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The influence of habitat preference on longitudinal population composition and distribution of Groupers (Serranidae) in Chumbe Island Coral Park, Zanzibar, Tanzania

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Abstract

A survey of six common grouper (Serranidae) species was conducted on both the western protected and eastern unprotected reefs around Chumbe Island, Zanzibar. Species, estimated maturity, and habitat were recorded using standardized categories. Fundamental niche and general habitat preference were extrapolated based on observed realized niche and qualified based on substrate, depth, slope position, and general reef region. Taking habitat preference into account, abundance and biomass density of serranid populations were compared between locations on the reef in order to best account for how habitat influences distribution and population health. The results of this study provide depth to previous research on the protected reef and indicate noteworthy shifts in population composition between 2014 and 2018 that favour species with less specified habitat preference, such as *Aethaloperca rogaea* and *Cephalopholis argus*. Surveys of Chumbe's nearby unprotected eastern reef indicate low levels of species abundance, which this study hypothesizes is the result of inappropriate habitat structure, increased fishing pressure, and decreased population health within the MPA. Ultimately, this study suggests that MPAs do not protect all species equally, and habitat preference must be taken into account when assessing MPA effectiveness at protecting different species. Indeed, especially as serranid habitat faces continued degradation, serranid conservation will depend even more on protection of each species' preferred habitat in coral systems. As such, assessing serranid populations as a whole fails to capture the changes in population distribution and composition that is occurring between species, which may be more indicative of shifts and disturbances in the ecosystem.

Keywords: marine protected areas, habitat preference, phase shift, groupers, Chumbe Island, Western Indian Ocean

Introduction

Coral reefs offer many ecosystem services, many of which operate in a synergistic relationship with one another. For example, a reef's capacity to support a biodiverse aquatic community is contingent, in part, on the degree to and manner in which it is fished by coastal communities, and vice versa. In Zanzibar, the rapid growth of coastal populations has resulted in unsustainable exploitation of the productive fishing grounds offered by nearby coral reefs. This overexploitation has not only diminished reef biodiversity, but also sapped these systems of the bountiful fisheries that attracted coastal populations to fish them in the first place.

Coral reefs are sensitive ecosystems, and many of the services they offer and much of the marine life that occupy them are contingent on a high standard of health (Richmond, 2011). Groupers (Serranidae) are apex predators that exhibit strong habitat preferences to structurally complex and healthy reefs and therefore are often regarded as an indicator of overall reef health (Hackradt *et al.*, 2014). The presence of groupers on a reef indicates (1) that the reef is not overexploited, (2) that the coral is healthy and complex, (3) that lower trophic levels are being balanced by natural predation (Hackradt *et al.*, 2014; Kelly and Ruhl, 2011), and (4) that the reef likely supports high abundances and biodiversity of marine life and offers noteworthy, stable

ecosystem services to the surrounding area (Hackradt *et al.*, 2014; Worm *et al.*, 2006). However, serranids are especially vulnerable to overfishing and ecosystem degradation due to their site fidelity and highly specific habitat preferences (Chiappone *et al.*, 2000; Kelly and Ruhl, 2011; Zeller, 1997, 2002); tendency to form spawning aggregates (Sadovy and Coiin, 1995); and long life, slow growth rate, and delayed sexual maturity (Hackradt *et al.*, 2014; Sadovy and Coiin, 1995), all of which result in low resilience to disturbances in population and habitat (Sadovy de Mitcheson *et al.*, 2013).

While the aforementioned qualities situate serranids as an indicator of reef health, in the face of coral degradation due to global climate change and ocean acidification, they also contribute to the vulnerability of Zanzibar's reef dwelling serranid populations. Additionally, in a burgeoning tourist economy like that of Zanzibar, groupers often generate a high market price, and their populations have suffered as a result. Moreover, in a reality in which comprehensive studies of grouper spawning aggregations, larval export, and population dynamics are lacking worldwide, longitudinal research into the persistence of grouper populations in the western Indian Ocean has fallen relatively by the wayside. While these factors contribute to groupers' vulnerability, they also render groupers an ideal case study for comprehensively assessing the effectiveness of Chumbe Island Coral Park Limited (CHICOP) at protecting serranids and restoring reef biodiversity, as well as promoting spillover and restoring fisheries in neighboring unprotected areas.

In order to best account for the rapid changes occurring on coral reefs in the face of climate change, this study aims to identify habitat preferences of six common species of grouper in order to inform best management strategies in the face of external pressures that cannot be eliminated by the boundaries of a no-take area (NTA). Habitat health and type have been shown to significantly influence not only the distribution, but also abundance and biomass of groupers (Hackradt *et al.*, 2014). Thus, defining the habitat preferences of these apex predators is of the utmost importance in order to appropriately attune management strategies in response to environmental change and to best ensure continued conservation of serranids under present and future threats (Berger and Possingham, 2008; Friedlander *et al.*, 2003). Comparisons between fundamental niche, or the habitat that a species is expected to occupy based on known preferences, and realized niche, the habitat that a species

actually occupies within CHICOP, serve as a foundation for discussion of the variables at play that might cause these two areas to be different, and an assessment of overall reef health (Buxton *et al.*, 2014). Accurate definitions of a species' fundamental niche allow for efficient and effective conservation of their habitat, if the population of that species is found to be in decline. Likewise, by methodically observing changes in a species realized range, one is able to extrapolate changes in overall ecosystem and reef health and better understand phenomena such as regime shifts and spillover effect (Rowly, 1994). Thus, a sound understanding of the relationship between a species and the habitat it occupies is foundational to their effective and long-term conservation.

CHICOP is a privately-owned marine protected area (MPA) off the western coast of central Unguja, Zanzibar, safeguarding ecological ecosystem services offered by coral reefs, which include buffering coastlines from wave action, sequestering carbon dioxide, and supporting the biodiversity of marine species that depend upon them (Richmond, 2011). Indeed, even small scale MPAs like CHICOP have been shown to consistently support higher abundance, biodiversity, and biomass of groupers and other predatory and commercially fished species than surrounding unprotected areas (Edgar *et al.*, 2014; Fenberg *et al.*, 2012; Hackradt *et al.*, 2014). In order to better understand the effectiveness of CHICOP in adequately meeting the needs of the reef – both in terms of ecological health and the aesthetics necessary to generate income from tourism to fuel management and research - and those of local fishermen, this study aimed to systematically assess serranid populations on the protected and unprotected areas and serves as an initial foray into a study of localized population dynamics around Chumbe Island (Francis *et al.*, 2002).

This report uses data gathered by Catherine Nesbitt in 2014 to compare population composition and biodiversity before and after a significant disturbance in coral reef health (2016 mass coral bleaching event). Nesbitt's study contextualizes the findings of this study and provides a basis for predicting the system's response to future threats. It is important to consider that this study draws its analytical power from the fact that it takes each species' habitat appropriateness into account when considering its respective abundance and biomass density. Moreover, focused investigation into realized niche offers amendment to current understanding of each species' fundamental

niche. Overall health of the reef is measured based on the abundance of groupers it currently supports and both the quality and type of habitat they occupy. By conducting research within an NTA that adheres to four out of the five features shown by Edgar *et al.* (2014) to exponentially benefit conservation suc-

study intends to lay a foundation for continued monitoring and research on population dynamics on and between protected and unprotected reefs and to generate an understanding of how grouper habitat might be better managed to maximize the benefit to reef health and local fishers.



Figure 1. Map of Chumbe Island in relation to Zanzibar and mainland Africa (adapted from Nesbitt and Richmond 2015).

cess (no-take, effective enforcement, isolation by deep water or sand, and more than 10 years of existence), changes in serranid populations may largely be attributed to the anthropogenic degradation of coral reefs via sea level and temperature rise, which unfortunately cannot be kept at bay by the boundaries of an MPA (Edgar *et al.*, 2014). Ultimately, this

Materials and methods

Study Site

Chumbe Island is located 6 km off the western coast of Zanzibar and 33 km off the eastern coast of Tanzania in the Zanzibar Channel. It measures a maximum of 1 km running north to south and is characterized by a fringing coral reefs on both sides.

Table 1. Description of focus species and respective fundamental niche (Debelius, 1999; Hiatt and Strasburg, 1960; Lieske and Myers, 1996; Kelly and Ruhl, 2011; Nesbit, 2014; Nesbit and Richmond, 2015; Unsworth *et al.*, 2007, IUCN.org).

Species	Description	Distinction of Maturity	Substrate	Depth	Reef Slope	IUCN Status	Notes
<i>Aethaloperca rogae</i> (Redmouth Grouper)	Dark body, red inside mouth; juveniles distinguished by white margin at end of tail and variable white bar on side	Reaches 34 cm Maximum length: 60 cm	Sparse coral Deep coral Deep sand	1 – 54 m	On and around reef slope and backreef	Data Deficient (Unknown trend)	Uncommon; not caught by fishermen; wide range
<i>Anyperodon leucogrammicus</i> (Slender Grouper)	Elongated body with flat, long snout and round tailfin; pink-brown with pale stripes; juveniles distinguished by white and yellow stripes	Reaches 30 cm and/or Color change Maximum length: 65 cm	Sparse coral Dense coral	1 – 50 m	Top of reef slope and backreef	Least Concern (Unknown trend)	Associates with table corals in shallow reefs; uncommon with generally low abundance
<i>Cephalopholis argus</i> (Peacock Grouper)	Dark brown or red with blue rimmed black spot and lighter bands toward tail	Reaches 22 cm Maximum length: 60 cm	Dense coral Deep sand	< 6 m	On and around reef slope	Least Concern (Stable)	Common on coral reefs
<i>Cephalopholis miniata</i> (Coral Grouper)	Orange-red body with small, blue spots with brown borders; juveniles distinguished by orange coloration with widely scattered blue spots	Reaches 26 cm Maximum length: 50 cm	Dense coral Deep sand	4 – 150 m	On and around reef slope; concentrated where steepest	Least Concern (Decreasing)	Common; caught in artisanal fisheries
<i>Epinephelus fuscoguttatus</i> (Brown Marbled Grouper)	Dark brown with light brown mottling	Reaches 50 cm Maximum length: 120 cm	Dense coral Deep sand	1 – 60 m	On and around reef slope	Near Threatened (Unknown trend)	Uncommon and wary; caught in artisanal fisheries
<i>Plectropomus laevis</i> (Black Saddled Grouper)	Red-brown, dark spots and white belly; five light bands on back and flanks; juveniles distinguished by yellow fins and five black bands across back	Color change Maximum length: 125 cm	Sparse coral Dense coral Deep sand	4 – 90 m	Bottom of reef slope	Vulnerable (Decreasing)	Strong habitat preference; wary

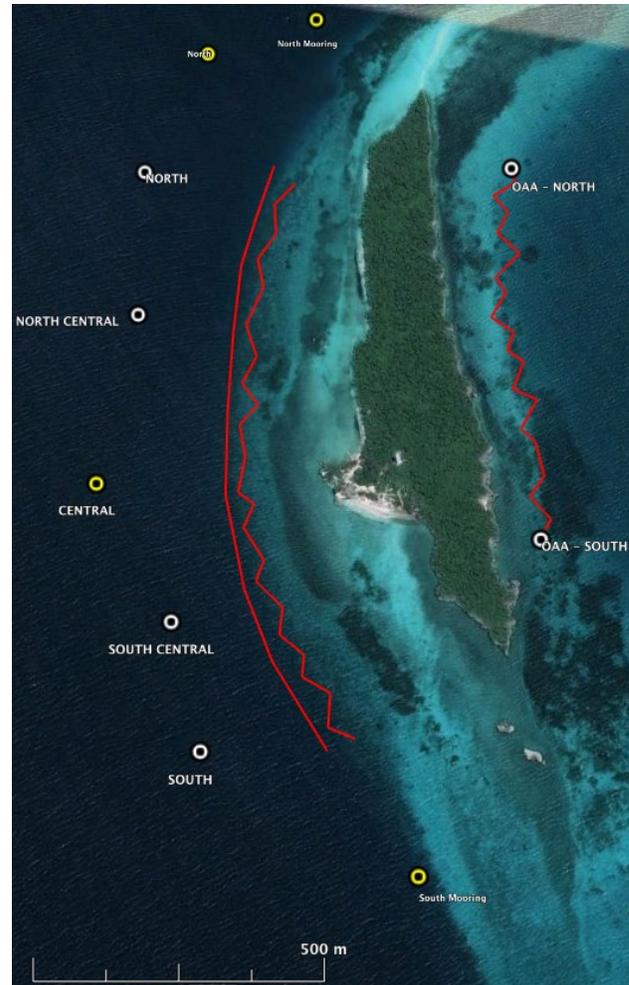
In accordance to Tanzania's commitment to protect 10 % of its marine ecosystems by 2012, Chumbe Island Coral Park Limited - which includes mangrove forests and other terrestrial ecosystems, as well as 55 hectares of the western fringing reef and associated backreef, seagrass beds, and coast – was established in 1994 by the semi-autonomous government of Zanzibar (Nordlund *et al.*, 2012). Chumbe's western fringing reef and abutting backreef and seagrass beds fall within the NTA, providing extensive research opportunities and vigilant protection by CHICOP. Even before the Park's inception in 2006, the western fringing reef supported a grouper population that was 300 % larger than that of the eastern unprotected reef (CHICOP, 2017). Chumbe's unprotected eastern fringing reef, however, has no protection, and, as a result, is vulnerable to over-exploitive and sometimes destructive fishing practices.

Focus Species

Table 1 includes brief descriptions of the six serranid species included in this study. These species are informally regarded as the most commonly observed within CHICOP. Fundamental niche and general habitat preference are informed both by external species profiles and Nesbitt's survey of these same species in the MPA in 2014, thereby attuning the descriptions to the populations specific to Chumbe's western reef. Other species were observed within the MPA, but were not included in this survey for the sake of continuity between this and Nesbitt's study. An understanding of general fundamental niche contextualizes and corroborates the validity of the realized niches of each species observed in this study.

Survey Methods

Visual under-water censuses were conducted on both the slope and backreef of the western no-take zone and the reef of the eastern open access area on either side of Chumbe Island, Zanzibar during the month of November 2018. The western reef was surveyed within the MPA between points at which coral becomes notably sparse and the slope disappears. Start and end locations in the southern- and northern-most reaches of the MPA were replicated relative to landmarks on the island and were approximated at 6°17.096'S, 39°10.571'E and 6°16.509'S, 39°10.483'E, respectively. Both the slope and the backreef were surveyed between these two points from south to north within prescribed zones approximated by visual landmarks on the island (Fig. 2). The slope was surveyed linearly from south to north, thereby



	Zone	Latitude	Longitude
MPA	NORTH	6° 16.509'S	39° 10.483'E
	NORTH CENTRAL	6° 16.664'S	39° 10.453'E
	CENTRAL	6° 16.837'S	39° 10.456'E
	SOUTH CENTRAL	6° 16.971'S	39° 10.494'E
	SOUTH	6° 17.096'S	39° 10.571'E
OAA	NORTH	6° 16.505'S	39° 10.730'E
	SOUTH	6° 16.892'S	39° 10.771'E

Figure 2. Map of Chumbe Island and estimated transects and zones. Red lines represent estimated transects. Yellow markers indicate buoys present at time of survey, white markers indicate imaginary points of differentiation. Capitalized labels indicate differentiation between zones, estimated latitude and longitude included in above table. Estimations of area surveyed were calculated based on these coordinates.

representing an informal transect. The reef slope was defined as the area of steepest bathymetric decline between dense coral and deep sand and was characterized by dense coral cover. The backreef was surveyed in a serpentine swim parallel to the slope at a minimum perpendicular distance of approximately 10 m (English *et al.*, 1997). Backreef was defined as the

area adjacent to the slope with no significant incline and was characterized by sparse to dense coral cover. The eastern reef was surveyed north to south in a serpentine swim parallel to Chumbe's coast and the area surveyed was bounded by landmarks on the island that corresponded to where coral begins and ends at the northern and southern ends of the informal transect, and were approximated at 6°16.505'S, 39°10.730'E and 6°16.892'S, 39°10.771'E, respectively. The western slope and backreef (hitherto, in addition to the east reef, referred to as 'regions') were divided into four 'zones' (north, north central, south central, and south) according to landmarks in order to compare serranid populations between eight distinct 'locations' (e.g. south central backreef). Southern zones were surveyed at low to mid tide, northern zones were surveyed at mid to high tide, and the eastern reef was surveyed exclusively at low tide.

Differentiation of 'zones' is explained in greater detail in Fig. 2. Yellow markers represent physical buoys that were present at the time of survey, and white markers represent markers that were approximated based on position relative to specified on-land markers. Markers with capitalized labels indicate differentiations between zones. The red lines represent approximate transects, the straight line represents slope surveys while the serpentine lines represent backreef swims.

The entire slope, backreef, and eastern slope were surveyed a total of three times, and the north and south-central zones were surveyed an additional three and two times respectively due to the importance of slope to serranid habitat. All individuals within 5 m of either side of the transect were included in the survey. Species and estimated length and/or maturity for each individual as well as habitat parameters such as depth, substrate, position on slope, and general notes for each sighting were recorded using a waterproof audio recorder attached to a floating ring. In addition to the time at which each species was sighted, time at which each zone was entered and exited, region surveyed, tide, and ambient weather conditions were recorded. Maturity was determined post-survey based on the information in Fig. 1, unless species maturity is indicated by color change (e.g. *Plectropomus laevis*), in which case it was determined in-field (Debelius, 1999; Nesbitt, 2014).

Results

Population distribution, composition, and diversity

A total of 362 individuals were observed around Chumbe Island, the majority of which were recorded within the MPA. Nearly twice as many individuals were observed on the slope compared to the backreef. There were 700 % more individuals on the protected backreef than the unprotected eastern reef, and the protected backreef supported a biomass density of 93.43 kg/ha compared to the eastern reef's 2.3 kg/ha (Table 3). Across all study locations, *Aethaloperca rogae* dominated the population and was observed more frequently than *Plectropomus laevis*, *Epinephelus fuscoguttatus*, *Cephalopholis miniata*, and *Anyperodon leucogrammicus* (Kruskal-Wallis, Dunn posthoc, $p < 0.0001$ for all species). There was no statistically significant difference observed between populations of *A. rogae* and *C. argus*, though *C. argus* was also observed more frequently than the aforementioned four species (Kruskal-Wallis, Dunn posthoc, $p = 0.0013$, $p = 0.0005$, $p = 0.0008$, $p = 0.0013$, respectively). *A. rogae* also exhibited a total biomass that is significantly higher than all study species except *C. argus* (Kruskal-Wallis, Dunn posthoc, $p = 0.0026$, $p = 0.0192$, $p = 0.0003$, $p = 0.0009$, respectively). Similar to abundance, no statistically significant difference in biomass between *A. rogae* and *C. argus* was observed, and the population biomass of *C. argus* was significantly higher than that of *P. laevis*, *C. miniata*, and *A. leucogrammicus* (Kruskal-Wallis, Dunn posthoc, $p = 0.0247$, $p = 0.0052$, $p = 0.0115$, respectively). Slope and backreef regions were dominated by *A. rogae*, both in relative species abundance and biomass density (Tables 2 and 3). *A. rogae* was only exceeded in biomass density in the north slope by *E. fuscoguttatus* (Fig. 4). With a relative abundance that was still less than half that of *A. rogae*, *C. argus* was observed to have the second highest relative abundance in both protected regions, and like *A. rogae*, its biomass density also fell behind that of *E. fuscoguttatus* (Fig. 4). The relative abundance and biomass density of *C. argus* remained relatively constant across locations, whereas both relative abundance and biomass density for populations of *A. rogae* spike in central sloping regions (Fig. 3 and 4). High relative abundances and biomass densities were shown on both central slopes across all species (Fig. 3 and 4). In keeping with their distribution within the population and across regions, relative species abundances of *P. laevis*, *E. fuscoguttatus*, *C. miniata*, and *A. leucogrammicus* were consistently lower than those of *A. rogae* and *C. argus*.

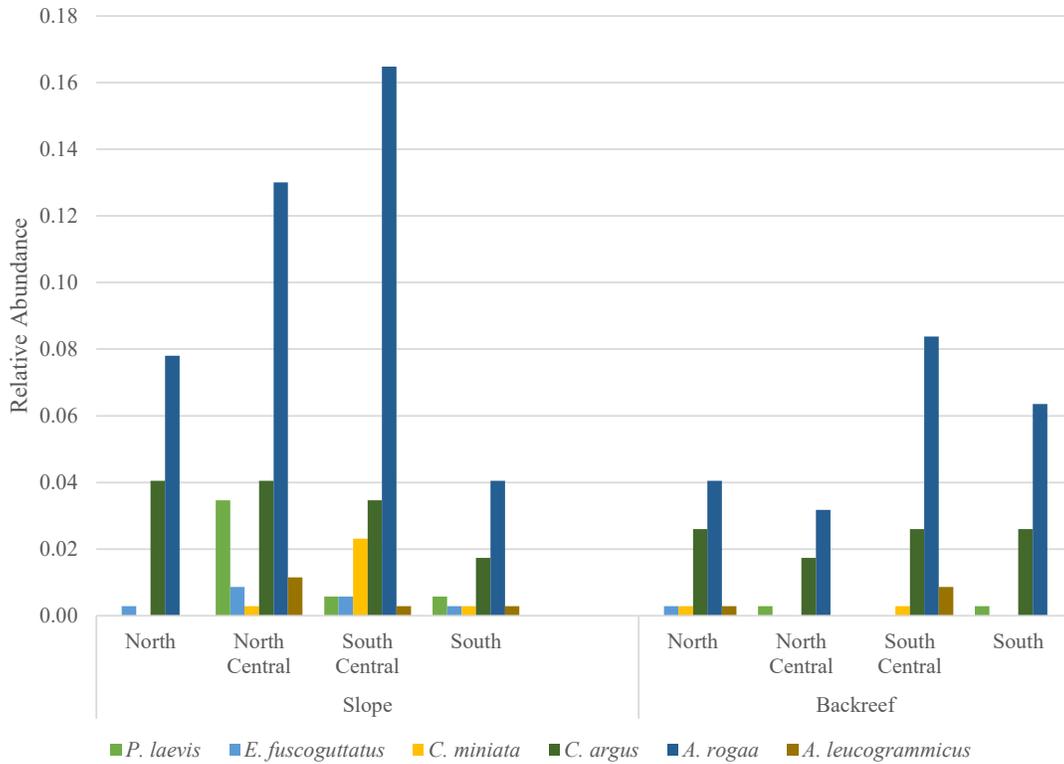


Figure 3. Total species abundance and relative abundance of six focus Serranidae species between regions and locations in Chumbe Island’s MPA. Table 3a. Relative species abundance calculated between regions out of region total population counts. East reef not included in “TOTAL” MPA species abundance and relative species abundance. Figure 3b. Relative species abundance calculated between ‘locations’ out of total reef population count. East reef not included.

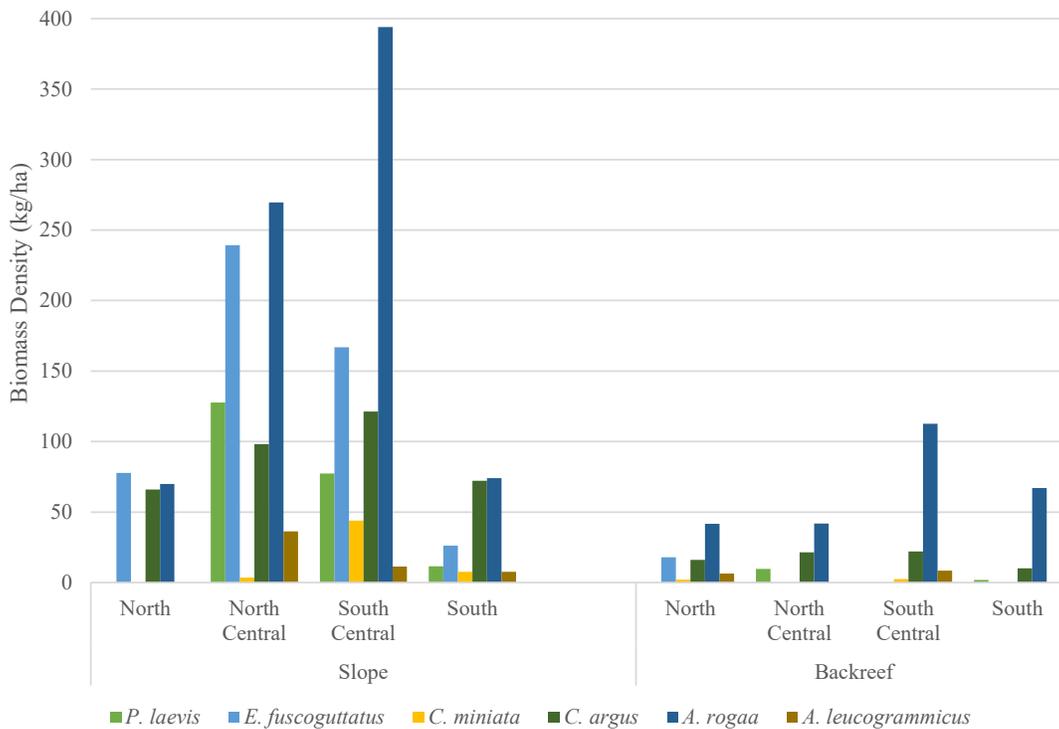


Figure 4. Total biomass density (kg/ha) of six focus Serranidae species between regions and locations in Chumbe Island’s MPA. Total hectares surveyed estimated by multiplying total transect length for each region by perpendicular width of area surveyed. Individual fish masses calculated according to length-weight relationships offered in “Biomass Calculator” Excel sheet available at Chumbe Office, Stonetown, Zanzibar. Table 3. Species biomass density calculated between regions out of total region hectareage. East reef not included in “TOTAL” MPA biomass density. Figure 4b. Species biomass density calculated between ‘locations’ out of total reef hectareage.

Table 2.

Total Abundance (Relative Abundance)				
	Slope	Backreef	Total	East Reef
<i>P. laevis</i>	16 (0.07)	2 (0.02)	18 (0.05)	0 (0)
<i>E. fuscoguttatus</i>	7 (0.03)	1 (0.01)	8 (0.02)	0 (0)
<i>C. miniata</i>	10 (0.04)	2(0.02)	12 (0.03)	1 (0.06)
<i>C. argus</i>	46 (0.20)	33 (0.28)	79 (0.23)	13 (0.81)
<i>A. rogae</i>	143 (0.63)	76 (0.63)	219 (0.63)	1 (0.06)
<i>A. leucogrammicus</i>	6 (0.03)	4 (0.03)	10 (0.03)	1 (0.06)
Total	228	118	346	16

Table 3.

Biomass Density (kg/ha)				
	Slope	Backreef	Total	East Reef
<i>P. laevis</i>	54.09	3.17	27.29	0.00
<i>E. fuscoguttatus</i>	128.01	4.68	63.10	0.00
<i>C. miniata</i>	12.57	1.10	6.55	0.05
<i>C. argus</i>	88.38	17.51	51.83	1.94
<i>A. rogae</i>	196.18	63.42	126.37	0.17
<i>A. leucogrammicus</i>	14.09	3.54	8.59	0.14
Total	493.31	93.43	283.74	2.30

Reef slope exhibited higher diversity than the backreef within the MPA, except in the northern zone (Table 4). The north central zones exhibited the highest diversity and the other three zones displayed diversity comparable to one another. In terms of both the Shannon-Weiner Index and general species richness, the lowest diversity occurred in the southern

backreef and northern slope. Diversity in the eastern open access area (OAA) was comparable to the southern backreef and northern slope, despite the fact that the total abundance and biomass density of the eastern reef were lower than these two locations. Overall, the western MPA exhibited a Shannon-Weiner Index of 1.09 and a species richness of 6.

Table 4. Shannon-Wiener Index of diversity and (species richness) by location on both protected and unprotected reefs around Chumbe Island.

MPA - West Reef	North	N. Central	S. Central	South	
Backreef	1.08 (5)	0.83 (3)	0.86 (4)	0.72 (3)	0.93 (6)
Slope	0.65 (3)	1.24 (6)	1.00 (6)	1.26 (6)	1.14 (6)
	0.90 (4)	1.20 (6)	0.99 (6)	1.01 (6)	
OAA - East Reef	0.69 (4)				

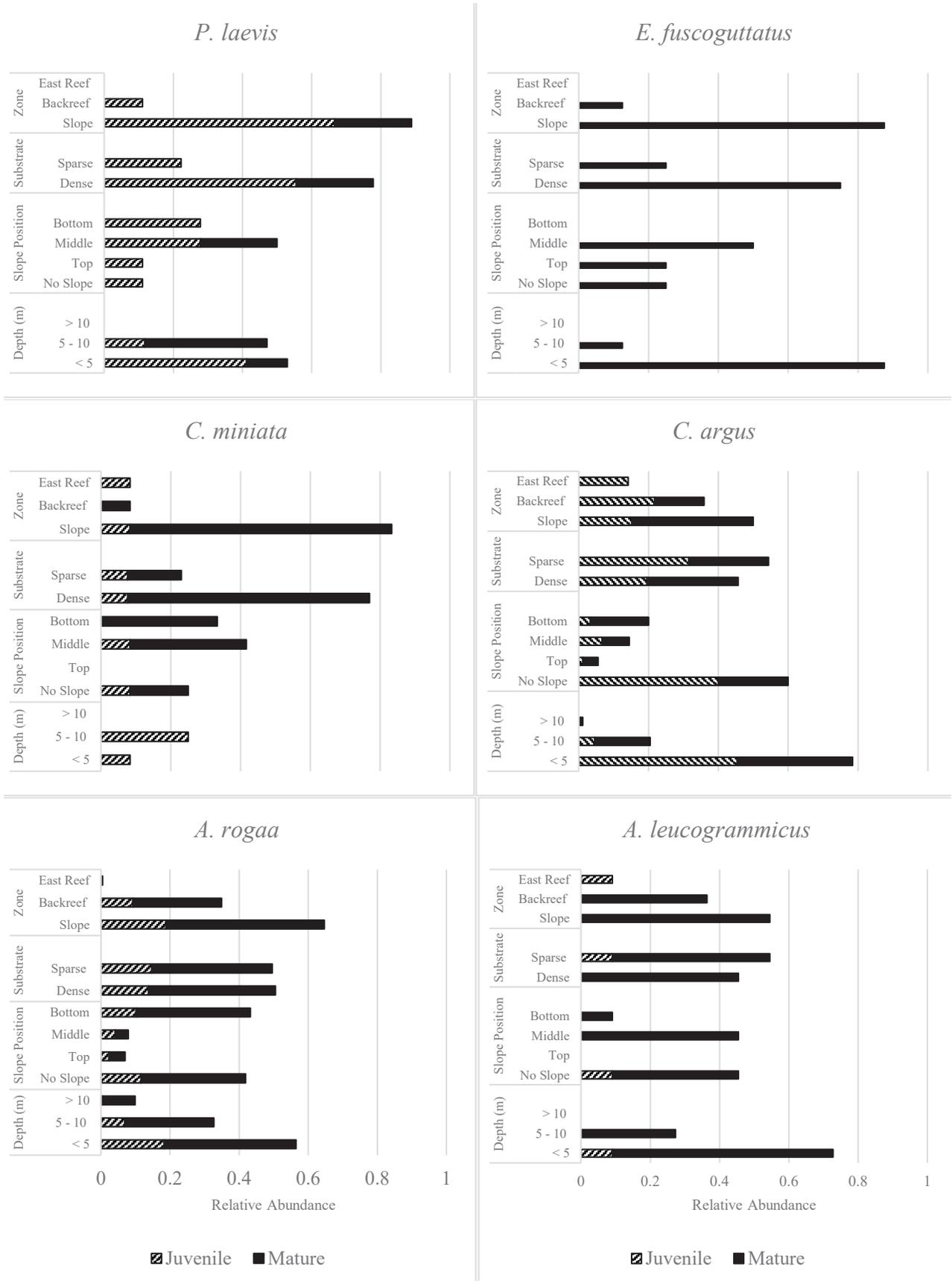


Figure 5. Habitat preferences of juvenile and mature individuals of each species according to the relative abundance of each age class observed in each qualifier. X-axis represents abundance relative to total population count on both the western and eastern reef. Distinctions between juvenile and mature individuals made according to parameters listed in Figure 1.

Habitat Preference

Significant relationships between maturity and habitat preference existed in *C. argus* and *A. rogaea*. There was a significant relationship between maturity of *A. rogaea* and slope and depth (Chi Squared Test, $p < 0.001$ and $p < 0.001$, respectively). Mature individuals favoured the bottom of the reef slope, and juvenile individuals favoured the middle of slope. Juvenile individuals were observed more frequently at depths of less than 5 meters, while mature individuals were observed most often at depths between 5 to 10 meters. There was also a significant relationship between maturity of *C. argus* and depth and slope, as well as region observed (Chi Squared, $p = 0.021$, $p < 0.001$, $p = 0.001$, respectively). Both mature individuals favoured non-sloping environments and the bottom of slopes, and juvenile individuals exhibited a strong preference to non-sloping environments. Both juveniles and mature individuals were observed more frequently at depths between 5 to 10 meters. Juvenile *C. argus* exhibited a preference to reef slopes, while mature individuals preferred backreef environments. No significant relationship between age and substrate existed for either *A. rogaea* or *C. argus* (Fig. 5).

C. argus and *A. leucogrammicus* were present in almost equal relative abundance in the slope and non-sloping environments. Only *A. rogaea* and *C. miniata* were observed at depths greater than 10 meters, and these two species were observed in all habitat categories. Out of all focus species, *A. rogaea* exhibited the largest relative abundance at depths greater than 10 meters

(Fig. 5). *P. laevis* was observed in all habitats except at depths greater than 10 meters and on the OAA eastern reef. *A. rogaea* and *C. argus* were observed in all habitat categories. *E. fuscoguttatus* was not observed in 3 habitat categories, with no sightings on the eastern backreef, at depths greater than 10 meters, and at the bottom of the reef slope.

Age Distribution

Very few mature *P. laevis* and very few juvenile *A. leucogrammicus* and *C. miniata* were recorded, and no juvenile *E. fuscoguttatus* were observed (Fig. 6). This small sample size renders it difficult to determine whether differences in habitat preference exist between age groups in these species. Comparatively, populations of *A. rogaea* and *C. argus* were more evenly distributed across maturities, and juvenile habitat preference mirrored that of the adult individuals. More juvenile *P. laevis* were observed than mature individuals, which is an age distribution unique to this species.

Abundance, biomass, and biodiversity between 2014 and 2018

A comparison between 2014 and 2018 survey data indicated a change in population composition over the four years. Relative species abundance decreased for all species, except *A. rogaea*, which exhibited an almost 100 % increase in relative abundance between 2014 and 2018 (Fig. 6). In conjunction with a spike in relative abundance, biomass of *A. rogaea* increased as well. Relative abundance of *C. miniata*, *A. leucogrammicus*, and *E. fuscoguttatus* all decreased minimally and

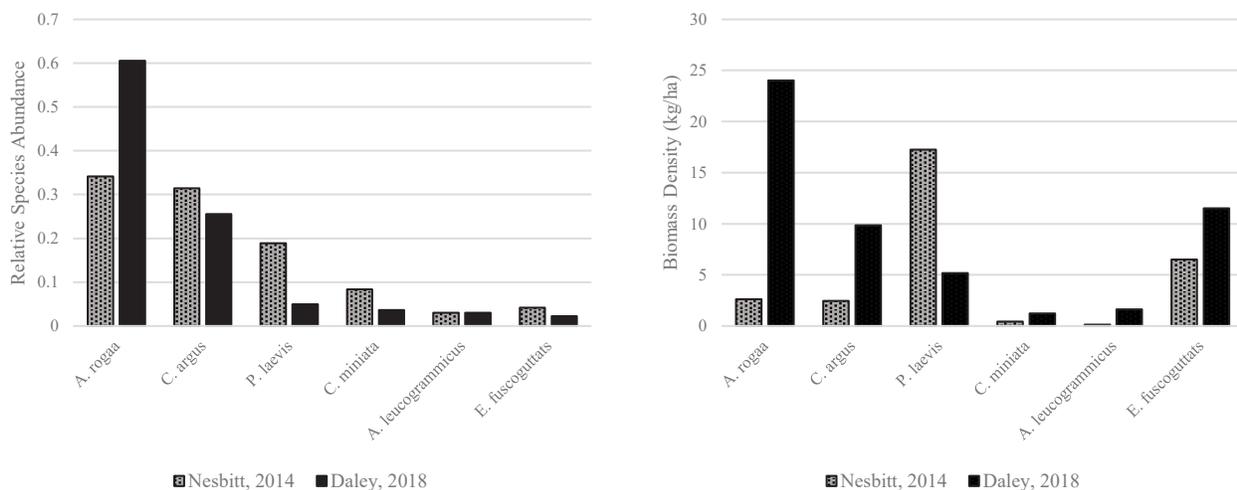


Figure 6. Comparison of relative species abundance and biomass density between serranid surveys conducted in 2014 and 2018 around Chumbe Island. Biomass density calculated over 12.5 hectares of coral reef within the NTA. The 2014 biomass calculated based on averaged weight categories.

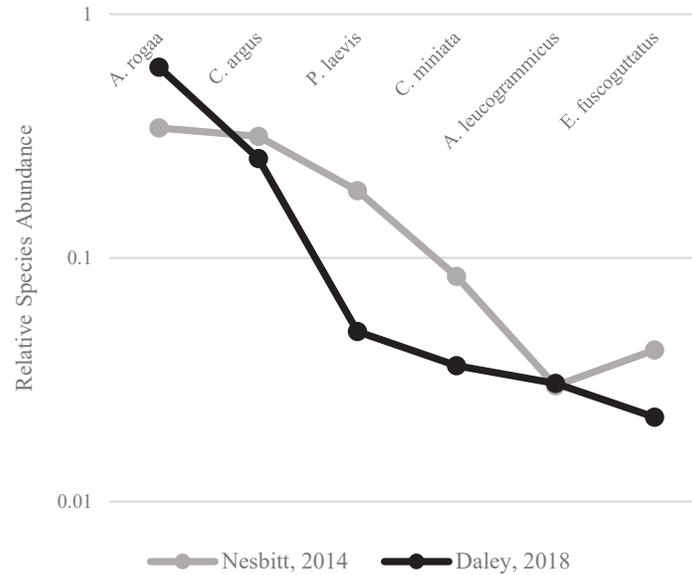


Figure 7. Comparison of average biomass per individual (kg) within the MPA between CHICOP's general long-term monitoring programme and Nesbitt's (2014) and Daley's (2018) focused surveys.

stayed below 0.1, but biomass density of all three species increased since 2014. *C. argus* experienced minimal decreases in relative abundance and an increase in biomass.

There was a 75 % decline in the already relatively low abundance of *P. laevis*, and a 66 % decline in biomass density (Fig. 7). These shifts in abundance are reflected in the decrease in serranid biodiversity from 1.49 in 2014 to 1.09 in 2018. All species except *A. rogea* experienced a decrease in relative abundance, and therefore the population experienced losses in both evenness and biodiversity. Though all species were represented in both years, this decrease in evenness is corroborated by the steep and concave appearance of the Whittaker plot in 2018 compared to the 2014 trendline (Fig. 7).

Discussion

Population distribution and composition

All six species exhibited lower abundance on the backreef than the slope, and a lower abundance and biomass density on the OAA than the protected backreef. This phenomenon was also observed by Nesbitt (2014) and suggests that most serranid species prefer deeper reef slopes to shallower, non-sloping environments (Chiappone *et al.*, 2000; Nesbitt and Richmond, 2015). Relative abundance and biomass density were generally higher for all species on the north and south central slopes, indicating that the continuity and complex reef structure of the central slopes attracted more and larger individuals than other

locations (García-Charton *et al.*, 2001). This pattern was not reflected in the central backreef locations. This is potentially due to the fact that while the central slopes are differentiated from the northern and southern slopes by steeper slope and higher structural complexity, there is less preference given to location on the more structurally homogeneous backreef.

A. rogea dominated the serranid population both in terms of abundance and biomass density, exhibiting significantly higher abundance and biomass density than all species except *C. argus*. The high biomass density of these two species is especially noteworthy considering *A. rogea* and *C. argus* share the second smallest maximum length (60cm) of the six focus species. *A. rogea* had the highest relative species abundance across all locations, with noteworthy increases on the central sloping locations. This increase in relative abundance suggests that while *A. rogea* thrives in a variety of habitat types, like all species observed, it prefers deeper sloping reefs. Thus, the fact that the biomass of *A. rogea* exceeded that of both *P. laevis* and *E. fuscoguttatus* (except on the northern slope) despite its relatively small maximum length speaks to the scale of its relative abundance (63 %) across all eight locations. Unlike many serranid species, *A. rogea* is known to have a wide fundamental niche and low site fidelity. Therefore, it is not surprising that a species with less distinct habitat preference dominates Chumbe's MPA and was most frequently observed pelagically on deep reef slopes.

C. argus exhibited the second highest abundance, with a more consistent relative abundance and biomass across locations. The biomass density of *C. argus* was surprisingly high given its small maximum length, which is likely attributable to the fact that its relative abundance is consistently second to that of *A. rogaea*. The low abundances and biomass densities of *E. fuscoguttatus*, *P. laevis*, *C. miniata*, and *A. leucogrammicus* reflect a patchy distribution and highly specified fundamental niche that was likely not adequately assessed by the survey methods employed by this study (Unsworth *et al.*, 2007). Despite this, potentially due to its large maximum size, *E. fuscoguttatus* surpassed *A. rogaea* in biomass density, but not relative abundance on the north slope. *E. fuscoguttatus* and *P. laevis* exhibited specific preference to the central slope, and *E. fuscoguttatus* displayed particular preference to the north central slope where coral begins to become sparse (Nesbitt, 2015).

Serranid diversity

A. rogaea dominated both Chumbe's western backreef and slope, and, as a result, the distribution of these six species was not even, which is attributable overwhelmingly to the fact that small MPAs do not protect all species equally. Although Chumbe meets four of the five qualifications for successful conservation via an MPA as listed by Edgar *et al.* (2014), it does not meet the minimum size (100 km²) cited to maximize marine park benefits. Small NTAs fail to adequately protect large serranid species and species that participate in spawning aggregations (Unsworth *et al.*, 2007). Moreover, small NTAs render rare species with specific habitat preferences especially vulnerable to density dependent intra and interspecific competition compared to more robust species that are able to thrive in more than one habitat or microhabitat (Donaldson, 2002).

As a region, the backreef supported a lower level of diversity than the slope. This finding was congruent with the decreased biomass density and relative abundance of all species in that region. The northern zone was the only zone in which the diversity of the slope exceeded that of the backreef. This discrepancy was likely due to the fact that the northern backreef extends further north than the slope, thereby providing a larger area of potential habitat. The central zones of each region exhibited higher levels of diversity according to the Shannon-Wiener Index than adjacent locations in the same region, which substantiates the hypothesis that all six *Serranid* species favor the complex central slope (García-Charton *et al.*, 2001).

Habitat preference and age distribution

The abundance of *A. rogaea* in all locations implies a broad fundamental niche (Nesbitt, 2015). The distribution of *A. rogaea* and *C. argus* revealed specific habitat preferences between species. While *A. rogaea* was observed in all habitat categories, the species indicated preference to the bottom of the slope and non-sloping environments and depths between 0 and 9 m. These preferences reflect a unique willingness to venture away from the structure of continuous reef, and *A. rogaea* was frequently observed swimming pelagically more than 10 m away from reef slope structure. Juveniles were observed in all habitat categories (except at depths greater than 10 m) in relative abundance proportionate to the mature population, indicating that the reef within the NTA was suitable to this species at all life stages and that the age distribution of this species was healthy.

The only other species that exhibited a healthy age distribution is *C. argus*, though there was a more distinct difference in preferred habitat between juvenile and mature individuals. Juvenile *C. argus* were more frequently observed on the backreef, non-sloping environments and mid reef slope. This population's apparent lack of preference for substrate and region and noticeable preference to depths less than 10 m allows it to exhibit high abundance and biomass density within the MPA, which is characterized by a dense reef slope and a sparse, shallow backreef.

P. laevis, *E. fuscoguttatus*, and *C. miniata* displayed high relative abundances on the slope and areas of dense coral cover, corroborating Nesbitt's observations that their habitat and range are limited and specific (Nesbitt, 2015). Their preference for these qualities explains the spike in relative abundance and biomass density in central sloping regions and on the slope in general. Indeed, the central slopes possess increased coral complexity and density as well as a wealth of vertical niches not offered by more shallow and non-sloping locations. This richness and variety predispose the north and south-central slopes to support higher abundances and biodiversity, and the presence of species with more specific niches in these regions reflects their complexity and health (García-Charton *et al.*, 2001).

Few to no juvenile *E. fuscoguttatus*, *C. miniata*, and *A. leucogrammicus* were observed, and therefore, no representative conclusions regarding difference in habitat preference and age can be drawn. It is not

surprising that few *A. leucogrammicus* were identified in surveys conducted by both Nesbitt and in the present study because they are notoriously furtive and generally uncommon (Hiatt and Strasburg, 1960; Nesbitt, 2015; Unsworth *et al.*, 2007). However, the absence of juveniles of all three species suggests an imbalance in age distribution. It is possible that larval import and juvenile migration into the MPA have been compromised either by these species' contribution to exploited spawning aggregations (Friedlander *et al.*, 2003; Sadovy de Mitcheson *et al.*, 2013), lack of connectivity between appropriate habitat (Fenberg *et al.* 2012), or the absence of other healthy ecosystems to contribute to larval export and from which developed individuals might migrate (García-Charton *et al.*, 2001). Additionally, the MPA may simply not include enough appropriate habitat to support high abundances of these species. These imbalances in maturity and population abundance as a whole have the potential to negatively impact reproductive health and generate a positive feedback loop that ultimately results in population collapse (Hackradt *et al.*, 2014). Thus, populations of *E. fuscoguttatus*, *C. miniata*, and *A. leucogrammicus* are especially at risk due to the fact that these reproductive stressors are exacerbated in small populations with limited and specific habitat niches (Hiatt and Stasburg, 1960).

The population of *P. laevis* was composed of fewer adults than juveniles, which exhibit a broad realized niche. Too few mature individuals were observed to determine representative differences in habitat preference between age groups. While the habitat preference of juvenile *P. laevis* was apparently broad, mature individuals most likely favour more specific habitats due to their large maximum size (Nesbitt, 2015). Their scarcity, as well as that of *E. fuscoguttatus*, may be attributed to the slow growth rate and limited spawning period of large species (Sadovy and Coiin, 1995). The population as a whole was still relatively small compared to those of *A. rogaea* and *C. argus* and exhibited a decrease in relative abundance and biomass densities since 2014. The scarcity of mature *P. laevis* and the general decline in population health is especially significant considering the species' status as "vulnerable" according to the IUCN and warrants further attention.

Regime shift between 2014 and 2018

Nesbitt (2015) conducted a foundational serranid survey within the MPA in order to establish long term monitoring efforts for these important species. This

study adopted her six species of focus and modified and expanded the methods slightly in order to compare serranid population composition and distribution before and after a mass coral beaching event that occurred within CHICOP in 2016. Between 2014 and 2018, the biomass density for all species except *P. laevis* increased, and in 2014, the population of *P. laevis* was divided evenly between juvenile and mature individuals. These changes in the population of *P. laevis*, in conjunction with a decrease in relative species abundance, suggest that fewer individuals are reaching maturity and that the population as a whole is in decline. Indeed, *P. laevis* exhibited the highest biomass density of all species in 2014, making its decline all the more alarming. While it is difficult to fully attribute the decline in *P. laevis* to changes in coral structure and complexity caused by the bleaching event, it is likely that they contribute in some way. The increase in biomass density within the MPA for all species except *P. laevis* further emphasizes the need to specifically investigate population composition and distribution of this species in order to best attune management toward conserving this vulnerable species both on Chumbe and other reefs in the Zanzibar archipelago.

While species' biomass density generally increased between 2014 and 2018, relative abundance of all species except *A. rogaea* decreased in the same time interval. *A. rogaea* held the highest relative abundance in 2014 by only 0.03 and supported only the third highest biomass density. Moreover, the decrease both in population biodiversity and evenness, in conjunction with *A. rogaea*'s increase in relative abundance and biomass density, suggest that an ecological regime shift may have occurred on Chumbe's western reef between 2014 and 2018. The coral bleaching event may have caused a disturbance large enough to alter not only the health of the coral, but the populations of grouper that depend heavily on specific coral habitats (Cheal *et al.*, 2008; Hackradt *et al.*, 2014). The surge in abundance and biomass density of serranid species with broader fundamental niches and less specific habitat preferences (*A. rogaea* and *C. argus*) and decline of species with narrower habitat niches between 2014 and 2018 is in keeping with this hypothesis (Russ and Alaca, 2011).

Indeed, the shift to complete dominance by *A. rogaea*, a species shown to exhibit generalist habitat preference and low site fidelity, reflects that change is occurring not only within the serranid population, but also in the coral reef that supports it (Nesbitt, 2015). In the

face of global climate change, even populations of coral dwelling groupers protected within MPAs are vulnerable to decline as their highly specialized and delicate habitat collapses (Berger and Possingham, 2008; Hackradt *et al.*, 2014). Thus, a comprehensive understanding of each species fundamental niche is paramount to successful management of serranids and other reef dwelling species as the static protection of even immensely successful MPAs like CHICOP proves insufficient (Berger and Possingham, 2008; Friendlander *et al.*, 2003).

Conclusion

Between 2014 and 2018, Chumbe's MPA has experienced a regime shift from a more even and biodiverse serranid population to one dominated by *A. rogae* and *C. argus*. The dominance of *A. rogae* and *C. argus* might be attributable to the fact that their fundamental niche was less specific than that of the other four species. Both this study and that conducted by Nesbitt (2015) noted that *C. miniata*, *A. fuscoguttatus*, *P. laevis*, and *A. leucogrammicus* exhibited highly specific habitat preferences. Overarching, in keeping with Nesbitt's findings, all species exhibited preference to the slope where it is most steep and complex in the central zones (Richmond and Nesbitt, 2015). The age distribution of *A. rogae* was balanced and indicated healthy reproductive capacity, while populations of *C. miniata*, *A. fuscoguttatus*, and *A. leucogrammicus* consisted of mostly adults and those of *P. laevis* were composed primarily of juvenile individuals (Claudet *et al.*, 2008; Fenberg *et al.*, 2012; García-Charton *et al.*, 2008; Lester *et al.*, 2009). High abundance and biomass across locations, wide range and unspecified realized niche, and balanced age composition suggest that populations of *A. rogae* and *C. argus* are healthy and thriving. Decreased abundance and biomass, high site fidelity and specified habitat, and unstable age composition of the remaining four species suggest that these populations are at risk in the face of continued degradation to their coral habitat despite the protection of the MPA.

The relationship between wide habitat range, relatively small maximum size, and high relative abundance and biomass density of *A. rogae* and *C. argus* further emphasizes the inequity in protection generated by small MPAs. These findings suggest that populations of species with restricted habitat preferences benefit minimally from small protected areas, and this unfortunate reality is compounded by the fact that many rare species must compete not only amongst each other for resources and habitat, but also

with dominant species that are able to inhabit less specialized niches. The overall health of the reef within CHICOP can be extrapolated based on the composition and distribution of groupers on the reef. Similarly, it can be deduced that declines in coral health will result in declines in the health of grouper populations, and vice versa. With this relationship in mind, the degradative impact of a bleaching event in addition to consistent destruction of coral ecosystems by global climate change, it should not be surprising that compositions of serranid populations are experiencing regime shifts in favor of species that are able to adapt and accommodate intense habitat disturbances.

Assessment of serranid populations within the context of their preferred habitat promotes more detailed understanding of the localized reasons behind population composition and distribution. Interestingly, many of the backreef locations resemble the eastern OAA with regard to biodiversity, but the OAA's comparatively low population and biomass density indicates that the shallow, discontinuous, and fished reef exhibits poor grouper population health compared to the NTA. Thus, the relatively small serranid populations on nearby open access reefs suggest that the ecosystems are unable to sustain healthy populations due to the stress of extractive fishing practices, the unsuitable coral reef structure, or to the fact the MPA might not support a healthy or large enough population to result in spillover into adjacent open access fishing areas.

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