

Before Determining the Density Threshold for Queen Conch Reproduction, Define “Density”
Antes de Determinar el Umbral de Densidad para la Reproducción del Caracol Rosado, Defina
"Densidad"

Avant de Déterminer le Seuil de Densité pour la Reproduction du Lambi, Définissez la "Densité"

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ABSTRACT

Queen conch can spawn frequently over the reproductive season. However, this requires some minimum density be maintained to promote both copulation in this slow-moving gastropod and sexual facilitation, wherein frequent sexual contact promotes gametogenesis. Field studies by Stoner and colleagues in The Bahamas found no mating activity below 56 adult conch/ha and no spawning below 48 conch/ha, suggesting a strong Allee effect. However, the interpretation of those figures to other areas are entirely dependent on how density is measured, both with respect to technique and spatial/population scale. Past studies estimated density, variously, over a whole shelf, within a portion of the shelf where conch may occur, within the area where spawning was most likely to occur, or within the core of conch aggregations. Measured baseline densities increase, respectively, across this spectrum. Methods giving localized density estimates best relate density to reproductive activity, but they require a large sample size or targeted allocation, whereas long transects more likely will encounter dense aggregations, but this density is diluted as transects span broad areas without conch. Even the threshold values of the Allee effect may be an artifact of methodology. Failure to appreciate how and over what scale density is measured has led to serious errors in the interpretation and application of Stoner and Ray-Culp’s density-reproduction relationship in population ecology, fisheries biology, regional connectivity, population assessment, and management. Lack of understanding of what constitutes a “spawning aggregation” and its relationship to overall conch population distribution prevents the development of a more generalized theory of conch reproduction versus density that could be applied to assessment and management.

KEYWORDS: Queen conch, Reproduction, Density, Thresholds, Allee effect

INTRODUCTION

The queen conch, *Aliger gigas*, is one of the most valuable and exploited fisheries resources of Caribbean coastal areas. It is widely distributed across Caribbean coastal shelves and occupies a variety of habitats. Intense exploitation led queen conch to be listed in 1992 under Appendix II of the Convention on International Trade in Endangered Species of Flora and Fauna (CITES), which requires documentation that all exports come from sustainable fishing (Theile 2001). More recently, queen conch has been proposed for listing as “Threatened” under the US Endangered Species Act (Horn et al. 2022). As a consequence, efforts to assess and manage conch fisheries have become more critical over time.

One focal point for assessment and management efforts has been the estimation of density as a proxy for stock abundance. Medley (2008) suggested that queen conch can sustain an annual harvest level of 8% of the exploitable stock biomass (but see Ehrhardt 2021), and this can be estimated from density if the size distribution and size-weight conversions are available. Density estimations are particularly valuable when monitoring changes in density over time as an indicator of changes in population size, as long as survey design and methodology are consistent over time (e.g., Friedlander et al. 1994, Singh-Renton et al. 2006, Baker et al. 2016, Doerr and Hill 2018, Ardila et al. 2020, Kong 2021). However, actual density estimations can vary spatially depending on a number of factors. These include those affecting the distribution of conch, such as the extent and geomorphology of the shelf, and the abundance and distribution of habitat types, and those factors related to survey sample design, methodology and spatial scope. These made it difficult to develop an object criteria or reference point based on single measures of density, although relative comparisons could still be informative (e.g., SEDAR 2007).

HABITAT AND DEPTH EFFECTS ON THE DISTRIBUTION OF QUEEN CONCH

Two of the main factors affecting conch distribution, and hence, density are habitat type and depth, with juveniles and adults responding differentially to these. For example, on the western platform of Puerto Rico, juvenile conch were most abundant in areas characterized by seagrass beds of *Thalassia testudinum*, *Syringodium filiforme*, and *Halophila wrightii*, often mixed with benthic macroalgae (Marshak et al. 2006). Within backreef areas along Exuma Sound in the Bahamas, Stoner et al. (1996) found most juvenile nursery areas within medium density beds of *T. testudinum*, but they also found no nursery areas greater than 5 km from the Sound inlet, indicating the significance of current flow for both larval supply and algal growth (food supply) (Jones and Stoner 1997). Movement out of these nursery areas was always away from the vast areas of the Exuma Bank and generally toward deeper water.

Adult queen conch inhabit a wider range of habitats (Torres-Rosado 1987; Stoner et al. 1994, Acosta 2001, Stoner and Davis 2010, Marshak et al. 2006, Boman et al. 2021). While in Puerto Rico adults were also found preferentially in the same habitat types as juveniles, these habitats only covered a combined 16% of the stations sampled on the western platform (Marshak et al. 2006). Adults were also found in areas of coral, coral rubble, and hardbottom – habitats that encompassed 20% of the stations sampled.

Conch are patchily distributed, but the exact causes for this may vary by area. Stoner et al. (1996), above, discussed the factors affecting the distribution of nursery areas along Exuma Sound. For adults, Boman et al. (2021) found a spatial dependence of adult densities on a scale of up to 7 km over the broad area of Saba Bank, which seems similar in scale to the clusters reported by Marshak et al. (2006) across the broad western platform off Puerto Rico. Boman et al. (2021) found spatial dependence at much smaller scales, 1 and 1.5 km, along the narrow shelves of St. Eustatius and Anguilla, respectively. Their results were not related to habitat distribution but may be related to the need for conch to aggregate during the spawning season. Along Exuma Sound in the Bahamas (Stoner and Ray-Culp 2000), the south coast of St John, USVI (Doerr and Hill 2006), and the foreereef of Glovers Reef, Belize (Tewfik et al. 2019), aggregations of breeding adults tend to form in deeper water at the mouth of bays or cuts through the reef.

Generally, queen conch are found most abundantly at depths less than 30 m (Brownell and Stevely 1981, Stoner and Schwarte 1994, Marshak et al. 2006), but this might be related to the general geomorphology of Caribbean shelves, particularly the presence of an abrupt shelf edge, as well as the practical depth limits of scuba-based surveys. Boman et al. (2021) found adult conch on Saba Bank widely distributed down to depths of 50 m, while off the west coast of Puerto Rico both juvenile and adult conch have been documented at mesophotic depths (Garcia-Sais 2012) down to 80 m (Garcia-Sais, ROV video, pers. comm.). The presence of small juveniles (Appeldoorn 1987) and adults with morphologies from shallow adults (Singh-Renton et al. 2006) clearly indicate that larval recruitment can occur over deeper portions of the platform. Interestingly, the conch recorded by Garcia-Sais at 80 m was a juvenile.

There is a general trend of conch densities declining with depth, especially when they tend to disperse from shallower nursery areas across a broad shelf. However, this general trend hides the fact that areas of higher density can be found in deeper water far from shallow areas (Marshak et al. 2006, Garcia-Sais 2012, Kough et al. 2017, Boman et al. 2021, Morris et al. 2023). In particular, Boman et al. (2021) suggested that the deeper aggregations along the western margin of Saba Bank were related to enhanced tidal currents at these locations.

During the reproductive season, conch aggregate in areas of suitable habitat to copulate and spawn. Conch are capable of copulating and spawning many times during the spawning season (Davis et al. 1984, Appeldoorn 2020) producing 10's of millions of eggs. Aggregation formation is critical, as conch reproduction is dependent on maintaining a sufficient density to allow for copulation and potentially sexual facilitation (gametogenic stimulation) during the spawning season (Appeldoorn 1988, 1995, 2020, Stoner and Ray-Culp 2000, Stoner et al. 2012, Delgado and Glazer 2020, Farmer and Doerr 2022). As such, density related to reproduction has become an important focal point for the assessment and management

of conch populations.

The work of Stoner and Ray-Culp (2000) in the Bahamas was, perhaps, the key turning point in this effort. They found that queen conch reproductive activity remained constant (% of adults active) over a broad range of densities but started to drop below densities of 200 adults/ha and reached zero at 56 adults/ha for mating and 48 adults/ha for spawning. These trends were verified in a follow-up study (Stoner et al. 2012). This seemed to provide an objective criterion for assessing conch populations on the bases of density, and many studies adopted such a criterion into assessments or management plans (e.g., Smikle 2010, Cala et al. 2013, Marco et al. 2021, Horn et al. 2022, Vaz et al. 2022, Morris et al. 2023). However, on the one hand Delgado and Glazer (2020) in Florida reported reproductive thresholds of 90 and 204 adults/ha for spawning and mating, respectively, while on the other hand, Baker et al. (2016) reported spawning activity off the west coast of Puerto Rico despite low adult densities in five surveys over a 26-year period, where mean density typically was below 10 adults/ha and the maximum observed never exceeded 56 adults/ha. These seemingly incompatible results point to the main problem in comparing and interpreting density surveys across areas, and that is how density is defined, both spatially and methodologically.

DEFINING DENSITY

Surveys of conch populations among different areas will result in different densities as a function of seascape factors such as habitat and depth distributions, but also in how the surveys are designed and conducted. For example, the study of Delgado and Glazer (2020) had a very narrow spatial focus, targeting sampling within known queen conch aggregations, most of which supported spawning activity. On a slightly larger spatial scale, Stoner and Ray-Culp (2000) concentrated their surveys in areas characterized by a depth range of 10 to 20 m on bare-sand habitat with shallow sand waves (height <10 cm) because past studies revealed that is where maximum reproductive activity occurs, despite adult conch being found from the intertidal zone to >30 m depth. Thus, their surveys cannot be characterized either as being of spawning aggregations or of being broad, cross shelf areas, although perhaps it leans toward the former. More broadly still, surveys on the western platform of Puerto Rico targeted areas previously identified by fishers as areas supporting, either currently or in the past, both juvenile and adult queen conch (Baker et al. 2016). These areas cover the vast proportion of the platform. In this case, then, the surveys are targeting a broad range of the platform (and even the "non-conch strata" is sampled to confirm absence of conch). An extreme example of total shelf coverage is the survey design for conch conducted on Pedro Bank, Jamaica. There, the entire bank is targeted down to 30 m (due to diving limitations), although there is stratification by depth (Morris et al. 2023). A similar example for the Bahamas was the 1980's study by Smith and van Nierop (undated), who surveyed across the broad area of the Great and Little Bahama Banks. In each of these examples, as the area

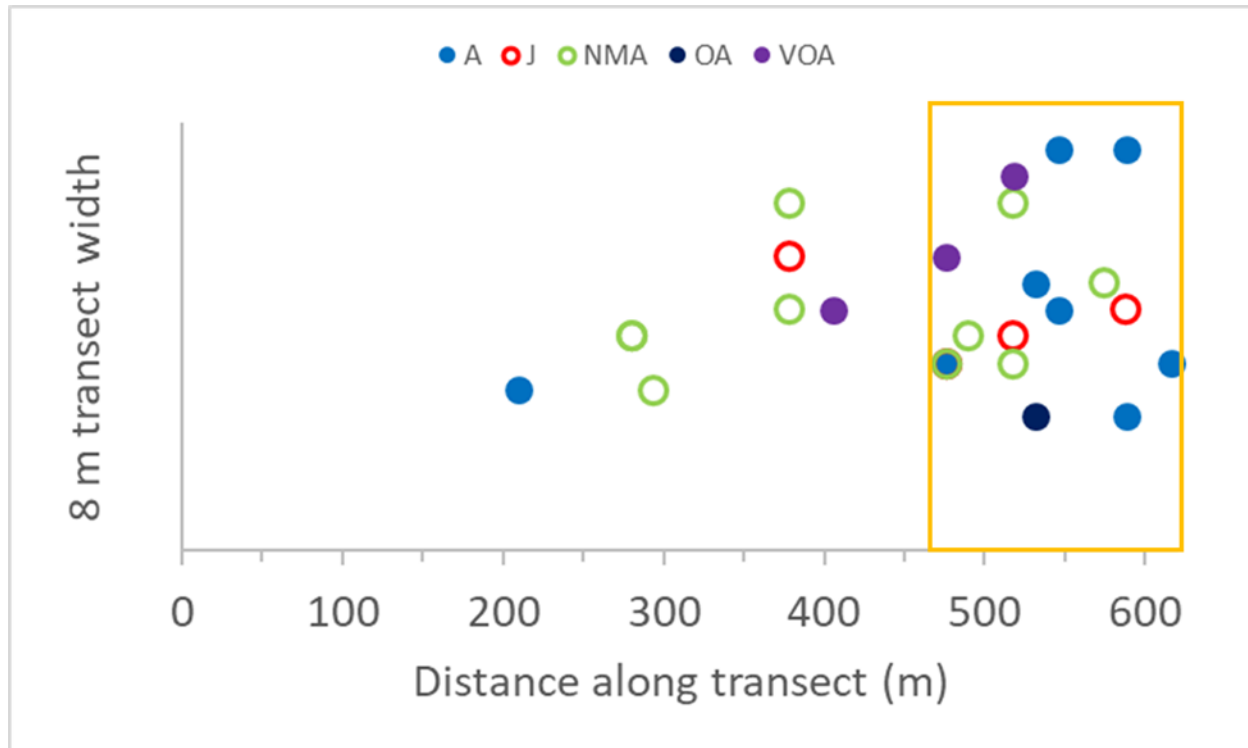


Figure 1. Distribution of conch along one transect off the west coast of Puerto Rico, showing juveniles (red), newly mature adults (NMA) (green), adults (blue), old adults (black) and very old adults (purple). Solid circles represent reproductively mature conch, defined as having a shell lip thickness ≥ 10 mm. Points are randomly distributed along the vertical axes to enhance clarity. Density (conch/ha) for the whole transect is 52.8, that of reproductively mature adults is 24.4, while their density within the orange box is 70.9.

broadens, the expected impact would be to lower average density, assuming other factors are similar, because more area of low or no conch abundance would be included in the samples.

How counts of queen conch are made at survey stations will also affect the estimation of density, and particularly the range and variance of these estimates. Samples from small areas can result in large sample sizes (number of stations) and give a more accurate impression of the magnitude and spatial variation in density, but risk having many stations recording zero conch unless the spatial extent of the surveys are well targeted. Thus, Delgado and Glazer (2020) sampled only up to $5 \times 200 \text{ m}^2$ transects within their aggregations (maximum total = $1,000 \text{ m}^2$). Stoner and Ray-Culp used circles of $1,256 \text{ m}^2$, combining three such circles at each site (total = $3,770 \text{ m}^2$). In their survey across the whole of Saba Bank, Boman et al. (2023) conduct video transects averaging only 525 m^2 , which resulted in 66.8% of stations showing no conch despite a reasonable average density of 125.7 adults/ha. In contrast, surveys done off the west coast of Puerto Rico consist of long, wide transects. In the most recent survey (Baker et al. 2016) the mean transect area was 0.814 ha and ranged from 0.3 ha to 3.93 ha. These large surveys help to minimize the number of stations with zero conch, but they result in a lower sample size ($N = 46$) and reduce the potential for identifying areas with high density because

these are combined along the transect with areas of low density. This is illustrated in Figure 1, which shows the distribution of conch along one transect. In this case, the bulk of the conch, particularly the reproductively mature conch, were found toward the end of the transect. Thus, while the overall density of reproductively mature adults was only 24.4 individuals/ha, well below a supposed threshold of 56/ha, the density within the orange box was 70.9 individuals/ha, which is above that threshold.

Differences in areas surveyed, the distribution of habitat and queen conch within those areas and the methods used to estimate density thus have a profound effect on the results obtained. This seriously questions whether there is any valid density threshold for reproduction that can be applied across areas. Another pertinent question here is: what is a spawning aggregation? Stoner and Sandt (1992) describe one such area at 18-m depth on the Exuma shelf. Here, during the spawning season adults moved between a sandy area, where spawning and copulation occurred, and hard bottom areas where feeding occurred. In contrast, Glazer and Kidney (2004) described a general aggregation of conch within which adults copulated and spawned over a disperse area, i.e., without a well-defined location identified for these activities. While the definition of what constitutes a spawning aggregation and how conch move within this and larger aggregations is beyond the scope of this review, it is clear that more work

needs to be done in this area. Especially important is how various sampling methods interact with aggregation distributions to produce the various density-reproductive activity patterns and thresholds observed (e.g., Stoner and Ray-Culp 2000, Stoner et al. 2012, Delgado and Glazer 2022).

CONSEQUENCES OF MISUNDERSTANDING THE DEFINITION OF DENSITY

Not understanding or appreciating what is being measured (i.e., target area relative to potential conch distribution) when queen conch densities are reported, including the methods used, can lead to dire consequences in the interpretation of results. This is illustrated with a couple of examples. Gascoigne and Lipcius (2004) present a population model showing a per capita reproductive index for conch that declines with increasing density, and then use this model to assess the potential for Allee effects. That model was supposedly developed from the data presented in Stoner and Ray-Culp (2000). However, Stoner and Ray-Culp (2000) focused on what was happening specific to spawning aggregations, not whole populations, and the issues in their study related to what defines a spawning aggregation and, given that slow moving conch must mate in order to copulate, at what densities do conch need to be at in order for that process to occur and be maximized. Importantly, there is no relationship between the density of any given spawning aggregation and population size as a whole. That is, in developing and parameterizing their model, Gascoigne and Lipcius (2024) falsely equated spawning density with population size.

Horn et al. (2022) conducted an in-depth review of conch biology, fisheries and population status that led to the recommendation that queen conch be listed as “threatened” under the US Endangered Species Act. However, a single factor was used most often to assess the risk to extinction, and that is that population densities were too low (i.e., <56 adult conch/ha) in many jurisdictions to support meaningful reproduction. This factor was used in six categories of risk evaluation (Abundance, Productivity, Connectivity, Commercial Fishing, IUU Fishing, and Regulatory Mechanisms). All of these are again subject to the flaw in equating population and spawning density and therefore also subject to the uncertainty inherent in interpreting any density threshold, including the one reported by Stoner and Ray-Culp (2000).

Vaz et al. (2022) developed a region-wide larval connectivity model for queen conch. This model both was incorporated into the Horn et al. (2022) review and assessment and utilized the population model that was developed for that assessment. That population model used whatever data were available to estimate queen conch densities in all jurisdictions throughout the region. Importantly, there was no assessment of what these densities represented relative to spawning. Vaz et al. (2022) interpreted these all as population density without consideration of the factors affecting these estimates. Furthermore, when assessing the implications of these

and past unfished densities on the potential for larval connectivity among regions, they misapplied the threshold of Stoner and Ray-Culp (2000) as also representing a population density. Areas below this density were then treated as not having viable larval production. This is clearly not the case, both because of the misinterpretation of the threshold as representing population density and because locations, e.g., Puerto Rico, with reported low population density may still have active spawning. To their credit, Vas et al. (2022) do test lower and higher densities than reported, thus potentially correcting for this effect using those higher densities. Nevertheless, the initial assumptions reduce the impact of their work to an elegant study of heuristic value, but not one that would have more immediate management inferences or applications.

CONCLUSIONS

Given the importance of reproduction in species conservation in general, and the specific importance of maintaining a density of mature adult conch sufficient to sustain copulation and spawning, it would be desirable to have reliable reference points based on density. However, any such reference points need to be developed using a standardized definition of density, that is, how is density being measured and over what area does it encompass. The studies of Stoner and Ray-Culp (2000), Stoner et al. (2012), and Delgado and Glazer (2022) support the existence of an Allee effect in queen conch, but differ in the threshold density at which this may occur. Yet, because of the specific way in which each study targeted the conch population, these values are not generally comparable or transportable to density estimates from other areas.

While the above thresholds cannot be universally applied in an absolute sense, they can still be useful as general guidelines. For example, in the survey of Saba Bank by Boman et al. (2023), the overall average density was 125.7 adults/ha, which by definition implies that there are a substantial number of sites with much higher densities. Indeed, they reported 22.1% of the sites had densities > 200 adults/ha and 12.2% had densities >300 adults/ha. Similarly, as reported by Stoner and Appeldoorn (2021), in the 2011 survey of Pedro Bank, the average density of reproductive adults was 103 conch/ha, with 37% and 17% of the stations having a density >56 and >200 adults/ha, respectively. Threshold density values can also be used as arbitrary reference points within a management context, although this should be done with caution as these values would be expected to underestimate real density thresholds in broad shelf surveys. For example, for the Pedro Bank fishery Smikle (2010) proposed a harvest control rule with a minimum exploitable density of 70 conch/ha, which was derived from values reported by Stoner and Ray-Culp (2000) but allowed for the fact that part of the exploitable population is still immature. This minimum density was later revised upwards to a more conservative level of 100 conch/ha (Kong 2021).

Table 1. Proposed guidelines for the use of density estimates for assessing population status (from Anon (2023)).

Target	Low Risk	Medium Risk	High Risk
Population Density	Harvestable population density > 100 conch/ha	Harvestable population density < 100 conch/ha but >50 conch/ha	Harvestable population density < 50 conch/ha
Spawning density	Spawning density (i.e., mature adults) > 300 conch/ha	Spawning density < 300 conch/ha but > 185 conch/ha	Spawning density < 185 conch/ha

Despite the caveats associated with the use of density as an assessment parameter, density is routinely estimated from field studies and remains one of the more common factors currently used in a management context. In an attempt to guide agencies in the use of density estimates for assessment purposes, Table 1 presents potential risk levels associated with various ranges of density within an aggregation or across broader areas of the shelf; these were developed within the context of assessing CITES Non Detriment Findings (NDF). Nevertheless, these guidelines still must be interpreted within the context of a specific situation. For example, the densities recorded in surveys in Puerto Rico would suggest the population is at high risk, but this must take into account just how broad an area is surveyed, how long the transects are, or the fact that a viable conch fishery has been maintained for decades despite the relative high risk. Bringing in these factors might suggest the fishery is overfished, but not near an Alee Effect threshold. With respect to spawning density, an important factor is the number of aggregations being surveyed. Fishing can serially deplete spawning aggregations, but if none of these are being surveyed, the results coming from those that are monitored will grossly underestimate the harvest impact. Additionally, conch aggregations may be subject to hyperstability, as has been observed in fish spawning aggregations (Erisman et al. 2011), so spawning density may not be the only relevant indicator, with total number of conch within the aggregation also being important. In summary, the use of density should not be done blindly, but when used it should be done with an abundance of precaution.

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