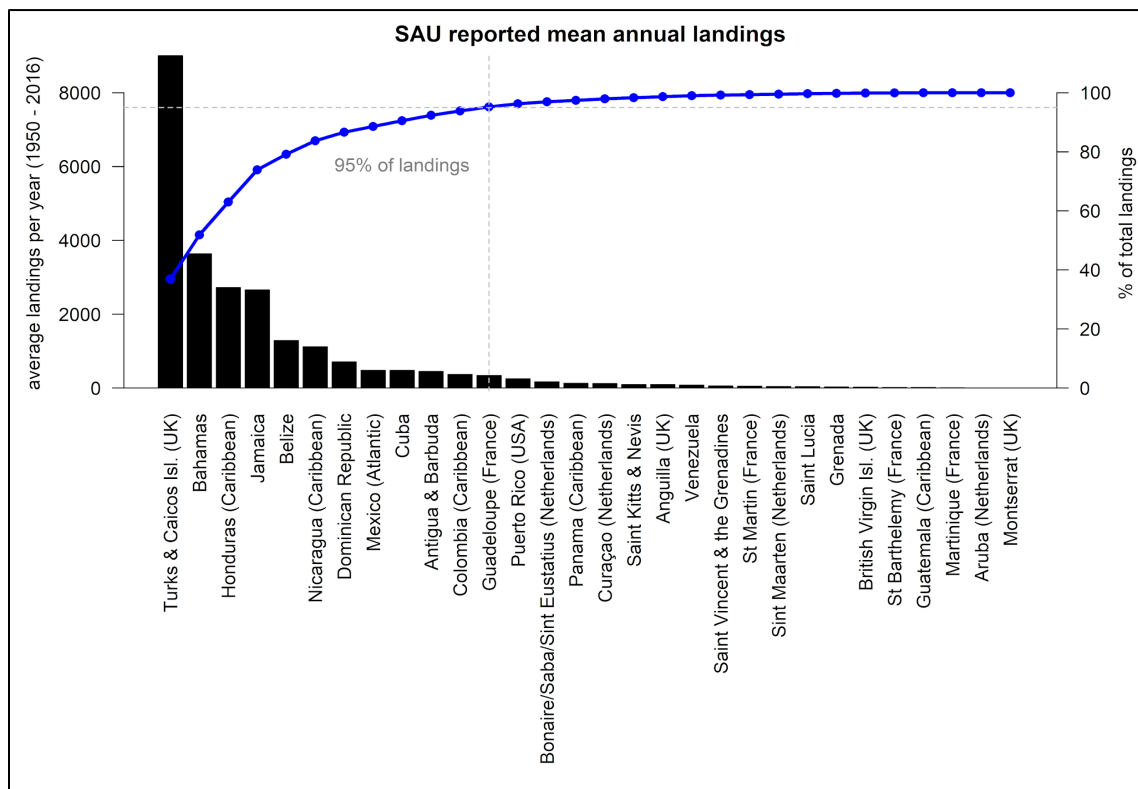


Figure 17. SAU reported mean annual landings (black bars) from 1950 – 2016; from Pauly et al. (2020). Blue line denotes percent of cumulative landings.

Spatial Effects of Fishing and Fishery Management

As mentioned above in the *Population Connectivity* section, genetic studies have examined evolutionary and ecological connectivity of queen conch across its range. Early studies using mitochondrial DNA suggested that the populations across the region were connected or panmictic. Subsequent studies found a break in distribution that suggested two major populations. One of the effects of the belief in a single mixed population or two largely connected populations was a general confusion about the effect of local fishing. If conch larvae are supplied to the fishing grounds from up-current locations then local fishing is less likely to affect local population conditions. The SRT’s modeling of connectivity (Vaz et al. 2022) suggests there are some connected segments that benefit from import of larvae from other

locations. These connections may provide benefits although the frequency with which genetic material is transported is poorly defined and may be less frequent than previously believed. These evolutionary connections maintain some genetic similarity between distant queen conch stocks but may not be ecologically significant in the shorter term. Recent genetic analyses with newer techniques suggest that even within The Bahamas there is genetic differentiation at distances of only a few hundred kilometers (Truelove et al. 2017). Similar evidence of population structuring between populations located short distances from one another have also been observed at Pedro Bank in Jamaica (Blythe-Mallett al. 2021) and in Puerto Rico (Beltrán et al 2019). This ecological isolation suggests that local fishing will have a greater impact on local populations than can be mitigated by long distance larval supply and successful recruitment.

Estimates of Exploitation Rate

Typical fishery assessments require information on fishery landings as well as effort or an index of relative stock abundance. As mentioned, few of the jurisdictions where queen conch is fished have been able to characterize the full extent of their fishery landings. Few jurisdictions collect adequate information from their fishery fleets to document indices of relative abundance such as catch per unit effort. Therefore, recent attempts to improve queen conch management across its range have recognized this lack of fishery dependent data and the lack of sufficient monitoring of all fishing pressures. An alternative metric using a combination of landings and density surveys has been recommended by working groups and fisheries managers. The alternate recommendation is to limit fishing to no more than 8% of mean or median fishable biomass (i.e., standing stock) as a precautionary sustainable yield if the stock is not depleted (FAO Western Central Atlantic Fishery Commission 2013). In this way, fishery independent estimates of abundance and fishery dependent landings data can substitute for full stock assessments that have proven difficult in these data-poor fisheries. While this approach can circumvent the problems with fishery dependent data collection being inadequate to judge landings from all fishing sectors, this approach also has some difficulties with implementation. It depends on statistically valid sampling to ensure that population extrapolations are an accurate indicator of population status. It also can depend on quantifying and/or mapping depths and habitats on which to base extrapolations. It is also recommended that the 8% target be down-adjusted for depleted or rebuilding fisheries (FAO Western Central Atlantic Fishery Commission 2013).

To estimate exploitation rate, the SRT first determined the number of conch landed per year by converting landings in weight to numbers. Landings data used in the calculation were the maximum estimated by FAO or SAU (Pauly 1998), for each particular year and location. The average landings for the period 2010 – 2018, reported in metric tons of dirty meat weight, were converted to kilograms (1 mt = 1000 kg) and then divided by the average weight of a conch, using the conversion factors from Theile (2001). Because the size of conch landed is highly variable and most of the weight is from the shell, we treated shell weight as variable from 0.7-1.5 kg, whereas the dirty meat weight was *assumed* to be fixed at 0.183 kg. The total expected weight of a conch was thus treated as a uniform distribution varying from 0.883-1.683 kg. Exploitation rates for each jurisdiction were calculated as the average numbers landed per year divided by the total abundance (adults only) across the shelf:

$$F_c = \frac{\frac{1}{9} \sum_{y=2010}^{y=2018} \max(SAU_{y,c}, FAO_{y,c}) / wt}{N_c}$$

where SAU and FAO are the reported landings for each year y and jurisdiction c , and both the weight of a conch w_t and the population abundance of conch N for each jurisdiction c are treated as distributions. Distributional estimates of F_c are created by taking 100,000 random draws from w_t and N_c and recalculating the annual exploitation rate for each set of draws (Figure 18).

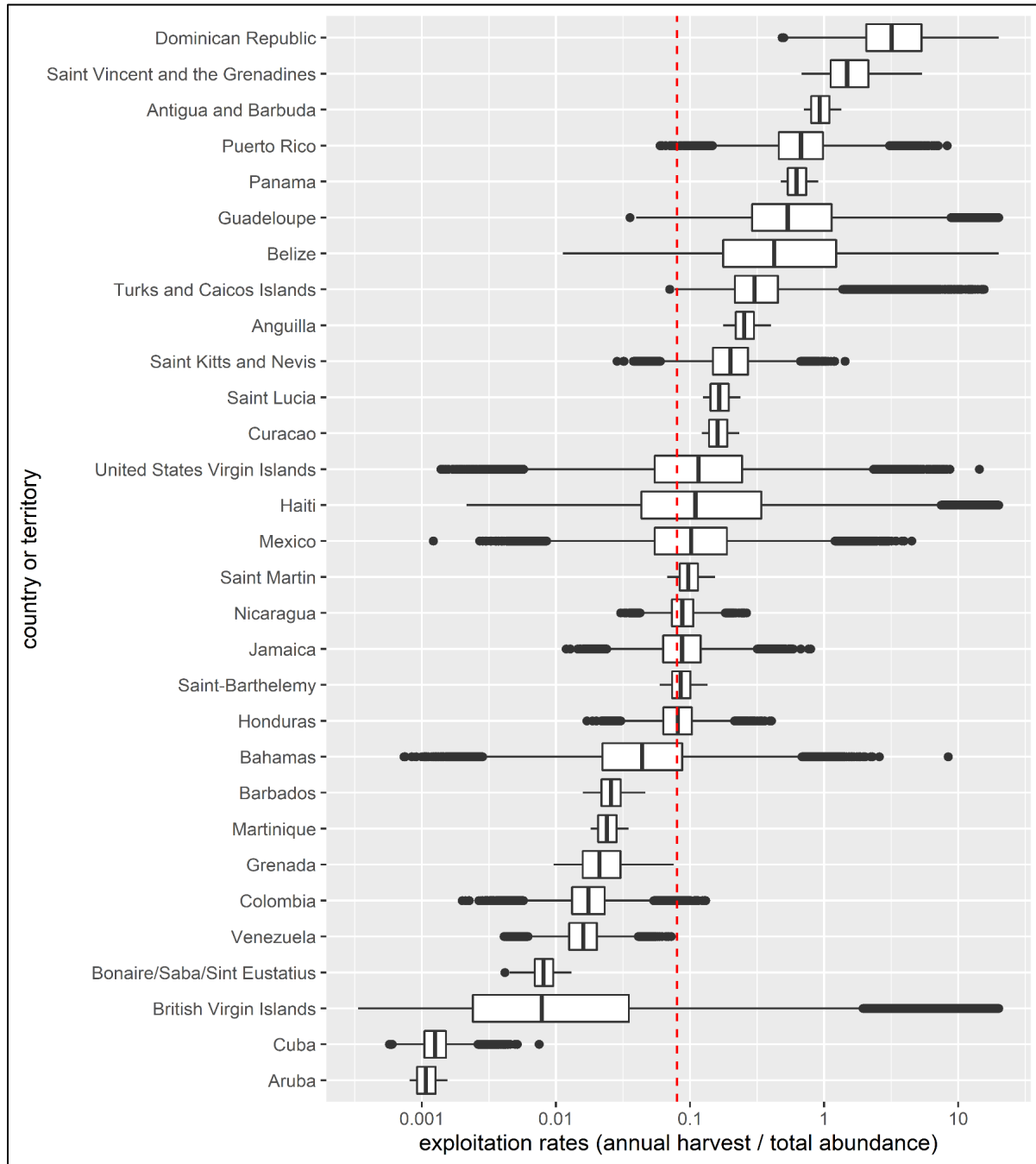


Figure 18. Estimated average annual exploitation rates for the period 2010 – 2018. Distributional estimates as box and whisker plots; boxes denote interquartile range and points denote the full range of possible estimates. An exploitation rate of 1 is equivalent to 100% of adult conch being exploited each year. The red line denotes the estimated 8% target for sustainable take.

In an effort to better understand whether adult conch densities can support exploitation rates, the SRT also plotted the estimated adult conch densities against recent landings (here the maximum

of either FAO or SAU) to look at regional trends in resource usage (Figure 18). Notably there are some jurisdictions with low densities, mostly in the Greater Antilles and Western Caribbean, which have continued to support high landings in recent years.

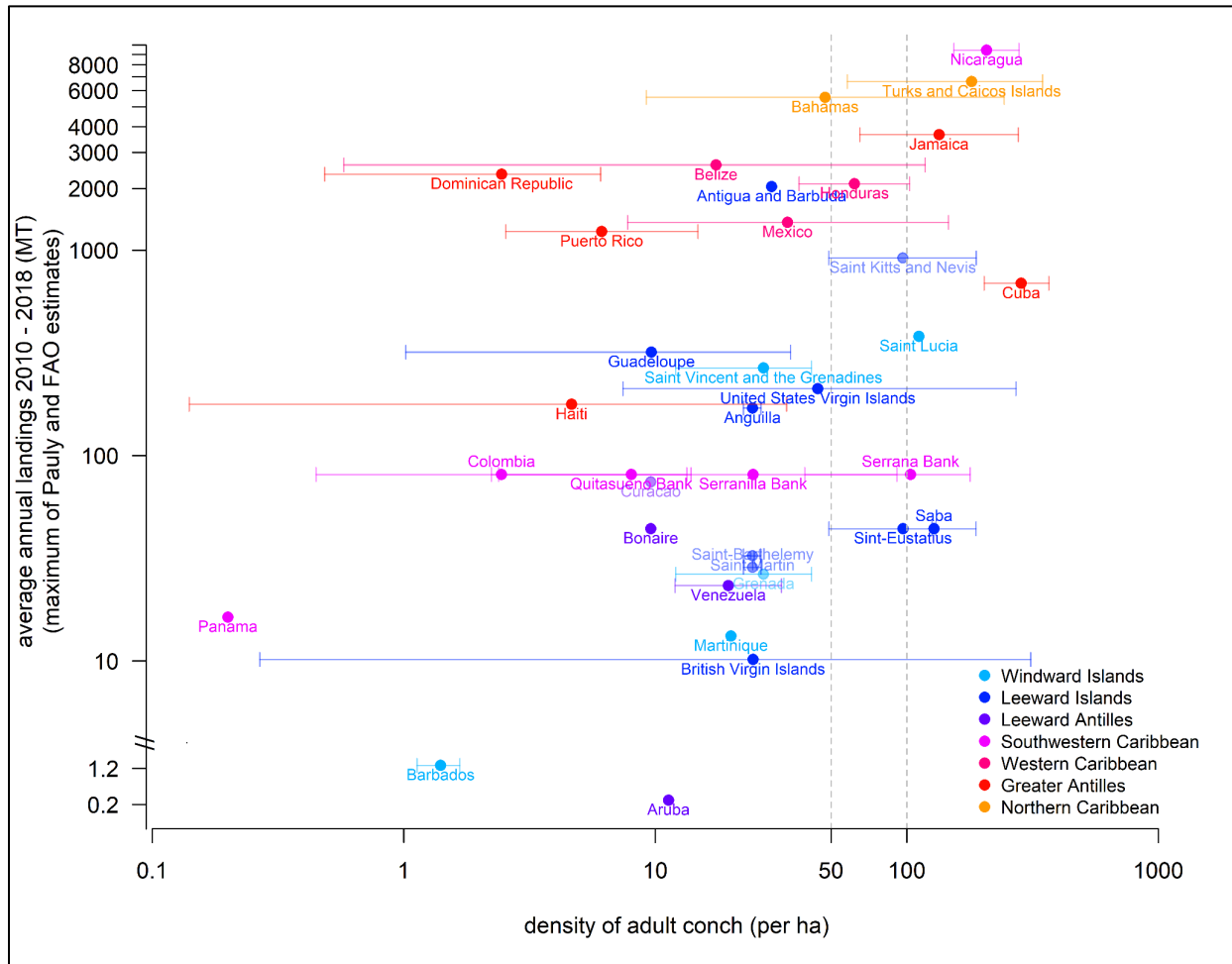


Figure 19. Estimated densities in adult conch per hectare are plotted against the annual average landings in metric tons. Points are median estimates and bars represent lower 5% and upper 95% bounds of distributions. Colors represent different regions, with cooler colors being more “up current” locations and warmer colors being “down current” locations with respect to the overall oceanographic flows in the region. Lighter labels represent countries for which no data were available and values were borrowed from nearest neighbors.

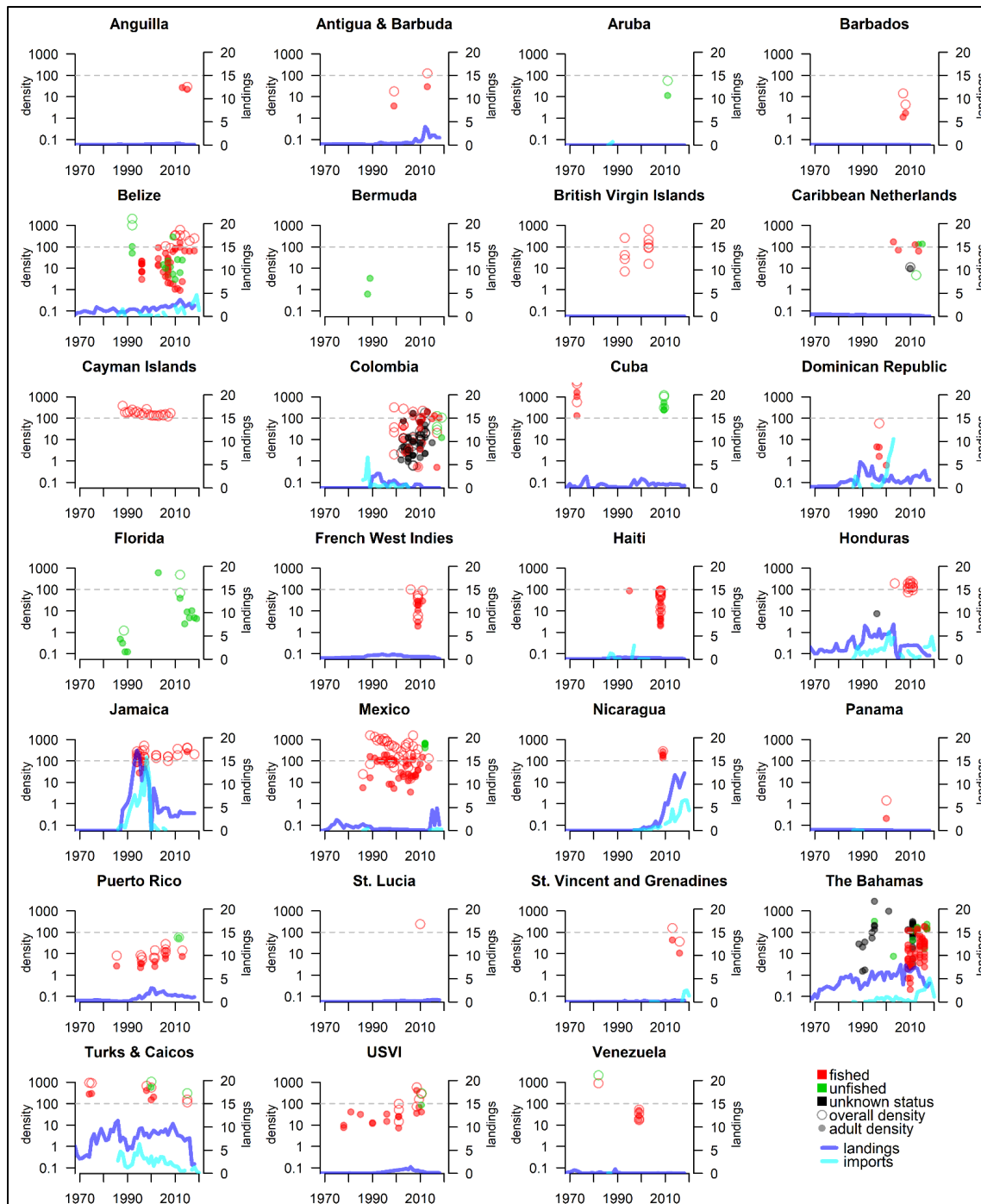


Figure 20. Time series of density estimates, landings, and imports. Density estimates are color coded by fished (red) or unfished (green) regions; open circles represent overall densities and closed circles represent adult densities. Landings are the maximum estimated by FAO or SAU for each year and are in units of thousands of metric tons. Note the primary and secondary y-axes are consistent across panels.

Compiled Information for Selected Jurisdictions

The SRT compared information derived from landings trends, as estimated or reconstructed for all fishing sectors, comprehensive surveys of conch densities, and recent exploitation rates, to estimate status of populations from the various jurisdictions in the region (Figures 18, 19). The

details for all jurisdictions for the greater Caribbean region are compiled in Supplemental File S1. The jurisdictions with highest landings are the Turks and Caicos Islands, The Bahamas, Honduras, Jamaica, Belize, and Nicaragua.

Turks and Caicos

According to the SAU database, Turks and Caicos has been by far the largest producer of queen conch since the 1950s, with sustained landings of approximately 8000 mt from 1960 – present; however, these landings are largely unreported and are subject to uncertainty. Sparse survey data on conch densities suggest that abundance levels are gradually decreasing over time (Figure 19); the most recent conch surveys conducted in 2015 indicate overall (adult and juvenile) conch densities of 154 conch/ha in fished areas and 312 conch/ha in unfished areas (Schultz and Lockhart 2017). The SRT estimated the current standing stock to be 17.6 million adult conch (95% C.I. 5.5-33.5 million), with an estimated exploitation rate of 30.1% (95% C.I. 13.1-134.7%; Figure 18) which is considerably higher than the recommended 8% target. However, the unreasonably high upper confidence interval limit suggests that either the landings are overestimated or the total the proportion of adults in the population is underestimated. Regardless, the available data suggest that fishing pressure may be unsustainable and this may explain why in 2010 – 2011, fishers were unable to catch enough conch to meet the annual export quota, resulting in quota reduction of about 40% for the 2012 – 2013 season (Ulman et al. 2016).

Honduras

According to the SAU database, Honduras (Caribbean) has been the third-largest producer of conch, with mean landings of 738.0 mt in the 1950s, 2239.7 mt in the 1960s, 1739.7 mt in the 1970s, and 3440.3 mt in the 1980s. Mean landings peaked in the 1990s (5272.4 mt) then decreased into the 2000s (2911.0 mt) and 2010s (2630.2 mt). Few survey data exist with which to assess the impact of fishing pressure on population trends (Figure 19). Surveys conducted in the nearshore area of Cayos Cochinos in the mid-1990s showed overall adult densities of 14.6 conch/ha (Tewfik et al. 1998); these low densities were attributed to intensive exploitation of the prior decades (CITES 2012). The Cayos Cochinos was declared a reserve and further harvest was prohibited. The fishery currently operates on vast offshore banks; surveys conducted in these areas from 2009 – 2011 estimated densities of 73-248 conch/ha (age classes not provided) with some stability at each site across the three-year time span. Average standing stock for the three banks was calculated as 21,143 mt (Regalado 2012). The mean landings from the 2010s represent about 12.3% of the standing stock, or more than 50% above the recommendation to fish at 8% of standing stock. The SRT's independent estimate of recent (2010 – present) exploitation in Honduras is a rate of 8.1% (95% C.I. 4.1%-16.4%) which is generally in agreement with the estimate by Regalado (2012).

Jamaica

Jamaica has had a more recent history with intensive conch fishing; little conch fishing was documented until the 1990s off Jamaica, at which point landings quickly increased to over 15,000 mt per year. Imports to the U.S. from Jamaica in some years in the late 1990s exceeded landings estimates, suggesting that landings may be underestimated. At one time, shelf edge waters around Jamaica supported some conch populations and fishing; however, almost all conch fishing now is conducted on an industrial scale on Pedro Bank. Abundance surveys on Pedro

Bank are conducted every 3-4 years (File S1; Jamaica) and these data show relatively stable trends from the 1990s – present. Management of the Pedro Bank fishery is conducted using abundance surveys and the 8% control rule: as long as densities remain above 100 conch/ha, harvest is capped at 8% of the exploitable biomass, when density surveys record between 50-100 conch/ha, the harvest is reduced, and if the survey densities are less than 50 conch/ha the fishery is closed. Although landings and densities have been relatively stable in the last 20 years (Figure 19), the fishery was closed in 2019 until February 2021 due to low densities (Jamaican Gleaner April 6, 2020; <http://jamaica-gleaner.com/article/news/20200406/ban-conch-fishing-extended-february-2021>). The SRT's independent estimate of the exploitation rate in Jamaica is 8.7% (95% C.I. 3.5%-22.4%; Figure 18), which suggests that the 8% control rule has largely been held to in the recent decade. However, management of queen conch on Pedro Bank is also complicated by IUU fishing by other jurisdictions.

Nicaragua

Landings of queen conch in Nicaragua have increased rapidly since the 2000s, and there are no time series data available with which to evaluate population trends over time (Figure 19). Systematic cross-shelf scientific surveys in 2009 showed adult conch densities ranging from 176-267 individuals/ha at different depths and times of the year. Notably, these surveys also indicated very high densities (>1000 conch/ha) in a number of locations within the 20-30 m depth range. The population consists of nearly all adults with very few juveniles recorded. The SRT's estimate of the exploitation rate in Nicaragua is 8.8% (95% C.I. 5.4-14.6%; Figure 18) which suggests that fishing effort is sustainable. However this estimate should be interpreted with some caution as it is based on surveys from a single year, and reports of poaching by other jurisdictions (see File S1; Nicaragua) adds additional pressure on this population.

Belize

According to the SAU database, Belize has been the fifth-largest producer of conch with landings increasing steadily from about 400 mt in the 1950s to over 3000 mt per year in recent years. In 2019 U.S. imports from Belize were over 4000 mt, suggesting that landings are still increasing. Surveys of conch densities in various regions of the jurisdiction have been carried out since the 1990s; densities are highly variable depending on year and location, but adult densities in some areas have remained at <100 conch/ha in the past three decades (Figure 19). The SRT estimated the current exploitation rate to be quite high at 46.1% (95% C.I. 5.0% - >>100%); the uncertainty in the estimate is very high due to the large variability in densities documented and lack of knowledge regarding the extent of habitat areas over which these densities should apply. The use of a small minimum size (178 mm shell length) allows for significant juvenile harvest; if harvest is composed heavily of juveniles, then the exploitation rate (calculated based on an average weight conversion to numbers) would be an underestimate. Despite these uncertainties, individual studies appear to concur that stocks in some of the major fishing areas are depleted. For example, in recent analyses of the Glover's Atoll, Tewfik et al. (2019) found that "Despite the existence of mature conchs and observations of reproductive behavior on the atoll, mean adult densities in all habitats fall below what has been commonly considered a minimum threshold to avoid the Allee effect and maintain reproductive behaviors." According to Tewfik et al. (2019), the fishery appears to have truncated the shell length of conch with a flared lip (i.e., adults) over the last 15 years, one of the signs of overexploitation. Conch fisheries in Belize may

be replenished by putative deep water spawning populations (FAO Western Central Atlantic Fishery Commission 2013).

The Bahamas

The Bahamas have been one of the top producers of conch throughout the historical record, with average landings equal to about half the landings of Turks and Caicos. Landings have increased gradually through the 1980s (5201 mt), 1990s (5714 mt), 2000s (5990 mt), and 2010s (6493 mt) but have decreased dramatically in the last decade. Extensive surveys have been carried out since the 1990s and these data suggest that adult conch densities have decreased over time (Figure 19). However, conch in The Bahamas are distributed over a large geographic area with widely varying habitat attributes and levels of exploitation, so trends vary widely by region. Densities in the Little Bahama Bank and Great Bahama Bank are generally <50 adult conch/ha whereas densities in the Jumentos and Ragged Keys and Cay Sal are much higher (>100 conch/ha). Because of the distributed nature of Bahamian fishing grounds across a large geographic area, it is difficult to estimate landings attributed to particular fishing areas. The SRT's exploitation estimate of 4.4% (95% C.I. 0.6-32.1%) should be interpreted as a jurisdiction-wide average. The high uncertainty in this estimate reflects the fact that densities are highly variable and that localized areas of depletion exist (Stoner et al. 2019a) while other areas are underexploited. Souza Jr. and Kough (2020) suggest the 134.1-158.8 adult conch/ha at Cay Sal Bank could be a potential source of larvae for the Great and Little Bahamas Banks, but warn that IUU fishing is likely a threat to this population.

Summary

Queen conch has been fished in the western tropical Atlantic since prehistoric times, but in the last four decades, fishing has increased and industrial scale fishing has developed (CITES 2003). In most range states, conch fishing continues although population densities are quite low; with conch populations, either experiencing reduced reproductive activity or densities are insufficient to support consistent reproductive activity. In this small fishery setting, the total impact of all fishing sectors can be difficult to quantify. Several indicators suggest that overfishing is affecting abundances, densities, spatial distributions, and reproductive outputs (FAO 2007). Many jurisdictions cite the loss of queen conch from shallow waters and the need for their fisheries to pursue conch with SCUBA or hookah in deeper waters. Regulations in a few jurisdictions prohibit the use of SCUBA to control fishing and subsequent depletion of deep-water stocks. Spatial distributions have also been affected by fishing. Adult densities in areas protected from fishing have been documented to be higher than those on the fishing grounds. In many locations the densities are below the minimum cross-shelf density (~50 adult conch/ha) at which reproductive activity largely ceases. It should be noted, however, that this minimum density pertains to density within reproductive populations and not necessarily cross-shelf densities; in reality, this threshold varies widely depending on scale and location. Continued recruitment in many areas is attributed to locations where reproductive activity is likely occurring in no-take reserves, deep-water populations, or larval supply from distant populations. The available data suggest that queen conch has been significantly depleted throughout its range with only a few exceptions. The best available information indicates that only Saba, St. Lucia, Colombia's Serrana Bank, Nicaragua, Jamaica's Pedro Bank, Costa Rica, Cuba, and portions of The Bahamas, and Turks and Caicos still have cross shelf densities above the 100 conch/ha threshold recommended by UNEP (2012). However, in these areas, the surveys are not comprehensively

performed and there is evidence of local overutilization of some populations, but it is likely that populations residing in inaccessible (difficult to fish) areas support some level of mating success and therefore recruitment.

Efforts to assess the condition of queen conch across its range are hampered by the lack of data collection for all fishing sectors. While many jurisdictions make an effort to collect data on the main commercial fisheries, including both industrial and artisanal, the collections are difficult in small scale fisheries. These fisheries typically land conch at a wide variety of locations, lack adequate centralized marketing outlets that can be monitored as a check on landings, and lack enforcement resources to ensure compliance with size, quotas, and other regulations. To cope with the short-comings of data collection, the SAU project made an attempt to reconstruct catches for most of the jurisdictions where queen conch is fished. While admittedly an underestimate of actual landings, the research attempted to provide best estimates of landings for all sectors. The SRT relied on these reconstructed landings as best available science to examine changes in landings over time and comparisons of landings with standing stock. The lack of reliable fishing indices across the region required us to investigate alternative metrics outside of formal stock assessments.

The combination of total estimated landings and information from abundance surveys allowed us to consider whether jurisdictions are achieving the working group goal of fishing no more than 8% of the estimated healthy stock where populations are not depleted (Prada et al. 2017). The analysis suggests that landings of the top producers in the region, Dominican Republic, Antigua and Barbuda, Belize, Turks and Caicos, and Mexico, exceed the 8% target. Nicaragua, Honduras, Jamaica, and The Bahamas fish very near the target, and Colombia (including nearshore areas and offshore banks) and Cuba fish below the 8% target (Figure 18). The majority of other conch producers within the Caribbean region (e.g., St. Vincent and the Grenadines, Puerto Rico, Panama, Guadeloupe, Anguilla, St. Lucia, St. Kitts and Nevis, St. Barthelemy, St. Maartin, Curaçao, U.S. Virgin Islands, and Haiti), are fishing well above the 8% rate (Figure 18) and their adult conch densities are well below minimum density threshold (50 adult conch/ha) (Figure 19), indicating overutilization is likely occurring. Notably, Aruba, Barbados, Colombia, The Bahamas, Bonaire, British Virgin Islands, Martinique, Venezuela, and Grenada, all fish below the 8% exploitation rate, but have very low adult densities (<50 adult conch/ha) which indicates that these populations are experiencing recruitment failure due to depensatory processes, despite the low exploitation rate (Figure 18). The combination of continued exploitation, depleted reproductive potentials, and unquantified fishing pressures is cause for concern for the status of queen conch.

Disease and Predation

Disease

Apicomplexan parasites commonly occur in invertebrates and especially in mollusks (Azevedo and Padovan 2004; Duszynski et al. 1998; Hillman et al. 1982; Lester and Davis 1981; Perkins 1988). Histological studies have suggested that there is a negative correlation between parasite abundance and reproduction in queen conch (Aldana Aranda et al. 2009a; Baqueiro Cárdenas et al. 2012). The Apicomplexa parasite can disperse through the feces of the host (Duszynski et al. 1998) and may spread to other benthic detritus feeders. The parasites appear to complete their life cycle within the digestive gland (Aldana Aranda et al. 2011). The parasites were found throughout the year with the maximum number observed in October and November (Aldana

Aranda et al. 2007; Baqueiro Cárdenas et al. 2007; Castro González et al. 2007). The Apicomplexa parasite was found in every conch sampled throughout the Caribbean (Table 3; (Aldana Aranda et al. 2007; Aldana Aranda et al. 2011).

Table 3. Apicomplexan parasite locations reported in the literature.

Jurisdiction	Site	Reference
Mexico	Alacranes	(Aldana Aranda et al. 2007)
Mexico	Chinchorro	(Aldana Aranda et al. 2011)
Florida, U.S.	East Sister Rock, Tinger Island	(Aldana Aranda et al. 2009b)
Belize	San Pedro	(Aldana Aranda et al. 2011)
Colombia	San Andres Archipelago	(Aldana Aranda et al. 2007; Baqueiro Cárdenas et al. 2012)
Venezuela	Margarita Island	(Aldana Aranda et al. 2011)
French West Islands	Martinique	(Aldana Aranda et al. 2011)
French West Islands	Guadeloupe	(Aldana Aranda et al. 2011)
French West Islands	Barthelemy	(Aldana Aranda et al. 2011)
Puerto Rico, U.S.	La Parguera	(Aldana Aranda et al. 2011)
Cuba	La Habana	(Aldana Aranda et al. 2011)

Aldana Aranda et al. (2007) observed that parasite abundance corresponded with irregularities observed in reproductive cycles, such as reduced gametogenesis and maturity in Alacranes, Mexico, and no gonad activity in San Andres Islands, Colombia. In addition, Baqueiro Cárdenas et al. (2007) reported the presence of an Apicomplexa parasite in the digestive gland of the queen conch population from San Andres Island, a population with attenuated reproduction (Castro González et al. 2007), which the authors attribute to the parasite. Aldana Aranda et al. (2009a) also found an inverse correlation between individual maturity and number of parasites in San Andres Islands, Colombia; specifically, the frequency of gametogenesis, maturity, and spawn stages diminished with increasing numbers of parasites. A gradual decrease in parasite abundance was observed from East to West of the Caribbean (Aldana Aranda et al. 2011). The lowest occurrence for this parasite was found in the Gulf of Honduras, Mexican Caribbean, and Campeche Bank, followed by the Colombian Archipelago and Venezuela Corridor, with the highest occurrence at French West Islands (Martinique and Guadeloupe) and Puerto Rico (Aldana Aranda et al. 2011). In Florida, the Apicomplexa parasite was also documented in offshore locations where queen conch reproductive activity is common (Pelican Shoal and Eastern Sambo) and in nearshore areas (East Sister Rock, Tinger Island) where queen conch reproduction has ceased (Aldana Aranda et al. 2009b). However, low gametogenesis may be related to other factors (pollution and/or water temperature) affecting conch reproductive systems in Florida's nearshore environment (Glazer and Delgado 2020).

While several histological studies indicate that Apicomplexan parasites have negative consequences for conch reproduction, Tiley et al. (2018a; 2018b) suggest that the organisms previously identified as parasitic are non-parasitic and pose no health implications for queen conch. These two studies assessed the digestive glands for features of parasites using histological, analytical chemistry, ultrastructural, and molecular techniques. Approximately 61 queen conch were sampled opportunistically from fishermen in St. Kitts from October 2015 to November 2016. The histopathological surveys found the characteristic “inclusion bodies” present in the digestive gland of 100% of the study specimens, which is consistent with other studies (Baqueiro Cárdenas et al. 2007; Gros et al. 2009). However, Tiley et al. (2018a; 2018b) found that parasitism did not represent infectious organisms, had little impact on the host’s health, and appeared to be incidental, representing normal physiology of queen conch. The authors hypothesize that the “inclusion bodies” represent a storage form for iron, and potentially other elements, within a protein matrix, as similar structures have been described in the digestive glands of other invertebrates. However, they note that disease impacting St. Kitts conch populations cannot be ruled out, particularly in individuals too young or small to be fished (Tiley et al. 2018a; 2018b).

In summary, the best available information on disease in queen conch indicates that an organism, which may be parasitic, is prevalent in all the sampled conch specimens throughout the Caribbean. Several studies suggest that the organisms are correlated with irregularities in reproductive cycles and reduced gametogenesis, while other studies are contradictory, suggesting that the organisms had no negative effects health or reproduction. Further, several studies also hypothesize that other factors, such as pollution and high water temperature, may be responsible for the irregularities reported in conch reproductive systems and may not be related to the organism’s occurrence. At this time, it appears that more research is needed to better understand the role of these organisms in the digestive glands and their implications on the health and reproduction of queen conch. Thus, it is important to continue to monitor queen conch population health in order to identify impediments to local or regional recoveries, or conditions which threaten further declines.

Predation

Similar to the larval stages of all marine organisms, the earlier life stages of queen conch are exposed to high rates of predation from stingrays, spiny lobster, octopus, nurse sharks, hermit crabs, predaceous snails, and other predators. Conch mortality is high during their planktonic life phase (Chávez and Arreguín-Sánchez 1994). Prior to the time that larval queen conch descend to the bottom to begin their benthos dwelling existence, they experience a large reduction in numbers (Iversen et al. 1986). Physical environmental factors also play an important role in the survivorship of this early life stage (Iversen et al. 1986). The predation rate of juveniles (5-16 cm) is estimated to be 60 percent annually (Iversen et al. 1986). Mortality due to predation decreases as the conch increases in size; specifically, predation was noted to decrease once the conch achieved a 10-15 cm shell length (Iversen et al. 1986). Juvenile queen conch have relatively thin shells and therefore are more vulnerable. Subsequently, juveniles rely on several defensive behaviors in addition to their shell. Juvenile queen conch burrow under the sand to avoid being seen by predators and they also form dense aggregations which make individuals difficult for predators to flip over and consume. Predator induced mortality on juveniles outside aggregations is significantly higher (Stoner and Ray 1993). The gregarious behavior observed in conch nurseries may provide an active mechanism for maintaining aggregated distribution and reducing mortality on earlier life stages (Stoner and Ray 1993). Smaller conch may also attempt

to escape predators with a flight response, extending their foot forward, grabbing the substrate, and hopping forward (Parker 1922).

Adult queen conch are afforded better protection from predation than juveniles by their larger size and thicker shell. The hard shell is very important in avoiding predation as conch are slow moving and unable to escape most predators (Delgado and Glazer 2007). Their nocturnal behavior (Randall 1964; Sandt and Stoner 1993) may also be a strategy to avoid visual detection. Some common predators of adult queen conch are tulip snails, apple murex, common octopus, spiny lobsters, queen triggerfish, spotted eagle rays, a variety of hermit crabs, and sharks (e.g., tiger sharks and nurse sharks) (Iversen et al. 1986; Jory and Iversen 1983; Stoner and Ray 1993). In the Berry Islands, Bahamas, tulip snails are common predators given the correlation of their abundance and the number of empty, undamaged conch shells (Iversen et al. 1986). In experimental releases of small hatchery-reared conch on an offshore algae plain, the most common method of predation (80%) involved crushing of the shell (Appeldoorn and Ballantine 1983). Predation decreases as the shell grows to 9 cm, as it is too strong to be crushed by the majority of predators (Davis 1992) and the number of predators is decreased to include only those able to destroy a strong shell such as sharks, rays, turtles, octopuses, and large hermit crabs (Brownell and Stevely 1981). However, information regarding natural predation rates of queen conch and how predation, particularly during larval stages, may affect the species is unavailable.

In summary, predation is not believed to currently be a factor that is influencing the status of queen conch. The role of juvenile aggregations in reducing predation does suggest, however, that as populations decline there could be compensatory feedback through increasing predation. In addition, warmer water temperatures and increased acidification resulting from climate change may increase predation rates, as juvenile conch will be unable to formulate strong shells (See Factor E).

Inadequacy of Existing Regulatory Mechanisms

This section examines the adequacy of current regulations in controlling threats to queen conch populations throughout the species range. This section summarizes the best available information on the status of queen conch populations, fisheries, and management, which is presented in its entirety in Supplemental File S1. The SRT examined the adequacy of each jurisdiction's specific regulations, including fisheries management, implementation, and enforcement, on the status of queen conch populations. The SRT used this information to elicit conclusions regarding the adequacy of existing regulatory mechanisms in controlling the overutilization of the species for each jurisdiction throughout the species range.

Bermuda

Queen conch were relatively abundant in Bermuda up until the late 1960s, but by the late 1970s populations had reached very low levels (Sarkis and Ward 2009). Bermuda subsequently closed the queen conch fishery in 1978 and listed it as "endangered" under the Bermuda Protected Species Act 2003. The queen conch population in Bermuda relies entirely on self-recruitment and currently has very little local retention. They have developed a recovery plan for queen conch with the primary goal to promote and enhance self-sustainability of the queen conch in Bermuda waters by increasing population levels through habitat protection, active breeding, and optimal self-recruitment. While current regulations appear adequate to control what was the main threat of overutilization, the fact that adult densities across the shelf are still low (and below the 50 adult conch/ha required to support reproductive activity) indicates that additional regulations

or management measures, such as those aimed at protecting habitat or water quality, may be warranted. The SRT's connectivity model (Vaz et al. 2022) indicates that the queen conch population in Bermuda relies entirely on self-recruitment and, thus, without management or regulatory measures that will protect but also help grow the adult breeding population, queen conch densities will likely decline in the future.

Cayman Islands

Concerns about overfishing of conch in the Cayman Islands began in the early 1980s and in 1988 the Department of Environment began monitoring the status of queen conch populations by conducting surveys annually. The surveys show a significant decreasing trend for queen conch densities, with a possible stabilization around 2007 – 2008, potentially due to regulations (Bothwell 2009); however, more recent survey data is unavailable. The Cayman Islands imports the majority of their conch meat, but there is a small fishery that harvests conch solely for domestic consumption (Bothwell 2009). Current regulations include closed fishing seasons (May 1 through October 31) and areas for queen conch, and a 5 conch per person or 10 conch per vessel per day bag limit. The use of SCUBA and hookah gears to harvest marine life is also prohibited in the Cayman Islands (Bothwell 2009; Ehrhardt and Valle-Esquivel 2008). However, Bothwell (2009) notes that local poaching and illegal harvest and export of queen conch are significant issues and regularly occur in protected areas of the Cayman Islands. Given the Cayman's small shelf area, Bothwell (2009) states that even a single poacher, who requires only simple fishing gear (i.e., mask and fins), can cause severe problems. Bothwell (2009) references a 2008 incident where a poacher had 56 conch, and noted that this amount of conch was twice as many conch than had been found in two hundred quadrats surveyed in a protected area over a two day period. Enforcement is also severely lacking, with border control noted as a severe weakness in the Cayman's queen conch management (Bothwell 2009). The SRT's connectivity analysis indicates that the Cayman Islands is largely a source for queen conch larvae to other jurisdictions (particularly Cuba), so as the Cayman Island conch populations are depleted, other jurisdictions are unlikely to receive recruits from the Cayman Islands (Figure 12). Given the significant decline in relative queen conch abundance, lack of enforcement capabilities, the easy access to queen conch for poachers, and evidence of significant IUU fishing, existing regulatory measures are likely inadequate to protect queen conch from overutilization and further decline in the future.

Cuba

The current status of queen conch populations in Cuba is highly uncertain due to a lack of available information; however, the few published surveys suggest relatively high densities, particularly in protected national parks (e.g., Jardines de la Reina National Park: 1108 conch/ha in 2005; Formoso et al. 2007; National Park Desembarco del Granma: 511-1723 conch/ha in 2009 to 2010; Cala et al. 2013). The commercial harvest of queen conch began in Cuba in the 1960s and the harvest level increased considerably in the mid to late 1970s. However, due to the largely unregulated and unmanaged harvest, the queen conch population collapsed and the fishery was closed in 1978. It reopened in the 1980s with harvest quotas; however, the quotas were inadequate to prevent overutilization and conch populations continued to decline. In 1998, the fishery was again closed for a year to conduct an abundance survey (Formoso 2001) and update quotas. Since then, the queen conch fishery has been managed under a catch quota system which is established by "zones" and set between 15% and 20% of the adult biomass, according to population assessments and monitoring. Regulations also include seasonal closures that co-

occur with peak spawning, depth limits on diving operations, a prohibition on SCUBA, and a lip thickness of greater than 10 mm; however, the regulations do not require that the animal be landed in a shell, so it is difficult to determine whether or not the minimum size requirements are adhered to by the fishery. Additionally, adherence to regulations appears to be a problem, with two previously allowed fishing “zones” closed in 2012 as fishermen were not complying with the regulatory requirements (FAO Western Central Atlantic Fishery Commission 2013). However, there is currently no directed commercial fishery for conch and the species is only harvested incidentally by fleets whose primary targets are lobster and reef fish. There is likely some limited illegal conch harvest that occurs in Cuba. A recent news article estimated that around 1000 vessels engaged in illegal fishing involving a total of around 2500 people, engage in the illegal harvest marine species, including conch, lobster, and shrimp (14ymedio 2019). However, there is very little information available on illegal harvest of conch in Cuba. In 2019 Cuba passed new fishery laws aimed at curbing illegal fishing by instituting a new licensing system and recovering fish populations through scientific assessments (14ymedio 2019). There is currently no information available on the implementation and enforcement of these new regulations at this time. Given the history of the conch fishery, including the rate at which declines in the population can occur with unsustainable quotas, poor management, and illegal harvest, it is important that the existing regulations are adequately enforced to protect the queen conch populations from overutilization in the future, particularly in the protected areas. However, without information on the status of the queen conch population or the implementation of the new regulations, the adequacy of existing regulations is highly uncertain at this time.

Leeward Islands (Anguilla, Antigua and Barbuda, British Virgin Islands, Guadeloupe, Montserrat, Saba, Saint Barthélemy, Saint Martin, St. Eustatius, Saint Kitts and Nevis, U.S. Virgin Islands)

Based on the available data as described in Supplemental File S1, many of the Leeward Islands have queen conch populations that are overexploited, with estimated population densities below those necessary for reproductive success. Existing regulatory mechanisms largely appear inadequate, resulting in overexploitation and illegal fishing, and have likely contributed to the decline in these populations and reproductive failure. For example, in Anguilla, surveys conducted in 2015 and 2016 reported 26 adult conch/ha, well below the minimum density threshold (50 adult conch/ha) and are likely not supporting reproductive activity (Izioka 2016). Despite this, fishing for conch is still allowed. In addition, existing regulatory mechanisms are also inadequate in preventing juvenile queen conch from being harvested. Currently, the minimum landing size for queen conch in Anguilla is 18 cm shell length; however, Wynne et al. (2016) found that up to 94% of individuals harvested at this size were immature.

In Antigua and Barbuda, surveys of populations also show low densities and low proportions of adult conch, suggesting that fishing pressure has significantly reduced the adult population to the point where Allee effects are occurring (Ruttenberg et al. 2018; Tewfik et al. 2001). For example, Tewfik et al. (2001) conducted 34 visual surveys (12.84 hectares total) off the southwestern side of Antigua. These surveys recorded adult density at 3.7 adults/ha, significantly below 50 adult conch/ha required to support reproductive activity. Overall conch density for Antigua was recorded as 17.2 conch/ha with juveniles making up about 78.4% of the population. Similarly, conch densities in Barbuda are also very low. Ruttenberg et al. (2018) recorded average densities of 0.29 ± 0.12 adult conch/100 m² (29 ± 12 adults/ha) and 0.96 ± 0.30 juvenile conch/100 m² (96 ± 30 juveniles/ha) (mean \pm SE). In terms of regulations, both jurisdictions

prohibit harvest of queen conch without a flared lip, in shells less than 180 mm, or animals whose meat is less than 225 g without the digestive gland. However, Horsford (2019) found over 20% of landed conch meat samples were below the minimum legal meat weight in 2018 and 2019, including within marine reserves. Evidence of the harvest of undersized and immature conch suggests a lack of enforcement of existing regulatory mechanisms. Additionally, based on the size distribution of queen conch in Barbuda, the current regulation allowing harvest of queen conch greater than 180 mm is inadequate to prevent harvesting of immature queen conch as juveniles can reach sizes greater than 180 mm and adults appear to have shell sizes that are greater than 200 mm.

In the British Virgin Islands there are regulations pertaining to the minimum size and weight limits to harvest queen conch, as well as a closed season, although enforcement of these regulations is questionable as the fishery appears to be essentially unmonitored (Gore and Llewellyn 2005). Given that surveys of queen conch populations in 1993 and 2003 both showed densities of queen conch on the order of <0.07 conch/ha indicates a severe inadequacy of regulatory mechanisms to protect queen conch populations from overexploitation with a subsequent failure in reproductive capacity likely leading to a collapse in recruitment (CITES 2003; Ehrhardt and Valle-Esquivel 2008; Gore and Llewellyn 2005).

In Guadeloupe and Martinique, there is high demand for local consumption of queen conch, which makes adequate regulatory measures essential for ensuring that queen conch populations are not overutilized. Martinique passed regulations in 1986 to prohibit the harvest of queen conch with a shell length of less than 22 cm, or shells without a flared lip, or animals whose meat weighs less than 250 g. The majority of landings in Martinique are meat only (FAO 2020), meaning that immature queen conch can potentially be harvested as long as the weight is greater than 250 g. In Martinique there is also a closed season that runs from January 1 through June 30, and the use of SCUBA to harvest conch is prohibited. However, minimum shell length, flared lip, and meat weight regulations are unreliable because large juveniles can have larger shells with a flared lip, and more meat than mature adult can. Similarly, studies on the reproductive cycle of queen conch in Martinique and Guadeloupe have concluded that the minimum shell length size is not an efficient criterion to base sexual maturity (Frenkiel et al. 2009; Reynal et al. 2009). Thus, the best available information indicates that these regulatory measures are inadequate to prevent the harvest of immature queen conch, and given the increasing demand, with the price of queen conch meat having doubled over the past 25 years (FAO 2020; FAO Western Central Atlantic Fishery Commission 2013), the existing regulations will likely contribute to further harvesting of immature queen conch and declines in queen conch populations in the future.

While the status of queen conch in Saba, St. Eustatius, and St. Kitts is unknown, there is a lack of adherence to or enforcement of existing regulatory measures. Evidence of illegal harvest and poaching of queen conch in marine parks, with no established quotas for queen conch fisheries (van Baren 2013), suggests current regulatory mechanisms are inadequate to prevent overutilization of queen conch in these areas.

In the U.S. Virgin Islands, the U.S. federal government has jurisdiction within the U.S. Virgin Island EEZ (i.e., those waters from 3-200 nautical miles [4.8-370 km] from the coast) and the Caribbean Fisheries Management Council (CFMC) and NMFS are responsible for management measures for U.S. Caribbean federal fisheries. The Government of the U.S. Virgin Islands manages marine resources from the shore out to the 3 nautical miles. At present, the U.S. Virgin

Islands manages fisheries resources cooperatively with the CFMC, although not all regulations are consistent across the state-federal boundary. Recently, the Secretary of Commerce approved new fishery management plans for the fishery resources managed by the CFMC in federal waters of each of St. Thomas/St. John and St. Croix. The St. Thomas/St. John FMP and the St. Croix FMP will transition fisheries management in the respective EEZ from the historic U.S. Caribbean-wide approach to an island-based approach, attentive to the unique biological, economic, and cultural attributes of each island/island group. This island-based approach to management does not alter existing regulations for the queen conch fishery.

In the U.S. Caribbean EEZ, no person may fish or possess on board a fishing vessel a Caribbean queen conch in or from the Caribbean EEZ, except from November 1 through May 31 in the area east of 64°34' W longitude which includes Lang Bank east of St. Croix, U.S. Virgin Islands (50 CFR 622.491 (a)). Fishing for queen conch is allowed in territorial waters of St. Croix, St. Thomas, and St. John from November 1 through May 31, or until the queen conch annual quota is reached. In 2008 a 22.7 mt (50,000 lbs) annual quota for St. Croix territorial waters and a 22.7 mt (50,000 lbs) annual quota for St. Thomas territorial waters and St. John territorial waters was established. The CFMC established a comparable ACL for harvest of queen conch in the area east of 64°34' W longitude, which includes Lang Bank east of St. Croix. When the ACL is reached or projected to be reached across territorial and federal waters, the federal queen conch fishery within the area east of 64°34' W longitude, including Lang Bank, is closed. From 2012 – 2020, commercial fishermen in St. Croix landed between 24-74 percent of their ACL; therefore, no closures of the queen conch fishery were necessary. Commercial trip limits and recreational bag limits are established for queen conch harvest in both territorial waters and federal waters of the U.S. Virgin Islands. The commercial trip limit in territorial waters and in the U.S. Caribbean EEZ off St. Croix is 200 queen conch per vessel per day (50 CFR 495). The recreational bag limit from the U.S. EEZ off St. Croix is three per person or, if more than four persons are aboard, 12 per boat (50 CFR 494). The recreational bag limit in territorial waters is six conch per day per person; not to exceed 24 conch per boat per day. In the U.S. EEZ off St. Croix and U.S. Virgin Islands territorial waters, regulations require a 22.9 cm minimum shell length or 9.5 mm lip thickness (50 CFR 622.492). In the U.S. EEZ off St. Croix and in territorial waters, queen conch must be landed alive with meat and shell intact. Federal regulations at 50 CFR 622.490(a) prohibit the use of hookah gear in the U.S. EEZ off St. Croix.

Survey of queen conch were conducted in the U.S. Virgin Islands in 2008 – 2010. While these surveys are dated, the median cross shelf adult density estimate suggests that adult conch densities are too low to support local reproductive activity. However, queen conch densities (at all the island groups) were higher in 2008 – 2010 compared to those recorded in 1980s and 1990s (Boulon 1987; Friedlander 1997; Friedlander et al. 1994; Gordon 2002; Wood and Olsen 1983). The population was composed mainly of juveniles (greater than 50 percent) with the remainder of the population spread evenly among the older age classes. Similarly, a more recent survey conducted in Buck Island Reef National Monument (a no-take reserve) estimated 68.5 adult conch/ha and 233.5 juvenile/ha (Doerr and Hill 2018). This age class structure suggests some successful recruitment in the area. However, given that queen conch have not been assessed in U.S. Virgin Islands in over a decade, their status is uncertain.

Overall, while queen conch regulations exist within the Leeward Islands to prohibit the harvest of immature queen conch and manage fisheries, many of these regulations use inadequate proxy measures for maturity, are poorly enforced, and lack monitoring controls. Given that the connectivity models (Vaz et al. 2022) show a reliance on self-recruitment for the Leeward

Islands, with larval transport mainly away from the islands, queen conch populations throughout the Leeward Islands will likely continue to decline in the future due to the inadequacy of the existing regulatory measures in protecting the Leeward Island conch populations from overutilization and limited larval supply from other locations.

Windward Islands (Barbados, Dominica, Grenada, Martinique, Saint Lucia, Saint Vincent and the Grenadines, Trinidad and Tobago)

In the Windward Islands, queen conch populations appear to be following the same trend as the Leeward Islands, likely due to Allee effects and an inability to self-recruit. Based on connectivity models (Vaz et al. 2022), local settlers comprise most of the settlers in the southern Windward Islands (i.e., Barbados, Grenada, and Trinidad and Tobago); however, due to low adult densities throughout the Windward Islands, there is little to no reproductive activity or recruitment occurring. The relatively low conch densities appear to be the result of overexploitation through sustained and unregulated or inadequately regulated fishing over the last few decades. For example, in Martinique, there is high demand for local consumption of queen conch, which makes adequate regulatory measures essential for ensuring that queen conch populations are not overutilized. However, the significant fishing pressure and declining yields, in addition to evidence of harvesting of juveniles, from the early 1980s to the mid-1990s indicates that regulatory measures were inadequate to prevent the queen conch from overexploitation (Rathier and Battaglia 1994). Subsequent regulations passed in 1999 prohibited the harvest of queen conch with a shell length of less than 22 cm, shells without a flared lip, and meat weight less than 250 g; however, the majority of landings in Martinique are meat only (FAO 2020), meaning that immature queen conch can potentially be harvested as long as the weight is greater than 250 g. Furthermore, studies of queen conch in waters greater than 40 m around Martinique have indicated that shell length is not an effective criterion for determination of sexual maturity, and only a lip thickness of greater than 6 mm appears to indicate maturity (Frenkiel et al. 2009; Rathier and Battaglia 1994). Given that landings have declined since 2000, from an estimated 98 mt live weight (meat + shell) to 2 mt in each year from 2013 to 2018, with Martinique now relying mainly on imported conch meat primarily from Jamaica to meet local demand (FAO 2020; FAO Western Central Atlantic Fishery Commission 2013), it appears that the existing regulatory measures are inadequate to protect the queen conch populations from further depletion. This is particularly concerning given that demand for queen conch has been increasing since 2013 and the price of queen conch meat in Martinique has doubled over the past 25 years (FAO 2020; FAO Western Central Atlantic Fishery Commission 2013) indicating that significant fishing pressure on queen conch will likely continue into the future.

In Barbados and Trinidad and Tobago, there is no management of the conch fishery or regulations pertaining specifically to conch harvesting or sale. Conch populations have been overfished and considered depleted in Trinidad and Tobago since the 1990s (CITES 2012), and in Barbados the catch is mainly comprised of immature conch, with estimates as high as 96% (Oxenford and Willoughby 2013), indicating highly unsustainable fishing of queen conch.

The jurisdiction of Grenada also lacks adequate regulatory measures to control the exploitation of queen conch in its waters and has been under a CITES trade suspension since May 2006 (notification to the Parties No. 2020/006). During the trade suspension, Grenada has continued to export conch to Trinidad, Tobago, and Martinique (exporting 249 mt from 2007 – 2018; File S2). However, Grenada recently indicated that it would be working towards a regional action plan for

queen conch in an effort to overcome the CITES trade suspension (Blue BioTrade Opportunities in the Caribbean, March 22-23, 2021)

Saint Vincent and the Grenadines have regulations in place that are supposed to ensure sustainable conch fishing (FAO 2016). However, management measures established in 1987 have not been modified due to the lack of any new recommendations for queen conch management and conservation (Isaacs 2014). Queen conch density has continued to decline since the late 1970s, with estimates of 73 to 78 percent declines, depending on depth area, from 2013 to 2016 (Rodriguez and Fanning 2018). Overall adult conch density estimates (10.4 conch/ha) are largely below the minimum required adult density needed to support any reproductive activity. Divers have begun using SCUBA to reach deep waters as populations have become depleted (CITES 2012). Current regulations prohibits the harvest of conch with a shell length less than 18 cm, without a flared lip, or with a total meat weight of less than 225 g. Seasonal closures have not been established and divers fish conch year round (Rodriguez and Fanning 2018; CITES 2012). An export quota was established based on one of the highest export years recorded in 2002; however, there appears to be no scientific basis for the establishment of the export quota (CITES 2012). In fact, the high level of exports that occurred in 2002 and 2004 was stated to be “influenced by market forces rather than stock abundance” (Management Authority of Saint Vincent and the Grenadines in litt. to CITES Secretariat, 2004, as cited in CITES 2012). The best available information indicates that existing regulatory measures are inadequate to protect spawning adults, as there is no seasonal closure, and deep waters are being fished with SCUBA. Furthermore, it is likely that juveniles are harvested, as minimum shell length regulations are inadequate to establish maturity and there is no evidence that an appropriate lip thickness regulation has been established. Arbitrary quotas and an apparent lack of monitoring of the fishery have likely contributed to the inadequacy of existing regulatory measures, resulting in continued depletion of queen conch populations.

St. Lucia Department of Fisheries implemented regulations in 1996 that include prohibitions on harvest of queen conch with weight less than 280 g, or a shell smaller than 18 cm, or a shell that does not have a flared lip (Hubert-Medar and Peter 2012). Queen conch are fished in St. Lucia mainly with SCUBA. There are no lip thickness regulations to prohibit the harvest of juveniles; as previously described, shell length is not a reliable indicator for maturity in conch. Regardless, while the Department of Fisheries requires queen conch to be landed whole in the shell, it appears the majority of conch meat is extracted at sea and the shell discarded (Williams-Peter 2021). Queen conch are fished year round; thus, fishing of spawning adults during their reproductive season is likely occurring. Information on stocks is still scarce, especially information on density, abundance, and distribution (Williams-Peter 2021). However, CPUE and landings data (1996 – 2007) shows that stocks have been in a steady decline (Hubert-Medar and Peter 2012; Williams-Peter 2021) indicating inadequate harvest controls. Both of these factors are likely contributing to the overexploitation of queen conch and observed decrease in CPUE in the fishery, and without adequate regulatory measures to control harvest and illegal trade, queen conch populations will continue to decline in the future.

Similar to the issues in the Leeward Islands, the Windward Islands lack adequate regulations to manage the queen conch fisheries, with inadequate proxy measures for maturity, lack of monitoring controls, poor enforcement, evidence of illegal fishing and trade, and arbitrary harvest quotas. Similar to the Leeward Islands, the models show a strong reliance on self-recruitment for the Windward Islands (although there is some exchange within islands), with

many acting as sources rather than sinks for queen conch larvae. As such, queen conch populations throughout the Windward Islands will likely continue to decline in the future due to the inadequacy of the existing regulatory measures in protecting the Windward Island conch populations from overutilization.

Venezuela

The commercial conch fishery in Venezuela has been closed since 2000 due to evidence of severely overfished populations (CITES 2012). Despite this extended closure, landings have continued to be reported to the FAO over the past decade (File S2). In 2016, 2017, and 2018 (the last year of the FAO reported data), Venezuela reported annual landings of 2 mt (File S2). This illegal harvest of queen conch, as well as poaching by other nations, is hypothesized to be the cause of the low densities and lack of recovery of the Venezuelan queen conch population (CITES 2003). Connectivity models show Venezuela is largely self-recruiting (Vaz et al. 2022); thus, Venezuela must support relatively high densities of reproductive adults to maintain queen conch populations within its waters. Without adequate enforcement of current regulations prohibiting the harvest of the local queen conch population, which are already depleted and unlikely to be successfully reproducing, densities will continue to decline into the future.

Western Caribbean (Mexico, Belize, Honduras)

The jurisdictions in the western Caribbean have a history of heavy exploitation of queen conch. In Mexico and Belize the queen conch fisheries saw rapid growth during the 1970s with subsequent declines in queen conch population and densities (CFMC and CFRAMP 1999). The exploitation was so heavy in Mexico that the government implemented temporary and permanent fishery closures throughout various areas in the 1990s (CITES 2012). Despite these closures and the more recent implementation of size limits, closed seasons, and quotas, queen conch populations have failed to recover in Mexico (CITES 2012). Density surveys conducted in 2009 show a population that is unlikely to be reproductively viable. In fact, during one of the surveys conducted in July, when spawning occurs in this region, no egg masses or spawning events were observed and mating was observed only once (De Jesús-Navarrete and Valencia-Hernández 2013). Although Mexico stated in 2018 that there have been no legal exports of specimens from the wild from Mexico in the last seven years (CITES 2018), this information contradicts the reported exports for queen conch in the FAO data (File S2), which show queen conch exports from Mexico increasing from 204 mt in 2003 to 623 mt in 2018. Given that harvest and export of the already depleted queen conch population in Mexico is still occurring, existing regulatory measures are inadequate to protect the species from overutilization and further decline. Additionally, illegal fishing of queen conch at both the Chinchorro and the Cozumel Banks and at Alacranes Reef is thought to be a significant factor inhibiting recovery (CITES 2012).

In Belize the heavy exploitation of conch populations almost led to a stock collapse in 1996 (CITES 2003). In response, the government prohibited the selling of diced conch (Government of Belize 2013), instituted minimum shell length and weight to prevent the harvest of immature conch, prohibited harvest by SCUBA, and established a total allowable catch (TAC) limit based on biennial surveys (Gongora et al. 2020). While the biennial surveys to determine TAC show relative stability in queen conch size classes over the past few years, it is likely that this is mainly due to the limitations of free-diving, which offers protection to putative offshore breeding populations. For example, Tewfik et al. (2019) documented a significant 15-year decline in the mean shell length of adult and sub-adult queen conch at Glover's Atoll, likely due to the

selective harvest of conch with a certain shell length size. However, smaller adults can affect the reproductive success of the conch population as they tend to have lower mating frequencies and smaller gonads (Tewfik et al. 2019), and could potentially lead to a decline in queen conch reproductive output. Additionally, Tewfik et al. (2019) found evidence that indicates Belize's minimum shell length size (178 mm) and market clean mass (85 g) regulations are inadequate to protect juveniles from harvest. Based on surveys of queen conch at Glover's Atoll, Tewfik et al. (2019) calculated a threshold for the size at 50% maturity to be a 10 mm thick shell lip and an associated 192 g market clean meat mass. They also found a significant amount of juveniles with shell length sizes over 178 mm and suggest lip thickness should instead be used as a proxy for maturity. However, most of the queen conch in Belize is landed without a shell. Therefore, current regulations are likely inadequate to protect juvenile queen conch from harvest and may lead to recruitment and growth overfishing in the future. In fact, the fishing of juveniles has been confirmed directly by fishermen and delegates, who note that imposing a lip thickness requirement would significantly affect their landings as "the majority of conch that is fished are juveniles" (Arzu 2019; FAO Western Central Atlantic Fishery Commission 2020). In addition, a study conducted by Huitric (2005) presented a historical review of conch fisheries and sequential exploitation. The overall objective of this study was to analyze how Belize's conch fisheries have developed and responded to changes in resource abundance. Huitric (2005) suggests that the use of new technology over time and space (by increasing the area of the fishing grounds), together with fossil fuel dependence, have sustained yields at the expense of depleted stocks, preventing learning about resource and ecosystem dynamics, and removing incentives to change fishing behavior and regulation.

Belize has established a network of marine reserves along the Belize Barrier Reef and two offshore atolls that are divided up into zones of varying levels of protection; however, enforcement of these regulations throughout the reserve is lacking. For example, long-term declines of reproductively active adult conch have been reported within the Port Honduras Marine Reserve (PHMR) in southern Belize, a no-take zone for queen conch. In fact, densities of conch have been continuously declining since 2009, falling below 88 conch/ha by 2013, and decreasing further to <56 conch/ha in 2014 (Foley 2016, unpubl., cited in Foley and Takahashi 2017). There have also been reports of poaching near Belize's border with Guatemala as well as reports of Honduras fishermen illegally selling seafood products from Belize (Arzu 2019). In 2017 the Belize Fisheries Department reported confiscating around 4.1 mt of queen conch that were harvested out of season (San Pedro Sun 2018). While existing regulations appear adequate to maintain a conch fishery in the short-term, because there are at least some large mature conch that are protected from fishing because they are below the depths usually accessed by free-diving (Singh-Renton et al. 2006; Tewfik et al. 2019), they will likely be ineffective in preventing overutilization of the species in the future, particularly given the evidence of significant harvesting of juvenile queen conch, the decreasing size of adult queen conch in the population, and the ongoing reports of IUU fishing and lack of enforcement capabilities. Further, Tewfik et al. (2019) found that the deep-water sites (i.e., fore-reef sites at Glover's Atoll), generally protected from fishing, displayed the lowest overall density (4-14 individuals/ha) and were dominated by significantly older individuals (lip thickness >20 mm) that have lower fecundity.

Honduras, which is one of the largest producers of queen conch, has also had a problem with overutilization and poaching, leading to low population densities in some areas. For example,

after decades of heavy exploitation (CITES 2012), surveys conducted in Cayos Cochinos in the mid-1990s showed overall adult conch densities of 14.6 conch/ha (Tewfik et al. 1998). These low adult densities indicate that there is no reproductive activity likely occurring in this population. Since these surveys were conducted, the Cayos Cochinos has been declared a reserve and further harvest has been prohibited. In the early 2000s, there was also evidence that a significant portion of the queen conch meat landed in and exported from Honduras was fished illegally from waters of neighboring jurisdictions. In particular, concerns were raised about the increase in queen conch meat exports from Honduras that coincided with the period when the Jamaican fishery at Pedro Bank was closed (2000 – 2001 and 2002), which led to an increase in poaching at the Bank by foreign vessels (including Honduran vessels) after the commercial moratorium (CITES 2003; CITES 2012). From 1999 – 2001, Honduras almost doubled their queen conch production, elevating concerns about illegal fishing, and this resulted in the imposition of a CITES moratorium (FAO 2016). Illegal fishers can have connections to drug trafficking, increasing the complexity of the issue for fisheries managers and the legal efforts in terms of enforcement (FAO 2016; Canadian Business.com, Illegal trade: raiders of the lost conch, April 28, 2008). Due to the high amount of exports, lack of landings records, evidence of illegal activity, and low population densities, Honduras was placed under a CITES trade suspension in 2003 and the Honduran government declared a moratorium on conch fishing from 2003 to 2006. From 2006 – 2012, export quotas were set annually for meat that is taken during scientific surveys (CITES 2012; Regalado 2012). However, based on surveys in 2009 – 2011 at the three main queen conch fishing banks (Regalado 2012), the mean queen conch landings from the 2010s represented about 12.3% of the standing stock, or more than 50% above the recommendation to fish at 8% of standing stock, indicating that quotas are being set too high to allow for sustainable fishing of these queen conch populations. In 2012 Honduras lost a substantial portion of their conch fishing grounds to Nicaragua in a marine dispute resolution (Grossman 2013). Subsequent to that determination, Honduras terminated their queen conch research program and temporarily ceased generating scientific reports to inform the annual quota allocation.

In 2017 Honduras developed and adopted a formal fishery management plan aimed at establishing legal and technical regulations contributing to the sustainable use of their queen conch populations. Regulations implemented in the plan established a quota of 310 mt of 100% clean conch meat to be distributed among 11 industrial fishing vessels. In 2018 – 2019, the total quota increased to 416 mt and was allocated among 13 vessels. Each vessel must carry a satellite monitoring and tracking system during operations and carry one inspector onboard. Up to 90.7 mt of cleaned conch can be harvested. Size limits were also established at 210 mm shell length and at least 18 mm lip thickness with a minimum meat weight of 125 g (4.41 oz), with fishing for juvenile conch explicitly prohibited. The most recent data for 2018 – 2019 show that approximately 416 mt of clean conch meat were landed by a fleet of 13 industrial vessels (Ortiz-Lobo 2019), in accordance with the set quota. However, 0.6 mt of conch meat was seized by the Honduran Navy onboard an unauthorized vessel in November 2018 (Ortiz-Lobo 2019), indicating illegal fishing and poaching are still a problem. In addition, fishermen who agreed to conduct population abundance and density surveys as part of the condition for being allowed to fish for queen conch under CITES, reversed their decision, and abundance surveys were not conducted (Ortiz-Lobo 2019). This suggests a lack of adequate management controls or enforcement capabilities that could ensure the sustainability of the conch fishery.

Nicaragua

The queen conch fishery in Nicaragua was not considered a major fishery until the mid-1990s (CITES 2012). The majority of the queen conch harvest is caught by fishermen targeting lobster, with the remainder made by divers during the lobster closed season (Barnutty Navarro and Salvador Castellon 2013) or incidentally (Escoto García 2004). Landings, export quotas, and exports have all increased significantly since the 1990s (Sánchez Baquero 2009). In 2003 Nicaragua implemented regulations that established a 200 mm minimum size, a minimal lip thickness of 9.5 mm, a seasonal closure between June 1 through September 30, and set the export quota at 45 mt (processed) (Barnutty Navarro and Salvador Castellon 2013; FAO Western Central Atlantic Fishery Commission 2020). Since then, the export quota has increased significantly. In 2009 the export quota was set at 341 mt of clean fillet and 41 mt for use for research purposes. In 2012 Nicaragua gained additional conch fishing grounds through the resolution of a maritime dispute with Honduras (International Court of Justice, Press Release 2012) and increased their export quota to 345 mt (Barnutty Navarro and Salvador Castellon 2013; FAO Western Central Atlantic Fishery Commission 2013). By 2019, this quota had almost doubled to an annual export quota of 638 mt (FAO Western Central Atlantic Fishery Commission 2020). The 2020 export quota increased to 680 mt (see CITES Export Quota). Whether or not these regulations are adequate to protect the queen conch population from overexploitation is unclear, but a comparison of conch densities over the years possibly suggests the current quota may be set too high. For example, results from a 2009 systematic cross-shelf scientific survey conducted by scuba divers showed adult conch densities ranging from 176-267 individuals/ha depending on the month (April, July, or November), location, and depth (10-30 m; Barnutty Navarro and Salvador Castellon 2013). More recent surveys, conducted in October 2016, March 2018, and October 2019, show a decrease in, presumably, adult densities to 70-109 individuals/ha (FAO Western Central Atlantic Fishery Commission 2020); however, details on these surveys were unavailable. Regardless, the available information suggests that adult densities have decreased by potentially over 50% since 2009, presumably due to the significant increase in the allowed export quota over the past few years. While the densities are still at a level that would allow some reproductive activity to occur in the queen conch population, the existing regulatory measures, including the current allowable quota, may not be adequate to prevent further declines in queen conch densities in the future. Based on the models, the queen conch in Nicaragua are reliant on high self-recruitment, and with the trends of decreasing queen conch densities and increasing export quotas over the past few years, there is an increasing likelihood of stock collapse in the future.

Costa Rica

Queen conch populations were reported to be declining in Costa Rica back in 2001, but there is limited information available (CITES 2003). Queen conch harvest has been prohibited since 1989 (CITES 2003; Mora 2012). In 2000 the commercial sale of incidentally captured conch was also prohibited, but conch caught as bycatch could be kept for personal consumption. Given that the status of the queen conch population in Costa Rica is unknown, the adequacy of existing regulatory measures in protecting queen conch from threats is highly uncertain.

The Bahamas

Landings data from the 1950s – 2018 have ranged between ~750-6000 mt, with a steady increasing trend over that period. Mean landings from the five middle years of a decade have exceeded 5000 mt over the last four decades. Prior to 1992, export of queen conch from The Bahamas was illegal. Presently, at least 51% of the landings are exported; export amounts and values have been increasing over the past two decades and the bulk of the product exported (99%) (Gittens and Braynen 2012) goes to the United States (Posada et al. 1997). The Bahamian government began implementing an export quota system in 1995 and more recently additional protective measures have been implemented, including: a SCUBA ban, limited use of compressed air, establishment of a network of marine protected areas, area closures, and take of only conch with well-formed flared lips (FAO 2007; Gittens and Braynen 2012). There is continued concern regarding illegal harvest and underreported landings, which is likely exacerbating the serial depletion that queen conch populations are experiencing throughout most of The Bahamas (Stoner et al. 2019b).

Several fishery-independent studies in both fished and unfished areas within The Bahamas have reported one or more of the following trends since the late 1990s: declines in adult densities ranging from 74-90%, a reduction in the size of adults on mating grounds, a reduction in the average age of individuals within populations, and a reduction in the number of juveniles within nursery grounds (Stoner et al. 2019a). Visual surveys spanning two decades showed that densities of mature individuals had a significant negative relationship with an index of fishing pressure: average shell length in a population was not related to fishing pressure, but shell lip thickness (an index of conch age) declined significantly with fishing pressure (Stoner et al. 2019a). Repeated surveys in three fishing grounds (Andros Island, Lee Stocking Island, and Berry Islands) revealed that densities of mature conch have declined in all of those locations and the populations have become younger with time. Densities have also declined significantly in three repeated surveys conducted over 22 years in a large no-take fishery reserve (Stoner et al. 2019a). Unlike fished populations, the protected population has aged and appears to be declining for lack of recruitment (Stoner et al. 2019a). Queen conch populations around Andros Island, the Berry Islands, Cape Eleuthera, and Exuma Cays are at or below critical densities for successful reproduction. A fishery closure in the Exuma Cays Land and Sea Park since 1986 has not been effective in reversing the collapse of the stock in this area (Stoner 2019).

Some areas of the southern Bahamas, including Cay Sal and Jumentos and Ragged Cays, maintain adult conch densities of >100 conch/ha (Souza Jr. and Kough 2020; Stoner et al. 2019a). However, fishing grounds in the central and northern Bahamas are depleted and regulatory measures are needed to reverse the downward trend (Souza Jr. and Kough 2020). Media reports from 2010 – 2020 show that remote Bahamian banks are increasingly threatened by poaching as fishers deplete more accessible areas (Souza Jr. and Kough 2020).

The Bahamas is largely self-recruiting, retaining the majority of conch larvae (Vaz et al. 2022). The Bahamas does not export a significant amount of larvae to any jurisdiction; however, it does receive a substantial amount of larvae from Turks and Caicos, and to a lesser extent Cuba (Vaz et al. 2022). The sustainability of queen conch populations in The Bahamas relies heavily on domestic regulations. Queen conch surveys show that densities of legal to harvest flared lip queen conch are well below the minimum threshold required to support reproductive activity (56 adult conch/ha; Stoner et al. 2012b; Stoner and Ray-Culp 2000) except in the most remote areas

(Stoner et al. 2019a). Substantial decreases in adult conch densities (up to 74%) observed in repeated surveys in three fishing grounds indicate that the conch population is collapsing. In fact, Stoner et al. (2019a) found that only one location of the 17 locations surveyed in 2011 and 2018 had adult conch densities above the 56 conch/ha threshold.

Other losses in juvenile populations were reported near Lee Stocking Island where aggregations associated with nursery grounds were estimated to have decreased by more than half between surveys conducted in the early 1990s and 2011 (Stoner et al. 2011; Stoner et al. 2019a). The current regulatory measures in The Bahamas are inadequate to protect queen conch populations from further declines.

Turks and Caicos

The Turks and Caicos has contributed substantially to the queen conch fishery, providing roughly 35% of the total landings reported for the greater Caribbean from 1950 – 2016. In 2007 CITES considered stocks in the Turks and Caicos to be among the most healthy in the Caribbean (Lockhart et al. 2007) and the most comprehensive fishery independent information from the early 2000s suggests that queen conch densities (~250 adult conch/ha) support reproductive activity and population growth. The following list of regulatory measures may have contributed to some of the purported success of the fishery: a catch quota system based on total allowable catch implemented in 1994, shell length and weight limits, requirement that all conch landed have a flared lip, prohibition of SCUBA and hookah, closed season on exports from July 15 – Oct. 15 beginning in 2000 (DEMA 2012), the establishment of several no-take reserves beginning in the early 1990s, and a satellite monitoring program proposed in 2012 to control poaching primarily from Hispaniola (DEMA 2012; Wood 2010a).

Two recent studies suggest that the level of exploitation of conch populations in Turks and Caicos may be higher than previously thought. The first study by Ulman et al. (2016) identified a significant problem with underreporting of fishery landings data from 1950 – 2012 by performing catch reconstructions. The authors found that the total reconstructed catch was approximately 2.8 times that reported by the Turks and Caicos to the FAO, and 86% higher than the export-adjusted national reported baseline. The discrepancies arose because local consumption was not reported and in fact the total local consumption of queen conch equated to almost the entire total allowable catch, before exported amounts were even considered. In other words, the exported catch was unsustainable. In response to this study, DEMA lowered the catch quota in 2013. A study by Schultz and Lockhart (2017) examined the demographics of conch populations inside and outside the East Harbor Conch and Lobster Reserve. There was a lack of algal plain habitat, smaller conch, and lower densities of conch in the reserve. Only one of 118 sites examined inside the reserve contained adult densities >50 conch/ha and none of the sites had densities >100 conch/ha. Outside of the reserve, only four of 96 sites had densities >50 conch/ha and only one site had a density of >100 conch/ha. Overall, the densities inside and outside the reserve were similar and had declined by at least an order of magnitude since 2000. The authors cited a lack of habitat inside the reserve and a lack of reserve compliance due to low enforcement presence as being the most likely reasons for an underperformance of the reserve for queen conch conservation.

The Turks and Caicos have been a top queen conch producer for decades, but recent trends suggest that the regulatory mechanisms in place may be inadequate to sustain viable populations. The jurisdiction supplies larvae to The Bahamas, does not receive larvae from overfished

populations up current, and is largely self-recruiting, thus local reproductive viability is important for sustaining the fishery and supporting species conservation.

Jamaica

Jamaica has been a major producer for the queen conch fishery since the 1990s (Aiken et al. 1999; Appeldoorn 1994b; Prada et al. 2009). The commercial fishery is focused on an offshore bank located approximately 50 miles (80 km) southwest of Jamaica (Pedro Bank). Fisheries-independent diver-based surveys began on Pedro Bank in 1994 and these surveys have helped establish total allowable catch limits for the fishery. Queen conch surveys are conducted about every 3-4 years (e.g., 1994, 1997, 2002, 2007, 2011, 2015, and 2018). Although density estimates for all life stages and depth strata from 1994 – 2018 have remained at a level that supports reproductive activity (142-405 conch/ha; National Environmental Planning Agency Jamaica 2020), the 2018 surveys recorded low enough densities (including low juvenile density) in some areas such that the National Fisheries Authority of Jamaica implemented a closure of the queen conch fishery from 2019 to 2020. Because funds to conduct a new survey have been unavailable, the closure was extended to February 2021 (Jamaica Gleaner, Ban on Conch Fishing Extended to February 2021; April 6, 2020).

Several management strategies have been employed to help sustain queen conch fishing in Jamaica. The queen conch fishery management plan established guidelines for management measures including a national total annual catch (NTAC) and individual quota system (Morris 2012) in 1994. There is a closed season from July 31 – February 1 (FAO Western Central Atlantic Fishery Commission 2013). Harvest of queen conch is prohibited at depths greater than 30 m and industrial fishers are not authorized to harvest conch within 5 miles of the Pedro Cays (Morris 2012). These measures are intended to conserve nursery and breeding areas as well as deep spawning stocks (Morris 2012). There is no closed season for the recreational fishery, but harvesting is limited to three conch per person per day (CITES 2003). Currently, annual quotas for Pedro Bank are determined through a control rule based on harvesting 8% of the estimated exploitable biomass (Smikle 2010). Under this scenario, the maximum catch is fixed when densities are above 100 conch/ha and are progressively reduced if the population density is reduced. The fishery would be closed if population density declined to 50 conch/ha. Additional management measures include: 1) all of the western bank is closed to fishing (due to depth) and represents a very large *de facto* protected spawning stock with plans to declare a second closed area on the eastern end in shallow areas near the keys utilized by the Jamaica Defense Force; 2) quotas cannot be increased unless supported by the results of an in-water survey; however, quotas can be lowered if there is evidence of problems, such as a drop in catch per unit effort or a survey indicating a lack of juveniles for future recruitment; and 3) field surveys are mandated at regular intervals. In 2012 the South West Cay Special Fisheries Conservation Area (SWCSFCA) was designated. Queen conch harvest is prohibited within the SWCSFCA which extends in a 2-km radius around Bird Key on Pedro Bank.

These management actions have not sufficiently addressed poaching, which is thought to be problematic based on a spike in catch statistics reported by Honduras and the Dominican Republic during two discrete periods between 2000 – 2002 when Jamaica's fishery on Pedro Bank was closed (CITES 2012). Per FAO Western Central Atlantic Fishery Commission (2020), a Jamaican national fisheries authority was newly declared but had an unfunded compliance branch, with the Jamaican Coast Guard and Marine Police also assisting but not prioritizing fisheries issues. With the large Jamaican EEZ, FAO Western Central Atlantic Fishery

Commission (2020) declares “As a result there is intense IUU fishing by vessels from jurisdictions such as Honduras, Dominican Republic and Nicaragua.”

Recent management actions taken by Jamaica have not addressed increased eutrophication in nursery habitats near Pedro Cays (NEPA 2020). In addition, Pedro Bank is geographically isolated and receives little gene flow from areas external to the Bank. The future of Pedro Bank’s queen conch fishery likely depends on local recruitment for sustaining its stocks (Kitson-Walters et al. 2018), thus highlighting the importance of conservative management measures on the Bank itself. The health of the Pedro Bank population may also be important to species connectivity throughout the greater Caribbean, as Jamaica has been identified as an important ecological corridor “stepping stone” and a source of larvae to down-current jurisdictions (Figures 12, 13).

In summary, management actions to date have helped to keep queen conch populations on Pedro Bank, on average, at levels above the necessary threshold required to support reproductive activity (i.e., >100 adult conch/ha); however there are some signs that suggest current regulations may not be adequate to control poaching, prevent habitat degradation, and reverse localized depletion in shallower areas.

Florida (United States)

Regulatory measures were put in place in the 1970s, 80s, and 90s (Florida Administrative Code, 1971, 1985, 1990) to first limit and then prohibit recreational and commercial take of queen conch in order to reverse the downward trend of queen conch populations in Florida (Florida Department of State 2021; Glazer and Berg Jr. 1994). The 1990 regulations also provided a stricter framework for shell possession. Habitat loss resulting from coastal developmental has also been implicated in the decline of queen conch populations during the 1980s and since that time, multiple state and federal regulations (e.g., Florida Department of Environmental Planning and the Florida Keys National Marine Sanctuary) have limited discharge, development, and other anthropogenic activities that may influence water quality and/or degrade coastal habitat.

To date, none of these measures have been effective in restoring sub-populations in the nearshore, shallow water, hardbottom habitats immediately adjacent to the Florida Keys island chain. In fact, three populations known to exist in the 1990s remain locally extinct despite 35 years of fishery closure (Glazer and Delgado 2020). Adults in the nearshore areas are not reproducing (Glazer et al. 2008) and densities remain low (<5 conch/ha from 1987 – 1990; (Berg Jr. and Glazer 1995). A causative agent responsible for reproductive failure has not been identified, although contaminants may play a role, and natural geographic barriers to movement (e.g. Hawks Channel) appear to be limiting opportunities for the formation of spawning aggregations that could restore viable populations in nearshore areas. Therefore, it is likely that these populations will continue to decline without additional intervention, despite the protective measures that have been in place over the past four decades.

Florida’s back-reef populations located in shallow water reef flats in habitats primarily consisting of coral rubble, sand, and seagrass (Glazer and Kidney 2004), have been the focus of fishery independent surveys since 1993 (Delgado and Glazer 2020). These surveys confirm that the adult abundance of queen conch on back reefs has been increasing slowly but steadily since 2007. As higher densities are reached, habitat expansion is occurring, with a statistically significant proportional shift into dense seagrass (FWC unpublished data). By 2013, with a few setbacks due to major hurricanes in 2004 and 2005, adult abundance reached approximately 65,000

individuals (Glazer and Delgado 2020). Delgado and Glazer (2020) have confirmed that adult spawning densities are high enough ($> \sim 100$ conch/ha) in these regions to support reproduction (i.e., egg laying), although the authors never observed mating when aggregation density was less than 204 adults/ha and spawning was not observed when densities were less than 90 adult conch/ha. Given that Florida is thought to be largely a self-recruiting population that receives little input from source populations outside of Florida, it is encouraging that back-reef populations have been increasing and are reproducing.

The State-sponsored experimental translocation program that began in the early 2000s may be partially responsible for the increase in back-reef populations. Approximately 3000 conch from nearshore sub-populations, where spawning does not occur, have been translocated to back-reef spawning aggregations to date. These individuals regained their reproductive capacity after approximately 3-6 months with no obvious adverse consequences relative to the genetic structure of populations or conspecific interactions resulting in the displacement of native back-reef conch (Delgado et al. 2004; Delgado and Glazer 2007). While it is promising that deep reef populations, seaward of the reef on sand plains in water depths of approximately 30 to 100 feet, are reproducing (FWC unpublished data) the impact of that reproduction on the overall health of South Florida conch populations is uncertain. Queen conch aggregations at these depths are difficult to consistently monitor and only a limited picture of their current status and overall reproductive contribution is possible at this time. The use of towed underwater cameras may improve monitoring capabilities in the future (Glazer and Delgado 2020).

In summary, queen conch populations in Florida have experienced large declines since the 1950s due to fisheries harvest and habitat degradation, despite protective regulations being put in place in the 1980s and 1990s. The best available data indicate that the density of large adults is still too low and/or compromised (i.e. non-reproductive adults in nearshore areas) to restore healthy populations across the three distribution zones in South Florida: nearshore, back reef, and deep-water. The median adult queen conch density in Florida is less than 50 conch/ha, too low for successful reproduction to be maintained throughout the region and for Florida to have a healthy self-recruiting population. Evidence of increasing abundance on back reefs and the restoration of the reproductive capacity of nearshore adult conch following translocation is promising. Fishery closures and other regulatory measures implemented up until the early 2000s may be partially responsible for some of the positive trends that have been observed within the last decade. Additional regulations and/or enforcement of existing measures that protect nearshore water quality and habitats may provide benefits to conch and may complement ongoing conservation efforts. Recent restoration measures through translocation implemented by the State suggest that queen conch populations may have the capacity to recover with sustained human intervention. Additional regulatory measures outside of Florida are unlikely to have a positive impact on Florida populations because connectivity modeling (Figures 12, 13) and genetic structure of populations (Truelove et al. 2017) throughout the queen conch range suggest that Florida receives very little larval input from other locations (i.e., Florida is largely a self-recruiting population).

Dominican Republic and Haiti

Populations of queen conch in the Dominican Republic and Haiti have been overfished (Mateo Pérez and Tejada 2008; Wood 2010b) since the 1970s (Brownell and Stevely 1981). Illegal fishing and trade is also common, as exemplified by the famous case known as operation Shell Game, where more than 20 mt of queen conch fillets were confiscated (FAO 2016). In another

example, from 1999 – 2001, the Dominican Republic almost doubled its queen conch production, elevating concerns about illegal fishing, and this resulted in the imposition of a CITES moratorium. Illegal fishers can have connections to drug trafficking, increasing the complexity of the issue for fisheries managers and the legal efforts in terms of enforcement (FAO 2016; Canadian Business.com, Illegal trade: raiders of the lost conch, April 28, 2008).

The sparse and outdated information that exists on conch populations in these jurisdictions indicates that adult densities are too low to support reproductive activity and recruitment locally and broadly to other Caribbean nations. The latter point is particularly relevant because the SRT's connectivity analysis suggests the Dominican Republic was an important ecological corridor for species connectivity throughout the region. Despite the implementation of national park designations, seasonal and spatial closures, shell size and lip thickness restrictions, fishing method restrictions, and CITES export suspension, most populations are continuing to decline. Although the rates of decline may be slowing in some areas since 2000 (Torres and Sullivan-Sealey 2002) and there is evidence of reproduction in some locations (Wood 2010b), there is no evidence that regulations have been effectively implemented and/or enforced. In addition, detailed, accurate, consistent, and unbiased reporting of fisheries data is a challenge and creates a barrier to recognizing and understanding the current status of populations (FAO Western Central Atlantic Fishery Commission 2020). Adult densities are well below what is required for healthy spawning populations at most locations (Posada et al. 1999; Wood 2010b) and continued declines may be irreversible without human intervention even if fishing pressure is significantly reduced or halted (Torres and Sullivan-Sealey 2002). Existing regulatory mechanisms are likely inadequate to reverse the decline of populations in the Dominican Republic and Haiti.

Puerto Rico

Queen conch populations in Puerto Rico showed signs of steady decline beginning in the 1980s. (CITES 2012). Estimated fishing mortality exceeded estimates of natural mortality, catch continued to decline while effort increased through 2011 (CITES 2012), and the catch became increasingly skewed to smaller sizes, all suggesting that Puerto Rican populations have been overfished for decades (Appeldoorn 1993; SEDAR 2007). Recently, studies by Jiménez (2007) and Baker et al. (2016) suggest that some of the downward demographic trends may be reversing. Larger size distributions, higher adult queen conch densities compared to three previous studies (but lower than the density reported in 2006), an increase in the proportion of older adults, and evidence of sustained recruitment suggest that populations are recovering to some extent.

There are several regulations associated with the Queen Conch Resources Fishery Management Plan of Puerto Rico and the U.S. Virgin Islands (CFMC 1996). In 1997 the U.S. Caribbean EEZ (with the exception of St. Croix) was closed to queen conch fishing and a territorial waters closed season (July 1 through September 30) was implemented. In 2004 additional regulations implemented in local waters included a 22.86 cm minimum shell length or 9.5 mm minimum lip thickness and daily bag limits of 150 per person and 450 per boat. As previously, minimum shell length and meat weight regulations are unreliable since large juveniles can have larger shells and more meat than mature adults can. The seasonal closure was amended to August 1 through October 31 in 2012. In 2013 the Puerto Rico Department of Natural Resources implemented an administrative order that lifted the prohibition on extracting conch meat from the shell while underwater (Puerto Rico Department of Natural and Environmental Resources Administrative Order 2013-14). The administrative order is still valid today. The relaxation of this regulation

coupled with a lack of proactive restoration interventions have negative consequences not only for queen conch populations in Puerto Rico, but also throughout the range of the species. The connectivity model (Vaz et al. 2022) indicates that Puerto Rico, specifically the deep mesophotic reef off the west coast of Puerto Rico, is a major stepping stone for maintaining connectivity between the Windward Islands and populations in the western Caribbean (Vaz et al. 2022).

Leeward Antilles (Aruba, Curaçao, and Bonaire)

There is no historic or current fisheries data from the Leeward Antilles islands. Fisheries were closed in Bonaire and Aruba in 1985 and 1987, respectively, but enforcement of the closure did not begin in Bonaire until the mid-1990s (van Baren 2013). Limited permits, allowing take of adult conch over 18 cm shell length or meat weight over 225 g, were issued in Bonaire through the 1990s, but a moratorium on permit issuance was reported in 2012 due to concern over the extremely low adult population size at that time (van Baren 2013). Current densities are too low to support fisheries despite being closed for greater than 30 years in two of the three islands. Queen conch are imported legally from Jamaica and Colombia and illegally from Venezuela to markets in Curaçao and Bonaire (FAO 2007).

Limited fisheries independent monitoring suggests that the island-wide density of conch in Bonaire is 21.8 conch/ha. On the island of Bonaire, a study was done in Lac Bay to assess the status of queen conch (Patitsas 2010). Within Lac Bay, conch density was recorded to be 11.24 conch/ha. The majority of conch in Lac Bay were adults, constituting 85% of the total found (Patitsas 2010). The previous density study in Lac Bay was conducted by Cynthia Lott (2001) who estimated the population to be around 22 conch/ha with an average age of 2.5 years (Patitsas 2010). Patitsas (2010) concluded the densities in Lac Bay are below the Allee effect threshold of 50 adult conch/ha (Stoner and Culp 2000). No surveys have been done to determine the density and the conditions of the populations in the island of Curaçao (Sanchez 2017). The only information located is presented in a 2017 thesis (Sanchez 2017) which studied the diet and size of queen conch around the island of Curaçao. While Sanchez (2017) did not provide density information, the author concluded that adult queen conch are very rare surrounding the island, and appear to only occur in restricted places, like the Sea Aquarium Basins, where poaching and predation is limited (Sanchez 2017). The average density of queen conch on the west side of Aruba was 11.3 conch/ha from 2009 – 2011 and the population was dominated by juveniles, suggesting Aruba populations on the west side of the island are not large enough for successful reproduction, though there are isolated areas of higher conch densities. There is evidence that illegal poaching continues and is further contributing to declines (Ho 2011; van Baren 2013).

Despite fisheries closures that have been in place in Bonaire and Aruba since the 1980s, the best available information indicates that there has been limited or no evidence of recovery. The most recent available survey, although dated (>10 years old), report very low conch densities and suggest further decline in Lac Bay, Bonaire. There is limited evidence of improving management, enforcement, and conservation planning strategies in Aruba, Curaçao, and Bonaire.

Colombia

The queen conch commercial fishery in Colombia shifted to the continental shelf Archipelago of San Andrés, Providencia, and Santa Catalina (ASPC), including its associated banks (Quitasueño, Serrana, Serranilla, and Roncador) in the 1970s when populations in San Bernardo and Rosario became severely depleted due to inadequate regulatory mechanisms (Mora 1994).

Even with the declaration of San Bernardo and Rosario as national parks that only allow subsistence fishing, further declines in adult abundance to very low levels (0.9-12.8 conch/ha, 0.2-12.9 juvenile conch/ha) suggest recruitment failure (Prada et al. 2009). Prada et al. (2009) noted that illegal queen conch harvest might represent 2-14% or 1.4-21.8 mt of clean meat.

During the 1980s and 1990s, a suite of regulatory measures was put in place to protect populations in the ASPC because it constituted almost all of Colombia's production. Regulatory agencies closed some areas, prohibited the use of SCUBA gear, lowered the total allowable catch, and placed weight limits on meat (Prada et al. 2009). In addition, the CITES listing in 1992 established international trade rules. Fishery-dependent data collected through the mid-1990s and early 2000s masked continued population declines, despite these measures, due to biases associated with reporting CPUE, incomplete data reporting (e.g., inconsistent reporting of landings in versus out of the shell and incomplete or absent key spatial information), and illegal trade both into and out of Colombia. Ultimately, management measures were ineffective as evidenced by decreased landings, increased effort, and low densities reported by diver-based visual surveys at two of the three offshore banks, 2.4 conch/ha at Quitasueño and 33.7 conch/ha at Roncador (Valderrama and Hernández 2000). The Colombian government responded to the alarming numbers by closing the fisheries at Serranilla and Roncador and reducing the export quota by 50% (CITES 2003). Still, these measures were inadequate and the entire archipelago closed from 2004 – 2007 due to illegal trade, conflicts between industrial and artisanal fishers, and discrepancies between landings and exports (Castro González et al. 2009). The fishery reopened in 2008 for Roncador and Serrana Banks, with annual production set at 100 mt (Castro González et al. 2011) only to close again in 2012 at Serrana Bank.

Beginning in the mid-2000s, establishment of marine protected areas, implementation of a restoration program, and more comprehensive monitoring occurred. Closed seasons/areas and TACs based on a quota system also continued. Although positive trends have been detected in some areas (Providencia and Santa Catalina islands; Azcarate et al. 2019), negative trends persist in San Andrés (Forbes Pacheco 2017) and overall, densities remain below the critical threshold required to support any reproductive activity throughout much of the region. Furthermore, fishing is permitted at a total adult density minimum of 50 conch/ha and collection of conch with a lip thickness greater than 5 mm is permitted. These thresholds are likely too low to adequately support spawning and protect immature individuals. Colombia has informally adopted a control rule for setting the quota based on population density, as developed by (Smikle 2010) for Jamaica, which may prove beneficial in the future.

The ASPC is not receiving significant larval input from source populations outside the area, so without local populations with sufficient adult densities, the region is unlikely to recover with the regulatory measures in place at this time. The lack of information for populations in deeper areas throughout the ASPC, which may be particularly important for recovery (Castro et al. 2011 unpublished), hinders Colombia's ability to make sound management decisions and illegal fishing activity continues to plague the region.

Panama

There is little information available on the status of queen conch or harvest of queen conch in Panama. Georges et al. (2010) suggested that the queen conch fishery in Panama may not have specific regulations, but recognized harvest using SCUBA is prohibited. In the 1970s a

subsistence fishery was centered in the San Blas Islands (Brownell and Stevely 1981). By the late 1990s landings data suggest that the population had collapsed (CITES 2003; Georges et al. 2010). In 2000 extremely low adult densities were observed at Bocas del Toro archipelago (~0.2 conch/ha; CITES 2003). The most recent information, although dated, indicates that the fishery was closed for five years in 2004 (CITES 2012). The SRT was not able to obtain more recent information on the status of the queen conch fishery in Panama. However, the SAU data indicate that queen conch are harvested (reported and unreported) for subsistence and by the artisan fishery (Pauly et al. 2020). Panama is largely isolated from source populations outside the region and cannot rely on external sources of larval supply for recovery. The current regulatory measures in place are inadequate to protect queen conch and bring about recovery of Panama's severely depleted populations.

Summary

Given the ongoing demand for queen conch, the issues with compliance, appropriateness of certain morphometric regulations, enforcement, and poaching, and the observed low densities and declining trends in many of the queen conch populations, the best available information indicates that existing regulatory mechanisms are inadequate to control the harvest and overutilization of queen conch throughout most of its range. Currently only a fraction of jurisdictions such as Belize, Jamaica, Nicaragua, Colombia, and The Bahamas, are conducting assessments and periodic surveys to gather relevant information on the status of their queen conch populations to inform their national management regimes (Queen conch population assessment workshop, Belize, 2019). Substantial commercial harvest has led to declines in many queen conch populations to the point where reproductive activity and recruitment has been significantly impacted, particularly throughout the eastern, southern, and northern Caribbean region. Despite fishery management regulations aimed at controlling commercial harvest, poor enforcement, inappropriate management measures, and significant IUU fishing demonstrate that the existing regulatory mechanisms throughout much of the range of the species are inadequate to achieve their purpose of protecting the queen conch from unsustainable harvest and continued population decline. Nonetheless, it should be noted that the integration of efforts by FAO, CFMC, OPESCA, and WECAFC to coordinate and improve management and combat IUU fishing region-wide, is an encouraging sign, as their goals are to improve fishery data collection and establish reliable landings data based on scientifically supported conversion factors and management measures.

Other Natural and Manmade Factors Affecting its Continued Existence

Climate Change - Direct Impacts

Queen conch reproduction is dependent on water temperature (Aldana Aranda et al. 2014; Randall 1964) and therefore alteration to water temperature regimes may limit the window for successful reproduction. The increase in mean sea-surface temperatures by 2100 is predicted to lie between 1.1 and 6.4°C (Intergovernmental Panel on Climate Change 2008) and the magnitude of estimated change differs markedly among regions. The current temperature range of the Caribbean Sea is between 24 and 30°C, and by 2100, the mean sea-surface temperature is predicted to be between $28.7 \pm 1.37^\circ\text{C}$ and $30.18 \pm 0.57^\circ\text{C}$ (Agard 2014; Chollett et al. 2012; Eakin et al. 2010; Smith et al. 2008, as cited in Aldana Aranda and Manzano 2017). Increasing ocean temperatures may have direct effects on the timing and length of the reproductive season and ultimately decrease reproductive output during peak spawning periods (Appeldoorn et al.

2011; Randall 1964). Queen conch reproduction begins at around 26-27°C and recent research has observed nearly all reproduction ceased when temperatures reached 31°C (Aldana Aranda and Manzano 2017).

Early life history stages of queen conch are particularly sensitive to ocean temperature (Brierley and Kingsford 2009; Byrne et al. 2011; Harley et al. 2006) and rising water temperatures may have a direct impact on larval and egg development (Aldana Aranda and Manzano 2017; Boettcher et al. 2003; Chávez Villegas et al. 2017). Aldana Aranda and Manzano (2017) tested the influence of climate change predicted in 2100 on queen conch larval development, growth, survival rate, and calcification by exposing egg masses and larvae to increased temperatures (28, 28.5, 29, 29.5, and 30°C) for 30 days. Egg masses exposed to water temperatures predicted for the year 2100 (up to 30°C) resulted in the highest larval growth rate, but also higher larval mortality (76%; Aldana Aranda and Manzano 2017). The authors found no link between elevated water temperatures and the calcification process in queen conch larvae. However, the concentrations of magnesium and boron, minerals important to overall shell strength, were significantly lower at the temperatures predicted for the year 2100 (30°C). Furthermore, heat stress can induce premature metamorphosis of queen conch leading to developmental abnormalities and lower survival (Boettcher et al. 2003). Higher ocean temperatures also accelerate growth rates and decrease the amount of time queen conch spend in vulnerable early stages. For example, faster growth of juveniles offers earlier protection from predators and shortens the time to reach sexual maturity. While growth may be optimized at higher temperatures up to a certain point, the evidence to date suggests that warming ocean conditions will also lead to higher mortality rates and possible disruption of the shell biomineralization process (Aldana Aranda and Manzano 2017; Chávez Villegas et al. 2017). Similarly, Davis (2000) found in a laboratory study that temperature and salinity impacted larval growth and survival. Development was arrested and mortality was high when temperatures reached 20°C regardless of salinity and at 45 ppt regardless of temperature (Davis 2000). These findings suggest that current and future increases in temperature in the Caribbean Sea are likely to have a negative effect on survival rates of queen conch early life stages.

Climate change will also adversely impact the Caribbean region through ocean acidification, which affects the calcification process of organisms with calcareous structures, like mollusks. Ocean acidification impedes calcareous shell formation and thereby impacts shell development (Aldana Aranda and Manzano 2017; Parker et al. 2013). Many mollusks deposit shells made from calcium carbonate (CaCO_3 ; in the form of aragonite and high-magnesium calcite) and these shells play a vital role in protection from predators, parasites, and unfavorable environmental conditions. There is mounting evidence that suggests increased acidic ocean water negatively impacts the shell biomineralization process in mollusks (Chávez Villegas et al. 2017; Doney 2006; Fitzer et al. 2018; Gazeau et al. 2013; Morash and Alter 2015; Parker et al. 2013). According to Parker et al. (2013) the absorption of CO_2 into the ocean surface has led to a global decline in mean pH levels of more than 0.1 units compared with pre-industrial levels (Raven et al. 2005). Assuming median emission scenarios predicted by the Intergovernmental Panel on Climate Change (IPCC) (2001) are correct, a further 0.3-0.4 unit decline is expected over this century as the partial pressure of CO_2 (pCO_2) reaches 800 parts per million, or ppm (Feely et al. 2004; Raven et al. 2005). At the same time there will be a reduction in the concentration of carbonate ions (CO_3^{2-}) which will lower the CaCO_3 saturation state in seawater making it less available to organisms that deposit CaCO_3 shells and skeletons (Cooley et al. 2009; Parker et al. 2013). Whether the impacts of ocean acidification persist over multiple generations and at large

enough spatial scales to affect the long-term viability of queen conch populations remains uncertain (Aldana Aranda and Manzano 2017; Gazeau et al. 2013). While it is likely that changes to ocean pH will upset the process of shell biomineralization through the reduction of carbonate available for shell production and challenge metabolic processes and energetic partitioning, acidic ocean conditions can be patchy in space and time and may develop slowly (Aldana Aranda and Manzano 2017). Recent research conducted by Aldana Aranda and Manzano (2017) observed that acidification conditions produced a 50% decrease in aragonite in larval shell calcification at pH 7.6 and 31°C, conditions predicted in year 2100 (Figure 21). As previously mentioned aragonite and high-magnesium calcite are the primary ingredients in queen conch shell formation. Intergovernmental Panel on Climate Change climate change models forecast an increase in CO₂ for 2100 resulting in negative impacts to shell formation as the water will be more acidic and potentially dissolve the shells of many mollusks (Woods Hole Oceanographic Institute; Ocean Acidification: A Risky Shell Game, Dec. 4, 2009).

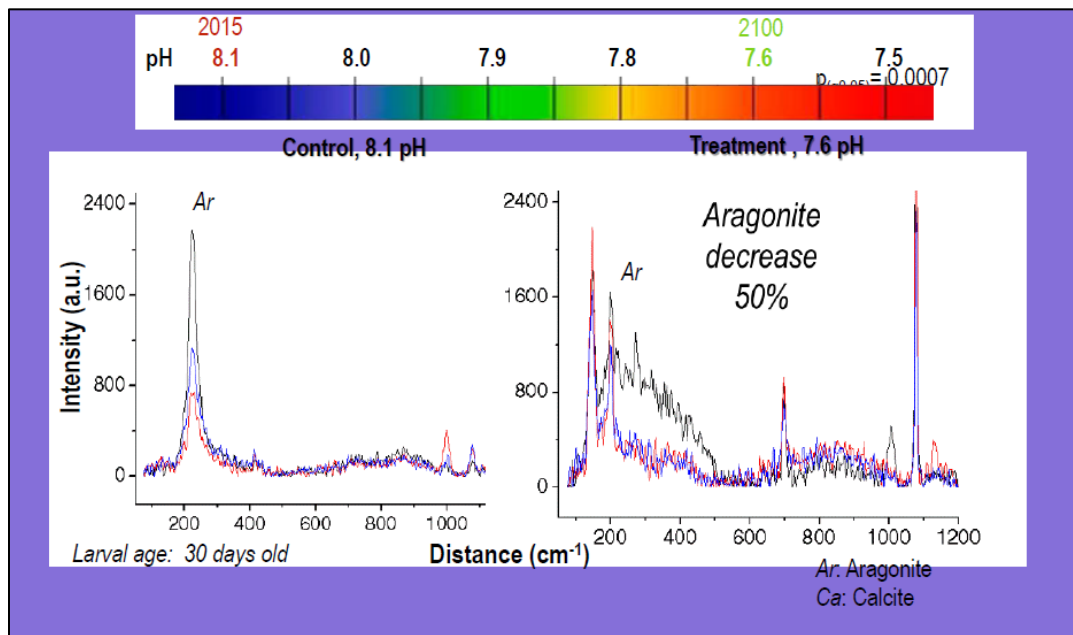


Figure 21. Ocean acidification and shell calcification. Acidification conditions produced a 50% decrease in aragonite in the larval shell calcification observed at pH 7.6 and 31°C; from Aldana Aranda et al. (2020).

Uncertainty with regard to the queen conch’s ability to adapt to predicted changing climate conditions, the potential costs of those adaptations, and the projections of future carbon dioxide emissions make it difficult to assess the severity and magnitude of this threat to the species. How queen conch specifically might be able to adapt to changing climate conditions and at what cost these adaptations will come are outstanding questions. Recent studies and reviews have stressed the importance of conducting multi-stressor (e.g., elevated water temperature and ocean acidity), multi-generational, and multi-predicted scenario experiments using animals from different areas in order to better understand the impacts of climate change on mollusks at species-wide levels (Aldana Aranda and Manzano 2017; Parker et al. 2013).

Climate Change - Indirect Impacts

Queen conch nursery habitat includes shallow and sheltered back reef areas that contain moderate amounts of seagrass. These areas are characterized by strong tidal currents and frequent exchange of clear seawater (Stoner et al. 1996). Sea level rise and associated erosion, rising sea surface temperatures and associated eutrophication, turbidity, siltation, and severity of tropical storms resulting from climate change can have both short- and long-term negative impacts on the water quality and health of seagrass meadows in these areas (Boman et al. 2019; Burkholder et al. 2007; Cullen-Unsworth et al. 2014; Duarte 2002; Grech et al. 2012; Orth et al. 2006; Short and Neckles 1999). Depending on the frequency, severity, and scale of climate change-induced conditions, seagrass meadow biomass may decrease at local and over larger scales resulting in conch larvae having lower encounter rates with appropriate settlement cues (i.e., *Thalassia testudinum* detritus and associated epiphytes) (Davis and Stoner 1994). Juveniles may experience lower growth and higher mortality rates if adequate food sources and shelter from predators, also provided by seagrass meadow communities, become limited (Appeldoorn and Baker 2013). The deposition of fine sediment or sediment with high organic content in a wider variety of habitats that adults depend upon (e.g., algal plains, coarse sand, coral rubble, seagrass meadows) could smother the algae they graze, limit nutrition, and have indirect impacts on their growth and gonad development (Appeldoorn and Baker 2013).

Queen conch are described as stenohaline (Stoner 2003), tolerating a narrow range of salinities (~34-36 ppt). The species' ability to adapt to short- or long-term intrusions of lower salinity water is uncertain, however in at least one groundwater-fed coastal area on the Yucatan Peninsula, queen conch movement and growth was not different from core habitat areas with more stable salinity and temperature signatures (Dujon et al. 2019; Stieglitz et al. 2020). Hypoxic or anoxic conditions may also affect the movement of juvenile queen conch (Dujon et al. 2019), which could make them more vulnerable to predation.

Changing climate may have subtler effects that could impact tidal flow, circulation patterns, the frequency and intensity of storm events, and larger scale current patterns (Franco et al. 2020; van Gennip et al. 2017). Changes in tidal flow and current patterns could alter the rate and condition of larval dispersal and the cycle of source and sink dynamics of queen conch populations throughout the Caribbean. Any changes in circulation patterns within the Caribbean would have significant implications for the species.

In summary, the two most significant impacts to queen conch resulting from climate change are increased ocean temperature and ocean acidification. The best available information suggests that future sea temperatures could significantly decrease or stop queen conch reproduction at 31°C. Current climate models predict that mean ocean temperature in the Caribbean Sea will be between 28.7°C and 30.18°C by 2100. Ocean temperature predicted by 2100 also resulted in higher larval growth rates, but also higher mortality rates (up to 76%) in laboratory studies. In addition, heat stress can induce premature metamorphosis leading to developmental abnormalities and lower survival rates. Furthermore, the IPCC forecasts an increase in CO₂ for 2100 resulting in negative impacts to shell formation as the water will be more acidic and potentially dissolve the shells of many mollusks. Studies have suggested a 50% decrease in aragonite in the larval shell calcification at conditions predicted for 2100 (pH 7.6) resulting in significantly weaker/thinner shells which may increase predation rates, thereby contributing to another source of mortality for the species in the foreseeable future. Similarly, changes in water

quality conditions (e.g., salinity, dissolved oxygen, pH) outside the range of those typically experienced by queen conch can impact their growth and survival and have negative consequences on the seagrass habitat upon which they depend. However, there is a high degree of uncertainty as the available studies do not span multiple generations or address the potential for queen conch to adapt to a changing climate. Even so, the available information is alarming as it indicates that the reproduction, growth, and survival of queen conch will likely be impacted by climate change based on the IPCC's climate predictions for 2100 (Intergovernmental Panel on Climate Change 2008).

Extinction Risk Analysis

Foreseeable Future

The appropriate time horizon for evaluating whether a species is more likely than not to be at risk of extinction in the foreseeable future depends on various case- and species-specific factors. For example, the time horizon may reflect certain life history characteristics (e.g., long generation time or late age-at-maturity) and should also reflect the time frame or rate over which identified threats are likely to impact the biological status of the species (e.g., the rate of disease spread). The appropriate time horizon is not limited to the period that status can be quantitatively modeled or predicted within predetermined limits of statistical confidence. The foreseeable future extends only so far into the future as can be reasonably determined that both the future threats and the species' responses to those threats are likely. It is based on the best available data, taking into account considerations such as the species' life-history characteristics, threat-projection timeframes, and environmental variability.

In determining an appropriate "foreseeable future" timeframe for our extinction risk analysis, the SRT first considered the life history of the queen conch. The longevity estimate for the queen conch is approximately 30 years. The SRT also considered how long it would take queen conch populations to show recovery after overexploitation. The SRT acknowledged that population recovery is likely dependent on when a closure is implemented and the status of the population at the time of the closure. For example, Florida, Bermuda, and Aruba prohibited all conch harvest in the mid 1980's (~30 years) yet their respective populations have yet to recover. Other recovery efforts such as those in Cuba and on Serrana Bank were started earlier and recoveries occurred over a shorter timeframe. Thus, the SRT concluded that it would likely take a minimum of 30 years for conservation management actions to be realized and reflected in the species status. Similarly, the impact of overutilization to the species could be realized in the form of noticeable population declines within this timeframe, as demonstrated in the available survey and fisheries data.

The SRT also determined that a separate timeframe needed to be considered for the threat of climate change because of the data available and the timescale over which the SRT could reasonably determine the impact of this threat on the species. The SRT considered the available information and current climate modeling scenarios and agreed that impacts on queen conch and its habitat from climate change could be predicted out to 2100. Based on the above, the SRT considered two foreseeable futures; the SRT considered the foreseeable future to be 2100 for determining the impact of climate change and 2050 for all other threats.

Methods

Demographic Risk Analysis

Threats to a species' long-term persistence, such as those evaluated in the analysis of the ESA Section 4(a)(1) factors section of this review, are manifested demographically as risks to its abundance, productivity, spatial structure and connectivity, and genetic and ecological diversity. These demographic risks provide the most direct indices or proxies of extinction risk. In this demographic risk analysis, the SRT assessed these risks by considering a set of questions adapted from McElhany et al. (2000). These questions are used as a guide to the types of considerations that are important to each of the broader demographic risk categories of abundance, productivity, spatial structure, and diversity.

After reviewing all relevant biological and commercial information for the species, each SRT member assigned a ranking to each of the four demographic criteria (abundance, growth rate/productivity, spatial structure/connectivity, diversity). Risks for each demographic criterion were ranked on a scale of 1 (low risk) to 3 (high risk). Below are the definitions that the team used for each ranking:

1. Low risk = This demographic factor indicates that the species is not presently at a high risk of extinction and this demographic factor is unlikely to significantly increase the species' extinction risk in the foreseeable future, but there is some concern that it may in combination with other Viable Population (VP) descriptors.
2. Moderate risk = This demographic factor indicates that the species is not presently at a high risk of extinction but this demographic factor may significantly increase the species' extinction risk in the foreseeable future.
3. High risk = This demographic factor indicates that the species is presently at a high risk of extinction.

The team members were provided a template and asked to fill out and rank the risk of each demographic factor. After rankings were provided, the team discussed the range of perspectives for each of the demographic risks and the supporting data on which they were based. Each team member was given the opportunity to revise scores, if desired, after the discussion. The rankings were reviewed by the SRT and considered in making the overall risk determination, which is presented at the end of this section. Although this process helps to integrate and summarize a large amount of diverse information, there is no simple way to translate the risk matrix ranking directly into a determination of overall extinction risk. Thus, the SRT emphasizes that this exercise was used as a tool to help the SRT organize the information and assist in their thought processes for determining overall risk of extinction for the species.

Threats Assessment

Section 4(a)(1) of the ESA requires the agency to determine whether the species is endangered or threatened because of any of the following factors:

- A. Present or Threatened Destruction, Modification, or Curtailment of its Habitat or Range;

- B. Overutilization for Commercial, Recreational, Scientific, or Educational purposes;
- C. Disease or Predation;
- D. Inadequacy of Existing Regulatory Mechanisms; or
- E. Other Natural or Human Factors Affecting its Continued Existence.

Similar to the demographics risk analysis, the SRT members were given a template to fill out and asked to rank the significance of each threat in terms of its contribution to the queen conch risk of extinction. Each threat was placed under the appropriate ESA Section 4(a)(1) factor within the template (File S3). Risks for each threat were ranked on a scale of 1 (low risk) to 3 (high risk). Below are the definitions that the team used to rank the threats:

1. Low risk = It is unlikely that this threat is significantly contributing to the species' extinction risk.
2. Moderate risk = This threat significantly contributes to the species' long-term extinction risk (through the foreseeable future of 30 years), but is not severe enough to drive the species towards extinction in a shorter time frame. NOTE: for climate change, the foreseeable future is considered to be year 2100.
3. High risk = This threat significantly contributes to the species' long-term extinction risk (through the foreseeable future of 30 years) and may be severe enough to drive the species towards extinction in a shorter time frame. NOTE: for climate change, the foreseeable future is considered to be year 2100.

After the rankings were provided, the team discussed the range of perspectives for each of the threats, and the supporting data on which they based their rankings, and were given the opportunity to revise rankings if desired after the discussion. The rankings were reviewed by the SRT and considered in making the overall risk determination. Again, it should be emphasized that this exercise was a tool to help the SRT organize the information and assist in their thought processes for determining the overall risk of extinction for the queen conch.

Overall Extinction Risk Analysis

Guided by the results from the demographic risk analysis and threats assessment, the SRT used their informed professional judgment to make an overall extinction risk determination for the queen conch. For these analyses, the SRT used three levels of extinction risk.

The risk categories are defined as:

1. Low risk = A species is at low risk of extinction if it is not at moderate or high level of extinction risk (see "Moderate risk" and "High risk" below). A species may be at low risk of extinction if it is not facing threats that result in declining trends in abundance, productivity, spatial structure, or diversity. A species at low risk of extinction is likely to show stable or increasing trends in abundance and productivity with connected, diverse populations.

2. Moderate risk = A species is at moderate risk of extinction if it is on a trajectory that puts it at a high level of extinction risk in the foreseeable future (see description of “High risk” below). A species may be at moderate risk of extinction due to current and/or projected threats or declining trends in abundance, productivity, spatial structure, or diversity. The appropriate time horizon for evaluating whether a species is more likely than not to be at high risk in the foreseeable future depends on various case- and species-specific factors.

3. High risk = A species with a high risk of extinction is at or near a level of abundance, productivity, spatial structure, and/or diversity that places its continued persistence in question. The demographics of a species at such a high level of risk may be highly uncertain and strongly influenced by stochastic or compensatory processes. Similarly, a species may be at high risk of extinction if it faces clear and present threats (e.g., confinement to a small geographic area; imminent destruction, modification, or curtailment of its habitat; or disease epidemic) that are likely to create imminent and substantial demographic risks.

To allow individuals to express uncertainty in determining the overall level of extinction risk facing the queen conch, the SRT adopted the “likelihood point” (FEMAT) method (Forest Ecosystem Management and Assessment Team 1993). This approach has been used in previous status reviews (e.g., Pacific salmon, Southern Resident Killer Whale, Puget Sound Rockfish, Pacific herring, and black abalone) to structure the team’s thinking and express levels of uncertainty in assigning threat risk categories. For this approach, each team member distributed 10 ‘likelihood points’ among the three extinction risk categories (File S3). The SRT provided their scores, which were assembled and presented to the team in aggregate. The SRT members discussed the range of perspectives, and the supporting data on which it was based. The SRT members were given the opportunity to revise scores, if desired, after the discussion.

Finally, the SRT did not make recommendations as to whether the queen conch should be listed as threatened or endangered. Rather, the SRT drew scientific conclusions about the overall risk of extinction faced by the species under present conditions and in the foreseeable future(s) based on an evaluation of the species’ demographic risks and assessment of threats.

Extinction Risk Results and Conclusions

Out of the four demographic factors analyzed in this ERA, all SRT members identified Spatial Structure and Connectivity as most concerning in terms of demographic risks that may contribute to the extinction risk of the queen conch (Figure 22). All SRT members (7 of 7) assigned a moderate risk to the Spatial Structure and Connectivity demographic factor. The Growth Rate/Productivity demographic factor also garnered significant concern, with all but one SRT member ranking this demographic factor as moderate. The SRT members all voiced concern related to the abundance and diversity demographic factors, but there was less agreement among members as to whether these demographic factors pose a moderate or low risk to the species. For example, four SRT members felt that the abundance was a moderate concern, whereas three members felt it was a low risk. Similarly, five SRT members ranked diversity as a low risk while two ranked it as a moderate risk.

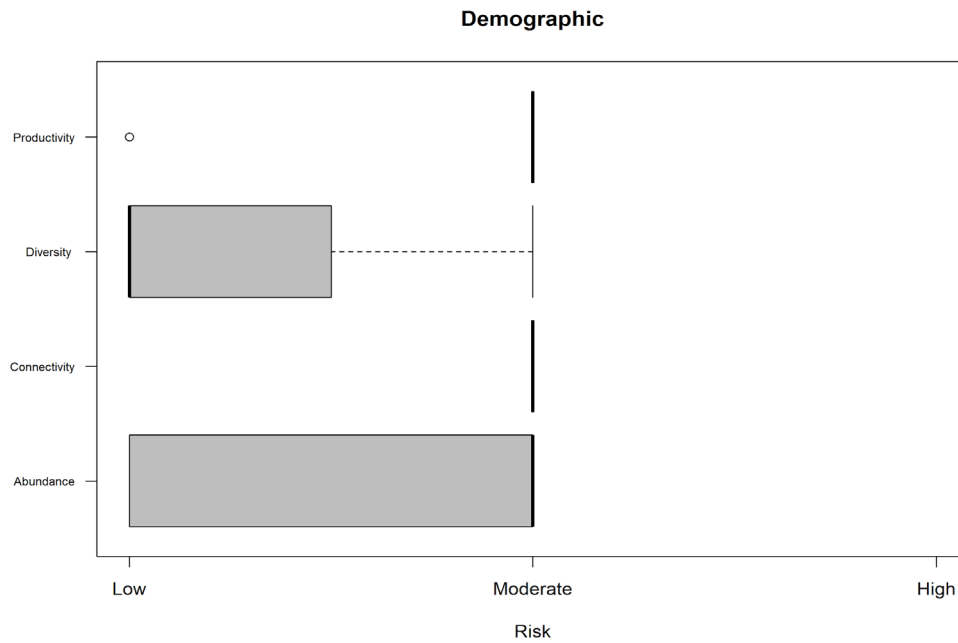


Figure 22. Demographic risk analysis results. The shaded area is the interquartile range (25% to 75% percentiles). The whiskers represent the minimum and maximum range. The single points represent outliers.

Spatial Structure and Connectivity

The connectivity modeling (Vaz et al. 2022) indicates that Allee effects are affecting queen conch dispersal rates Caribbean-wide. Compared to the models that showed uniform spawning, it is clear that many important connections for queen conch dispersal have been lost over the past 30 years (Figures 12, 13). Many of the larval connections between the Windward and Leeward Islands, as well as the Leeward Antilles and a large portion of the Greater Antilles, are no longer viable due to the reproductive depression/failure of the queen conch populations within these areas. Many of the Windward Islands that once served as source populations are no longer able to contribute to recruitment, as their densities are too low to support successful reproduction. The models show that the Dominican Republic, Puerto Rico, Colombia, Jamaica, and Cuba are jurisdictions that are central to keeping the network integrity for larval dispersal, and, therefore, likely serve as important ecological corridors. The loss (or significant reduction in larvae contributions) of critical up-current source populations (Windward and Leeward Islands, Leeward Antilles, Puerto Rico) has placed the species at an increased risk of extinction. The Dominican Republic, Puerto Rico, and Colombia all have populations with cross-shelf densities that are below the critical threshold required to support reproductive activity. As such, it is likely that these important ecological corridors may be lost in the foreseeable future, contributing to an increase in the species' extinction risk by significantly altering natural rates of dispersion among populations and metapopulations. Furthermore, the best available information indicates that critical populations within many of the Central American reefs (specifically Quitasueño Bank, Serrana Bank, Serranilla Bank) are likely overexploited, as those populations have low adult densities and are likely experiencing Allee effects. Based on the results from the connectivity model and genetic studies (Truelove et al. 2017), these Central America Reefs appear to be important populations for facilitating connectivity within the Caribbean region. In addition, the connectivity model indicates that the southeastern portion of the species range historically

functioned as a source of larvae (and genetic exchange) for the western Caribbean. Presently, however, it appears that only the mesophotic population in Puerto Rico is maintaining this connection and is currently at densities that put this recruitment/exchange at significant risk. Populations in Cuba, Jamaica (Pedro Bank), Nicaragua, Turks and Caicos, and the southern Bahamas appear to contain conch populations that achieve some level of reproductive activity, but they appear to be largely self-recruiting, offering limited connectivity via larval exports/dispersal to neighboring jurisdictions and, subsequently, providing limited genetic exchange. While exchange still exists between populations within the central/southwestern Caribbean, the continued fishing pressure, illegal fishing, and poor enforcement of existing regulations are likely to place these populations at increased risk of extinction in the foreseeable future.

The SRT noted that while the connectivity modeling indicates that Allee effects are potentially affecting dispersal rates Caribbean-wide, limited adult abundance estimates from surveys and unknown survey methodologies contributed to the connectivity model uncertainty in assumptions of decreased reproduction across the species range. It was also assumed that some level of reduced reproduction might continue in areas the connectivity models found to have no larval production. Such reproduction, if it occurs, may be from local remnant aggregations with sufficient local densities of conch that are less impacted by compensatory processes. If these aggregations persist, the connectivity that was presumed lost among these areas may still exist but just at a reduced level (i.e., many fewer larvae transported).

Overall, compensatory processes are likely limiting reproduction throughout the species' range. The loss of reproductively viable queen conch populations appears likely to have occurred in many areas throughout the Caribbean. The subsequent reduced larval production has resulted in the loss of connectivity among many queen conch populations, further contributing to declines in those populations dependent on source larvae. Thus, based on the best available information, the SRT concluded that loss of Spatial Structure and Connectivity throughout the species' range poses a moderate extinction risk to the queen conch in the foreseeable future.

Growth Rate/Productivity

The SRT noted that while the species is highly productive, queen conch require a minimum density for successful reproduction. However, many queen conch populations are presently below the densities required to support reproductive activity due to low encounter rates or mate finding (See *Spawning Density Section*). Based on the available data, it is likely that recruitment failure is occurring throughout a large portion of the species' range. Continued declines in abundance and evidence of overfishing suggest that population growth rates are below replacement. There are only a handful of jurisdictions [i.e., St. Lucia, Saba, Jamaica (Pedro Bank), Nicaragua, Turks and Caicos, Costa Rica, Cuba, Colombia (Serrana Bank), and The Bahamas (Cay Sal Bank and Jumentos and Ragged Cays)] that have adult conch densities (>100 adult conch/ha) sufficient to sustain successful reproductive activity. The majority of jurisdictions have adult densities below the critical threshold of 50 adult conch/ha required for any reproductive activity (i.e., Anguilla, Antigua and Barbuda, Aruba, The Bahamas' Western/Central Great Bahama's Bank, Little Bahama's Bank, Barbados, Belize, Bermuda, Bonaire, British Virgin Islands, Colombia's mainland, Quitasueño and Serranilla Bank, Curaçao, Dominica, Dominican Republic, Grenada, Guadeloupe, Haiti, Martinique, Mexico, Monserrat, Panama, St. Maarten, St. Vincent and the Grenadines, St. Barthelemy, Trinidad and Tobago, Florida, Puerto Rico, U.S. Virgin Islands, and Venezuela). Several, additional jurisdictions have

densities that are below the 100 adult conch/ha minimum threshold for successful reproductive activity (i.e., Cayman Islands, Honduras, St. Eustatius, Saint Kitts and Nevis, and Puerto Rico's mesophotic reef). In other words, the population growth rates in the majority of jurisdictions are likely below replacement levels given their lower densities and thus are at increased risk for negative impacts due to compensatory processes. There is also evidence of growth overfishing of queen conch, such as in Belize, which has led to the development of smaller adult conch. Since smaller conch are thought to be less productive (i.e., lower mating frequencies, smaller gonads, fewer eggs), the decrease in the sizes of adult queen conch will likely lead to decreases in abundance and lower densities, further contributing to declines in populations in the foreseeable future.

Several SRT members also noted that queen conch could likely withstand moderate harvest levels, as the species is very productive and may have the ability to compensate. However, given the extremely high levels of harvest occurring throughout the species' range, including high levels of IUU/poaching, harvesting of juveniles, and evidence of significant population declines throughout most of the Caribbean, the majority (6 of 7) of SRT members found that current population growth and productivity rates present a moderate risk to the species, significantly contributing to its long-term extinction risk. One SRT member, however, concluded that growth rate/productivity was a low risk, but close to moderate, primarily because successful reproduction is likely to continue in numerous areas within the region, including those areas with the largest populations of adults (e.g., Cuba), in the foreseeable future.

Abundance

There are no region-wide population estimates for queen conch. To assess species abundance, the SRT considered numerous sources of information including abundance estimates, stock assessments, surveys, landings and trends, habitat availability, and other biological indicators. Our total population abundance estimate ranges from 451 million to 1.49 billion individuals, based on the 10th and 90th percentile abundance estimates across jurisdictions. Those estimates, however, required numerous assumptions, in particular the assumed extent of conch habitat. In addition, for many areas, available survey data were limited, were outdated (may have been collected decades ago), or were unavailable. In many cases, survey methods and data collected (e.g., was abundance of adults or of all conch reported) were poorly described. Many density estimates were also unavailable or unable to be calculated because the survey methods were poorly described. These data limitations and analytical assumptions contribute to high uncertainty in our abundance estimates.

Considering these limitations, the SRT concluded that the best available data suggest queen conch populations are experiencing Allee effects, as densities are consistently very low and insufficient to support mate finding and reproductive activity. There remain several populations of queen conch that appear reproductively active based on the available survey data, but those are limited to Cuba, Costa Rica, Colombia (Serrana Bank), Jamaica (Pedro Bank), Nicaragua, Saba, Saint Lucia, The Bahamas (Cay Sal Bank and Jumento/Ragged islands), and Turks and Caicos, where population surveys in some cases are dated, highly uncertain, or unavailable (Table 2; Figure 7). In some cases, the exploitation rates are significantly above the recommended maximum harvest rate of 8% of the standing stock for a healthy population. Specifically, the SRT found that approximately half of the jurisdictions reviewed had exploitation rates significantly above the recommended maximum 8% harvest for healthy populations. Significant harvest levels and regulatory enforcement issues (e.g., harvest of

juveniles, poaching, etc.) will only continue to slow population growth and recruitment by decreasing abundances and potentially leading to extirpations into the foreseeable future. Any local disturbances (natural or anthropogenic) or environmental catastrophe (e.g., hurricanes) that affects those jurisdictions in the future could result in population declines that would have extensive negative implications for the species overall given the depensatory issues occurring in the wider Caribbean.

The majority of the SRT (4 of 7) concluded that abundance is a moderate risk, while not presently placing the species at a high risk of extinction, as low and/or declining abundances may significantly increase the species' extinction risk in the foreseeable future. Members of the SRT acknowledged that Cuba, southern Bahamas, Turks and Caicos, Jamaica, and Nicaragua have populations with higher abundance and densities that indicate successful reproductive activity is occurring. However, all these jurisdictions, with the exception of Cuba, heavily fish their conch populations with evidence of significant poaching/IUU and harvest of juveniles occurring, exemplifying the inadequate regulatory measures and lack of enforcement. As previously discussed, the majority of the SRT felt that while some jurisdictions have higher abundance, most jurisdictions throughout the species' range have very low densities which are insufficient to support reproduction and therefore recruitment. Thus, while the abundance estimates indicate that queen conch are not presently at a high risk of extinction, the majority of the SRT felt that the likelihood of declining abundance and lower population densities in the foreseeable future will significantly increase the species' extinction risk. Conversely, three SRT members considered abundance to be a low demographic risk, based on the data uncertainty, limited data available, and the fact that there are potentially millions of conch distributed across the region.

Diversity

The majority of the SRT (4 of 7) concluded that diversity was unlikely to significantly contribute to the species extinction risk. Early genetic studies of queen conch using electrophoretic methods found a high degree of gene flow among populations dispersed over the species' geographic distribution, with definitive separation observed only between populations in Bermuda and those in the Caribbean basin (Mitton et al. 1989). At the local level, Pérez-Enriquez et al. (2011) and Zamora-Bustillos et al. (2011) found, with mitochondrial DNA and microsatellites, respectively, low genetic differentiation among locations in the Mexican Caribbean. In the Florida Keys and Bimini, Campton et al. (1992) also found low genetic differentiation. Although Mitton et al. (1989) found limited evidence of population structure in the Caribbean, the authors hypothesized that the complex ocean currents of the Caribbean may restrict gene flow among Caribbean populations, even though larvae may disperse long distances throughout the Caribbean during their 16-28 day pelagic larval duration. Truelove et al. (2017) used microsatellite markers and a comprehensive sampling strategy to perform a detailed study of queen conch spatial genetic structure across the greater Caribbean seascape. Microsatellite genetics identified significant levels of genetic differentiation among Caribbean sub regions (e.g., Florida Keys, Mesoamerican Barrier Reef, Lesser Antilles, Honduran/Jamaican Banks, Greater Antilles, and Bahamas) and between the eastern and western Caribbean regions (Truelove et al. 2017). The connectivity model (Vaz et al. 2022) indicates there are several important jurisdictions that act as stepping-stones in facilitating population connectivity in the Caribbean region. For example, loss of Puerto Rico mesophotic populations would likely result in the loss of the genetic connectivity between the southeastern and western Caribbean. Furthermore, the connectivity model and literature suggest that the Nicaraguan rise, which includes the territorial seas of Honduras, Nicaragua, Colombia, and Jamaica, is likely to be an important region for maintaining population

connectivity over larger spatial scales. These findings are similar to those observed in Truelove et al. (2017). Many of these jurisdictions are currently overexploiting their conch populations. If this trend continues, those populations will likely continue to decrease to the point of impaired reproduction in the foreseeable future, further disrupting the flow of larvae throughout the region and decreasing genetic diversity. The SRT noted low genetic diversity may pose a risk in the future in combination with low densities/abundance and continued overexploitation. However, at this time, the evidence is not substantial enough to suggest that significant changes in or loss of phenotypic or genetic traits are altering genetic diversity to the extent that it is significantly contributing to the species long-term extinction risk.

Threats Assessment

Based on the best available scientific and commercial information, the SRT identified the threats of commercial and artisanal fishing, IUU fishing, existing regulations, enforcement, and climate change as threats that are significantly contributing to the species’ extinction risk (Figure 23). Below is a brief discussion of the SRT’s rationales and conclusions regarding the threats assessment, organized by the five ESA Section 4(a)(1) factors.

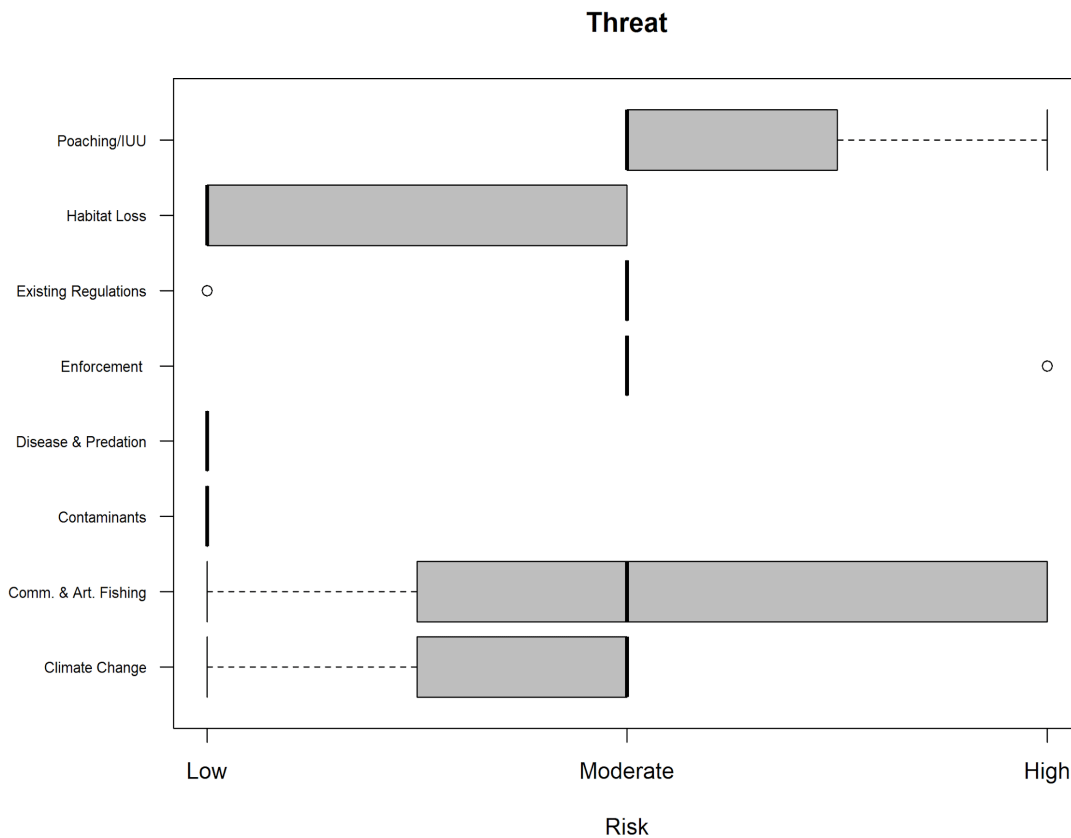


Figure 23. Threats assessment results. The shaded area is the interquartile range (25% to 75% percentiles). The whiskers represent the minimum and maximum range. The single points represent outliers.

Present or Threatened Destruction, Modification, or Curtailment of its Habitat or Range

The SRT considered threats of seagrass habitat loss, degradation, and impacts to conch reproduction and survival resulting from environmental contaminants (i.e., heavy metals and

pesticides). The SRT concluded that pesticides and other contaminants are not contributing to the species' risk of extinction. While there is evidence that contaminants affect reproductive potential and/or fitness, those impacts are generally localized, affecting only a small proportion of a queen conch population (for example, those near marinas or closer nearshore where contaminants may be concentrated). Additionally, without available ecotoxicity thresholds, it is unknown whether current levels of known contaminants within queen conch populations are affecting queen conch reproduction and/or survival locally or on a regional scale. Therefore, the SRT did not find that environmental contaminants are significantly increasing the species' extinction risk. The SRT noted, however, that early life stages of conch occur in nearshore areas where widespread use of pesticides is common, but the potential risk to the viability of the species is currently unknown.

The SRT also evaluated whether the species is at risk due to the loss or degradation of seagrass habitat as seagrass and associated substrates provide many benefits to queen conch throughout their life cycle. The loss of habitat, particularly nursery or mating habitats, could have impacts on queen conch survival and reproduction. However, queen conch have the ability to utilize a variety of habitats during their life cycle, and this flexibility may give the species some protection from short-term disturbances to habitat areas such as seagrass meadows and sand patches. The SRT noted that destruction of this habitat tends to occur in localized areas and nearshore, and is usually the result of coastal development and dredging and associated water quality impacts from these activities. Extensive seagrass loss, in particular, would have negative implications for conch, especially early life stages; however, there is limited information available on seagrass trends in the Caribbean. While there is evidence of a declining trend in seagrass meadows worldwide, seagrass is still fairly prevalent in the Caribbean and there is no information to suggest widespread destruction of seagrass in the range of the queen conch that would significantly affect its extinction risk in the foreseeable future. In some parts of the range of queen conch, like the U.S. Virgin Islands, an increase was noted in the spatial extent of seagrass meadows over the course of 28 years (Waycott et al. 2009). Additionally, for the queen conch populations located in protected marine areas, it is unlikely that these areas will be developed in the foreseeable future and the seagrass will remain protected. Although the SRT shared concerns regarding the implications of observed trends in decreasing native seagrass coverage and increasing invasive seagrass, the SRT did not find substantial evidence indicating that there have been or will be drastic declines in overall seagrass habitat availability in the Caribbean. Thus, while the SRT noted that extensive seagrass loss in the Caribbean would have significant implications for queen conch, the best available information does not suggest that habitat destruction, modification, or curtailment is a threat that is significantly contributing to the species extinction risk. The majority (4 of 7) of SRT members scored this threat as low risk.

Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

Fishing for queen conch substantially increased in the 1970s and 1980s, reaching peak landings in the mid-1990s. It was during this time that many of the conch fisheries collapsed due to overfishing of the populations. In shallow waters, where conch are most accessible to both subsistence and commercial fishing, significant depletions have been recorded, with fishermen having to pursue the species into progressively deeper waters. Overfishing has caused population collapses throughout the range of the conch, leaving adult densities below that which would indicate successful reproduction [e.g., Anguilla, Antigua and Barbuda, Aruba, northern Bahamas, Belize, Bermuda, Bonaire, British Virgin Islands, Cayman Islands, portions of

Colombia, Dominican Republic, Guadeloupe, Haiti, Martinique, Mexico, Panama, Saint Vincent and the Grenadines, Puerto Rico, U.S. Virgin Islands, Florida (US), and Venezuela]. Only a handful of jurisdictions in the Caribbean have conch populations with densities high enough to support continued reproduction [e.g., Cuba, Costa Rica, Colombia (Serrana Bank), Jamaica (Pedro Bank), Nicaragua, Saba, Saint Lucia, The Bahamas (Cay Sal Bank and Jumento/Ragged islands), and Turks and Caicos], with the viability of the species likely dependent on the persistence of those populations. However, as discussed below, many of these jurisdictions have extensive conch landings and problems with poaching which are placing these populations at increased risk of collapse from fishing pressure.

In terms of the Leeward Islands (Anguilla, Antigua and Barbuda, British Virgin Islands, Guadeloupe, Montserrat, Saba, Saint Barthélemy, Saint Martin, St. Eustatius, Saint Kitts and Nevis) and Windward Islands (Barbados, Dominica, Grenada, Martinique, Saint Lucia, Saint Vincent and the Grenadines, Trinidad and Tobago) in the eastern Caribbean, historically these queen conch populations served as important larval sources to the central/western Caribbean. However, overfishing has resulted in declines of these populations to the point where they have likely little to no active reproduction (<50 adult conch/ha). Although the SRT noted the possibility of recruitment from undescribed deep-water populations, the Leeward Islands' conch populations are unlikely to recover given they are primarily self-recruiting and up-current from most larval sources.

According to the SAU database there are 12 jurisdictions that have produced 95% of the conch landings from 1950 – present: Turks and Caicos, The Bahamas, Honduras, Jamaica, Belize, Nicaragua, Dominican Republic, Mexico, Cuba, Antigua and Barbuda, Colombia, and Guadeloupe (in order from highest landings producers to lower producers) (Figure 17). The exploitation rate analysis indicates that The Bahamas, Honduras, Jamaica (Pedro Bank), and Nicaragua conch population are likely exploited very near the targeted 8% rate of standing stock to maintain a healthy population. Of the other top-producing jurisdictions in the region, Dominican Republic, Antigua and Barbuda, Belize, Turks and Caicos, and Mexico's landings significantly exceed the 8% exploitation rate target (Figure 18). For example, the estimated exploitation rate for the Turks and Caicos is 30% of the stock, significantly higher than the recommended rate. These unsustainable fishing levels are of particular concern in these jurisdictions as, at present, many of these jurisdictions have adult queen conch density levels that are below the minimum density required to support reproductive activity/mate finding. Furthermore, the SRT was concerned about the largely self-reporting of landings data to FAO by each jurisdiction and the inadequacy and inconsistency in the reported data. In addition, many jurisdictions have different measures they report based on their traditional processing methods. Differences in the processing of queen conch meat affect the estimation of catch data in terms of overall yield and numbers of individuals. Few jurisdictions (e.g., Antigua and Barbuda, Belize, Honduras, Nicaragua, and Jamaica) have conducted intensive sampling and developed specific conversion factors to enable extrapolation from various processing grades to nominal weight (live weight plus shell). Generic conversion factors have been recommended for jurisdictions that lack specific conversion factors; however, jurisdiction-specific factors need to be developed for the remaining jurisdictions to ensure consistent reporting over time and among all the reporting jurisdictions. The FAO data are also uncertain since these data do not include commercial landings intended for local markets and internal consumption. Queen conch catch data are often incomplete, poorly organized, represent short time periods, and/or are based on processors' purchase reports. The efficiency of effort often changes over time by virtue of

changes in fishing techniques and fishing grounds. Fishing effort is a key variable because most conch fisheries management models use CPUE as a measure of abundance. Recreational and subsistence fishing are also rarely tracked during data collection efforts, and the collective impacts of these activities, as well as IUU fishing captures (discussed below), can at times be equal to or greater than the pressure from commercial fisheries. Taking into account these uncertainties along with the available adult density data, the SRT found that there was a high likelihood of underreporting in the landings data and had significant concerns regarding the current harvest levels of queen conch throughout its range, concluding that, at current rates, queen conch populations will likely continue to decline into the foreseeable future. The SRT responses regarding the extinction risk associated with this threat were variable; of the 7 SRT members, 3 scored overutilization by commercial and artisanal fishing as high risk, 2 as moderate, and 2 as low risk.

The SRT determined illegal, unreported, and unregulated (IUU) fishing to be a moderate risk factor in the sustainability of conch populations, with substantial uncertainty regarding the magnitude of this threat. The best estimates of unreported catch, including those from illegal harvest and poaching, are most likely underestimated and account for a significant portion (>15%) of total catch. IUU fishing of queen conch is a significant problem throughout the range of the species, and particularly within Nicaragua, Honduras, Jamaica, the Dominican Republic, Haiti, and Colombia (File S1). IUU fishing has led to declines in queen conch abundance and has prevented recovery in many populations (e.g., Bonaire, Cayman Islands, St. Eustatius). In the few jurisdictions with reproductively active populations, which are essentially protecting the species from extinction in the short-term, poaching is a serious threat as these queen conch removals are not considered in the management of fishing quotas, and, therefore, harvest levels are likely exceeding what is potentially sustainable for the species. In the Turks and Caicos Islands, large-scale poaching operations from neighboring Hispaniola, involving a “mother ship” with several smaller dinghy-type vessels, branch out along the edge of the Turks and Caicos banks to illegally fish. Jamaica also has a significant poaching problem. In fact, poaching estimates have been greater than the Total Allowable Catch in previous years. Currently, annual quotas for Jamaica are determined through a more sustainable control rule based on harvesting 8% of the estimated exploitable biomass. Under this scenario, the maximum catch is fixed when queen conch densities are above 100 conch/ha and are progressively reduced if the population density is reduced, with the fishery closed at 50 conch/ha or below. However, since 2019, Jamaica has been unable to meet these metrics to allow for queen conch fishing, potentially due to poaching impacts. The fishery was closed, but was posed to reopen in April 1, 2021 (Jamaican Gleaner, Green Warns Poachers as Conch Season Restarts, January 29, 2021). Given the available information, IUU appears to be a significant threat, particularly to the currently reproductive stocks of queen conch. The unregulated harvesting of these populations will likely lead to decreasing adult densities and potential for reproductive depression/failure in the long-term. There is no evidence to suggest that poaching will decline in the foreseeable future - in fact, it will likely intensify as other queen conch populations become depleted and more conch fisheries close. Of the 7 SRT members, 5 felt Poaching/IUU placed conch populations at moderate risk and 2 felt they placed conch populations at high risk.

Overall, given the high likelihood of underreporting of harvest data due to inconsistencies with data collection, IUU fishing of queen conch, coupled with the evidence of significant declines in queen conch populations with density levels at which Allee effects can limit effective reproduction, the SRT concluded that the available information suggests queen conch

populations are subject to unsustainable exploitation rates throughout their range, with overutilization significantly contributing to the species' risk of extinction through the foreseeable future.

Disease or Predation

The SRT considered whether disease increases the queen conch's extinction risk. The research on the Apicomplexa parasite is relatively recent and it is possible that this parasite has been present in conch for many generations prior to its discovery. The most recent study suggests that this organism may, in fact, be non-parasitic and pose no adverse health issues. Since Apicomplexa has been found in individuals throughout the conch's range, including in reproductively active areas, it is possible that prior observations of reduced gametogenesis in queen conch infected by the parasite is coincidental, resulting from other causes such as low density due to overfishing. The SRT concluded that further information is needed to fully understand the impacts of disease on conch populations. Other than observations of the Apicomplexa parasite, no other diseases specific to queen conch have been reported. The SRT also evaluated the threat of predation and its contribution to the species' extinction risk. Predation has the greatest impact on queen conch populations during the larval and juvenile stages. Although estimated predation rates on larval and <1 year old juveniles are quite high, the enormous quantities of eggs and egg masses produced may offset this loss from predation. The SRT also noted that climate change may change the composition of conch shells in the future, potentially making them weaker, which could increase the queen conch's susceptibility to predation; however, at this time, these impacts are highly uncertain. There is no information to suggest that predation rates have increased to a point where predation is now considered a threat significantly contributing to the species' extinction risk. Therefore, based on the best available scientific and commercial information, the SRT concluded that disease and predation are unlikely to be threats significantly contributing to the species' extinction risk.

Inadequacy of Existing Regulatory Mechanisms

Queen conch populations have declined throughout a large portion of the species' range, and the best available information indicates that many populations continue to decline, particularly in the eastern and central/southern Caribbean; thus, it is evident that many of the current regulatory measures are inadequate to prevent overfishing of the species. There are still some jurisdictions throughout the conch's range that have not implemented any regulatory mechanisms, and of those that have regulations many are insufficient to maintain existing conch stocks (e.g., Dominican Republic, Haiti, and Puerto Rico). While there are regulations in many jurisdictions that are aimed at prohibiting the take, sale, or possession of immature queen conch, some of these are established through setting a minimum queen conch shell length, weight, or lip thickness or a combination of these. Recent studies conducted on established maturation criteria have demonstrated that most jurisdictions' minimum lip thickness regulations do not protect spawning and allow for harvest of immature conch. Similarly, minimum shell length and meat weight regulations are unreliable since large juveniles and subadults can have larger shells and more meat than mature adult conch. In addition, many fisheries do not require conch to be landed in the shell, an allowance that is inadequate to ensure that only mature individuals are being harvested because there is no way to determine whether minimum size limits were followed. While meat weight is also used to indicate maturity, it is of minimal conservation benefit as underweight animals have already been removed from the shell and, as previously mentioned, meat weight is not a reliable indicator of maturity.

The SRT noted that MPAs and seasonal closures can be effective regulatory controls if they are established in appropriate habitats, encompass reproductive seasons, and are enforced. Reproductive seasons also vary in timing and duration in different regions of the Caribbean, spanning between 4- to 9-month periods between April and October, but most often between June and September. Similarly, prohibitions on SCUBA/Hookah are helpful in preserving deep water populations if jurisdictions have the ability to monitor and enforce these prohibitions. The SRT noted only a few jurisdictions currently prohibit the use of SCUBA in their queen conch fisheries. The poor enforcement of the existing regulations is a significant issue throughout the Caribbean. Jurisdictions that establish appropriate regulations are often plagued by poor enforcement and poaching. Queen conch, in particular, tend to be harvested by individual divers, and given the large shelf habitats and remoteness of fishing grounds, it is difficult to patrol and enforce conch harvesting regulations. Furthermore, the available jurisdiction-specific information regarding the status of queen conch populations makes significant reference to illegal poaching. It appears to be a well-documented issue throughout the Caribbean and is acknowledged by most, if not all, management mechanisms (CFMC, OPSECA, CITES, etc.).

Overall, given the ongoing demand for queen conch, the issues with compliance, appropriateness of certain morphometric regulations, enforcement, and poaching, and the observed low densities and declining trends observed in most queen conch populations, the SRT concluded that the existing regulatory mechanisms are inadequate to control the harvest and overutilization of queen conch throughout its range. Overall, 6 of 7 SRT members felt this threat was contributing to the species' moderate risk of extinction.

Other Natural or Manmade Factors Affecting its Continued Existence

The SRT identified increasing ocean temperatures and ocean acidification, two consequences of climate change, as threats that are likely to affect queen conch. As described under Factor E, queen conch reproduction is dependent on temperature, thus changes in water temperature may limit the window for successful reproduction. A recent study found that nearly all queen conch reproduction stopped when temperatures reached 31°C. Current climate models predict that mean ocean temperatures in the Caribbean Sea will be between 28.7°C and 30.18°C by 2100. These findings suggest that future sea temperatures could significantly decrease queen conch reproduction. In addition, larval growth and mortality were also impacted by the water temperatures predicted for 2100 (30°C). Laboratory studies showed that increased ocean temperatures resulted in high growth rates for queen conch, but also higher mortality rates (up to 76%). It is difficult to predict how queen conch may adapt to these changing environmental conditions and whether higher growth rates would offset the higher mortality.

The predicted increased acidity associated with ocean warming will likely impact shell biomineralization processes, potentially leading to weaker, thinner shells for queen conch. Recent studies have suggested a 50% decrease in aragonite in the larval shell calcification at conditions predicted for 2100 (pH 7.6). These weaker shells may increase predation rates, thereby contributing to another source of mortality for the species in the foreseeable future. As the current reproductively active populations rely significantly on self-recruitment of their larvae, these higher rates of mortality could have significant implications for the species' viability. The SRT also noted significant concern regarding altered larval transport resulting from potential changes in ocean circulation at both a local and regional scale. Over time, ocean warming may result in geographic shifts and impacts to pelagic larvae and possibly settlement habitat

throughout the Caribbean. Any changes in circulation patterns within the Caribbean would have significant implications for the species. While the available information suggests that changes to ocean circulation patterns are likely to influence larval supply dynamics, pelagic larval stage survival, as well as their condition upon settlement, information is lacking on how changes in circulation patterns will affect local populations or how they will alter population connectivity on a regional scale. The majority (5 of 7) of the SRT concluded, and we agree, that climate change is a threat that will significantly contribute to the species extinction risk through the foreseeable future (of 2100).

Overall Risk Summary

Guided by the results and discussions from the demographics risk analysis and threats assessment, the SRT analyzed the overall risk of extinction to queen conch. In this process, the SRT considered the best available scientific and commercial information on queen conch populations throughout the Caribbean to collectively assess the species’ overall extinction risk. Table 4 and Figure 24 provides the results of the likelihood point distribution. Likelihood points were tallied and the totals (n = 70) are presented for the overall level of extinction risk. The SRT expressed uncertainty by placing some likelihood points in the high, moderate, and low risk categories.

Table 4. Overall extinction risk likelihood point distribution.

Overall Extinction Risk for the Queen Conch			
	Low risk	Moderate risk	High risk
Distribution of likelihood points	21	41	8

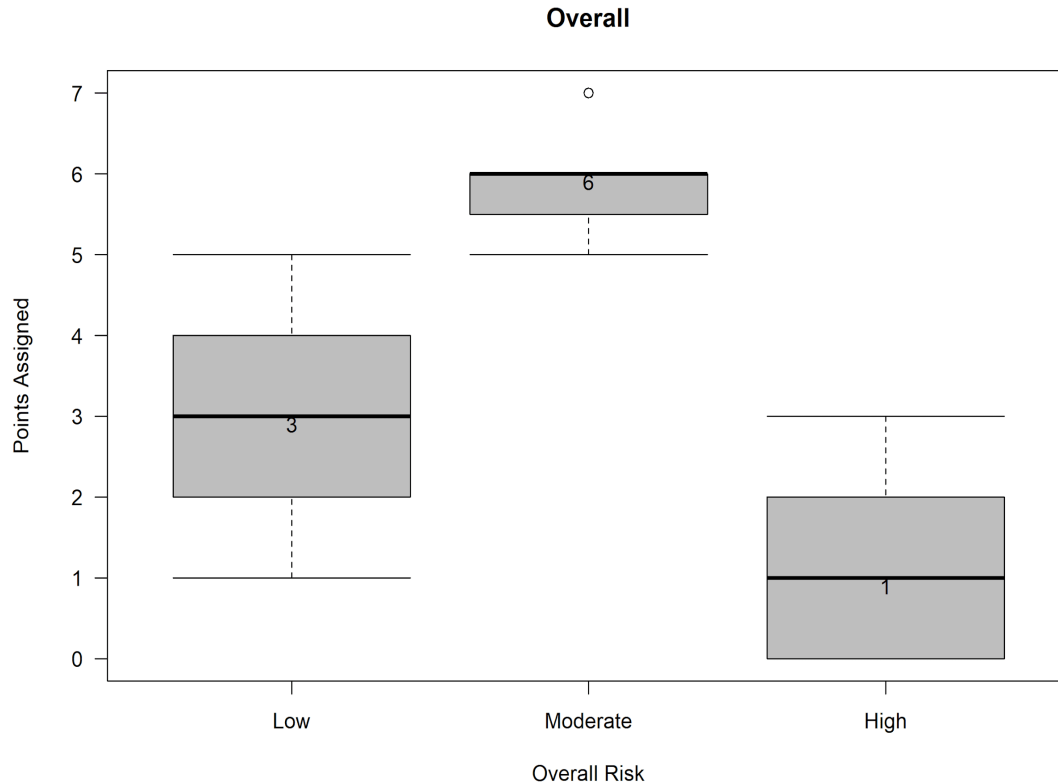


Figure 24. Boxplot of overall extinction risk across SRT members allocated 10 points each to assign to Low/Moderate/High categories. The shaded area is the interquartile range (25% to 75% percentiles). The whiskers represent the minimum and maximum range. The single points represent outliers.

The SRT was largely in agreement concerning the overall extinction risk for the queen conch, with the majority of likelihood points (59%) being assigned to the moderate risk category. Due to uncertainty regarding the inconsistent reporting of landings and survey methodologies, team members placed some of their likelihood points in the “low risk” (30%) and “high risk” (11%) categories as well.

The SRT recognized that one of the most critical factors in the long-term survival of the species are localized densities of reproductively active adults. The results of a jurisdiction analysis showed that of jurisdictions reviewed throughout the range of the queen conch, 27 (69%) have adult density levels below the critical threshold of 50 adult conch/ha, and another five (13%) have densities that are below 100 adult conch/ha. There are only nine jurisdictions (i.e., St. Lucia, Saba, Jamaica (Pedro Bank), Nicaragua, Turks and Caicos, Costa Rica, Cuba, Colombia (Serrana Bank), and the Bahamas (Cay Sal Bank and Jumentos/Ragged Cays) that have adult conch densities (greater than 100 adult conch/ha) sufficient to sustain reproductive activity. Note this is true for a portion of conch habitats in The Bahamas and Jamaica. Given that the SRT’s biophysical modeling assumed no reproductive output from areas where conch populations are depleted (<50 conch/ha), results from the model indicate that connectivity has been significantly impacted across the Caribbean region. A number of important ecological corridors for larval flow no longer function in that respect, and most of the queen conch populations that historically served as sources of larvae have collapsed. However, the SRT acknowledged that the available

density data can be difficult to interpret as survey methods varied, surveys were lacking from many areas and, in some cases, surveys were decades old. In addition, the connectivity modeling scenario provided density estimates that represent jurisdiction-wide averages, and the SRT acknowledges that conch are not distributed evenly across space. Even in jurisdictions with very low densities, there likely exist some areas above the critical density threshold where reproduction continues to take place (e.g., Florida). In terms of the extrapolated total abundance estimates, which suggest there are millions of conch in the Caribbean, the SRT noted that this was primarily based on highly uncertain population estimates from seven jurisdictions (i.e., The Bahamas, Jamaica, Turks and Caicos, Cuba, Nicaragua, Honduras, and Mexico account for 95% of all adult conch). Furthermore, the SRT notes that density is a stronger indicator of a population's status than total abundance, as adult conch density directly influences the probability of locating a receptive mate (Farmer and Doerr 2022). If high numbers of conch exist but are widely distributed over a given area, their low mobility reduces the likelihood of a reproductive encounter between two adults, thus limiting overall productivity of the population. The SRT determined that the best available density and abundance information, despite its limitations, suggests that there are localized depletions in many jurisdictions that have led to near-reproductive failure in most cases. As it stands, population growth rate is below replacement for much of the range of the queen conch and recruitment failure is occurring throughout a large part of the species' range.

Further declines in queen conch populations and adult densities are expected into the foreseeable future as the species remains at risk from overutilization and the inadequacy of existing regulatory mechanisms. Overfishing has been the main threat to queen conch for several decades, creating patchy, disconnected populations and resulting in low local densities, and there is very little indication that current protective measures will reverse this trend in the greater Caribbean. Many existing regulatory measures are either poorly enforced or use inappropriate metrics for managing the queen conch fishery. In fact, the combination of overutilization and inadequate regulations has led to the decline of many queen conch populations, particularly those in the northern, eastern, and southern parts of the Caribbean, where these populations have become so depleted that they can no longer support fisheries and are experiencing recruitment failure. Therefore, the viability of the species is currently reliant on the populations in the central Caribbean, specifically those found off Cuba, southern Bahamas, Turks and Caicos, Jamaica, and Nicaragua. While these jurisdictions support queen conch populations that are likely reproductively active (based on current adult density estimates), they also operate queen conch fisheries that are unlikely to remain sustainable over the next 30 years. This is mainly due to the threats of overharvesting, illegal fishing, and inadequate enforcement. As these jurisdictions are largely self-recruiting, overharvesting of these populations will lead to direct declines in the populations and have significant impacts on the reproductive output and overall viability of the species in the foreseeable future. This is particularly concerning as Jamaica is an important connector, or ecological corridor, for the exchange of larvae throughout the region. As such, if Jamaica's populations become reproductively impaired, this would lead to a loss in gene flow and genetic diversity, creating additional susceptibilities for the remaining conch populations. Furthermore, IUU is a significant issue for Cuba, Turks and Caicos, Bahamas, Jamaica, and the Colombia/Honduras banks. This additional mortality on the conch populations will likely accelerate the declines in abundance and associated densities over the next 30 years. As already evident in Jamaica, despite trying to operate a sustainable fishery, Jamaica has had to close its queen conch fishery in recent years due to declining adult densities that were likely the result of poaching. As conch fisheries continue to close and populations become depleted, poaching will

likely continue or increase, and without adequate enforcement to halt this illegal harvest of conch, the species will be on a downward trajectory and at risk of extinction over the next 30 years. The SRT acknowledged that the implementation and enforcement of appropriate management measures could reduce the threat of overutilization to the queen conch, but found that current regulations and more importantly the enforcement of these regulations are presently inadequate and/or lacking altogether across the species' range, significantly contributing to the species' extinction risk in the foreseeable future.

With respect to climate change, several SRT members noted that the effects of warming ocean waters and increased acidification would further exacerbate the projected declines above as this threat will lead to higher mortality rates of larvae and therefore a decrease of recruitment to already declining populations. Several SRT members also shared concerns about negative impacts to shell formation resulting from ocean acidification brought on by climate change. However, the SRT noted that while climate modeling provides some indication of the types of changes that may occur, there is uncertainty as to the timing of any shifts that may occur, as well as the spatial scale over which it will occur, in the foreseeable future.

Overall, given the best available scientific and commercial information, though not free from uncertainty, the SRT found the queen conch to meet the definition of species at a moderate risk of extinction throughout its range. The species currently suffers from low population densities and poor recruitment throughout a vast majority of its range and experiences limited larval dispersal and disturbed population connectivity. While there are some populations that are still reproductively active with relatively high adult densities, they, along with the other queen conch populations found throughout the species' range, are threatened with overutilization (through commercial, artisanal, and IUU fishing) due to inadequate management and poor enforcement of existing regulations. As such, the SRT concluded based on the best scientific and commercial information, that these threats and demographic risks are placing the species at a moderate risk of extinction, which is defined as a species that "is on a trajectory that puts it at a high risk of extinction over the next 30 years."

Determination of Status Throughout a Significant Portion of its Range (SPR)

Under the ESA a species may warrant listing if it is in danger of extinction or likely to become so in the foreseeable future throughout all or a significant portion of its range. The court in *Center for Biological Diversity v. Everson*, 2020 WL 437289 (D.D.C. Jan. 28, 2020) (Center for Biological Diversity or CBD), vacated the aspect of the 2014 Significant Portion of its Range Policy that provided that the Services do not undertake an analysis of significant portions of a species' range if the species warrants listing as threatened throughout all of its range.

Because the SRT recommended a "Moderate" risk of extinction for queen conch throughout its range, they also evaluated whether there is any portion of the species' range for which both (1) the portion is significant; and (2) the species is at a "High" risk in that portion (as defined in the Overall Extinction Risk Analysis section).

The team defined "significance" in the context of the species' demographic characteristics. Specifically, the SRT considered information pertaining to population abundance and productivity, spatial structure and connectivity, and diversity to help identify any portions that may be *biologically* important, and, therefore significant, to the species. These demographic

components are important for ensuring populations are well represented and distributed across diverse habitats and geographic regions, helping to promote population resilience. For example, a population should have sufficient abundance in order to provide for population-level persistence in the face of year-to-year variations due to environmental and anthropogenic perturbations. Additionally, because queen conch produce planktonic larvae, with transport and recruitment patterns largely influenced by regional hydrodynamics of the Caribbean Sea, maintaining the connectivity of queen conch larval dispersal throughout its range allows the species access to a wider array of environments and suitable habitats than it would without this network. This connectivity could protect the species against short-term spatial and temporal environmental changes, and provide evolutionary resilience to long-term environmental changes through the exchange of larvae and maintenance of genetic diversity.

The SRT developed an assessment tool to determine whether any portion of the species range is *potentially* at a high risk of extinction and *potentially* significant, where both have to be true for the SRT to further evaluate the portion as qualifying as a SPR. Because the majority of relevant queen conch data (i.e., connectivity, density, landings/exploitation rates) were collected or summarized at the “jurisdiction” subpopulation level, and the primary identified threats to queen conch (i.e., overutilization, illegal harvest, and inadequate regulations) are managed at the “jurisdiction” level, the SRT evaluated portions at the level of “jurisdiction” subpopulations. At this level of resolution, the SRT felt that it could more accurately evaluate the risk and potential significance of a portion. Use of this standardized assessment tool with documented criteria provided a consistent frame of reference for determining potential risk level and significance across the 44 identified “jurisdiction” subpopulations.

SPR Assessment Tool Criteria

Under the standardized assessment tool, to determine whether a subpopulation was potentially at a high risk, one of the following must be true:

1. Exploitation Rate is $>8\%$.

OR

2. Density <50 adults/ha.

The assessment tool’s decision framework flags jurisdictions exceeding the 8% target exploitation rate, which has been used as a region-wide guideline for establishing sustainable queen conch fisheries (i.e., fishing should remove no more than 8% of the biomass of a healthy stock [Prada et al. 2017]). Given that the goal for the 8% exploitation rate is “sustainability” of queen conch fisheries, flagging jurisdictions exceeding this sustainability benchmark is a conservative approach for identifying possibly high-risk populations. The SRT also considered subpopulations with densities <50 adults/ha as potentially high risk, as sub-populations with adult densities below this threshold are at significant risk of reproductive depression/failure.

To determine whether a subpopulation was potentially significant, the SRT examined its contemporary contributions to population abundance, its capacity for carrying a substantial portion of population abundance based on available habitat, and its ability to make meaningful contributions to the broader population, as indicated by a high relative Betweenness Centrality

(BC) value (Figure 25). In order to be deemed potentially significant, a subpopulation had to meet the criteria in number 1 or 2 below *and* the criteria in 3:

1. Abundance in the portion is greater than 5% of the overall population abundance. Abundance is computed from contemporary cross-shelf density estimates and estimated habitat availability. The 5% threshold for significance is a commonly accepted statistical threshold (e.g., $\alpha = 0.05$) and also accounts for the fact that “habitat” has been coarsely identified, where high contemporary abundance may reflect high-quality habitat that is significantly contributing (currently) to the population’s viability.

OR

2. Habitat in the portion is greater than 5% of all available queen conch habitat. The threshold of >5% habitat accounts for the fact that there is a very large amount of conch habitat (73,058 km²) that is broadly distributed but poorly defined with regards to quality or carrying capacity.

The union of habitat and abundance thresholds provides a meaningful way of quantitatively identifying capacity to contribute meaningful numbers of individuals to the viability of the conch population.

AND

3. Jurisdictions with a high BC value (above median) are important ecological corridors. The BC values utilized were from the pre-exploitation (“uniform”) connectivity run (Vaz et al. 2022), which accounts for spawning habitat availability rather than historical exploitation patterns. This pre-exploitation BC measure is a better representation of the “potential” of the portion to contribute to the connectivity of the overall population. Use of the pre-exploitation BC measure in the analysis is: 1) a more conservative approach because it evaluated all portions’ contributions to spatial connectivity even if they are currently suffering from overexploitation and reproductive depression/failure; 2) a comprehensive approach because it evaluates the relative impact of each portion’s removal on overall spatial connectivity; and 3) a complete representation of the “potential” of each portion’s contribution to the connectivity of the overall population.

As explained above, the SRT identified important ecological corridors among spawning and settlement sites of queen conch larvae by using graph theoretical network analyses and calculated the betweenness centrality of all sites to identify multi-generational connections (Treml et al. 2008; Treml and Halpin 2012). Those jurisdictions with high betweenness centrality are generally important for maintaining the connectivity of the species through its range and its genetic diversity (i.e., if reproductive output from portions with high centrality were to decline significantly, reduced genetic mixing over the region as a whole would be expected). In short, jurisdictions with a high BC value act as ecological corridors (or bridges) facilitating larval and genetic flows, and preventing the fragmentation of the range.

SPR Assessment Tool Results

By using this assessment tool, the SRT identified 30 potentially high-risk conch subpopulations and 3 potentially significant subpopulations (File S4). Only the Nicaragua subpopulation met both the potentially high risk and potentially significant criteria. Notably, Nicaragua's high BC value (which contributed to it meeting the potentially significant criteria) was only present in the Mercator simulations, but not the Glb-HyCOM simulations (Figure 25). No other portions of the species range were identified that met both the potentially high-risk and potentially significant criteria (File S4). The SRT concluded, by consensus, that no other portions warranted further consideration.

Nicaragua Evaluation

Based on the results of the assessment tool, the Nicaraguan portion of the species range was further evaluated to determine whether this portion is both significant and at a "High" risk of extinction. Because both must be true for SPR to apply, regardless of which question is addressed first, if a negative answer is reached with respect to the first question addressed, the other question does not need to be evaluated for that portion of the species' range. In undertaking the SPR analysis for queen conch, the SRT chose to address the status question first.

A species with a high risk of extinction is at or near a level of abundance, productivity, spatial structure, and/or diversity that places its continued persistence in question. The demographics of a species at such a "High" level of risk may be highly uncertain and strongly influenced by stochastic or compensatory processes. Similarly, a species may be at "High" risk of extinction if it faces clear and present threats (e.g., confinement to a small geographic area; imminent destruction, modification, or curtailment of its habitat; or disease epidemic) that are likely to create imminent and substantial demographic risks.

The most significant threat to queen conch is overutilization (through commercial; artisanal; and illegal, unreported, unregulated fishing) for commercial purposes. Nicaragua is one of the primary producers of queen conch meat in the Caribbean, with their landings and fishing quotas having increased substantially since the mid-1990s. For example, in 2003, Nicaragua set its quota at 45 mt (processed meat), but in 2009, the quota had increased to 341 mt and 41 mt for use for research purposes (bringing the total queen conch quota to ~382 mt). By 2019 this quota had almost doubled to an annual export quota of 628 mt, distributed among the licensed fishing fleet (FAO Western Central Atlantic Fishery Commission 2020). The most recent density estimates, conducted in 2016, 2017, and 2018, indicate that densities are sufficient to support some recruitment; however, comparisons between survey years suggest a declining trend. For example, surveys conducted in 2009 observed approximately 176-267 conch/ha, while surveys conducted in October 2016, March 2018, and October 2019, reported 70-109 conch/ha suggesting a reduction in densities (FAO Western Central Atlantic Fishery Commission 2020). Furthermore, no information was provided on the age classes for the more recent survey or survey methodology (i.e., no location, season, area). Thus, it is conceivable that the recent densities include adults as well as immature conch.

Compensatory issues are a major factor limiting the recovery of overharvested queen conch populations (Appeldoorn 1995; Stoner et al. 2012b). In addition, Nicaragua's subpopulation is heavily reliant on self-recruitment (Vaz et al. 2022), which means that depletion of the

subpopulation would have negative implications on its ability to recover. However, while the decline in densities is concerning, this subpopulation remains at a level which likely is still reproducing and therefore recruiting, indicating that this subpopulation is not presently strongly influenced by depensatory processes.

Based on the available information, the SRT concluded that the decreasing trend in queen conch densities coupled with the increasing quotas suggests inadequate management of the conch fishery and a likelihood of unsustainable fishing of the stock. However, the SRT noted that the current estimated exploitation rate (i.e., 8.8%) was only slightly above the 8% target for sustainable fishing, which is not synonymous with risk of extinction. Rather, it suggests that current exploitation levels are at or slightly above sustainable levels for a reproductively active subpopulation. Considering the exploitation rate (and potential for increases in this rate, given the trend in the quota-setting over the years) and declining trend in conch densities, the SRT concluded that the best available information indicates that this subpopulation is on a trajectory that will put it at a “High” level of extinction risk in the foreseeable future (i.e., at “Moderate” risk), but it is not presently at a “High” level of extinction risk.

Given the above analysis, the SRT concluded that there are no portions of the queen conch range that are both significant and presently at a “High” risk of extinction. In making this finding, the SRT attempted to be consistent with the Courts’ holdings in *Desert Survivors v. Department of the Interior*, No. 16-cv- 01165-JCS, 2018 WL 4053447 (N.D. Cal. Aug. 24, 2018); *Center for Biological Diversity v. Jewell*, 248 F. Supp. 3d, 946, 959 (D. Ariz. 2017); and *Center for Biological Diversity v. Everson*, 2020 WL 437289 (D.D.C. Jan. 28, 2020).

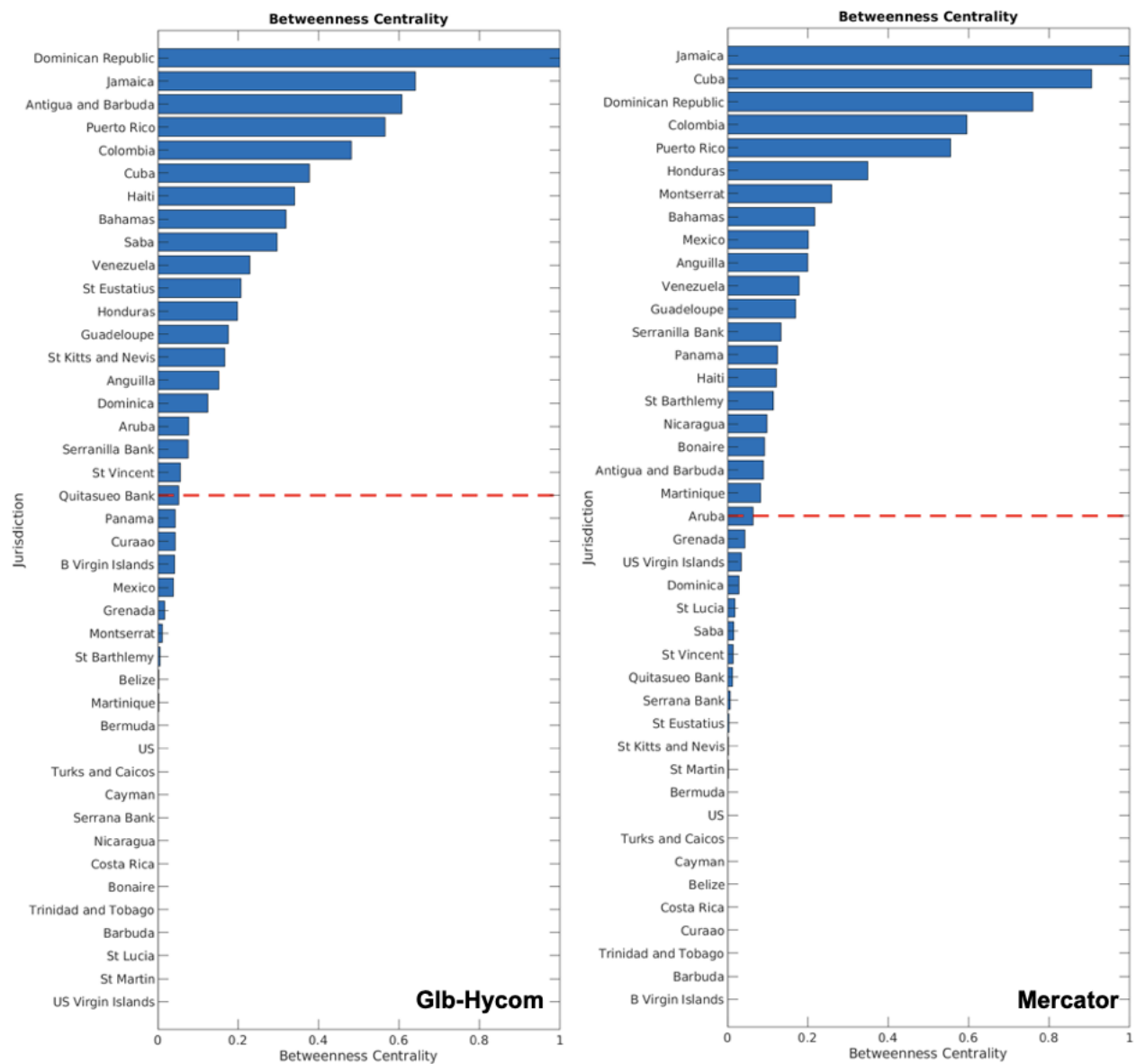


Figure 25. Relative Betweenness Centrality (pre-exploitation) for each jurisdiction within the queen conch’s range. The BC measures the fraction of shortest paths passing through a node (country) - higher values represent most central nodes (i.e. ecological corridors). Red line denotes the median value. BC values utilized were from the pre-exploitation (“uniform”) connectivity run. Results are combined for the 5-year simulation period (2013 – 2017), where larvae are advected with the Global Hycom and the Mercator GLORYS12V1 Reanalysis (Vaz et al. 2022).

Acknowledgements

The National Marine Fisheries Service (NMFS) gratefully acknowledges the commitment and efforts of the Status Review Team (SRT) members and thank them for generously contributing their time and expertise to the development of this status review report.

Several individual fishery scientists and managers provided information that aided in preparation of this report and deserve special thanks. We particularly wish to thank Dr. Ana Carolina Vaz, Dr. Stephanie Martinez, Ms. Kim Johnson, Ms. Samantha Flounders, Dr. Robert Glazer, Mr. Gabriel Delgado, Mr. Joe Heublein, and Mr. Miguel Lugo.

We would also like to thank the peer reviewers Dr. Allan Stoner, Dr. Martha Prada, and Dr. Dalila Aldana Aranda for their professional review of this report.

Supplemental Files

Supplemental 1: Jurisdiction summaries for the queen conch status review report (Horn et al. 2022). This file provides information on the queen conch population status, fisheries, and regulations, where available for jurisdictions within the species range (PDF, 95 pages).

Supplemental 2: Fishery and Aquaculture Statistics. Queen conch landings data by production source 1950 – 2018. FAO Fisheries Aquaculture Department. Rome. Updated 2020. www.fao.org/fishery/statistics/software/fishstatj/en (Excel file).

Supplemental 3: Queen conch extinction risk analysis results and example worksheet. This file provides the results of the extinction risk assessment conducted by the seven status review team members (Excel file).

Supplemental 4: Significant Portion of its Range Assessment Tool. This file provides the assessment tool developed by the status review team to determine whether queen conch subpopulations would meet the SPR criteria (Excel file).

Supplemental 5: Estimated queen conch densities for subpopulations throughout the wider Caribbean region. This file provides data used by the status review team to estimate queen conch densities by jurisdiction. The dataset includes but is not limited to location, survey years, total area surveyed, status (fished and unfished) of the area surveyed, survey methods, and data source or references (Excel file).

Original supplemental files available upon request to: Calusa.Horn@noaa.gov

References

- 14ymedio. 2019. Cuban Government Tries to Stop Illegal Fishing with New Legislation. Translating Cuba, Cuba.
- Acosta, C. A. 2001. Assessment of the functional effects of a harvest refuge on spiny lobster and queen conch populations at Glover's Reef, Belize. Pages 212-221 *in* Proceedings of the 52nd Gulf and Caribbean Fisheries Institute, volume 52. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Acosta, C. A. 2006. Impending trade suspensions of Caribbean queen conch under CITES: A case study on fishery impacts and potential for stock recovery. *Fisheries* 31(12):601-606.
- Agard, J. B. R. 2014. Climate and water: Global to local Caribbean socio-economic climate change scenarios. University of West Indies, Global Water Partnership Annual Lecture, June 28, 2014, Trinidad.
- Aiken, K. A., G. A. Kong, S. Smikle, R. Mahon, and R. S. Appeldoorn. 1999. The queen conch fishery on Pedro Bank, Jamaica: Discovery, development, management. *Ocean & Coastal Management* 42(12):1069-1081.
- Alcolado, P. M. 1976. Crecimiento, variaciones morfológicas de la concha y algunos datos biológicos del cobo *Strombus gigas* L. (Mollusca, Mesogastropoda). *Academia de Ciencias de Cuba, Instituto de Oceanología* 34:1-36.
- Aldana Aranda, D., E. R. Baqueiro Cárdenas, I. Martínez Morales, R. I. Ochoa, and T. Brulé. 2003a. Reproductive patterns of *Strombus gigas* from Alacranes Reef versus Chinchorro Bank of Mexico. Pages 202-225 *in* Proceedings of the 54th Gulf and Caribbean Fisheries Institute, volume 54. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Aldana Aranda, D., E. Baqueiro Cárdenas, I. Martínez Morales, A. Zetina Zárata, and T. Brulé. 2003b. A review of the reproductive patterns of gastropod mollusks from Mexico. *Bulletin of Marine Science* 73(3):629-641.
- Aldana Aranda, D., E. Baqueiro Cárdenas, I. Martínez Morales, R. I. Ochoa Baez, and T. Brulé. 2003c. Gonad behavior during peak reproduction period of *Strombus gigas* from Banco Chinchorro. *Bulletin of Marine Science* 33(1):241-248.
- Aldana Aranda, D., and L. Frenkiel. 2007. Lip thickness of *Strombus gigas* (Mollusca: Gastropoda) versus maturity: A Management Measure. Pages 407-418 *in* Proceedings of the 58th Gulf and Caribbean Fisheries Institute, volume 58. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Aldana Aranda, D., E. R. Baqueiro-Cárdenas, J. Montero, and L. Frenkiel. 2009a. Attenuated reproduction of *Strombus gigas* by an Apicomplexa parasite. Proceedings of the 61st Gulf and Caribbean Fisheries Institute, volume 61. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.

- Aldana Aranda, D., J. F. Chávez-Villegas, and M. Sánchez Crespo. 2014. Is the queen conch *Strombus gigas* (Mesogastropoda: Strombidae) a species with Allee effect? *Revista de Biología Tropical* 62(Supplement 3):207-213.
- Aldana Aranda, D., and coauthors. 2007. Geographic distribution of Apicomplexa infecting *Strombus gigas*. Pages 321-326 in *Proceedings of the 59th Gulf and Caribbean Fisheries Institute*, volume 59. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Aldana Aranda, D., L. Frenkiel, T. Brulé, J. Montero, and E. R. Baqueiro Cárdenas. 2011. Occurrence of Apicomplexa-like structures in the digestive gland of *Strombus gigas* throughout the Caribbean. *Journal of Invertebrate Pathology* 106(2):174-178.
- Aldana Aranda, D., R. Glazer, G. Delgado, E. Baqueiro, and J. Montero. 2009b. Occurrence of Apicomplexa infecting queen conch, *Strombus gigas*, from off shore and near shore in Florida. Pages 491-497 in *Proceedings of the 61st Gulf and Caribbean Fisheries Institute*, volume 61. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Aldana Aranda, D., and N. B. Manzano. 2017. Effects of near-future-predicted ocean temperatures on early development and calcification of the queen conch *Strombus gigas*. *Aquaculture International* 25(5):1869-1881.
- Allee, W. C. 1931. *Animal Aggregations: A Study in General Sociology*. The University of Chicago Press, Chicago, IL.
- Allen Coral Atlas. 2020. CoralMapping/AllenCoralAtlas: DOI release (v1.0). Zenodo. <https://doi.org/10.5281/zenodo.3833246>.
- Andréfouët, S. 2008. Coral reef habitat mapping using remote sensing: A user vs producer perspective. Implications for research, management and capacity building. *Journal of Spatial Science* 53:113-129.
- Apeti, D. A., and coauthors. 2014. An assessment of contaminant body burdens in the coral (*Porites astreoides*) and queen conch (*Strombus gigas*) from the St. Thomas East End Reserves (STEER). U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Centers for Coastal Ocean Science Center for Coastal Monitoring and Assessment, NOAA Technical Memorandum NOS/NCCOS 177, Silver Spring, MD.
- Appeldoorn, R. S. 1985. Growth, mortality and dispersion of juvenile, laboratory-reared conchs, *Strombus gigas* and *S. costatus*, released at an offshore site. *Bulletin of Marine Science* 37(3):785-793.
- Appeldoorn, R. S. 1987. Practical considerations in the assessment of queen conch fisheries and population dynamics. Pages 307-324 in *Proceedings of the 38th Gulf and Caribbean Fisheries Institute*, volume 38. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Appeldoorn, R. S. 1988a. Ontogenetic changes in natural mortality rate of queen conch, *Strombus gigas* (Mollusca: Mesogastropoda). *Bulletin of Marine Science* 42(2):159-165.

- Appeldoorn, R. S. 1988b. Age determination, growth, mortality and age of first reproduction in adult queen conch, *Strombus gigas* L., off Puerto Rico. *Fisheries Research* 6(4):363-378.
- Appeldoorn, R. S. 1988c. Fishing pressure and reproductive potential in strombid conchs: Is there a critical stock density for reproduction? *Memoria de la Sociedad de Ciencias Naturales La Salle* 48(Supplement 3):275-288.
- Appeldoorn, R. S. 1992. Development of a combined model of growth in weight for juvenile and adult queen conch (*Strombus gigas*) and its application to the population off La Parguera, Puerto Rico. Pages 13-20 *in* Proceedings of the 42nd Gulf and Caribbean Fisheries Institute, volume 42. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Appeldoorn, R. S. 1993. Reproduction, spawning potential ratio and larval abundance of queen conch off La Parguera, Puerto Rico. University of Puerto Rico, Department of Marine Sciences, Manuscript Report to Caribbean Fishery Management Council. San Juan, Puerto Rico, Mayaguez, Puerto Rico.
- Appeldoorn, R. S. 1994a. Spatial variability in the morphology of queen conch and its implications for management regulations. Pages 145-157 *in* R. S. Appeldoorn, and B. Rodríguez Q., editors. Queen Conch Biology, Fisheries, and Mariculture. Fundación Científica Los Roques, Caracas, Venezuela.
- Appeldoorn, R. S. 1994b. Queen conch management and research: Status, needs and priorities. Pages 301-319 *in* R. S. Appeldoorn, and B. Rodríguez Q., editors. Queen Conch Biology, Fisheries and Mariculture. Fundación Científica Los Roques, Caracas, Venezuela.
- Appeldoorn, R. S. 1995. Potential compensatory mechanisms operating on reproductive output in gonochoristic molluscs, with particular reference to strombid gastropods. Pages 13-18 *in* ICES Marine Science Symposia, volume 199. International Council for the Exploration of the Sea, Copenhagen, Denmark.
- Appeldoorn, R. S. 1996. Deep water spatial variability in the morphology of queen conch and its implication for management regulations. CARICOM Fisheries Resource Assessment and Management Programme (CFRAMP), Report of the Conch and Lobster Subproject Specification and Training Workshop, October 9-12, 1995, CARICOM Fishery Research Document No. 19, Kingston, Jamaica.
- Appeldoorn, R. S. 2020. Size at maturation, spawning variability, and fecundity in the queen conch, *Aliger gigas*. *Gulf and Caribbean Research* 31(1):GCFI 10-GCFI 19.
- Appeldoorn, R. S., and N. E. Baker. 2013. A literature review of the queen conch, *Strombus gigas*. University of Puerto Rico, Department of Marine Sciences, Mayaguez, Puerto Rico.
- Appeldoorn, R. S., and D. L. Ballantine. 1983. Field release of cultured queen conch in Puerto Rico: Implications for stock restoration. Pages 89-98 *in* Proceedings of the 35th Gulf and Caribbean Fisheries Institute, volume 35. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.

- Appeldoorn, R. S., E. R. Castro González, R. Glazer, and M. C. Prada. 2011. 12 chapter. Applying EBM to queen conch fisheries in the Caribbean. Pages 177-186 in L. Fanning, R. Mahon, and P. McConney, editors. Towards Marine Ecosystem-Based Management in the Wider Caribbean. Amsterdam University Press, Amsterdam, Netherlands.
- Arzu, D. 2019. What if you could no longer enjoy Belizean conch soup or ceviché? Ambergris Today Online, December 18, 2019.
- Atkinson, S., M. J. Atkinson, and A. M. Tarrant. 2003. Estrogens from sewage in coastal marine environments. *Environmental Health Perspectives* 111(4):531-535.
- Ault, J. S., S. G. Smith, J. Luo, M. E. Monaco, and R. S. Appeldoorn. 2008. Length-based assessment of sustainability benchmarks for coral reef fishes in Puerto Rico. *Environmental Conservation* 35(3):221-231.
- Avila-Poveda, O. H., and E. R. Baqueiro-Cárdenas. 2006. Size at sexual maturity in the queen conch *Strombus gigas* from Colombia. *Bulletin of Marine and Coastal Research* 35(1):223-233.
- Avila-Poveda, O. H., and E. R. Baqueiro-Cárdenas. 2009. Reproductive cycle of *Strombus gigas* Linnaeus 1758 (Caenogastropoda: Strombidae) from Archipelago of San Andres, Providencia and Santa Catalina, Colombia. *Invertebrate Reproduction and Development* 53(1):1-12.
- Azcarate, R., A. Rojas-Archbold, E. Castro, C. Ballesteros, and D. Lucía Gomez, 2019. Current status (2017) of the queen conch (*Lobatus gigas*) (Linnaeus, 1758) populations in the Seaflower Biosphere Reserve, Serranilla Bank, Courtown and Southwest Cays. Pages 139-145 in Proceedings of the 71st Gulf and Caribbean Fisheries Institute, volume 71. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Azevedo, C., and I. Padovan. 2004. *Nematopsis gigas* n. sp. (Apicomplexa), a parasite of *Nerita ascensionis* (Gastropoda, Neritidae) from Brazil. *Journal of Eukaryotic Microbiology* 51(2):214-219.
- Baker, N., R. S. Appeldoorn, and P. A. Torres-Saavedra. 2016. Fishery-independent surveys of the queen conch stock in western Puerto Rico, with an assessment of historical trends and management effectiveness. *Marine and Coastal Fisheries* 8(1):567-579.
- Ballantine, D. L., and R. S. Appeldoorn. 1983. Queen conch culture and future prospects in Puerto Rico. Pages 57-63 in Proceedings of the 35th Gulf and Caribbean Fisheries Institute, volume 35. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Baqueiro Cárdenas, E. R., L. Frenkiel, and D. Aldana Aranda. 2007. One more threat for the queen conch *Strombus gigas*? Coccidian (Apicomplexa) infection of *S. gigas* digestive gland: Preliminary results. Pages 397-402 in Proceedings of the 58th Gulf and Caribbean Fisheries Institute, volume 58. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.

- Baqueiro Cárdenas, E. R., J. Montero, L. Frenkiel, and D. Aldana Aranda. 2012. Attenuated reproduction of *Strombus gigas* by an Apicomplexa: Emeriidae-like parasite in the digestive gland. *Journal of Invertebrate Pathology* 110(3):398-400.
- Barile, P. J., A. W. Stoner, and C. M. Young. 1994. Phototaxis and vertical migration of the queen conch (*Strombus gigas* Linne) veliger larvae. *Journal of Experimental Marine Biology and Ecology* 183(2):147-162.
- Barnutty Navarro, R., and R. Salvador Castellon. 2013. Informe nacional de Nicaragua. Pages 124-129 in Report of the First Meeting of the CFMC/OSPESCA/WECAFC/CRFM Working Group on Queen Conch, Panama City, Panama 23-25 October 2012. Food and Agriculture Organization of the United Nations (FAO) Western Central Atlantic Fishery Commission, Rome, Italy.
- Becking, L. E., T. van Bussel, M. S. Engel, M. J. A. Christianen, and A. O. Debrot. 2014. Proximate response of fish, conch, and sea turtles to the presence of the invasive seagrass *Halophila stipulacea* in Bonaire. IMARES - Institute for Marine Resources & Ecosystem Studies, Report Number C118/14, Wageningen, Netherlands.
- Beltrán, D. M. 2019. Phenotypic and genomic variation of the queen conch (*Lobatus gigas*) in Puerto Rico. Technical Report. San Juan, PR, Puerto Rico Department of Natural and Environmental Resources.
- Berg Jr., C. J., F. Couper, K. Nisbet, and J. Ward. 1992. Stock assessment of queen conch, *Strombus gigas*, and harbour conch, *S. costatus*, in Bermuda. Pages 433-438 in Proceedings of the 41st Gulf and Caribbean Fisheries Institute, volume 41. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Berg Jr., C. J., and R. A. Glazer. 1995. Stock assessment of a large marine gastropod (*Strombus gigas*) using randomized and stratified towed-diver censusing. Pages 247-258 in ICES Marine Science Symposia, volume 199. International Council for the Exploration of the Sea, Copenhagen, Denmark.
- Berg Jr., C. J., and D. A. Olsen. 1989. 18 chapter. Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. Pages 421-442 in J. F. Caddy, editor. Marine Invertebrate Fisheries: Their Assessment and Management. Wiley and Sons New York, NY.
- Bissada, C. E. 2011. Aspects of the biology of queen conch *Strombus gigas* in Barbados with implications for fisheries management. Master's Thesis. University of the West Indies, Cave Hill, Barbados.
- Blackburn, M., C. A. S. Mazzacano, C. Fallon, and S. H. Black. 2014. Oil in our oceans: A review of the impacts of oil spills on marine invertebrates. The Xerces Society for Invertebrate Conservation, Portland, OR.
- Blythe-Mallett, A., K. A. Aiken, I. Segura-Garcia, N. K. Truelove, M. K. Webber, M. E. Roye, and St. J. Box. 2021. Genetic composition of queen conch (*Lobatus gigas*) population on Pedro Bank, Jamaica and its use in fisheries management. *PLoS ONE* 16(4):e0245703.

- Boettcher, A. A., H. Long, and A. Duque. 2003. The impact of heat stress on queen conch larval metamorphosis. Pages 226-229 in Proceedings of the 54th Gulf and Caribbean Fisheries Institute, volume 54. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Boidron-Metairon, I. F. 1992. A new approach to comparative studies of *Strombus gigas* larvae at the developmental and nutritional levels. Pages 459-467 in Proceedings of the 41st Gulf and Caribbean Fisheries Institute, volume 41. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Boman, E. M., and coauthors. 2019. Diet and growth of juvenile queen conch *Lobatus gigas* (Gastropoda: Strombidae) in native, mixed and invasive seagrass habitats. Marine Ecology Progress Series 621:143-154.
- Boman, E. M., and coauthors. 2018. Variability in size at maturity and reproductive season of queen conch *Lobatus gigas* (Gastropoda: Strombidae) in the Wider Caribbean Region. Fisheries Research 201:18-25.
- Botero, L. 1984. Observaciones sobre una población de *Strombus gigas* L. en la Ensenada de Nenguange, Caribe colombiano. Anales del Instituto de Investigaciones Marinas de Punta Betín 14:47-66.
- Bothwell, J. 2009. Conchs in the Cayman Islands: Population, CITES and IUU fishery status. Pages 38-40 in M. C. Prada, and E. Castro, editors. Proceedings of Regional Workshop for the Improvement of the Queen Conch Collaborative Management and Enforcement in the Southwestern Caribbean, Section 2. Current Situation of the Queen Conch in the Southwestern Caribbean, July 28-31, 2008, San Andres Island, Colombia.
- Brierley, A. S., and M. J. Kingsford. 2009. Impacts of climate change on marine organisms and ecosystems. Current Biology 19(14):R602-R614.
- Brownell, W. N. 1977. Reproduction, laboratory culture, and growth of *Strombus gigas*, *S. costatus* and *S. pugilus* in Los Roques, Venezuela. Bulletin of Marine Science 27(4):668-680.
- Brownell, W. N., and J. M. Stevely. 1981. The biology, fisheries, and management of the queen conch, *Strombus gigas*. Marine Fisheries Review 43(7):1-12.
- Brownscombe, J. W., and coauthors. 2015. Individual differences in activity and habitat selection of juvenile queen conch evaluated using acceleration biologgers. Endangered Species Research 27(2):181-188.
- Buckland, B. J. 1989. Reproduction and growth of the queen conch, *Strombus gigas*, off St. Christopher and Nevis in the Eastern Caribbean. Master's Thesis. University of Guelph, Guelph, Ontario, Canada.
- Burkholder, J. M., D. A. Tomasko, and B. W. Touchette. 2007. Seagrasses and eutrophication. Journal of Experimental Marine Biology and Ecology 350(1-2):46-72.
- Burry, L. A. 1949. A new *Strombus* species. Shell Notes 2(7, 8, 9):106-109.

- Byrne, M., P. Selvakumaraswamy, M. A. Ho, E. Woolsey, and H. D. Nguyen. 2011. Sea urchin development in a global change hotspot, potential for southerly migration of thermotolerant propagules. *Deep Sea Research Part II: Topical Studies in Oceanography* 58(5):712-719.
- Cala, Y. R., A. de Jesús-Navarrete, F. A. Ocaña, and J. Oliva-Rivera. 2013. Density and reproduction of the queen conch *Eustrombus gigas* (Mesogastropoda: Strombidae) at Cabo Cruz, Desembarco del Granma National Park, Cuba. *Revista de Biología Tropical* 61(2):645-655.
- Campton, D. E., C. J. Berg Jr., L. M. Robison, and R. A. Glazer. 1992. Genetic patchiness among populations of queen conch *Strombus gigas* in the Florida Keys and Bimini. *Fishery Bulletin* 90(2):250-259.
- Castro González, E. R., L. Frenkiel, E. Baqueiro Cárdenas, and D. Aldana Aranda. 2007. Atypical reproductive cycle of the queen conch *Strombus gigas* (Mollusca: Gastropoda). Pages 419-426 in *Proceedings of the 58th Gulf and Caribbean Fisheries Institute*, volume 58. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Castro, E., M. Prada, E. Taylor, C. Pomare, and H. Robinson. 2009. Conservation and fishery management of the queen conch (*Strombus gigas*): Challenges and achievements in the Seaflower Biosphere Reserve, Colombia. Pages 20-27 in M. C. Prada, and E. Castro, editors. *Proceedings of Regional Workshop for the Improvement of the Queen Conch Collaborative Management and Enforcement in the Southwestern Caribbean, Section 2. Current Situation of the Queen Conch in the Southwestern Caribbean, July 28-31, 2008, San Andres Island, Colombia.*
- Castro, E., and coauthors. 2011. Estado actual de las poblaciones del caracol *Strombus gigas* en el sector norte del área marina protegida Seaflower, Colombia. Universidad Nacional de Colombia, Departamento Archipiélago de San Andrés, Providencia y Santa Catalina, Coralina, Reporte Técnico, San Andrés isla 23.
- CFMC. 1996. Fishery management plan, regulatory impact review, and final environmental impact statement for the queen conch resources of Puerto Rico and the United States Virgin Islands. Caribbean Fishery Management Council, EPA No. 960154D, San Juan, Puerto Rico.
- CFMC and CFRAMP. 1999. Report on the queen conch stock assessment and management workshop. Caribbean Fishery Management Council (CFMC) and CARICOM Fisheries Resource Assessment and Management Program (CFRAMP), Belize City, Belize.
- Chau, Y. K., R. J. Maguire, M. Brown, F. Yang, and S. P. Batchelor. 1997. Occurrence of organotin compounds in the Canadian aquatic environment five years after the regulation of antifouling uses of tributyltin. *Water Quality Research Journal* 32(3):453-522.
- Chávez, E. A., and F. Arreguín-Sánchez. 1994. Simulation modelling for conch fishery management. Pages 125-136 in R. S. Appeldoorn, and B. Rodriguez Q., editors. *Queen Conch Biology, Fisheries and Mariculture*. Fundación Científica Los Roques, Caracas, Venezuela.

- Chávez Villegas, J. F., M. Enríquez Díaz, and D. Aldana Aranda. 2017. Efecto de la temperatura y la acidificación en larvas de *Strombus gigas* (Mesogastropoda: Strombidae). *Revista de Biología Tropical* 65(2):505-515.
- Chollett, I., P. J. Mumby, F. E. Müller-Karger, and C. Hu. 2012. Physical environments of the Caribbean Sea. *Limnology and Oceanography* 57(4):1233-1244.
- CITES. 2003. Progress on the implementation of the review of significant trade (Phases IV and V), Review of significant trade in specimens of Appendix-II species. Secretariat of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), AC19 Doc. 8.3 (Rev. 1), 18–21 August 2003, Geneva, Switzerland.
- CITES. 2012. Evaluation of the review of significant trade: Case studies [Decision 13.67 (REV. COP14)]. Secretariat of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), AC26/PC20 Doc. 7, Annex 5, Dublin, Ireland.
- CITES. 2018. Species specific matters. Aquatic species. Queen conch (*Strombus gigas*). Secretariat of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), AC30 Doc. 22, 16-21 July 2018, Geneva, Switzerland.
- Clench, W. J. 1937. Descriptions of new land and marine shells from the Bahama Islands. *Proceedings of the New England Zoological Club* 16:17-26.
- Clerveaux, W., A. J. Danylchuk, and V. Clerveaux. 2005. Variation in queen conch morphology: Management implications in the Turks and Caicos Islands, BWI. Pages 715-724 in *Proceedings of the 56th Gulf and Caribbean Fisheries Institute*, volume 56. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Cœurdassier, M., A. de Vaufleury, N. Crini, R. Scheifler, and P. M. Badot. 2005. Assessment of whole effluent toxicity on aquatic snails: Bioaccumulation of Cr, Zn, and Fe, and individual effects in bioassays. *Environmental Toxicology and Chemistry* 24(1):198-204.
- Coleman, F., C. C. Koenig, and L. A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental Biology of Fishes* 47:129-141.
- Cooley, S. R., and S. C. Doney. 2009. Anticipating ocean acidification's economic consequences for commercial fisheries. *Environmental Research Letters* 4, 024007.
- Corral, J. L., and J. Ogawa. 1987. Cultivo masivo de larva de caracol *Strombus gigas* en estanques de concreto. Pages 345-352 in *Proceedings of the 38th Gulf and Caribbean Fisheries Institute*, volume 38. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Coulston, M. L., R. W. Berey, A. C. Dempsey, and P. Odum. 1987. Assessment of the queen conch (*Strombus gigas*) population and predation studies of hatchery reared juveniles in Salt River Canyon, St. Croix, U.S. Virgin Islands. Pages 294-306 in *Proceedings of the 38th Gulf and Caribbean Fisheries Institute*, volume 38. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.

- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* 14(10):405-410.
- Creswell, R. L. 1994. An historical overview of queen conch mariculture. Pages 223-230 in R. S. Appeldoorn, and B. Rodriguez Q., editors. *Queen Conch Biology, Fisheries and Mariculture*. Fundación Científica Los Roques, Caracas, Venezuela.
- Cruz S., R. 1986. Avances en la experimentacion de producción massiva de caracol en Quintana Roo, Mexico. Pages 12-20 in *Proceedings of the 37th Gulf and Caribbean Fisheries Institute*, volume 37. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Cullen-Unsworth, L. C., and coauthors. 2014. Seagrass meadows globally as a coupled social-ecological system: Implications for human wellbeing. *Marine Pollution Bulletin* 83(2):387-397.
- D'Asaro, C. N. 1965. Organogenesis, development, and metamorphosis in the queen conch, *Strombus gigas*, with notes on breeding habits. *Bulletin of Marine Science* 15(2):359-416.
- Dahlgren, C. P. 2014. Review of the benefits of no-take zones. Wildlife Conservation Society, Belize City, Belize.
- Davis, M. 1992. Predation on hatchery-reared juvenile queen conch, *Strombus gigas* (L.) by juvenile spiny lobsters, *Panulirus argus* (L.). Master's Thesis. Florida Institute of Technology, Melbourne, FL.
- Davis, M. 1994. Mariculture techniques for queen conch (*Strombus gigas* Linne): Egg mass to juvenile stage. Pages 231-252 in R. S. Appeldoorn, and B. Rodriguez Q., editors. *Queen Conch Biology, Fisheries and Mariculture*. Fundación Científica Los Roques, Caracas, Venezuela.
- Davis, M. 2000. The combined effects of temperature and salinity on growth, development, and survival for tropical gastropod veligers of *Strombus gigas*. *Journal of Shellfish Research* 19(2):883-889.
- Davis, M. 2005. Species profile: Queen conch, *Strombus gigas*, Southern Regional Aquaculture Center Publication No. 7203.
- Davis, M., and C. Hesse. 1983. Third world level conch mariculture in the Turks and Caicos Islands. Pages 73-82 in *Proceedings of the 35th Gulf and Caribbean Fisheries Institute*, volume 35. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Davis, M., B. A. Mitchell, and J. L. Brown. 1984. Breeding behavior of the queen conch *Strombus gigas* Linné held in a natural enclosed habitat. *Journal of Shellfish Research* 4(1):17-21.
- Davis, M., and A. W. Stoner. 1994. Trophic cues induce metamorphosis of queen conch larvae (*Strombus gigas* Linnaeus). *Journal of Experimental Marine Biology and Ecology* 180(1):83-102.

- de Graaf, M., M. Meijer zu Schlochtern, and E. K. Boman. 2014. Non-detriment finding regarding the export of queen conch (*Lobatus gigas*) from St. Eustatius (Caribbean Netherlands). Institute for Marine Resources & Ecosystem Studies, IMARES Report C173/14, Wageningen, Netherlands.
- De Jesús-Navarrete, A., and A. Valencia-Hernández. 2013. Declining densities and reproductive activities of the queen conch *Strombus gigas* (Mesogastropoda: Strombidae) in Banco Chinchorro, Eastern Caribbean, Mexico. *Revista de Biología Tropical* 61(4):1671-1679.
- Delgado, G. A., C. T. Bartels, R. A. Glazer, N. J. Brown-Peterson, and K. J. McCarthy. 2004. Translocation as a strategy to rehabilitate the queen conch (*Strombus gigas*) population in the Florida Keys. *Fishery Bulletin* 102(2):278-288.
- Delgado, G. A., and R. A. Glazer. 2007. Interactions between translocated and native queen conch *Strombus gigas*: Evaluating a restoration strategy. *Endangered Species Research* 3(3):259-266.
- Delgado, G. A., and R. A. Glazer. 2020. Demographics influence reproductive output in queen conch (*Lobatus gigas*): Implications for fishery management. *Bulletin of Marine Science* 96(4):707-721.
- Delgado, G. A., R. A. Glazer, and N. J. Brown-Peterson. 2019. Arrested sexual development in queen conch (*Lobatus gigas*) linked to abnormalities in the cerebral ganglia. *The Biological Bulletin* 237(3):241-249.
- Delgado, G. A., R. A. Glazer, and N. J. Stewart. 2002. Predator-induced behavioral and morphological plasticity in the tropical marine gastropod *Strombus gigas*. *The Biological Bulletin* 203(1):112-120.
- Delgado, G. A., R. A. Glazer, and D. Wetzel. 2007. The effects of water quality on embryogenesis and larval development of queen conch: Implications for recruitment to and coastal development of the Florida Keys. Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute and Mote Marine Laboratory, Final Report to the South Florida Water Management District, SFWMD #OT050676, Marathon, FL.
- DEMA. 2012. Status of the queen conch fishery in the Turks and Caicos Islands. Turks and Caicos Islands Department of Environment and Maritime Affairs (DEMA), Presentation at the Queen Conch Working Group, Panama, October 2012, Panama.
- Doerr, J. C., and R. L. Hill. 2013. Home range, movement rates, and habitat use of queen conch, *Strombus gigas*, in St. John, U.S. Virgin Islands. *Caribbean Journal of Science* 47(2-3):251-259.
- Doerr, J. C., and R. L. Hill. 2018. Spatial distribution, density, and habitat associations of queen conch *Strombus gigas* in St. Croix, US Virgin Islands. *Marine Ecology Progress Series* 594:119-133.
- Doney, S. C. 2006. The dangers of ocean acidification. *Scientific American* 294(3):58-65.

- Douglas, M. R., T. K. Chafin, J. E. Claussen, D. P. Philipp, and M. E. Douglas. 2021. Are populations of economically important bonefish and queen conch ‘open’ or ‘closed’ in the northern Caribbean basin? *Marine Ecology* 42(2):1-14.
- Duarte, C. M. 2002. The future of seagrass meadows. *Environmental Conservation* 29(2):192-206.
- Ducrot, V., and coauthors. 2007. Dynamic energy budget as a basis to model population-level effects of zinc-spiked sediments in the gastropod *Valvata piscinalis*. *Environmental Toxicology and Chemistry* 26(8):1774-1783.
- Dujon, A. M., T. Stieglitz, E. Amice, and D. M. Webber. 2019. Snail leaps and bounds: Drivers of the diel movement pattern of a large invertebrate, the Caribbean queen conch in a marginal inshore habitat. *Canadian Journal of Zoology* 97(5):436-445.
- Duszynski, D. W., S. J. Upton, and L. Couch. 1998. The coccidia of the world: A unified database. *Parasitology International* 47(Supplement 1):286.
- Eakin, C. M., and coauthors. 2010. Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. *PLoS ONE* 5(11):e13969.
- Egan, B. D. 1985. Aspects of the reproductive biology of *Strombus gigas*. Master’s Thesis. University of British Columbia, Vancouver, B.C., Canada.
- Ehrhardt, N. M., and M. Valle-Esquivel. 2008. Conch (*Strombus gigas*) stock assessment manual. Caribbean Fishery Management Council, San Juan, Puerto Rico.
- Erisman, B., and coauthors. 2017. Fish spawning aggregations: Where well-placed management actions can yield big benefits for fisheries and conservation. *Fish and Fisheries* 18(1):128-144.
- Escoto García, R. 2004. Situación de la pesca del caracol, *Strombus gigas*, en Nicaragua. Pages 1000-1001 in *Proceedings of the 55th Gulf and Caribbean Fisheries Institute*, volume 55. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- FAO. 2007. Regional workshop on the monitoring and management of queen conch, *Strombus gigas*. Food and Agriculture Organization of the United Nations (FAO), FAO Fisheries Report. No. 832, Kingston, Jamaica, 1–5 May 2006, Rome, Italy.
- FAO. 2016. Report of the second meeting of the CFMC/OSPESCA/WECAFC/CRFM Working Group on Queen Conch, Panama City, Panama.
- FAO. 2020. Queen conch fisheries: Guadeloupe, Martinique and Saint-Barthélemy. Pages 18 in *Western Central Atlantic Fishery Commission, Report of the Fourth Meeting of the CFMC/OSPESCA/WECAFC/CRFM/CITES Working Group on Queen Conch*, San Juan, Puerto Rico, 16–17 December 2019. Food and Agriculture Organization of the United Nations (FAO) Western Central Atlantic Fishery Commission, Rome, Italy.

- FAO Western Central Atlantic Fishery Commission. 2013. Report of the first meeting of the CFMC/OSPESCA/WECAFC/CRFM Working Group on Queen Conch, Panama City, Panama, 23–25 October 2012. Food and Agriculture Organization of the United Nations (FAO), FAO Fisheries and Aquaculture Report No. 1029, Bridgetown, Barbados.
- FAO Western Central Atlantic Fishery Commission. 2020. Report of the Fourth Meeting of CFMC/OSPESCA/WECAFC/CRFM/CITES Working Group on Queen Conch, San Juan, Puerto Rico, 16–17 December 2019. Food and Agriculture Organization of the United Nations (FAO), FAO Fisheries and Aquaculture Report No. 1326, Bridgetown, Barbados.
- Farmer, N. A., and J. C. Doerr. 2022. Limiting factors for queen conch (*Strombus gigas*) reproduction: A simulation-based evaluation. PLoS ONE 17(3):e0251219.
- Feely, R. A., and coauthors. 2004. Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. Science 305(5682):362.
- Fitzer, S. C., and coauthors. 2018. Coastal acidification impacts on shell mineral structure of bivalve mollusks. Ecology and Evolution 8(17):8973-8984.
- Florida Department of State. 2021. Florida Administrative Code & Florida Administrative Register, 68B-16.002: Definitions. <https://www.flrules.org/>.
- Foley, J. R., and M. Takahashi. 2017. Shell lip thickness is the most reliable proxy to sexual maturity in queen conch (*Lobatus gigas*) of Port Honduras Marine Reserve, Belize: Informing management to reduce the risk of growth overfishing. Frontiers in Marine Science 4:179.
- Forbes Pacheco, T. Y. 2017. Distribución y densidad del caracol pala, *Lobatus gigas* (Linnaeus, 1758) en San Andrés Isla, Caribe Insular Colombiano. Corporación para el Desarrollo Sostenible del Archipiélago de San Andrés, San Andrés Isla, Colombia.
- Forest Ecosystem Management Team. 1993. Forest ecosystem management: An ecological, economic, and social assessment. U.S. Department of Agriculture, Forest Service, Washington, DC.
- Formoso, G. 2001. Stock assessment and fishery management of queen conch (*Strombus gigas*) in major fishing grounds of the Cuban shelf. Second International Queen Conch Conference, 18–20 July 2001, Juan Dolio, Dominican Republic.
- Formoso, M., B. D. González, and S. Alfonso. Queen conch (*Strombus gigas*) commercial population monitoring in Doce Leguas, eastern region of Jardines de la Reina National Park, Cuba. Pages 384-387 in Proceedings of the 58th Gulf and Caribbean Fisheries Institute, volume 58. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Franco, B. C., and coauthors. 2020. Climate change impacts on the atmospheric circulation, ocean, and fisheries in the southwest South Atlantic Ocean: A review. Climatic Change 162(4):2359-2377.

- Frenkiel, L., and coauthors. 2009. Reproductive cycle of the queen conch *Strombus gigas* L. 1758 in Guadeloupe FWI. Pages 518-520 in Proceedings of the 61st Gulf and Caribbean Fisheries Institute, volume 61. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- García-Sais, J. R., J. Sabater-Clavell, R. Esteves, and M. Carlo. 2012. Fishery-independent survey of commercially exploited fish and shellfish populations from mesophotic reefs within the Puerto Rican Exclusive Economic Zone: Final report. Caribbean Fisheries Management Council, San Juan, Puerto Rico.
- García E., M. I., J. M. Mow P., J. R. Cantera K., and F. H. Pineda P. 1992. The study of the populations of the queen conch (*Strombus gigas*) with fisheries management implications in the different areas of the Archipelago of San Andrés and Providencia, Colombia. Pages 172-189 in Proceedings of the 42nd Gulf and Caribbean Fisheries Institute, volume 42. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Gascoigne, J., and R. N. Lipcius. 2004. Conserving populations at low abundance: Delayed functional maturity and Allee effects in reproductive behaviour of the queen conch *Strombus gigas*. Marine Ecology Progress Series 284:185-194.
- Gazeau, F., and coauthors. 2013. Impacts of ocean acidification on marine shelled molluscs. Marine Biology 160(8):2207-2245.
- Georges, J., R. Ramdeen, and H. A. Oxenford. 2010. Fishing and marketing of queen conch (*Strombus gigas*) in Tobago. University of the West Indies, Centre for Resource Management and Environmental Studies (CERMES), CERMES Technical Report No. 23, Cave Hill Campus, Barbados.
- Gittens, L., and M. Braynen. 2012. Bahamas National Report. Government of The Bahamas, Department of Marine Resources.
- Glazer, R. A., and C. J. Berg Jr. 1994. Queen conch research in Florida: An overview. Pages 79-95 in R. S. Appeldoorn, and B. Rodriguez Q., editors. Queen Conch Biology, Fisheries and Mariculture. Fundación Científica Los Roques, Caracas, Venezuela.
- Glazer, R., and G. Delgado. 2020. Information to support initiation of a status review for queen conch. Florida Fish and Wildlife Conservation Commission, Marathon, FL.
- Glazer, R. A., G. A. Delgado, and J. A. Kidney. 2003. Estimating queen conch (*Strombus gigas*) home ranges using acoustic telemetry: Implications for the design of marine fishery reserves. Gulf and Caribbean Research 14(2):79-89.
- Glazer, R., and coauthors. 2008. Anthropogenic effects on queen conch reproductive development in South Florida: Final report. Florida Fish and Wildlife Conservation Commission, University of Florida, University of Southern Mississippi, and North Carolina State University, EPA Identifier: X7974799-03, FWC File Code: F2410-03-08-F, Marathon, FL.

- Glazer, R. A., and J. A. Kidney. 2004. Habitat associations of adult queen conch (*Strombus gigas* L.) in an unfished Florida Keys back reef: Applications to essential fish habitat. *Bulletin of Marine Science* 75(2):205-224.
- Gómez-Campo, K., M. Rueda, and C. García-Valencia. 2010. Distribución espacial, abundancia y relación con características del hábitat del caracol Pala *Eustrombus gigas* (Linnaeus) (Mollusca: Strombidae) en el archipiélago Nuestra Señora del Rosario, Caribe colombiano. *Boletín Investigaciones Marinas y Costeras* 39(1):137-159.
- Gongora, M., K. Esquivel, and A. Quiroz. 2020. Information on the queen conch fishery of Belize. Ministry of Forestry, Fisheries and Sustainable Development, Belize Fisheries Department, Belize City, Belize.
- Gordillo-Morales, G. 1996. Estadios gónadales del caracol rosa *Strombus gigas* Linneo 1758 (Mollusca: Gasteropoda: Strombidae) en Banco Chinchorro, Quintana Roo, Mexico. Bachelor's Thesis. University of Veracruz, Xalapa, Veracruz, México.
- Gore, S., and A. Llewellyn. 2005. Distribution and abundance of *Strombus gigas* in the British Virgin Islands. Pages 697-704 in *Proceedings of the 56th Gulf and Caribbean Fisheries Institute*, volume 56. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Government of Belize. 2013. The situation of the queen conch (*Strombus gigas*) stock of Belize. Ministry of Forestry, Fisheries and Sustainable Development, Belize Fisheries Department, Capture Fisheries Unit, Technical document being submitted to NOAA Fisheries in rejection of the petition to list the queen conch (*Strombus gigas*) as endangered or threatened species under the Endangered Species Act of the United States, Belize City, Belize.
- Grech, A., and coauthors. 2012. A comparison of threats, vulnerabilities and management approaches in global seagrass bioregions. *Environmental Research Letters* 7(024006):8.
- Green, E. P., and F. T. Short. 2003. *World Atlas of Seagrasses*. UNEP-WCMC, London.
- Gros, O., L. Frenkiel, and D. Aldana Aranda. 2009. Structural analysis of the digestive gland of the queen conch *Strombus gigas* Linnaeus, 1758 and its intracellular parasites. *Journal of Molluscan Studies* 75:59-68.
- Grossman, N. 2013. Territorial and maritime dispute (Nicaragua v. Colombia). *The American Journal of International Law* 107(2):396-403.
- Harley, C. D. G., and coauthors. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9(2):228-41.
- Hennessey, M. K., H. N. Nigg, and D. H. Habeck. 1992. Mosquito (Diptera: Culicidae) adulticide drift into wildlife refuges of the Florida Keys. *Environmental Entomology* 21(4):714-721.
- Hesse, K. O. 1976. An ecological study of the queen conch, *Strombus gigas*. Master's Thesis. University of Connecticut, Storrs, CT.

- Hesse, K. O. 1979. Movement and migration of the queen conch, *Strombus gigas*, in the Turks and Caicos Islands. *Bulletin of Marine Science* 29(3):303-311.
- Hillman, R. E., N. J. Maciolek, J. I. Lahey, and C. I. Belmore. 1982. Effects of a haplosporidian parasite, *Haplosporidium sp.*, on species of the molluscan woodborer *Teredo* in Barnegat Bay, New Jersey. *Journal of Invertebrate Pathology* 40(3):307-319.
- Ho, A. L. F. C. 2011. Population assessment of queen conch, *Strombus gigas*, in Western waters of Aruba. Report of the research team charged with assessing queen conch (*Strombus gigas*) population in Aruba, Report No. DLVV/R11.01.003, Oranjestad, Aruba.
- Holstein, D. M., C. B. Paris, and P. J. Mumby. 2014. Consistency and inconsistency in multispecies population network dynamics of coral reef ecosystems. *Marine Ecology Progress Series* 499:1-18.
- Horsford, I. S. 2019. Antigua and Barbuda: Status of implementation of the regional Queen Conch Fisheries Management Plan (QCFMP) in 2019. Antigua Ministry of Agriculture, Lands, Fisheries and Barbuda Affairs, Fisheries Division, St. John's, Antigua.
- Huitric, M. 2005. Lobster and conch fisheries of Belize: A history of sequential exploitation. *Ecology and Society* 10(1):21.
- Ilano, A. S., K. Fujinaga, and S. Nakao. 2004. Mating, development and effects of female size on offspring number and size in the neogastropod *Buccinum isaotakii* (Kira, 1959). *Journal of Molluscan Studies* 70(3):277-282.
- IMaRS-USF (Institute for Marine Remote Sensing-University of South Florida). 2005. Millennium Coral Reef Mapping Project. Unvalidated maps. These maps are unendorsed by IRD, but were further interpreted by UNEP World Conservation Monitoring Centre. Cambridge (UK): UNEP World Conservation Monitoring Centre.
- IMaRS-USF, IRD (Institut de Recherche pour le Developpement). 2005. Millennium Coral Reef Mapping Project. Validated maps. Cambridge (UK): UNEP World Conservation Monitoring Centre.
- International Court of Justice. 2012. Territorial and Maritime Dispute (Nicaragua v. Colombia). Press Release. [No. 2012/32](#). 8 November 2012.
- Intergovernmental Panel on Climate Change. 2001. Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, Cambridge, United Kingdom.
- Intergovernmental Panel on Climate Change. 2008. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

- Iversen, E. S., D. E. Jory, and S. P. Bannerot. 1986. Predation on queen conchs, *Strombus gigas*, in the Bahamas. *Bulletin of Marine Science* 39(1):61-75.
- Iversen, E. S., E. S. Rutherford, S. P. Bannerot, and D. E. Jory. 1987. Biological data on Berry Islands (Bahamas) queen conchs, *Strombus gigas*, with mariculture and fisheries management implications. *Fishery Bulletin* 85(2):299-310.
- Izioka, A. K. 2016. Population status and distribution of the queen conch (*Lobatus gigas*) in the waters of Anguilla. Wageningen University & Research, Wageningen, The Netherlands.
- Jiménez, N. M. 2007. Queen conch, *Strombus gigas*, population assessment around Puerto Rico.
- Jones, R. L., and A. W. Stoner. 1997. The integration of GIS and remote sensing in an ecological study of queen conch, *Strombus gigas*, nursery habitat. Pages 523-530 in *Proceedings of the 49th Gulf and Caribbean Fisheries Institute*, volume 49. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Jory, D. E., and E. S. Iversen. 1983. Queen conch predators: Not a roadblock to mariculture. Pages 108-111 in *Proceedings of the 35th Gulf and Caribbean Fisheries Institute*, volume 35. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Kitson-Walters, K. A., and coauthors. 2018. Fine-scale population structure of *Lobatus gigas* in Jamaica's exclusive economic zone considering hydrodynamic influences. *Fisheries Research* 199:53-62.
- Kough, A. S., C. A. Belak, C. B. Paris, A. Lundy, H. Cronin, G. Gnanalingam, S. Hagedorn, R. Skubel, A. C. Weiler, and A. W. Stoner. 2019. Ecological spillover from a marine protected area replenishes an over-exploited population across an island chain. *Conservation Science and Practice* 1(3):1-9.
- Kruczynski, W. L. 1999. Water quality concerns in the Florida Keys: Sources, effects, and solutions. EPA 904-R-99-005. Water Quality Protection Program, Florida Keys National Marine Sanctuary Report, Marathon, FL.
- Lagos-Bayona, A. L., S. Hernández-Barrero, H. Rodríguez-Gómez, and P. Victoria-Daza. 1996. Algunos aspectos bioecológicos y reproductivos del caracol pala *Strombus gigas* Linnaeus, 1758 en el Archipiélago de San Bernardo, Caribe Colombiano. *Boletín Científico del Instituto Nacional de Pesca y Acuicultura (INPA)* 4:141-160.
- Landau, B. M., M. Harzhauser, and A. G. Beu. 2009. A revision of the Tonnoidea (Caenogastropoda, Gastropoda) from the Miocene Paratethys and their palaeobiogeographic implications. *Jahrbuch der Geologischen Bundesanstalt* 149(1):61-109.
- Laskowski, R., and S. P. Hopkin. 1996. Effect of Zn, Cu, Pb, and Cd on fitness in snails (*Helix aspersa*). *Ecotoxicology and Environmental Safety* 34(1):59-69.

- Latiolais, J. M., M. S. Taylor, K. Roy, and M. E. Hellberg. 2006. A molecular phylogenetic analysis of strombid gastropod morphological diversity. *Molecular Phylogenetics and Evolution* 41(2):436-444.
- León-Pérez, M. C., W. J. Hernández, and R. A. Armstrong. 2019. Characterization and distribution of seagrass habitats in a Caribbean nature reserve using high-resolution satellite imagery and field sampling. *Journal of Coastal Research* 35(5):937-947.
- Lester, R. J. G., and G. H. G. Davis. 1981. A new *Perkinsus* species (Apicomplexa, Perkinsea) from the abalone *Haliotis ruber*. *Journal of Invertebrate Pathology* 37(2):181-187.
- Lockhart, K., C. de Fontaubert, and W. Clerveaux. 2007. Fisheries of the Turks and Caicos Islands: Status and threats. Pages 66-71 in *Proceedings of the 58th Gulf and Caribbean Fisheries Institute*, volume 58. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Lott, C. E. 2001. Lac Bay: Then and now...a historical interpretation of environmental change during the 1900s. Report prepared for Bonaire Marine Park.
- Machkour-M'Rabet, S., J. Cruz-Medina, F. J. García-De León, A. de Jesús-Navarrete, and Y. Hénaut. 2017. Connectivity and genetic structure of the queen conch on the Mesoamerican Reef. *Coral Reefs* 36(2):535-548.
- Márquez-Pretel, E., E. O. Davila-Vila, and J. Gallo-Nieto. 1994. Dinámica poblacional y pesquera del caracol pala *Strombus gigas* Linnaeus, 1758 en las Islas de Providencia y Santa Catalina. *Boletín Científico del Instituto Nacional de Pesca y Acuicultura (INPA)* 2:110-123.
- Márquez-Pretel, E., and coauthors. 2013. Genetic analysis of queen conch *Strombus gigas* from the Southwest Caribbean. Pages 410-416 in *Proceedings of the 65th Gulf and Caribbean Fisheries Institute*, volume 65. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Marshak, A. R., R. S. Appeldoorn, and N. Jiménez. 2006. Utilization of GIS mapping in the measurement of the spatial distribution of queen conch (*Strombus gigas*) in Puerto Rico. Pages 31-47 in *Proceedings of the 57th Gulf and Caribbean Fisheries Institute*, volume 57. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Martín-Mora, E., F. C. James, and A. W. Stoner. 1995. Developmental plasticity in the shell of the queen conch *Strombus gigas*. *Ecology* 76(3):981-994.
- Mateo, J., and J. C. Tejada. 2008. The queen conch, *Strombus gigas*, resource in the Dominican Republic. Pages 519-524 in *Proceedings of the 60th Gulf and Caribbean Fisheries Institute*, volume 60. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Maxwell, S. J., A. M. Dekkers, T. L. Rymer, and B. C. Congdon. 2020. Towards resolving the American and West African Strombidae (Mollusca: Gastropoda: Neostromboidae) using integrated taxonomy. *The Festivus* 52(1):3-38.

- McCarthy, K. 2007. A review of queen conch (*Strombus gigas*) life-history. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, SEDAR 14-DW-4, Miami, FL.
- McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. NOAA Technical Memorandum NMFS-NWFSC 42.
- McGinty, T. L. 1946. A new Florida strombus, *S. gigas verrilli*. Pages 46-48 in H. A. Pilsbry, and H. B. Baker, editors. The Nautilus, volume 60.
- McIntyre, M., R. A. Glazer, and G. A. Delgado. 2006. The effects of the pesticides Biomist 30/30® and Dibrom® on queen conch (*Strombus gigas*) embryos and larvae: A pilot study. Pages 731-741 in Proceedings of the 57th Gulf and Caribbean Fisheries Institute, volume 57. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- McKenzie, L. J., L. M. Nordlund, B. L. Jones, L. C. Cullen-Unsworth, C. Roelfsema, and R. K. F. Unsworth. 2020. The global distribution of seagrass meadows. Environmental Research Letters 15(7). <https://doi.org/10.1088/1748-9326/ab7d06>.
- Medley, P. 2008. Monitoring and managing queen conch fisheries: A manual. Food and Agriculture Organization of the United Nations, FAO Fisheries Technical Paper. No. 514, Rome, Italy.
- Meijer zu Schlochtern, M. 2014. Population status and reproductive biology of queen conch (*Lobatus gigas*) in the coastal waters around St. Eustatius. Master's Thesis. Wageningen University, Wageningen, Netherlands.
- Mianmanus, R. T. 1988. Induction of settlement and metamorphosis in larvae of *Aplysia brasiliensis* and *Strombus gigas* (Mollusca: Gastropoda). Ph.D. Dissertation. University of Miami, Miami, FL.
- Mitton, J. B., C. J. Berg Jr., and K. S. Orr. 1989. Population structure, larval dispersal, and gene flow in the queen conch, *Strombus gigas*, of the Caribbean. The Biological Bulletin 177(3):356-362.
- Mora, J. L. C. 2012. Situación de cambute (*Strombus gigas*) en el Caribe costarricense. Instituto Costarricense de Pesca y Acuicultura.
- Mora, O. 1994. Análisis de la pesquería del caracol pala (*Strombus gigas* L.) en Colombia. Pages 137-144 in R. S. Appeldoorn, and B. Rodríguez Q., editors. Queen Conch Biology, Fisheries and Mariculture. Fundación Científica Los Roques, Caracas, Venezuela.
- Morales, F. 2004. Metapopulation structure of the queen conch, *Strombus gigas* (Linne, 1758) throughout the Intra-Americas Sea. Ph.D. Dissertation. Florida Institute of Technology, Melbourne, FL.

- Morash, A. J., and K. Alter. 2015. Effects of environmental and farm stress on abalone physiology: Perspectives for abalone aquaculture in the face of global climate change. *Reviews in Aquaculture* 7(4):1-27.
- Morris, R. A. 2012. Jamaica national queen conch (*Strombus gigas*) report. Jamaica Ministry of Agriculture and Fisheries, Fisheries Division, Kingston, Jamaica.
- Nadeau, R. J., and E. T. Bergquist. 1977. Effects of the March 18, 1973 oil spill near Cabo Rojo, Puerto Rico on tropical marine communities. Pages 535-538 *in* International Oil Spill Conference Proceedings, volume 1977. American Petroleum Institute, Washington, D.C.
- National Environmental Planning Agency Jamaica. 2020. Information on queen conch for the Endangered Species Act, status review from Jamaica 2020. National Environment and Planning Agency, Kingston, Jamaica.
- Orth, R. J., and coauthors. 2006. A global crisis for seagrass ecosystems. *Bioscience* 56(12):987-996.
- Ortiz-Lobo, N. D. 2019. Informe final del Proyecto Caracol (*Strombus gigas*) en el marco de implementación del Plan de Manejo Caracol para la Temporada 2018–2019. Secretaría de Agricultura y Ganadería de Honduras / Dirección General de Pesca y Agricultura, Acuerdo Ministerial SAG 139-2018, La Ceiba, Atlántida.
- Oxenford, H. A., and S. Willoughby. 2013. Status of the queen conch fishery in Barbados. Pages 74-79 *in* Report of the First Meeting of the CFMC/OSPESCA/WCAFC/CRFM Working Group on Queen Conch, Panama City, Panama, 23–25 October 2012. Food and Agriculture Organization of the United Nations (FAO) Western Central Atlantic Fishery Commission, Rome, Italy.
- Paris, C. B., D. Aldana-Aranda, M. Perez-Perez, and J. Kool. 2008. Connectivity of queen conch, *Strombus gigas*, populations from Mexico. Pages 439-443 *in* B. Riegl, and R. E. Dodge, editors. Proceedings of the 11th International Coral Reef Symposium, volume 11. Nova Southeastern University, National Coral Reef Institute, Davie, FL.
- Parker, G. H. 1922. The leaping of the stromb (*Strombus gigas* Linn.). *Journal of Experimental Zoology* 36(2):205-209.
- Parker, L. M., and coauthors. 2013. Predicting the response of molluscs to the impact of ocean acidification. *Biology* 2(2):651-692.
- Patitsas, P. 2010. Abundance, density, and distribution of queen conch (*Strombus gigas*) in Lac Bay, Bonaire, Dutch Caribbean. *Physis* 8:49-55.
- Paul, J. H., M. R. McLaughlin, D. W. Griffin, E. K. Lipp, R. Stokes, and J. B. Rose. 2000. Rapid movement of wastewater from on-site disposal systems into surface waters in the lower Florida Keys. *Estuaries* 23(5):662-668.
- Pauly, D. 1998. Rationale for reconstructing catch time series. *EC Fisheries Cooperation Bulletin* 11(2):4-7.

- Pauly, D., D. Zeller, and M. L. D. Palomares (editors). 2020. Sea Around Us Concepts, Design and Data. www.seaaroundus.org.
- Peel, J. R., and D. Aldana Aranda. 2012. 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. Pages 383-390 in Proceedings of the 64th Gulf and Caribbean Fisheries Institute, volume 64. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Pérez-Enriquez, R., F. J. Garcia-Rodriguez, G. Mendoza-Carrion, and C. Padilla. 2011. Geographical variation in the genetic diversity and composition of the endangered queen conch *Strombus gigas* (Mesogastropoda: Strombidae) from Yucatán, México. *Revista de Biología Tropical* 59(3):1115-1126.
- Pérez-Pérez, M., and D. Aldana Aranda. 2003. Actividad reproductiva de *Strombus gigas* (Mesogasteropoda: Strombidae) en diferentes hábitats del Arrecife Alacranes, Yucatán. *Revista de Biología Tropical* 51(Supplement 4):119-126.
- Perkins, F. O. 1988. Structure of protistan parasites found in bivalve molluscs. Pages 93-111 in W. S. Fisher, editor. *Disease Processes in Marine Bivalve Molluscs*, volume Special Publication 18. American Fisheries Society, Bethesda, MD.
- Petuch, E. J. 1994. *Atlas of Florida Fossil Shells (Pliocene and Pleistocene Marine Gastropods)*. Chicago Spectrum Press, Evanston, IL.
- Phillip, O. S. 2000. The relationship between masculinized female conch (*Strombus gigas*) and tributyltin-based antifouling paints in coastal waters of the British Virgin Islands. Master's Thesis, University of Plymouth, Plymouth, United Kingdom.
- Phillips, M. A., C. E. Bissada-Gooding, and H. A. Oxenford. 2010. Preliminary investigation of the movements, density, and growth of juvenile queen conch in a nursery area in Barbados. Pages 427-434 in Proceedings of the 63rd Gulf and Caribbean Fisheries Institute, volume 63. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Pierce, R. H., M. S. Henry, T. C. Blum, and E. M. Mueller. 2005. Aerial and tidal transport of mosquito control pesticides into the Florida Keys National Marine Sanctuary. *Revista de Biología Tropical* 53:117-125.
- Posada, J. M., and R. S. Appeldoorn. 1994. Preliminary observations on the distribution of *Strombus* larvae in the eastern Caribbean. Pages 191-199 in R. S. Appeldoorn, and B. Rodriguez Q., editors. *Queen Conch Biology, Fisheries and Mariculture*. Fundación Científica Los Roques, Caracas, Venezuela.
- Posada, J. M., G. García-Moliner, and I. N. Oliveras (editors). 1997. Proceedings International Queen Conch Conference *Strombus gigas*. Caribbean Fishery Management Council, NOAA award No. NA77FC0004, San Juan, Puerto Rico.

- Posada, J. M., I. M. Rabelo, and M. Nemeth. 1999. Occurrence, abundance, and length frequency distribution of queen conch, *Strombus gigas* (Gastropoda) on shallow waters of the Jaragua National Park, Dominican Republic. *Caribbean Journal of Science* 35(1-2):70-82.
- Prada, M. C., R. S. Appeldoorn, S. van Eijs, and M. Pérez M. 2017. Regional queen conch fisheries management and conservation plan. Food and Agriculture Organization of the United Nations (FAO), FAO Fisheries and Aquaculture Technical Paper No. 610, Rome, Italy.
- Prada, M. C., and coauthors. 2009. Non-detrimental findings for the queen conch (*Strombus gigas*) in Colombia. CORALINA, NDF Workshop Case Studies, WG 9 – Aquatic Invertebrates, Case Study 3.
- Randall, J. E. 1964. Contributions to the biology of the queen conch, *Strombus gigas*. *Bulletin of Marine Science* 14(2):246-295.
- Rathier, I., and A. Battaglia. 1994. Assessment of the Martinique queen conch fishery and management perspectives. Pages 29-49 in R. S. Appeldoorn, and B. Rodríguez Q., editors. *Queen Conch Biology, Fisheries and Mariculture*. Fundación Científica Los Roques, Caracas, Venezuela.
- Raven, J., and coauthors. 2005. Ocean acidification due to increasing atmospheric carbon dioxide. The Royal Society, London, UK.
- Ray, M., and A. W. Stoner. 1995. Growth, survivorship, and habitat choice in a newly settled seagrass gastropod, *Strombus gigas*. *Marine Ecology Progress Series* 123:83-94.
- Regalado, J. 2012. Response of the Government of Honduras to the request made by NOAA regarding the Petition made to the U.S. Department of Commerce to list the queen conch, *Strombus gigas*, as “threatened” or “endangered” under the Endangered Species Act. Government of Honduras in the Ministry of Agriculture and Livestock, CODE 0648–XB140, 18th October 2012, Honduras.
- Reynal, L., M. Enríquez Díaz, and D. Aldana Aranda. 2009. First results of reproductive cycle of deep-sea queen conch, *Strombus gigas*, from FWI, Martinique. Pages 506-508 in *Proceedings of the 61st Gulf and Caribbean Fisheries Institute*, volume 61. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Ríos-Jara, E., M. Pérez-Peña, R. Beas-Luna, E. López-Urriarte, and E. Juárez-Carrillo. 2001. Gastropods and bivalves of commercial interest from the continental shelf of Jalisco and Colima, México. *Revista de Biología Tropical* 49(3-4):859-863.
- Rizo, O. D., and coauthors. 2010. Copper, zinc and lead bioaccumulation in marine snail, *Strombus gigas*, from Guacanayabo Gulf, Cuba. *Bulletin of Environmental Contamination and Toxicology* 85(3):330-333.
- Robertson, R. 1959. Observations on the spawn and veligers of conchs (*Strombus*) in the Bahamas. *Journal of Molluscan Studies* 33(4):164-171.

- Rossetto, M., F. Micheli, A. Saenz-Arroyo, J. A. E. Montes, and G. A. De Leo. 2015. No-take marine reserves can enhance population persistence and support the fishery of abalone. *Canadian Journal of Fisheries and Aquatic Sciences* 72(10):1503-1517.
- Rumbold, D. G., and S. C. Snedaker. 1997. Evaluation of bioassays to monitor surface microlayer toxicity in tropical marine waters. *Archives of Environmental Contamination and Toxicology* 32(2):135-140.
- Ruttenberg, B., and coauthors. 2018. Ecological assessment of the marine ecosystems of Barbuda, West Indies: Using rapid scientific assessment to inform ocean zoning and fisheries management. *PLoS ONE* 13(1):20.
- Salley, S. 1986. Development of the statocyst of the queen conch larva, *Strombus gigas* L. (Gastropoda: Prosobranchia). Master's Thesis. McGill University, Montreal, Canada.
- San Pedro Sun. 2018. The queen conch season is officially open; illegal conch fishing continues to be a challenge, October 3, 2018.
- Sánchez Baquero, R. 2009. National report of queen conch (*Strombus gigas*) fishery in the Republic of Nicaragua. Pages 28-31 in M. C. Prada, and E. Castro, editors. Proceedings of Regional Workshop for the Improvement of the Queen Conch Collaborative Management and Enforcement in the Southwestern Caribbean, Section 2. Current Situation of the Queen Conch in the Southwestern Caribbean, July 28–31, 2008, San Andres Island, Colombia.
- Sánchez, F. C., M. E. Díaz, E. M. Rodríguez, and D. Aldana Aranda. 2019. First use of a non-invasive technique for determination of sex hormones in the queen conch *Lobatus gigas*, Mollusca Gastropoda. *Aquaculture International* 27(2):437-448.
- Sánchez, V. 2017. Diet and maximum size of Queen conch (*Lobatus gigas*) around the island of Curaçao. Master's Thesis, Utrecht University, The Netherlands.
- Sanders, I. M. 1984. Sublethal effects of copper on juveniles of the queen conch *Strombus gigas* Linné. *Journal of Shellfish Research* 4(1):31-35.
- Sandt, V. J., and A. W. Stoner. 1993. Ontogenetic shift in habitat by early juvenile queen conch, *Strombus gigas*: Patterns and potential mechanisms. *Fishery Bulletin* 91:516-525.
- Santana Flores, P. A., and D. Aldana Aranda. 2013. Temporalidad y esfuerzo reproductivo del caracol *Strombus gigas*. Pages 458-460 in Proceedings of the 66th Gulf and Caribbean Fisheries Institute, volume 66. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Sarkis, S., and J. Ward. 2009. Recovery plan for the queen conch, *Strombus gigas*, in Bermuda. Government of Bermuda, Department Conservation Services, Bermuda.
- Schill, S. R., V. P. McNulty, F. J. Pollock, F. Lühthje, J. Li, D. E. Knapp, J. D. Kington, T. McDonald, G. T. Raber, X. Escovar-Fadul, and G. P. Asner. 2021. Regional high-

- resolution benthic habitat data from Planet Dove imagery for conservation decision-making and marine planning. *Remote Sensing* 13, 4215.
- Schultz, H. K., and K. Lockhart. 2017. Evaluation of queen conch (*Strombus gigas*) populations inside and outside of the East Harbor Conch and Lobster Reserve in the Turks and Caicos Islands. Bachelor's Thesis. University of Puget Sound, Tacoma, WA.
- SEDAR. 2007. Caribbean queen conch. Southeast Data, Assessment, and Review (SEDAR), SEDAR 14, Stock Assessment Report 3, North Charleston, SC.
- Serviere-Zaragoza, E., A. Mazariegos-Villareal, and D. Aldana Aranda. 2009. Preliminary observation of natural feed of queen conch *Strombus gigas*. Pages 514-517 in *Proceedings of the 61st Gulf and Caribbean Fisheries Institute*, volume 61. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *The Quarterly Review of Biology* 64(4):419-461.
- Short, F. T., and H. A. Neckles. 1999. The effects of global climate change on seagrasses. *Aquatic Botany* 63(3-4):169-196.
- Simone, L. R. L. 2005. Comparative morphological study of representatives of the three families of Stromboidea and the Xenophoroidea (Mollusca, Caenogastropoda), with an assessment of their phylogeny. *Arquivos de Zoologia* 37(2):141-267.
- Singh-Renton, S., R. S. Appeldoorn, and M. Gongora. 2006. Report of workshop to analyse data collected during visual abundance survey of queen conch conducted in Belize. CRFM Technical and Advisory Document.
- Smikle, S. G. 2010. Pedro Bank queen conch fishery, assessment and TAC recommendation. Jamaica Ministry of Agriculture, Fisheries Division, Jamaica.
- Smith, M. 1940. World-wide Sea Shells: Illustrations, Geographical Range and Other Data Covering More Than Sixteen Hundred Species and Sub-species of Molluscs. Tropical Photographic Laboratory, Lantana, FL.
- Smith, T. M., R. W. Reynolds, T. C. Peterson, and J. Lawrimore. 2008. Improvements to NOAA's historical merged land-ocean surface temperature analysis (1880 – 2006). *Journal of Climate* 21(10):2283-2296.
- Snyman, R. G., A. J. Reinecke, and S. A. Reinecke. 2004. Changes in oocyte numbers in the ovotestis of *Helix aspersa*, after experimental exposure to the fungicide copper oxychloride. *Bulletin of Environmental Contamination and Toxicology* 73:398-403.
- Souza Jr., P. M., and A. S. Kough. 2020. Queen conch *Lobatus gigas* population estimates and age structure suggest a potential natural refuge on the Cay Sal Bank, The Bahamas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 30(7):1276-1290.

- Spade, D. J., and coauthors. 2010. Queen conch (*Strombus gigas*) testis regresses during the reproductive season at nearshore sites in the Florida Keys. PLoS ONE 5(9):e12737.
- Spalding, M. D., C. Ravilious, and E. P. Green. 2001. World Atlas of Coral Reefs. Berkeley (California, USA): The University of California Press. 436 pp.
- Staaterman, E., and C. B. Paris. 2013. Modelling larval fish navigation: The way forward. ICES Journal of Marine Science 71(4):918-924.
- Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? Oikos 87(1):185-190.
- Stieglitz, T. C., A. M. Dujon, J. R. Peel, and E. Amice. 2020. The potential of marginal coastal nursery habitats for the conservation of a culturally important Caribbean marine species. Diversity and Distributions 26(5):565-574.
- Stoner, A., M. Davis, and C. Booker. 2011. Surveys of queen conch populations and reproductive biology at Lee Stocking Island and the Exuma Cays Land and Sea Park, The Bahamas, Community Conch, Bahamas.
- Stoner, A. W. 1989a. Density-dependent growth and grazing effects of juvenile queen conch *Strombus gigas* L. in a tropical seagrass meadow. Journal of Experimental Marine Biology and Ecology 130(2):119-133.
- Stoner, A. W. 1989b. Winter mass migration of juvenile queen conch *Strombus gigas* and their influence on the benthic environment. Marine Ecology Progress Series 56(1):99-104.
- Stoner, A. W. 2003. What constitutes essential nursery habitat for a marine species? A case study of habitat form and function for queen conch. Marine Ecology Progress Series 257:275-289.
- Stoner, A. W. 2019. Forty years of field and laboratory experiments with hatchery-reared queen conch: The case for conserving natural stocks. Reviews in Fisheries Science & Aquaculture 27(4):490-516.
- Stoner, A. W., and M. Davis. 1997. Abundance and distribution of queen conch veligers (*Strombus gigas* Linne) in the central Bahamas. I. Horizontal patterns in relation to reproductive and nursery grounds. Journal of Shellfish Research 16(1):7-18.
- Stoner, A. W., and M. H. Davis. 2010. Queen conch stock assessment historical fishing grounds Andros Island, Bahamas. Community Conch, Report by Community Conch to the Nature Conservancy, Nassau, Bahamas.
- Stoner, A. W., M. H. Davis, and C. J. Booker. 2012a. Maturation and age in queen conch (*Strombus gigas*): Urgent need for changes in harvest criteria. Fisheries Research 131-133:76-84.

- Stoner, A. W., M. H. Davis, and C. J. Booker. 2012b. Negative consequences of Allee effect are compounded by fishing pressure: Comparison of queen conch reproduction in fishing grounds and a marine protected area. *Bulletin of Marine Science* 88(1):89-104.
- Stoner, A. W., M. H. Davis, and A. S. Kough. 2019a. Relationships between fishing pressure and stock structure in queen conch (*Lobatus gigas*) populations: Synthesis of long-term surveys and evidence for overfishing in The Bahamas. *Reviews in Fisheries Science & Aquaculture* 27(1):51-71.
- Stoner, A. W., C. J. Booker, E. M. Cash, M. H. Davis, A. S. Kough, and C. McKinney-Lambert. 2019b. Queen conch harvest in The Bahamas during the last decade: shell middens provide more evidence of overfishing. Tech. Rept. Nassau, The Bahamas: Ministry of Agriculture and Marine Resources, The Bahamas, 17 p. Available at: www.communityconch.org.
- Stoner, A. W., and R. A. Glazer. 1998. Variation in natural mortality: Implications for queen conch stock enhancement. *Bulletin of Marine Science* 62(2):427-442.
- Stoner, A. W., R. A. Glazer, and P. J. Barile. 1996. Larval supply to queen conch nurseries: Relationships with recruitment process and population size in Florida and the Bahamas. *Journal of Shellfish Research* 15(2):407-420.
- Stoner, A. W., M. D. Hanisak, N. P. Smith, and R. A. Armstrong. 1994. Large-scale distribution of queen conch nursery habitats: Implications for stock enhancement. Pages 169-189 in R. S. Appeldoorn, and B. Rodriguez Q., editors. *Queen Conch Biology, Fisheries and Mariculture*. Fundación Científica Los Roques, Caracas, Venezuela.
- Stoner, A. W., and J. Lally. 1994. High-density aggregation in queen conch *Strombus gigas*: Formation, patterns, and ecological significance. *Marine Ecology Progress Series* 106:73-84.
- Stoner, A. W., K. W. Mueller, N. J. Brown-Peterson, M. H. Davis, and C. J. Booker. 2012c. Evidence for a significant decline in queen conch in the Bahamas, including the population in a marine protected area. Pages 349-361 in *Proceedings of the 64th Gulf and Caribbean Fisheries Institute*, volume 64. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Stoner, A. W., and M. Ray-Culp. 2000. Evidence for Allee effects in an over-harvested marine gastropod: Density-dependent mating and egg production. *Marine Ecology Progress Series* 202:297-302.
- Stoner, A. W., and M. Ray. 1993. Aggregation dynamics in juvenile queen conch (*Strombus gigas*): Population structure, mortality, growth, and migration. *Marine Biology* 116(4):571-582.
- Stoner, A. W., M. Ray, and J. M. Waite. 1995. Effects of a large herbivorous gastropod on macrofauna communities in tropical seagrass meadows. *Marine Ecology Progress Series* 121:125-137.

- Stoner, A. W., and V. J. Sandt. 1992. Population structure, seasonal movements and feeding of queen conch, *Strombus gigas*, in deep-water habitats of the Bahamas. *Bulletin of Marine Science* 51(3):287-300.
- Stoner, A. W., and K. C. Schwarte. 1994. Queen conch, *Strombus gigas*, reproductive stocks in the central Bahamas: distribution and probable sources. *Fishery Bulletin* 92:171-179.
- Stoner, A. W., V. J. Sandt, and I. F. Boidron-Metairon. 1992. Seasonality in reproductive activity and larval abundance of queen conch *Strombus gigas*. *Fishery Bulletin* 90(1):161-170.
- Stoner, A. W., and J. M. Waite. 1991. Trophic biology of *Strombus gigas* in nursery habitats: Diets and food sources in seagrass meadows. *Journal of Molluscan Studies* 57(4):451-460.
- Tello-Cetina, J. A., L. A. Rodríguez-Gil, and F. Rodríguez-Romero. 2005. Population genetics of the pink snail *Strombus gigas* in the Yucatan Peninsula: Implications for its management and fishery. *Ciencias Marinas* 31(2):379-386.
- Tewfik, A., E. A. Babcock, R. S. Appeldoorn, and J. Gibson. 2019. Declining size of adults and juvenile harvest threatens sustainability of a tropical gastropod, *Lobatus gigas*, fishery. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29(10):1587-1607.
- Tewfik, A., E. A. Babcock, J. Gibson, V. R. Burns Perez, and S. Strindberg. 2017. Benefits of a replenishment zone revealed through trends in focal species at Glover's Atoll, Belize. *Marine Ecology Progress Series* 580:37-56.
- Tewfik, A., S. Archibald, P. James, and I. S. Horsford. 2001. Antigua and Barbuda queen conch abundance survey (1999). CARICOM Fisheries Unit, CARICOM Fishery Report No. 7, Belize City, Belize.
- Tewfik, A., H. M. Guzmán, and G. Jácome. 1998. Assessment of the queen conch *Strombus gigas* (Gastropoda: Strombidae) population in Cayos Cochinos, Honduras. *Revista de Biología Tropical* 46(Supplement 4):137-150.
- Theile, S. 2001. Queen conch fisheries and their management in the Caribbean. TRAFFIC Europe, Technical report to the CITES Secretariat in completion of contract A-2000/01, Brussels, Belgium.
- Theile, S. 2005. Status of the queen conch *Strombus gigas* stocks, management and trade in the Caribbean: A CITES review. Pages 675-694 in *Proceedings of the 56th Gulf and Caribbean Fisheries Institute*, volume 56. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Tiley, K., and coauthors. 2018a. Digestive gland inclusion bodies in queen conch (*Lobatus gigas*) are non-parasitic. *Journal of Invertebrate Pathology* 157:4-8.
- Tiley, K., M. A. Freeman, and M. M. Dennis. 2018b. Pathology and reproductive health of queen conch (*Lobatus gigas*) in St. Kitts. *Journal of Invertebrate Pathology* 155:32-37.

- Titley-O'Neal, C. P., B. A. MacDonald, É. Pelletier, R. Saint-Louis, and O. S. Phillip. 2011. The relationship between imposex and tributyltin (TBT) concentration in *Strombus gigas* from the British Virgin Islands. *Bulletin of Marine Science* 87(3):421-435.
- Torres, R. E., and K. M. Sullivan-Sealey. 2002. Abundance, size frequency, and spatial distribution of queen conch (*Strombus gigas*) in southeastern Dominican Republic: A four-year population study in Parque Nacional del Este. Pages 120-128 in *Proceedings of the 53rd Gulf and Caribbean Fisheries Institute*, volume 53. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Torres Rosado, Z. A. 1987. Distribution of two mesogastropods, the queen conch, *Strombus gigas* Linnaeus, and the milk conch, *Strombus costatus* Gmelin in La Parguera, Lajas, Puerto Rico. Master's Thesis. University of Puerto Rico, Mayagüez Campus, Mayagüez, Puerto Rico.
- Treml, E. A., P. Halpin, D. Urban, and L. Pratson. 2008. Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landscape Ecology* 23:19-36.
- Treml, E. A., and P. N. Halpin. 2012. Marine population connectivity identifies ecological neighbors for conservation planning in the Coral Triangle. *Conservation Letters* 5(6):441-449.
- Truelove, N. K., and coauthors. 2017. Isolation by oceanic distance and spatial genetic structure in an overharvested international fishery. *Diversity and Distributions* 23(11):1292-1300.
- Ulman, A., L. Burke, E. Hind, R. Ramdeen, and D. Zeller. 2016. Conched out: Total reconstructed fisheries catches for the Turks and Caicos Islands uncover unsustainable resource usage. *Frontiers in Marine Science* 3(71):1-9.
- UNEP-WCMC, Short FT. 2021. Global distribution of seagrasses (version 7.1). Seventh update to the data layer used in Green and Short (2003). Cambridge (UK): UN Environment World Conservation Monitoring Centre. Data DOI: <https://doi.org/10.34892/x6r3-d211>
- UNEP-WCMC, WorldFish Centre, WRI, TNC. 2021. Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project. Version 4.1. Includes contributions from IMaRS-USF and IRD (2005), IMaRS-USF (2005) and Spalding et al. (2001). Cambridge (UK): UN Environment World Conservation Monitoring Centre. Data DOI: <https://doi.org/10.34892/t2wk-5t34>
- UNEP. 2012. Report of the Queen Conch Expert Workshop. United Nations Environment Programme (UNEP), May 22–24, Miami, FL.
- Valderrama B., M., and S. Hernández B. 2000. Determinación de la abundancia del recurso caracol de pala *Strombus gigas* en los bajos Serrana, Serranilla, Roncador y Quitasueño como base para la definición de cuotas de pesca en el Archipiélago de San Andrés y Providencia, Caribe Colombiano. Instituto Nacional de Pesca y Acuicultura.

- Vallés, H., and H. A. Oxenford. 2012. Queen conch (*Strombus gigas*) in Barbados: Density, distribution, and habitat correlates. *Bulletin of Marine Science* 88(4):947-969.
- van Baren, P. K. 2013. Status of queen conch fisheries in The Caribbean Netherlands. Pages 85-91 in Report of the First Meeting of the CFMC/OSPESCA/WECAFC/CRFM Working Group on Queen Conch, Panama City, Panama, 23–25 October 2012. Food and Agriculture Organization of the United Nations (FAO) Western Central Atlantic Fishery Commission, Rome, Italy.
- van Gennip, S. J., and coauthors. 2017. Going with the flow: The role of ocean circulation in global marine ecosystems under a changing climate. *Global Change Biology* 23(7):2602-2617.
- van Tussenbroek, B. I., and J. K. van Dijk. 2007. Spatial and temporal variability in biomass and production of psammopyhtic *Halimeda incrassata* (Bryopsidales, Chlorophyta) in a Caribbean reef lagoon. *Journal of Phycology* 43:69-77.
- van Tussenbroek, B. I., J. Cortés, R. Collin, A. C. Fonseca, P. M. H. Gayle, H. M. Guzmán, G. E. Jácome, R. Juman, K. H. Koltés, H. A. Oxenford, A. Rodríguez-Ramirez, J. Samper-Villarreal, S. R. Smith, J. J. Tschirky, and E. Weil. 2014. Caribbean-wide, long-term study of seagrass beds reveals local variation, shifts in community structure and occasional collapse. *PLoS ONE* 9(3):e90600.
- Vaz, A. C., M. Karnauskas, C. B. Paris-Limouzy, J. C. Doerr, R. L. Hill, C. Horn, M. H. Miller, M. Neuman, K. J. McCarthy, and N. A. Farmer. 2022. Exploitation drives changes in the population connectivity of queen conch (*Aliger gigas*). *Frontiers in Marine Science* 9:841027.
- Waycott, M., and coauthors. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* 106(30):12377-12381.
- Weil, E. M., and R. G. Laughlin. 1984. Biology, population dynamics, and reproduction of the queen conch *Strombus gigas* Linné in the Archipiélago de Los Roques National Park. *Journal of Shellfish Research* 4(1):45-62.
- Whitall, D. R., and coauthors. 2016. Contaminants in queen conch (*Strombus gigas*) in Vieques, Puerto Rico. *Regional Studies in Marine Science* 5:80-86.
- Wicklund, R. I., L. J. Hepp, and G. A. Wenz. 1991. Preliminary studies on the early life history of the queen conch (*Strombus gigas*) in the Exuma Cays, Bahamas. Pages 283-298 in Proceedings of the 40th Gulf and Caribbean Fisheries Institute, volume 40. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.
- Wilkins, R. M., M. H. Goodwin, and D. M. Reid. 1987. Research applied to conch resource management in St. Kitts/Nevis. Pages 370-375 in Proceedings of the 38th Gulf and Caribbean Fisheries Institute, volume 38. Gulf and Caribbean Fisheries Institute, North Fort Pierce, FL.

- Willette, D. A., and R. F. Ambrose. 2012. Effects of the invasive seagrass *Halophila stipulacea* on the native seagrass, *Syringodium filiforme*, and associated fish and epibiota communities in the Eastern Caribbean. *Aquatic Botany* 103:74-82.
- Willette, D. A., and coauthors. 2014. Continued expansion of the trans-Atlantic invasive marine angiosperm *Halophila stipulacea* in the Eastern Caribbean. *Aquatic Botany* 112:98-102.
- Wood, E. 2010b. Status and management of queen conch in Haiti. Marine Conservation Society, Ross-on-Wye, United Kingdom.
- Wood, K. M. 2010a. Petition to include queen conch (*Strombus gigas*) on the U.S. Endangered Species List. Turks and Caicos Island Government, Department of Environment and Maritime Affairs, Ministry of Environment and Home Affairs, 0648-XB140, Providenciales, Turks and Caicos Islands.
- Wynne, S. P., I. A. Kuramae, and E. M. Boman. 2016. Summary of queen conch (*Lobatus gigas*) research undertaken in Anguilla and the implications for current management practices. *Anguilla Fisheries and Marine Resources Research Bulletin* No 3.
- Zamora-Bustillos, R., R. Rodríguez-Canul, F. J. García de León, and J. Tello Cetina. 2011. Diversidad genética de dos poblaciones del caracol *Strombus gigas* (Gastropoda: Strombidae) en Yucatán, México, con microsatélite. *Revista de Biología Tropical* 59(3):1127-1134.
- Zeller, D., S. Booth, G. Davis, and D. Pauly. 2007. Re-estimation of small-scale fishery catches for U.S. flag-associated island areas in the western Pacific: The last 50 years. *Fishery Bulletin* 105(2):266-277.
- Zeller, D., R. Graham, and S. Harper. 2011. Reconstruction of total marine fisheries catches for Belize, 1950–2008. Pages 142-151 in M. L. D. Palomares, and D. Pauly, editors. *Too Precious to Drill: the Marine Biodiversity of Belize*, Fisheries Centre Research Reports, volume 19. University of British Columbia, Fisheries Centre, Vancouver, B.C., Canada.