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Spatiotemporal Patterns of Parrotfish (Scaridae) Population Structure Across Florida's Coral Reef

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Thesis of Zachary T. Graff

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF ARTS AND SCIENCES

Spatiotemporal Patterns of Parrotfish (Scaridae) Population Structure Across Florida's Coral
Reef

By
Zachary T Graff

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Masters of Science with a specialty in:

Marine Science

Nova Southeastern University
May 2024

Abstract

This study conducted a population assessment of parrotfish density, biomass, occurrence, and size class frequencies in south Florida utilizing a decade of previously collected National Coral Reef Monitoring Program (NCRMP) Reef Visual Census (RVC) fish count data from 2012-2022. Larger parrotfish have the ability to remove large amounts of macroalgae during feeding which may clear habitat for assisting with reef repair via benthic settlement of beneficial organisms such as coral and CCA. Therefore, the parrotfish population over 30 cm in total length were also examined separately. Results illustrated size classes heavily skewed towards smaller individuals with 46.76% parrotfish below 11 cm in total length and 82.68% under our 30 cm. The majority of parrotfishes in Florida are not of sufficient size to have the capacity to remove a large biomass of macroalgae from Florida's coral reefs. Highest densities and biomass of larger individuals were observed in the Florida Keys and the lowest were located in the Coral ECA region. Densities and biomass in the Florida Keys were significantly lower in 2018, likely due to hurricane Irma, and have not recovered to previous levels since. Since parrotfish are short lived, several generations should have matured since 2018. The lack of post disturbance recovery may be due to the continually degraded nearshore and offshore habitats in Florida that juvenile and adult parrotfishes depend upon, limiting population recovery.

Keywords: marine protected areas, biogeography, ecological impact, conservation, macroalgae removal and control

Acknowledgements

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Introduction

Parrotfishes (Labriformes: Scaridae) are important herbivores on Caribbean coral ecosystems capable of controlling algal coverage on benthic ecosystems (Mumby et al., 2006; Williams & Polunin, 2001) and have likely been essential to reef function for millennia (Cramer et al., 2017, 2021). Parrotfish feeding and ingestion rates exponentially increase with body size (Arim et al., 2010), making larger individuals ecologically valuable in terms of their ability to clear larger areas of benthic space (Bruggemann et al., 1994, 1996; Lange et al., 2020; Petchey et al., 2008).

Increasing anthropogenic stressors including land-based source nutrients, increasing water temperature, storm events, and overfishing have concomitantly caused decadal Caribbean-wide increases in benthic macroalgae coverage (Adam et al., 2018; Dell et al., 2020; Holbrook et al., 2016). In healthy coral reef systems, corals and macroalgae compete for space and substrates cleared of macroalgae promote the settlement and growth of new generations of coral larvae potentially assisting in the natural reef recovery (Harrington et al., 2004; Paddock et al., 2006). Intense herbivory clears space in benthic ecosystems allowing other important habitat building organisms such as corals and crustose coralline algae to become established (Charendoff et al., 2023; Harrington et al., 2004; Mumby, 2009; Mumby et al., 2007; Steneck & Dethier, 1994). Historically *Diadema* urchins were a primary macroalgal grazer in the Caribbean but a basin-wide disease outbreak in 1983 decimated urchin populations (Foster, 1987; Hylkema et al., 2023). This massive population decline left parrotfish as a dominant grazer on many Caribbean coral reefs capable of clearing reef space (Bonaldo et al., 2014; Lange et al., 2020; Williams & Polunin, 2001).

In many Caribbean nations, parrotfish population metrics are useful in estimating fishing and other anthropogenic pressures on stressed coral reef ecosystems (Vallès & Oxenford, 2014). Fishing pressure on parrotfish has increased as other fisheries (e.g. snapper, grouper) become diminished past the point of profitability or sustenance (Valdivia et al., 2017). Parrotfish biomass in many Caribbean nations has dropped drastically in recent years, studies show from 71g/m² to less than 30 g/m² (Steneck & Arnold, 2009). Recently 73% of surveyed Caribbean countries report that fishers are actively targeting parrotfish and larger size classes are generally preferred for local markets (Callwood, 2021). This overfishing alters natural reef fish size frequency distributions.

In the Bahamas, parrotfish under 11 cm in length composed nearly 70% of the population while on protected reefs parrotfish under 11 cm composed less than 25% of the overall population (Shantz et al., 2020). Removing larger sized reef herbivorous fish has been shown to increase macroalgae biomass (Bulleri et al., 2018; Shantz et al., 2020; Zhang et al., 2022) because smaller parrotfish size classes generally do not effectively compensate for the loss of the larger fish (Garcia et al., 2012).

The establishment of no-take areas can meet or exceed pre-exploited parrotfish biomass levels after 10 years of protection (Mumby et al., 2021). Although no-take areas may not increase parrotfish density, they can increase biomass indicating larger and more ecologically important parrotfish within (Nugraha et al., 2017). However, since parrotfish are highly habitat dependent, fishing restriction location must be chosen carefully as habitat has a great effect on parrotfish population metrics (Zuercher, Kochan, & Harborne, 2023).

Despite their ecological importance in coral reef ecosystems, historical publications have been relatively sparse on Florida's parrotfish population dynamics. Parrotfish have been managed by the state since the early 1990's with only a small number allowed to be taken for the personal aquariums by recreational divers, all parrotfish harvested must be under 30 cm in size, must be kept alive, and commercial sale is prohibited (FWC, 2022). Previous research has focused on density and biomass (Bozec et al., 2016; Morais & Bellwood, 2020; Mumby et al., 2021), however size distribution changes may not be evident in the overall biomass of a population as smaller bodied parrotfish fill the biomass gap in higher densities than in an unfished population (Morais & Bellwood, 2020; Shantz et al., 2020; Vallès & Oxenford, 2014). Therefore, this study investigated regional temporal comparisons of density, biomass, and size demographics of Florida's coral reef tract parrotfish population in context of their potential to clear space for new benthic settlers like corals. Differences in large parrotfish (>30 cm) capable of excavating substrate were analyzed to determine if the state-wide protected status of parrotfish has provided a natural demographic that supports high densities of larger bodies parrotfish that may be capable of clearing space on Florida's coral reef ecosystems.

Methods

NCRMP Data collection

National Coral Reef Monitoring Program (NCRMP) Reef Visual Census (RVC) surveys conducted between 2012–2022 were compiled to explore spatial-temporal patterns in parrotfish population size structure across Florida’s Coral Reef (FCR). The NCRMP dataset spans 10 years of standardized data on fish and benthic communities across the Florida Reef Tract, providing an extensive and under-utilized dataset for researchers. We extracted survey data on the biomass/size, abundance/density, and size class frequencies NCRMP encompasses mapped hardbottom habitats shallower than 33 m. A pair of divers each record fish species present within their respective 15 m cylinder for a 15 minute period (Bohnsack & Bannerot, 1986; Walker, 2012). The arithmetic average of the stationary counts for a buddy team of two divers is then calculated from the collected data.

Analysis

Parrotfish density, biomass, and size class frequency were analyzed between and among three regions across Southern Florida: the Kristen Jacob’s Coral Reef Ecosystem Conservation Area (Coral ECA), the Florida Keys (FLA KEYS), and the Dry Tortugas (DRY TORT)(Figure 1). Parrotfish assemblages were also evaluated by fishing protection status throughout the Florida Keys and Dry Tortugas to determine if the restriction of all forms of fishing is influencing demographics.

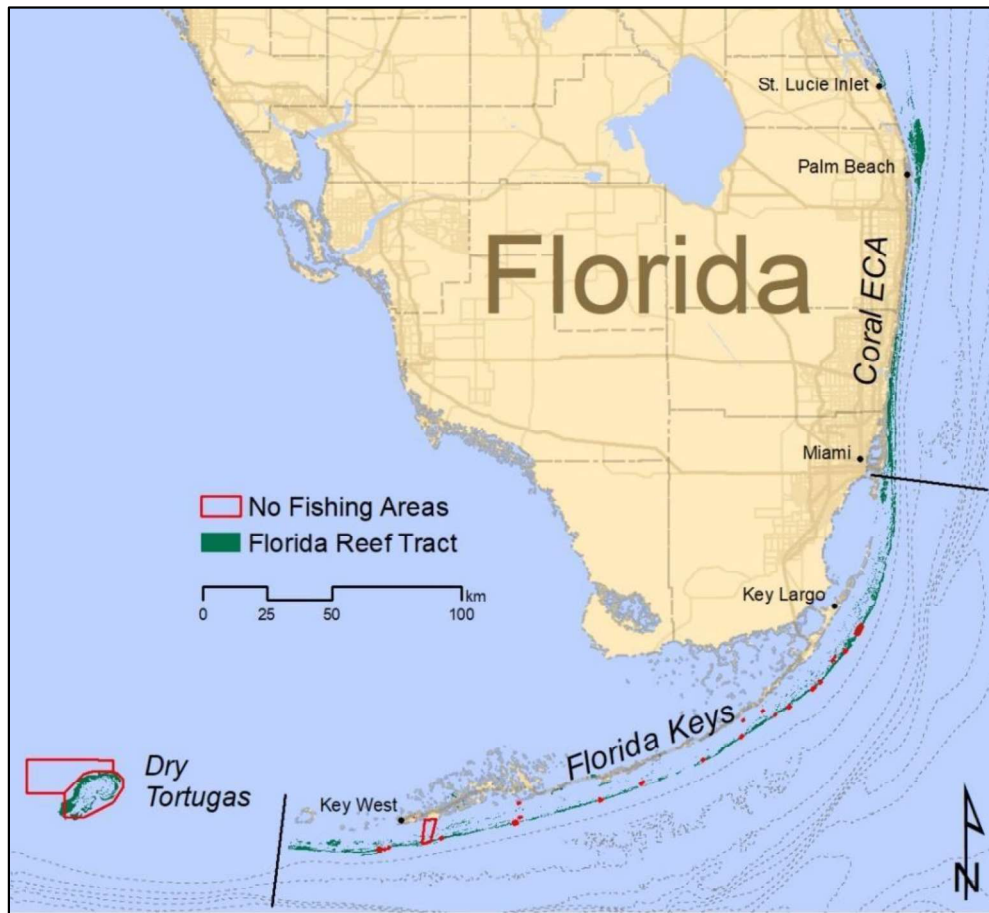


Figure 1: Three regions of southern Florida

Metrics Measured

Total parrotfish density, biomass, and size class frequency of 14 species (Table 1) were compared among regions, years, and protection status. Specialized R-code designed for the NCRMP dataset (Blondeau & Ganz, 2015) was used for the analysis. This R-code estimates means and variances of the various metrics following standard procedures for two-stage stratified random surveys (Lohr, 2010). Computational details are provided in Smith et al. (Smith et al., 2011). SAS and Microsoft Excel software were used for data exploration and quality control. Kruskal-Wallis statistical tests were used to find significance of the overall population between regions and ANOVA statistical tests were used to find significance among priority individual species among regions.

Seven species >30 cm total length (TL) (Stoplight, Blue, Redtail, Yellowtail, Midnight, Queen, and Rainbow) were selected for further analyses based upon the ability of these species to

regularly exceed the 30 cm threshold which allows these individuals to have an exponentially increased ability to clear reef space (Arim et al., 2010; Lange et al., 2020; Petchey et al., 2008). Survey region-year estimates of density and biomass for the suite of large parrotfish species were scaled to overall study means (Grove et al., 2024; Viehman et al., 2024), analogous to a parametric ANOVA, to evaluate (i) within-year differences among regions and (ii) within-region differences among years.

Table 1: Parrotfish species of southern Florida, scientific name (left), common name (middle), and NCRMP abbreviation code (right). Species capable of regularly exceeding 30cm in total length highlighted in grey.

Parrotfish Species in Southern Florida		
<i>Scarus coeruleus</i>	(Blue parrotfish)	SCA COER
<i>Sparisoma viride</i>	(Stoplight parrotfish)	SPA VIRI
<i>Scarus vetula</i>	(Queen parrotfish)	SCA VETU
<i>Sparisoma chrysopterygion</i>	(Redtail parrotfish)	SPA CHRY
<i>Sparisoma rubripinne</i>	(Yellowtail parrotfish)	SPA RUBR
<i>Scarus guacamaia</i>	(Rainbow parrotfish)	SCA GUAC
<i>Scarus coelestinus</i>	(Midnight parrotfish)	SCA COEL
<i>Scarus iseri</i>	(Striped parrotfish)	SCA ISER
<i>Cryptotomus roseus</i>	(Bluelip parrotfish)	CRY ROSE
<i>Sparisoma atomarium</i>	(Greenblotch parrotfish)	SPA ATOM
<i>Sparisoma radians</i>	(Bucktooth parrotfish)	SPA RADI
<i>Scarus taeniopterus</i>	(Princess parrotfish)	SCA TAEN
<i>Nicholsina usta</i>	(Emerald parrotfish)	NIC USTA
<i>Sparisoma aurofrenatum</i>	(Redband parrotfish)	SPA AURO

Results

All parrotfish Species and Size Classes

Domain wide patterns in density, biomass, length frequency distribution

Total parrotfish population density was dominated by three species: Striped at 43% (14.3±1.00), Redband at 27.1% (9.0±0.47), and Greenblotch at 9.3% (3.01±0.32). Total parrotfish biomass was dominated by three species: Stoplight at 26.3% (0.55±0.05), Redband at 16.3% (0.34±0.03), and Blue at 13.2% (0.28±0.09). 46.7% of Florida's parrotfish were less than 11 cm

and 82.7% parrotfish less than 30 cm. Only 17.3% of the parrotfish in the survey timeframe were over 30 cm in total length (Figure 2).

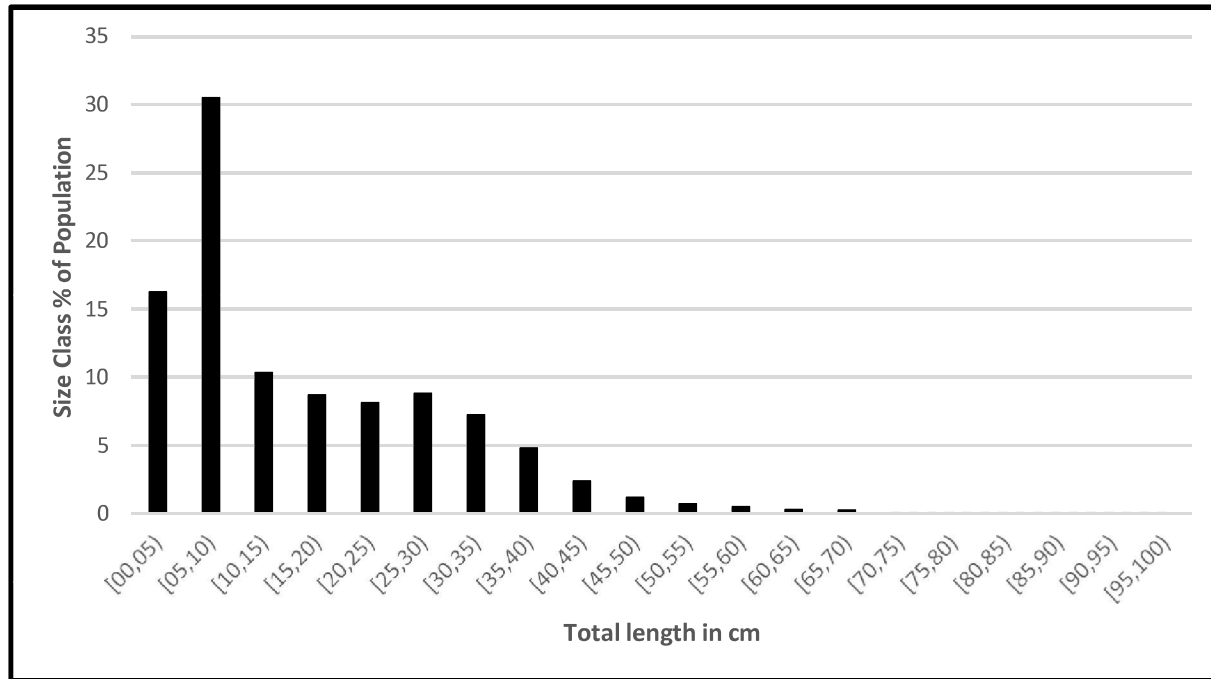


Figure 2. Domain size frequency distribution of parrotfishes in southern Florida

Regional patterns of density, biomass, and length frequency

Total mean parrotfish density differed significantly across regions. Density in the Coral ECA was low (0.69 ± 0.075 parrotfish per 177m^2) and similar in the Dry Tortugas (1.44 ± 0.115 parrotfish per 177m^2) and Florida Keys regions (1.42 ± 0.104 parrotfish per 177m^2). Kruskal-Wallis chi-squared multiple comparison significance testing showed a significant difference in overall parrotfish density between the Florida Keys and Coral ECA regions (26.70 / p-value 0.038). Biomass was low in the Coral ECA (0.040 ± 0.009 kg 177m^2), intermediate in the Dry Tortugas (0.069 ± 0.014 kg per 177m^2), and highest in Florida Keys (0.113 ± 0.020 kg per 177m^2) (Figure 3). A Kruskal-Wallis rank sum test and Dunn’s test of multiple comparisons showed significant differences between parrotfish overall biomasses of the Dry Tortugas and Florida Keys regions (27.58 / p-value 0.0345), as well as significant differences between the Coral ECA and Florida Keys regions (-35.64 / p-value 0.0026) (Figure 3).

Density in all three regions was dominated by small-bodied species: Striped, Redband, and Greenblotch. An ANOVA statistical test showed Striped density was significantly different between the Dry Tortugas and Coral ECA regions (0.826 / p-value 0.00) and significantly different between the Florida Keys and Coral ECA regions (0.675 / p-value 0.00). Redband density was significantly different between the Florida Keys and Coral ECA regions (0.155 / p-value 0.038) and significantly different between the Florida Keys and Dry Tortugas regions (0.206 / p-value 0.011). Greenblotch density showed no significance among regions (p-value 0.165) (Figure 4). Biomass fluctuated with primary species, Stoplight dominated biomass in the Florida Keys and the Dry Tortugas regions while Redband appeared to dominate biomass in the Coral ECA region. An ANOVA statistical test showed Stoplight biomass was significantly different between the Dry Tortugas and Coral ECA regions (0.238 / p-value 0.003) and significantly different between the Florida Keys and Coral ECA regions (0.204 / p-value 0.010). Redband showed no significant differences between any of the three regions (p-value 0.938). And Blue showed significant differences between the Dry Tortugas and Coral ECA (0.835 / p-value 0.00) as well as between the Florida Keys and the Coral ECA (1.262 / p-value 0.00) (Figure 5). Redband appeared to be the most frequently occurring species in the Florida Keys and Coral ECA, while Striped appeared to be the most frequently occurring species in the Dry Tortugas. There was a significant difference in occurrence of Striped between the Dry Tortugas and Coral ECA (0.575 / p-value 0.00), between Florida Keys and Coral ECA (0.485 / p-value 0.00) and between the Florida Keys and Dry Tortugas (-0.089 / p-value 0.037). Redband showed significant differences in occurrence between the Dry Tortugas and Coral ECA regions (0.257 / p-value 0.00) and significant differences between the Florida Keys and Coral ECA regions (0.296 / p-value 0.00). Greenblotch showed significant differences between the Dry Tortugas and the Coral ECA (0.115 / p-value 0.041) (Figure 6).

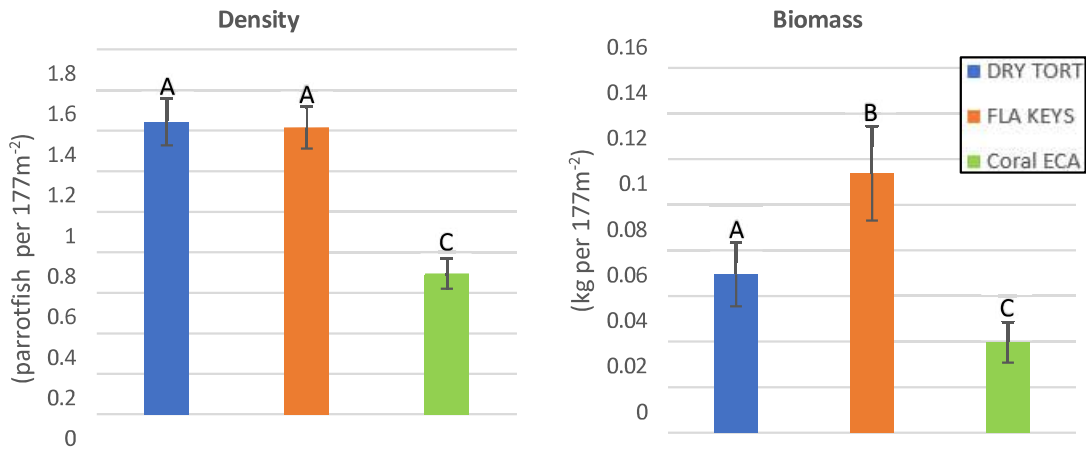


Figure 3. Florida's Coral Reef parrotfish density and biomass. Densities were similarly high in the Dry Tortugas and Florida Keys regions and lowest in the Coral ECA. Asterisk demotes significance ($p < 0.05$). Biomass was highest in the Florida Keys and lowest in the Coral ECA. Error bars represent one standard error of the mean.

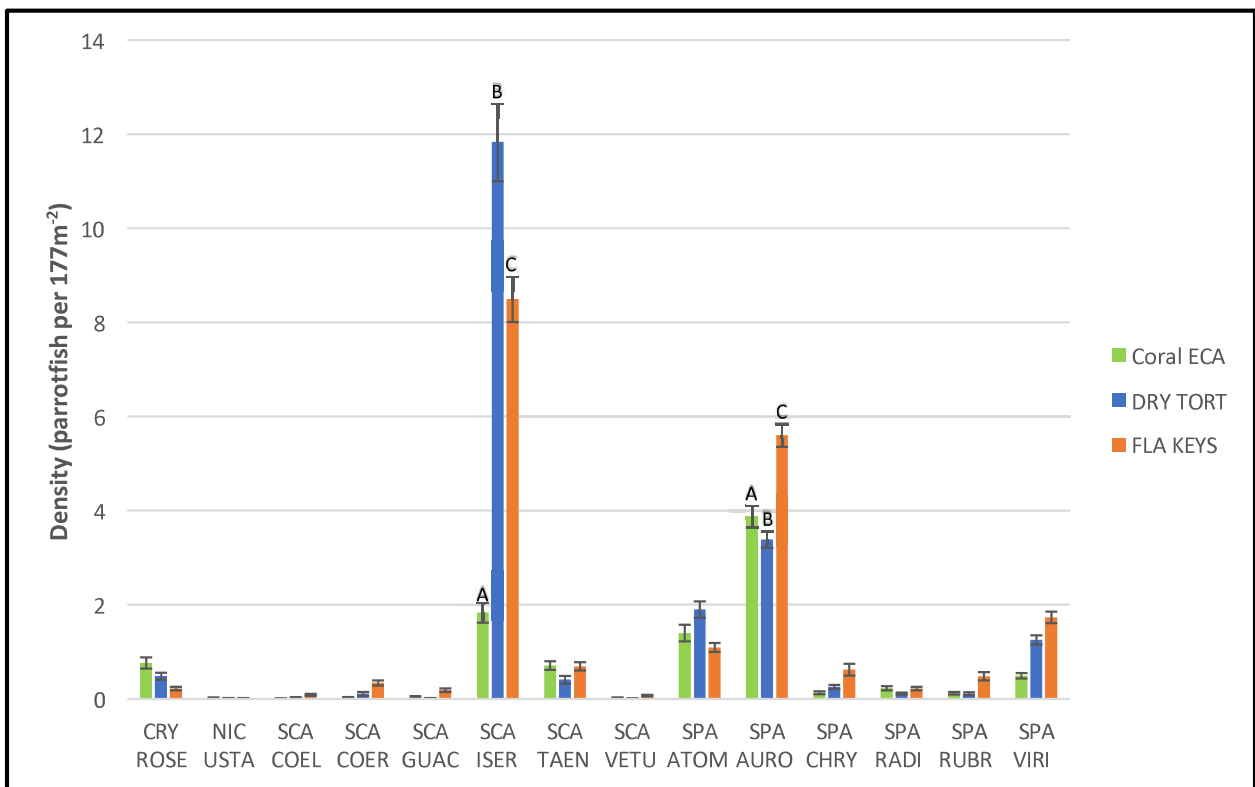


Figure 4. Mean density per species by region. Density in all three regions was dominated by three small bodied species: *S. iseri* (Striped), *S. aurofrenatum* (Redband), and *S. atomarium* (Greenblotch). A, B, and C above error bars represent significance between each region. Error bars represent one standard error of the mean.

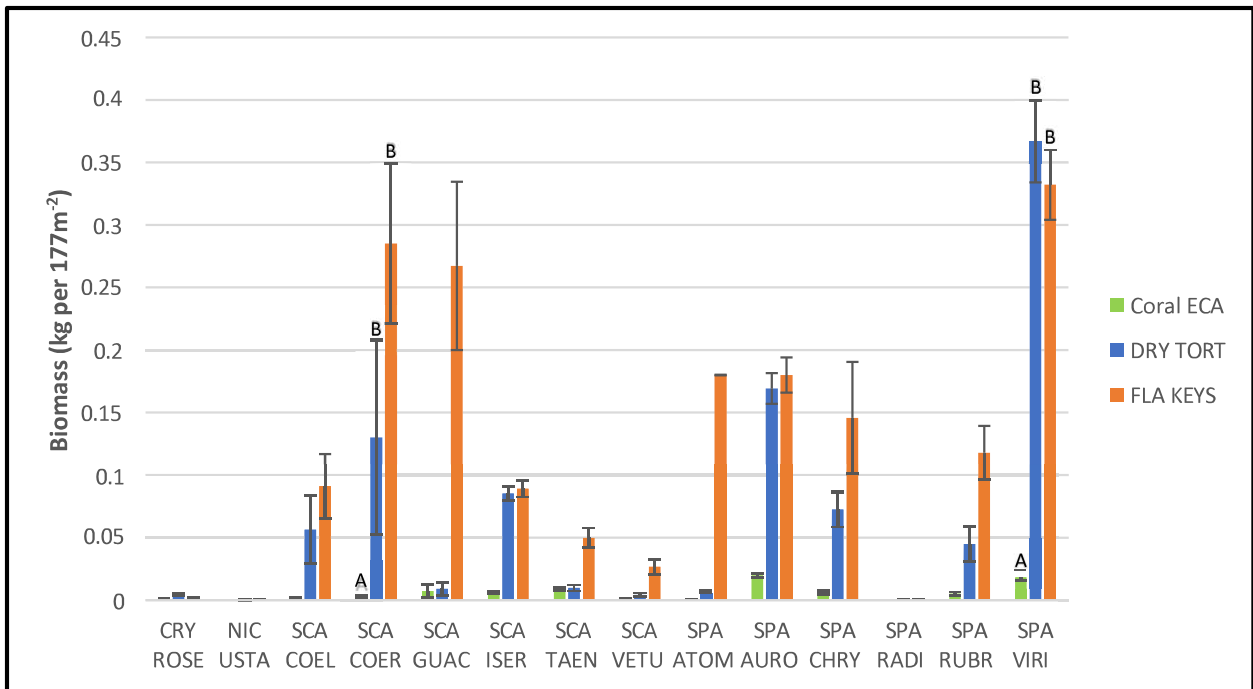


Figure 5. Mean biomass per species by region. Biomass was dominated by *S. viride* (Stoplight), *S. aurofrenatum* (Redband), and *S. coeruleus* (Blue). A, B, and C above error bars represent significance between each region. Error bars represent one standard error of the mean.

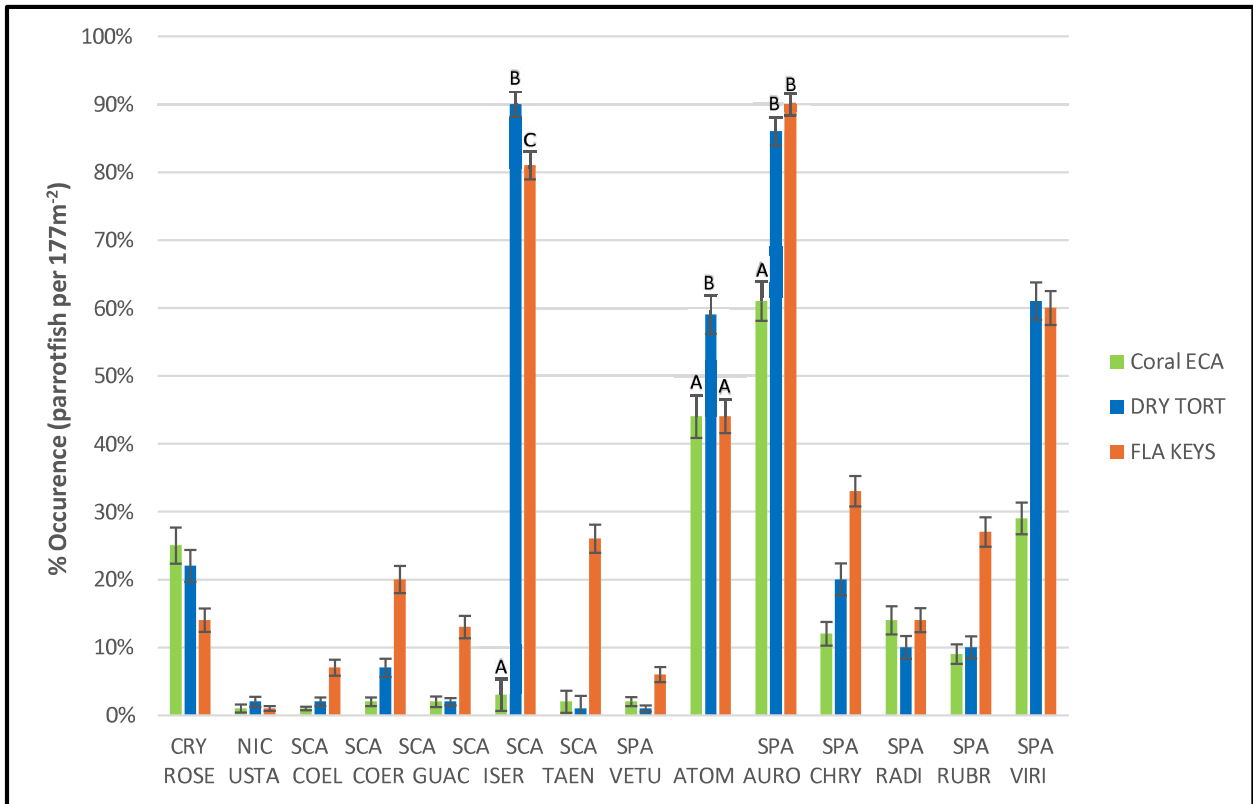


Figure 6. Mean % occurrence per species by region. % Occurrence was dominated by *S. Iseri* (Striped), *S. aurofrenatum* (Redband), and *S. Atomarium* (Greenblotch). A, B, and C above error

bars represent significance between each region. Error bars represent one standard error of the mean.

Region temporal density and biomass

Total parrotfish density varied across time and region (Figure 7). In the Dry Tortugas, density was highest in 2012 (1.64 ± 0.09), declined 25% in 2016 (1.24 ± 0.09), and then maintained a lower level of density thereafter. Density was highest in the Florida Keys in 2014 (1.77 ± 0.12) and 2016 (1.66 ± 0.10), then declined 31.5% in 2018 (1.14 ± 0.07) and 2022 (1.10 ± 1.13). Densities were lowest in the Coral ECA throughout the study and stayed around 0.6 except in 2016 where they were significantly higher (0.99 ± 0.09).

Total parrotfish biomass varied through time within each region similar to density (Figure 8). Biomass was highest in the Florida Keys throughout the study period (mean~1.59). Biomass in the Florida Keys dropped significantly by 54% between 2016 (2.17 ± 0.03) and 2018 (1.0 ± 0.01), then increased 20% in 2022 (1.26 ± 0.02). Biomass was lowest in the Coral ECA throughout the study and was fairly stable (mean~0.55) except in 2016 where it was significantly higher (0.86 ± 0.01) matching the Dry Tortugas. Dry Tortugas biomass was highest in 2014 (1.31 ± 0.03), declined 37% in 2016 (0.83 ± 0.01) and an additional 22% in 2018 (0.65 ± 0.01), then increased 34% in 2022 (0.87 ± 0.01).

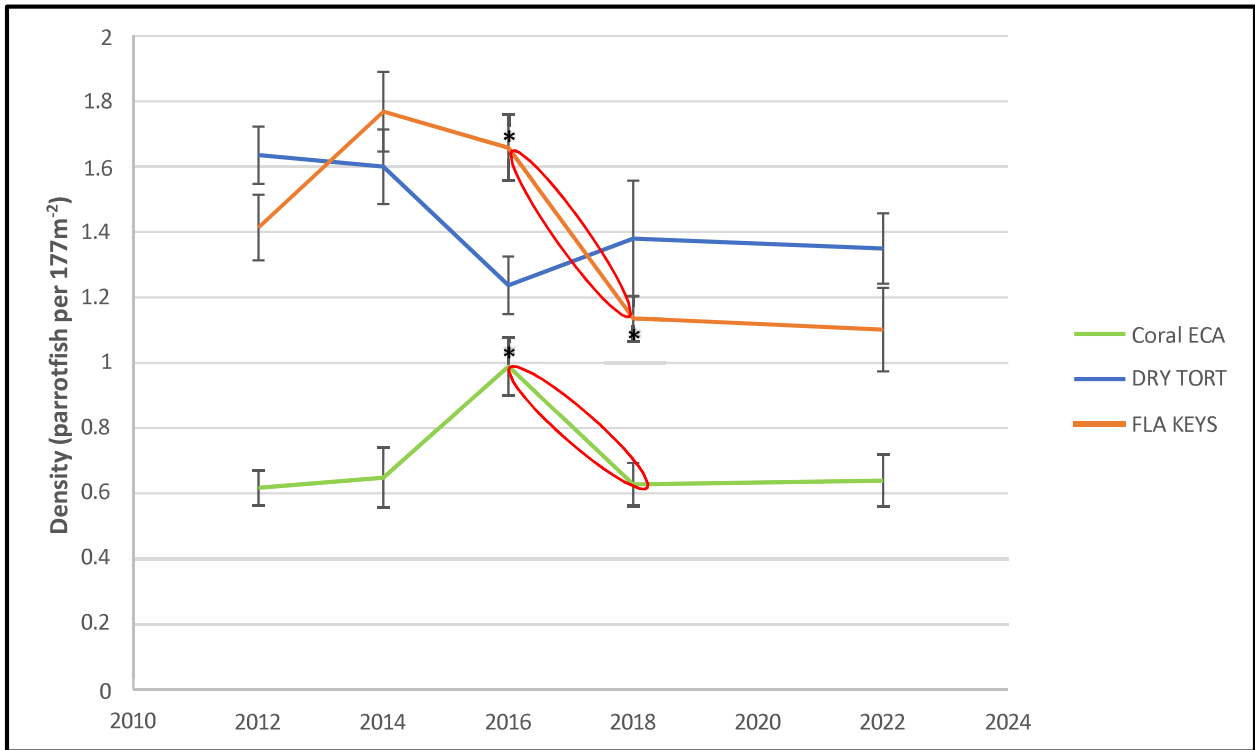


Figure 7. Total density by region by year. Density was highest in the Florida Keys and Dry Tortugas and lowest in the Coral ECA. Significant changes occurred in 2016 where Dry Tortugas densities dropped and Coral ECA increased. Florida Key and Coral ECA densities dropped significantly in 2018 (see areas circled in red). Error bars represent one standard error of the mean.

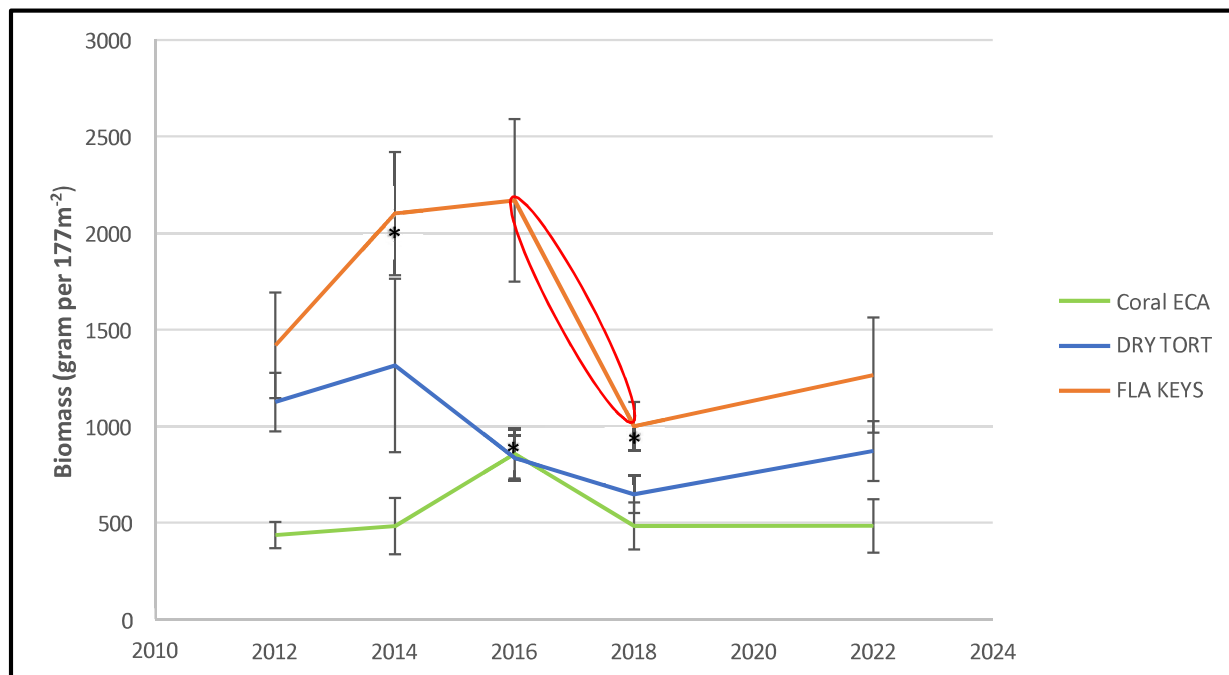


Figure 8. Total biomass by region by year. Biomass was highest in the Florida Keys and lowest in the Coral ECA. Significant changes occurred in 2016 where Dry Tortugas biomass dropped and Coral ECA increased. The Florida Key biomass dropped significantly in 2018 (see area circled in red). Error bars represent one standard error of the mean.

Large parrotfish (>30 cm)

Domain density, biomass, and length frequency

Total mean density of large parrotfish was (0.62 ± 0.08) domain-wide across all years. The highest domain-wide densities occurred in 2014 (0.79 ± 0.06) and the lowest in 2018 (0.44 ± 0.03) . Total mean biomass was 0.59 ± 0.07 domain-wide across all years. Temporal biomass patterns matched density with the highest in 2014 (0.79 ± 0.07) and the lowest in 2018 (0.41 ± 0.03) . Of the 17.32% of parrotfish exceeding the 30 cm threshold, 15.52% were between 30-50 cm in total length, and only 1.79% of parrotfishes in NCRMP reef fish surveys were >50 cm supermales.

Region temporal density and biomass

Mean density of large parrotfish in the Florida Keys (0.84 ± 0.14) was significantly higher than the Dry Tortugas (0.43 ± 0.05) and Coral ECA (0.20 ± 0.04) (Figure 9). Density in the Florida Keys was highest in 2014 (1.14 ± 0.11) and lowest in 2018 (0.54 ± 0.05) . Density in the Dry Tortugas

was highest in 2012 (0.55 ± 0.06) and 2022 (0.52 ± 0.08) and lowest in 2016 (0.28 ± 0.04). Mean density of large parrotfish in the Coral ECA was not significantly different across years.

Deviance from the domain mean for each region was tested to identify years where density was significantly higher or lower than the domain mean (Figures 9 and 10, Table 2). Large parrotfish density in the Dry Tortugas region was significantly lower than the domain mean in 2014 and 2016. The Florida Keys large parrotfish density was significantly higher than the domain mean in 2014 and lower in 2018. The Coral ECA large parrotfish density was significantly lower than the domain mean for all years.

For year differences within region, in the Dry Tortugas density was only significantly different from the mean in 2016 (Table 3). In the Florida Keys, density was significantly higher than the mean in 2014 and significantly lower in 2018. There were no significant deviances from the mean in the Coral ECA.

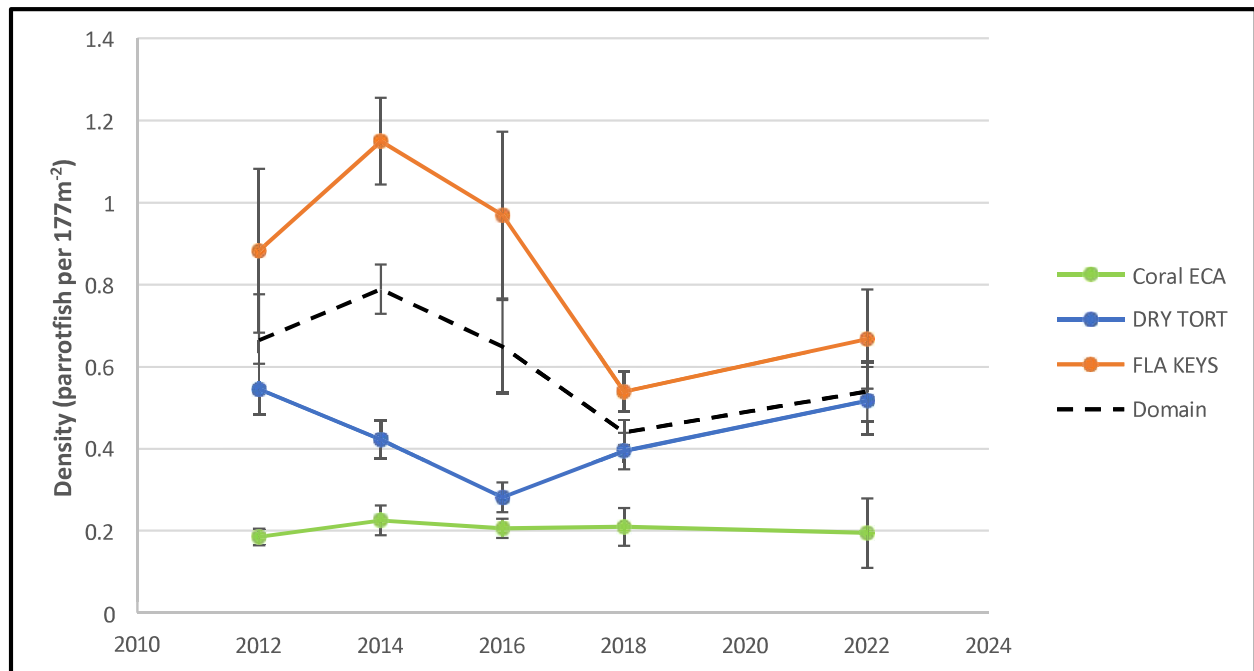


Figure 9. Total large parrotfish density by region by year. Density was highest in the Florida Keys and lowest in the Coral ECA. Error bars represent one standard error of the mean. Refer to table 3 for significance details.

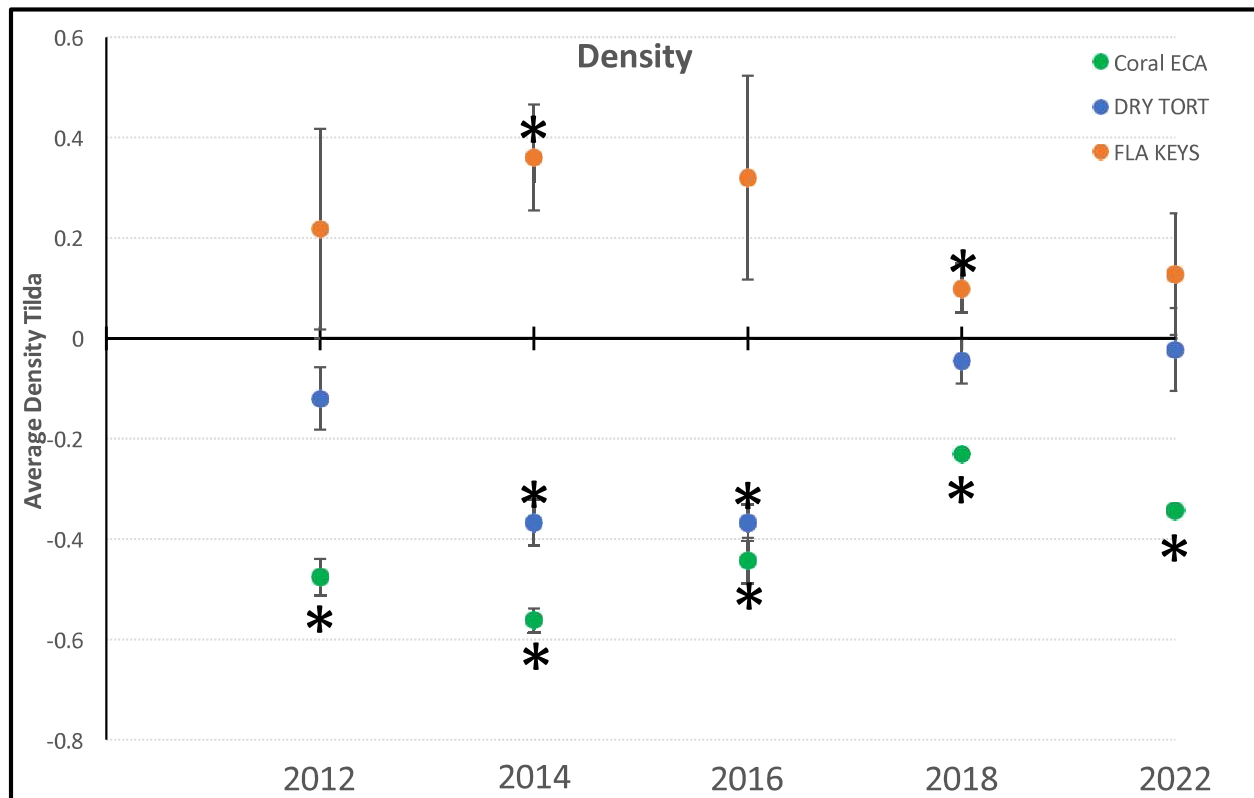


Figure 10. Visual example of significance among region within time: Mean large parrotfish density scaled to the domain mean by region by year. Asterisk denotes significant deviance from the domain mean. Error bars represent one standard error of the mean. See all results in tables 2 and 3.

Mean biomass of large parrotfish in the Florida Keys (0.80 ± 0.12) was significantly higher than the Dry Tortugas (0.42 ± 0.07) and Coral ECA (0.18 ± 0.04) (Figure 11). Biomass in the Florida Keys was highest in 2014 (1.12 ± 0.13) and lowest in 2018 (0.51 ± 0.05). Biomass in the Dry Tortugas was highest in 2012 (0.51 ± 0.09) and 2022 (0.43 ± 0.08) and lowest in 2016 (0.27 ± 0.04). Mean biomass of 30 cm and up large parrotfish in the Coral ECA was not significantly different across years.

Large parrotfish in the Dry Tortugas region was significantly lower than the domain mean in 2014 and 2016 (Table 2). The Florida Keys large parrotfish biomass was significantly higher than the domain mean every year. The Coral ECA 30 cm and above large parrotfish biomass was significantly lower than the domain mean for all years.

In the Dry Tortugas, large parrotfish biomass was only significantly different from the mean in 2016 (Table 3). In the Florida Keys, biomass was significantly higher than the mean in 2014 and significantly lower in 2018. There were no significant deviances from the mean in the Coral ECA.

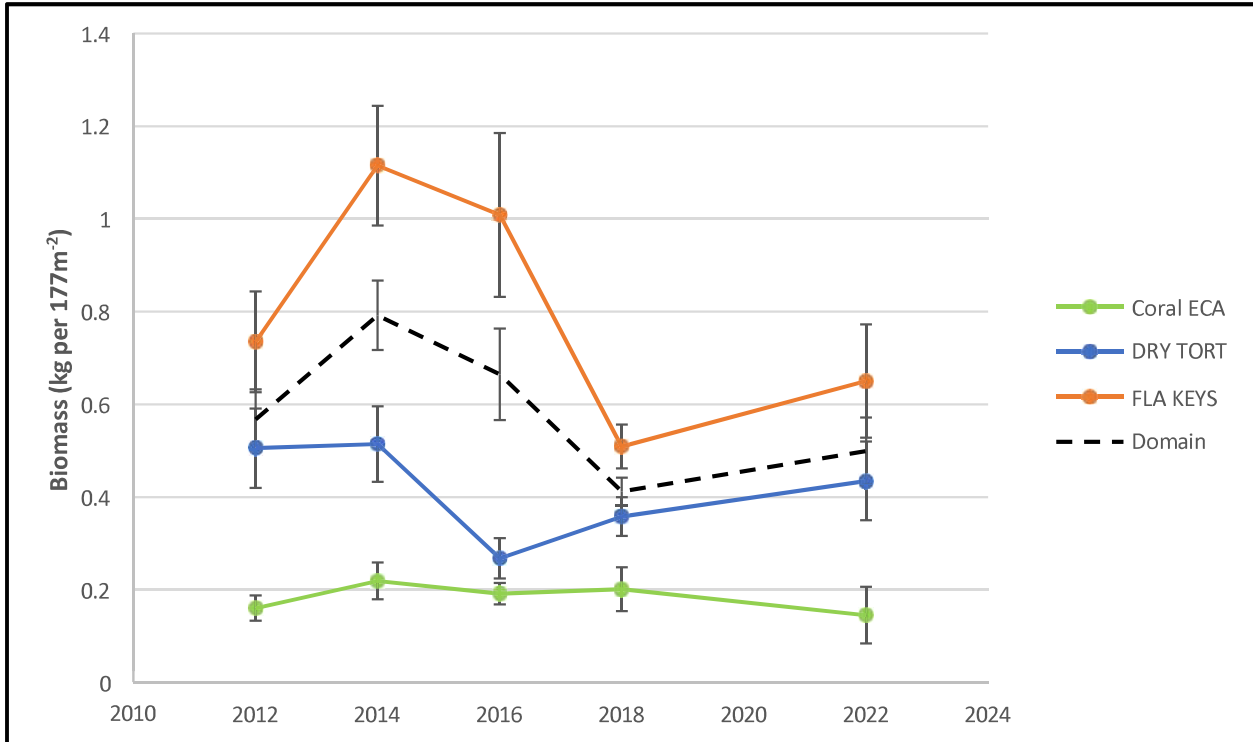


Figure 11. Total large parrotfish biomass by region by year. Biomass was highest in the Florida Keys and lowest in the Coral ECA. Error bars represent one standard error of the mean. Refer to table 3 for significance details.

Table 2: Significance testing results, region effect within time

metric	Year	Region effect	Description
Density	2012	p<0.05	FLA KEYS and DRY TORT are greater than the Coral ECA
	2014	p<0.05	FLA KEYS is greater than the DRY TORT which is greater than the Coral ECA
	2016	p<0.05	FLA KEYS is greater than the DRY TORT and Coral ECA
	2018	p<0.05	FLA KEYS and DRY TORT are greater than the Coral ECA
	2022	p<0.05	FLA KEYS and DRY TORT are greater than the Coral ECA
Biomass	2012	p<0.05	FLA KEYS and DRY TORT are greater than the Coral ECA
	2014	p<0.05	FLA KEYS is greater than the DRY TORT which is greater than the Coral ECA
	2016	p<0.05	FLA KEYS is greater than the DRY TORT and Coral ECA
	2018	p<0.05	FLA KEYS is greater than the DRY TORT which is greater than the Coral ECA
	2022	p<0.05	FLA KEYS and DRY TORT are greater than the Coral ECA

Table 3: Significance testing results, time effect within region. Deviance from domain mean for each region was tested to identify years where density or biomass were significantly higher or lower than the domain mean.

Metric	Region	Time Effect	Description
Density	FLA KEYS	p<0.05	Significant increase in density in 2014 followed by a significant decrease 2018 compared to other years
	DRY TORT	p<0.05	Significant decrease in density in 2016 compared to other years
	Coral ECA	No Significance	n/a
Biomass	FLA KEYS	p<0.05	Significant increase in biomass in 2014 followed by a significant decrease in 2018 compared to other years
	DRY TORT	p<0.05	Significant decrease in biomass in 2016 compared to other years
	Coral ECA	No Significance	n/a

No-take versus open to fishing areas by region

Florida Keys

In the Florida Keys, the total mean density of all parrotfish was not significantly different between no-take (1.44 ± 0.16) and open to fishing areas (1.41 ± 0.11) after a Mann-Whitney Wilcox test (p-value 0.4358). Total mean biomass of all parrotfish was not significantly different between no-take (0.20 ± 0.05) and open to fishing areas (0.11 ± 0.02) after Wilcox rank sum test with continuity correction (p-value 0.07583) (Figure 12).

Dry Tortugas

In the Dry Tortugas, total mean density of all parrotfish was not significantly different between no-take (1.45 ± 0.16) and open to fishing areas (1.20 ± 0.21) after a Wilcox rank sum test with continuity correction (p-value 0.9089). Total mean biomass of all parrotfish was not significantly different between no-take (0.07 ± 0.02) and open to fishing areas (0.07 ± 0.02) after a Wilcox rank sum test with continuity correction (p-value 0.9089) (Figure 13).

Length frequency

In Florida Keys open areas, 80.1% of parrotfish were below 11 cm and 4.3% were over 30 cm. In Florida Keys no-take areas, 76.4% of parrotfish were below 11 cm and 7.2% were over 30 cm (Figure 14). In Dry Tortugas open areas, 88.2% of parrotfish were under 11 cm and 2.4% were over 30 cm. In Dry Tortugas no-take areas, 89.1% of parrotfish were below 11 cm and 2.1% were

over 30 cm (Figure 15). In the Florida Keys region parrotfish size classes of 50-105 cm were seen exclusively in protected areas in 2024 and composed of four species, Rainbow, Blue, Midnight, and Stoplight (Figure 16).

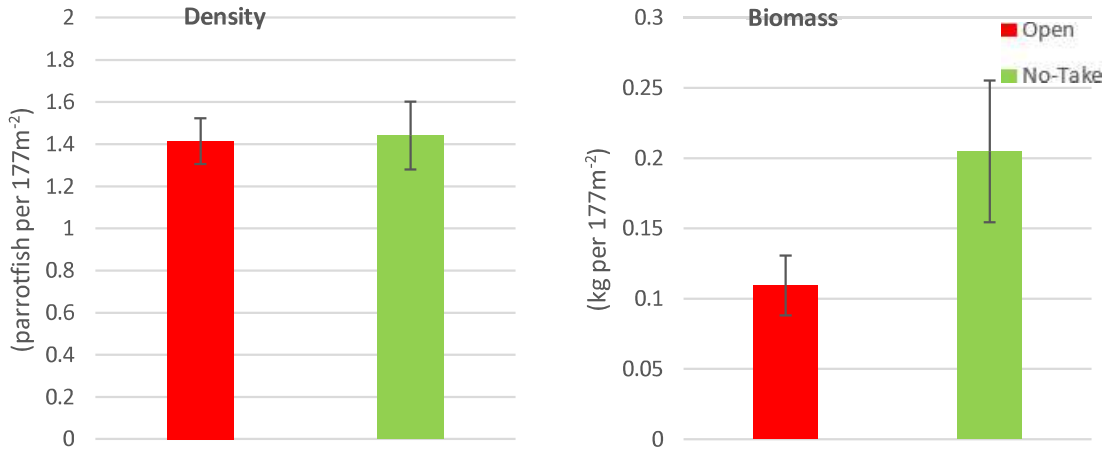


Figure 12. Florida Keys open vs no-take density and biomass (left), biomass (right) between no-take and open fishing areas.

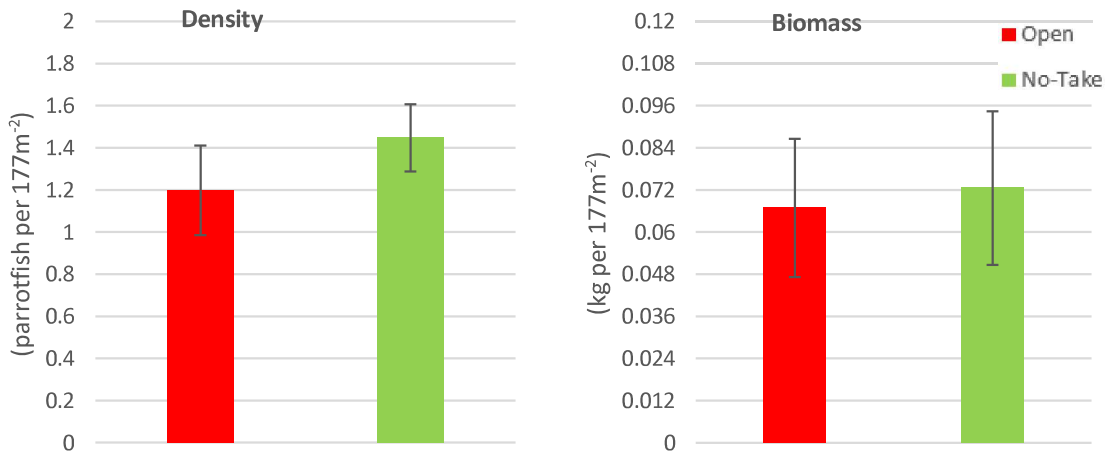


Figure 13. Dry Tortugas open vs no-take density and biomass (left), biomass (right) between no-take and open fishing areas.

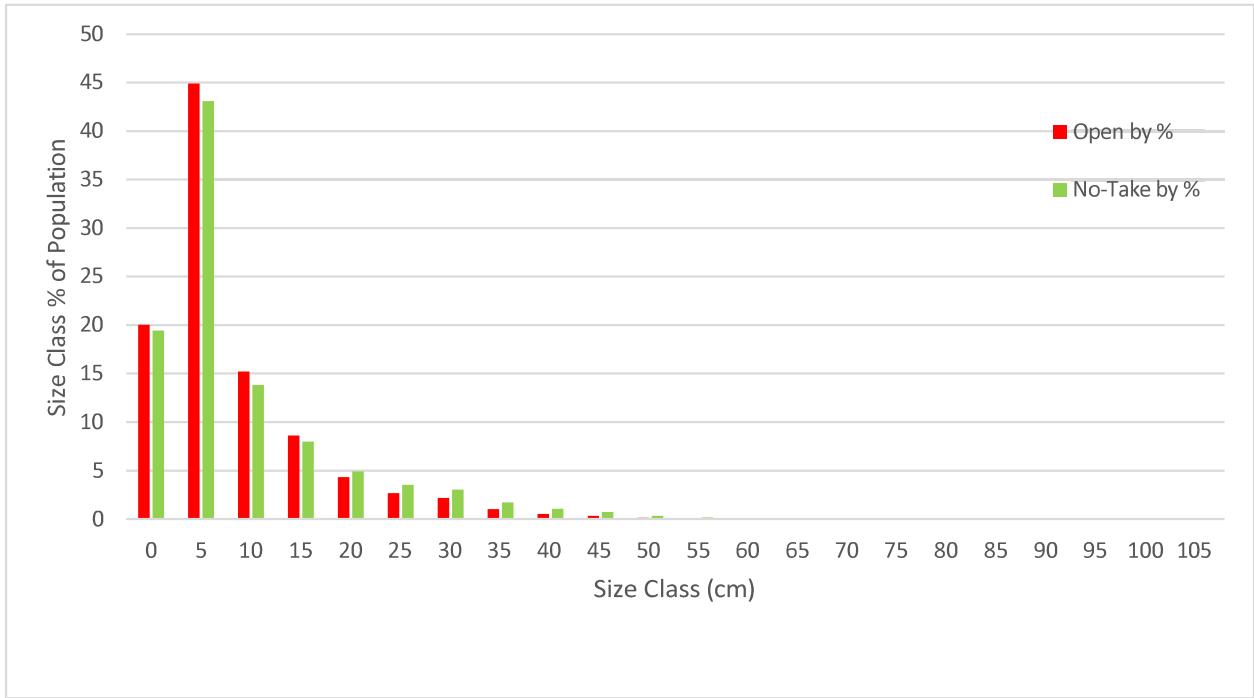


Figure 14. Florida Keys open vs no-take size class frequencies

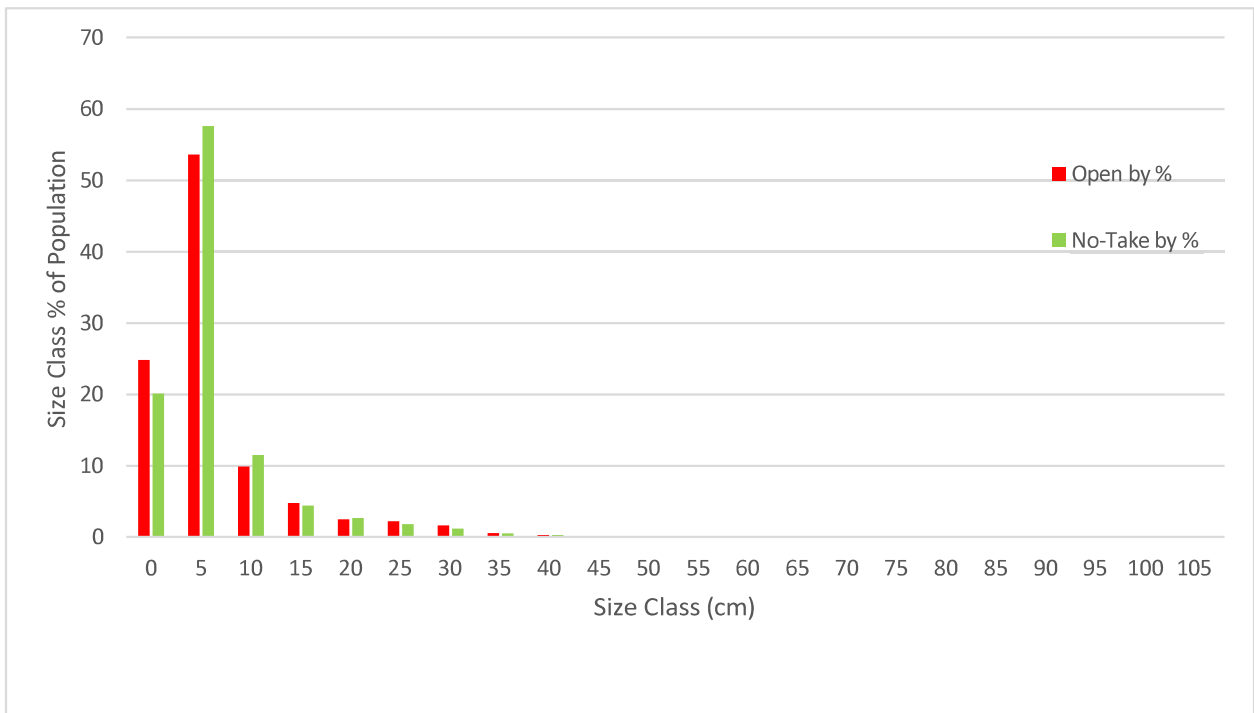


Figure 15. Dry Tortugas open vs no-take size class frequencies



Figure 16. Length frequency of all fish larger than 30 cm and above by species

Discussion

Parrotfishes are a key functional group in facilitating the recovery of coral reefs from recurrent disturbances by exerting top-down control of algae communities (Bonaldo et al., 2014; Charendoff et al., 2023; Mumby, 2009). Despite their importance, the density and biomass of large-bodied parrotfishes across Florida's Coral Reef remains unresolved hampering our ability to study and understand their ecology. This study showed that parrotfish density, biomass, and occurrence is lower in the Coral ECA than in other regions in the Caribbean. The Florida Keys and Dry Tortugas had mean density of 1.4 fish 177 m^{-2} and mean biomass of 110 g 177 m^{-2} , whereas combined surveys from across the Bahamas archipelago have reported mean densities ranging from 4.5 to 38.8 fish 120 m^{-2} and mean biomass ranging from 587 to 1,767 g 120 m^{-2} using different survey methods (Roff et al., 2011; Sherman et al., 2022). Combined surveys from Florida, Bahamas, Turks and Caicos, Haiti, Navassa, St. Vincent, Grenada, Jamaica, Colombia, Honduras, Guatemala, Belize, and Mexico show densities ranging between 5 and 40 fish 100 m^{-2} depending on the size classes and mean biomass ranging from 800 to 4,500 g 100 m^{-2} (Shantz et al., 2020). And contrary to the characterization that Florida's parrotfish population is less impacted due to its protected status (Shantz et al., 2020), Florida reefs were dominated by small bodied species namely Striped, Redband, and Greenblotch, that do not reach 30 cm TL. The majority of parrotfish (46%) were <11 cm TL and 82% fish were <30 cm TL, indicating that Florida's parrotfish community may not be as robust as previously reported given their protected status.

Numerous factors contribute to the disparity in mean density and biomass values between Florida and the Caribbean including differences in latitude, suitable habitat (high coral richness, cover, and density; proximity to sea grass and mangroves), fishing (poaching), and storm frequency. Outside of the Flower Gardens banks and Bermuda, the northern Bahamas and Florida are the highest latitude systems in the Caribbean. Florida's Coral Reef resides along a latitudinal gradient that transitions from tropical to subtropical communities that affect benthic habitat types, fish assemblages, and coral reef communities (Stallings, 2009; Vallès & Oxenford, 2014; Zuercher, Kochan, & Harborne, 2023). Latitude correlates with so many other variables related to parrotfish in Florida that it must be removed from statistical models (Zuercher, Kochan, Brumbaugh, et al., 2023). Region comparisons account for latitude in their design where the Dry Tortugas and Florida Keys are more tropical and the Coral ECA captures the transition to subtropical ecotone (Walker et al., 2023). The Dry Tortugas and Florida Keys had twice the parrotfish density higher mean biomass and occurrence than the Coral ECA. The reduced

parrotfish population in the Coral ECA coincided with the ecotone differences between regions. Since the Florida Keys and Dry Tortugas are high latitude compared to the rest of the Caribbean, reductions in density and biomass may be expected. However, after a 59% decadal decrease in parrotfish density, northern Bahamian reefs (New Providence - latitude equivalent with Key Largo) still have much higher mean densities (~11 fish 100 m⁻²) than Florida. Mean parrotfish density on Bermuda reefs have also been reported much higher (4 - 42 fish 100 m⁻²) (Hammond et al., 2008). These higher densities at similar and higher latitudes, indicate other factors contribute to Florida's comparably low parrotfish metrics.

Macroalgae control & Reef Repair

Florida's coral reefs are in a net carbonate structure loss (Toth et al., 2023) and as stony coral tissue loss disease (SCTLD) accelerated the loss of reef habitat, models by Swaminathan et al. 2024 showed potential reef fish decline associated with SCTLD in correlation with loss of habitat complexity. Larger bodied parrotfish have been shown to be a primary driver of coral reef algal biomass (Sheppard et al., 2023) and can reduce algal biomass by up to 600% more than nearby reefs with diminished parrotfish size classes (Zaneveld et al., 2016) which can double the recruitment of habitat building *Porites* spp. and *Agaricia* spp corals (Mumby et al., 2007). Natural herbivory provided by parrotfishes clears space on benthic ecosystems assisting with natural reef repair as other important habitat building organisms such as corals and crustose coralline algae establish themselves in this new algae free space (Charendoff et al., 2023; Harrington et al., 2004; Mumby, 2009; Mumby et al., 2007; Steneck & Dethier, 1994). Our results indicate that Florida parrotfish populations are dominated by small scrapers and browsers that are not capable of removing macroalgae or clearing substrate for new benthic settlers.

It has been suggested that Caribbean algal cover is near the upper threshold that parrotfish can control, making coral reefs macroalgae biomass susceptible to parrotfish exploitation (Cheal et al., 2010; Mumby et al., 2007). Previous studies have shown that even robust herbivorous fish populations may only maintain 50–65% cropped algae cover (Williams & Polunin, 2001). Between 2000 and 2003, an analysis of algal production and consumption by herbivores (47% parrotfish) in the Keys concluded that herbivores were capable of consuming the majority of new algal production, but not removing it (Paddack et al., 2006). Although their reported estimates were for all herbivores, parrotfish comprised 47% of the fish counted with *S. viride* comprising 29% of the fish on high relief reefs, 32% on low relief reefs, and 22% on patch reefs. Mean density of

herbivorous fish was between 0.5 and 2 fish m⁻² and mean biomass ranged from 25–200 g m⁻² across all reef habitats and sample periods in the Florida Keys. These estimates are orders of magnitude higher than our estimates (mean density = 1.4 fish 177m⁻² = 0.008 fish per m⁻²; mean biomass = 800 g 177 m² = 4.5 g m⁻²). This could be an indication of drastic changes in Florida's parrotfish population.

Fishing

Fishing for parrotfish occurs throughout many Caribbean countries and overseas territories with the Stoplight Parrotfish and *Sc. vetula* being the most frequently targeted species (Harms-Tuohy, 2021; Kramer & Heck, 2007) and populations are known to be skewed towards smaller size classes in heavily fished populations (Kramer & Heck, 2007). Shantz et al (2020) found that no-take areas in Florida had demographic community different from heavily fished areas around the Caribbean. This study did not support their findings. Although harvesting parrotfish for consumption in Florida is illegal, there are signs that parrotfish are being fished. Zuercher et al (2023) suggest that parrotfishes are recorded as bycatch in recent creel surveys of recreational and small operation commercial fishers (Florida Fish and Wildlife Conservation Commission, unpublished data) but data is lacking for these numbers. Size frequency data of all years combined in this study showed a higher percentage of >70 cm TL rainbow and midnight parrotfish that occurred almost exclusively in the Keys no-take areas in the year 2014 but have not been observed since. This was a curious finding without explanation. Outside of this occurrence, there were no indications of a fishing effect between take and no-take areas.

Storms and other impacts

Large storms (e.g. hurricanes, typhoons) can have major impacts on coral reef fish populations (Anticamara & Go, 2017) and are capable of cutting reef fish density in half (Gavriel et al., 2023). Mean density and biomass of parrotfish significantly declined in the Florida Keys from 2016 to 2018 coinciding with Hurricane Irma that hit the lower keys in 2017 causing extensive damage. Hurricane Irma was the most notable event to happen between the 2016 and 2018 sampling and measurable drops in reef fish densities from Irma were reported in the Virgin Islands (Langwiser et al., 2023). Total mean density remained low in 2022, five years after the storm. Mean biomass increased 21.4% between 2018 and 2022 indicating some recovery, but still 24.9% lower than pre-storm levels. This lack of recovery is concerning. Parrotfish are not a long lived reef fish, with adults typically not surviving beyond 8 years (Bellwood & Choat, 1989;

Paddack et al., 2006). Therefore, five years after the event, subadults should be reaching maximum maturity. With storm frequencies predicted to increase, the population may not be able to recover to previous sizes due to continually diminishing juvenile and adult habitat due to increasing anthropogenic effects and SCTL (Swaminathan et al., 2024; Toth et al., 2023) .

Suitable habitat limitations

Habitat reduction has been posed as one of parrotfish's main threats in south Florida (Machemer et al., 2012). Caribbean parrotfish are positively correlated with coral cover, reef topographic complexity, the proximity of seagrass and mangroves, and the biomass of other parrotfishes (Charendoff et al., 2023; Jackson et al., 2012; Paddack et al., 2006; Shideler et al., 2017; Zuercher, Kochan, & Harborne, 2023). Studies have shown that these factors are declining in Florida, especially in the Coral ECA region where lowest parrotfish densities and biomass occurred. South Florida coral cover has declined for decades (Fisher, 2023; Porter & Meier, 1992) but has more recently accelerated with the persistence of stony coral tissue loss disease (Toth et al., 2023; Walton et al., 2018). Between 2016 to 2022 reef-accretion potential declined by >70% across the Florida Keys and reefs have become measurably flatter (Fisher, 2023) and less complex (Yates et al., 2016). Habitat loss remains one the biggest threats to Florida mangroves and probable predictions are the total collapse of existing mangrove forests from sea level rise by 2100 (Parkinson & Wdowinski, 2022). The historic 80% reduction in mangrove coverage has resulted in a substantial loss of potential parrotfish habitat (Machemer et al., 2012; Snedaker, 1996). This is especially important for the Rainbow parrotfish whose juveniles have obligate, functional dependence on mangroves (Mumby et al., 2006). Since the proximity of dense mangroves can double the biomass of large excavating parrotfishes (Mumby et al., 2004), it may help explain regional parrotfish differences. In Florida, the proximity of mangroves played the most substantial role in the diversity of nearby reef fish populations, including parrotfish (Shideler et al., 2017). The presence of high mangrove cover explained large percentages in the difference of eight parrotfish species: Striped (44%), Stoplight (39%), Blue (27%), Redband (24%), Yellowtail (17%), Midnight (15%), Redtail (13%), and Greenblotch (12%). Mangrove cover was a strong predictor in the occurrence of all parrotfish species except the small bodied Greenblotch parrotfish. My analyses found the highest parrotfish densities and biomass in the Florida Keys where mangroves cover approximately 2,900 km of the Florida Keys National Marine Sanctuary shoreline and the lowest in the Coral ECA where only 826 hectares remain (Radabaugh et al., 2017). In the Coral ECA, where mangrove cover is minimal/low (Shideler et al 2017), mean

density was 50% less and mean biomass was 64% less than the Florida Keys. In the Dry Tortugas, where mangroves are also limited in cover, mean biomass was 36% less than the Florida Keys.

Conclusion

Poor water quality, high nutrients, thermal stress, coastal development, and stony coral tissue loss disease have put Florida's coral reef under great pressure (Cramer et al., 2017, 2021; Hayes et al., 2022; Lirman et al., 2011; Manzello, 2015; Zaneveld et al., 2016). Over 70% of Florida's coral reefs are in a state of net erosion as the reef-building corals die and cease to produce vital habitat forming carbonate structures (Morris et al., 2022). Parrotfish may assist with natural reef recovery as they clear new reef space allowing beneficial habitat providing organisms such as CCA and coral to settle and rebuild reef complexity (Charendoff et al., 2023; Harrington et al., 2004; Mumby, 2009; Mumby et al., 2007; Steneck & Dethier, 1994). The analyses herein suggest that the Florida's parrotfish populations are potentially in peril. There were much lower densities than reported 20 years prior (Paddack et al., 2006), the population is overwhelmingly dominated by small individuals, and steep declines in density were found associated with the timing of hurricane Irma that have not recovered. Storms have been shown to effect reef fish population dynamics in other areas of the world but fish but affected fish populations usually quickly recover (Langwiser et al., 2023). Since parrotfish distributions are strongly affected by habitat proximity and affinity, it is possible that habitat degradation is impairing the resilience of Florida's parrotfish populations, which may be limiting their recovery from disturbance. This possibility is a call to arms for more detailed analyses on parrotfish temporal demographics, habitat associations, spatial utilization, and recovery potential from disturbances.

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