Impacts of fishing on parrotfish grazing in St. Croix –A case study on the ecological impacts of fishery management actions: Final Report

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Sc. coelestinus and *Sc. guacamaia* foraging on a reef in the Florida Keys. Both species were once abundant throughout the Caribbean but are now ecologically extinct in St. Croix.

Project Summary and Management Recommendations

This report summarizes information from a three year study to evaluate the impacts of fishing on parrotfish grazing in St. Croix, U. S. Virgin Islands. The largest parrotfish fishery in the U. S. Caribbean is located on St. Croix. For many years, commercial landings of parrotfishes on St. Croix had approached or exceeded 400,000 lbs. annually, with parrotfishes accounting for nearly one third of landings. There is concern that these high levels of parrotfish fishing in St. Croix may negatively impact coral reef ecosystems through a reduction in parrotfish grazing, resulting in an increase in algae that can inhibit the recruitment, growth, and survivorship of reef-building corals. In order to quantify potential impacts of the parrotfish fishery on coral reefs around St. Croix, we combined data on parrotfish foraging behavior with data sets on parrotfish abundance and size-structure from fishery-dependent and fishery-independent monitoring efforts. The project had three interlinked components. First, we conducted behavioral observations of parrotfishes on coral reefs in St. Croix to parameterize species- and size-specific models of parrotfish grazing. Next, we applied these species- and size-specific models of parrotfish grazing to NOAA monitoring data sets on the abundance and size-structure of fishes to understand how the grazing impacts of parrotfishes vary spatially around St. Croix. Finally, we synthesized data on parrotfish populations, parrotfish foraging behavior, and the parrotfish fishery to predict the ecosystem-level impacts of the fishery in St Croix. Our results suggest strong fishing impacts on parrotfish populations and ecosystem level processes, and we conclude with a series of management recommendations for ways to reduce negative impacts of parrotfish fisheries on reef ecosystems in St. Croix.

We collected data on the feeding behavior of the dominant species of parrotfishes on St. Croix at three locations on the north shore of St. Croix during June and July 2015. These data confirmed that the seven common species of parrotfishes on shallow high-relief reefs in St. Croix belong to three distinct functional groups (browsers, excavators, and scrapers), with each group being differentially responsible for carrying out key ecological processes (see Table 1). These processes include: 1) clearing space on the reef via the removal of turf algae, 2) removing macroalgae that can compete with established corals and also inhibit coral recruitment, and 3) bioerosion of existing dead coral framework. Data from the behavioral observations were used to parameterize species- and size-specific grazing models, which were then combined with data on the density, size structure, and species composition of parrotfish assemblages from diver surveys. These surveys revealed that parrotfish biomass and modeled grazing impacts varied greatly among depths and habitat types, with highest rates of parrotfish grazing, macroalgal consumption, and bioerosion occurring on shallow, architecturally complex reefs compared to deeper areas and areas of low relief.

According to port sampling by NOAA, the parrotfish fishery in St. Croix is dominated by two species, *Sp. chrysopterum* and *Sp. viride*, which together account for over 80% of the landings by weight. These species belong to different functional groups and are responsible for different ecological processes. As an excavating grazer, feeding by *Sp. viride* results in deep grazing scars denuded of algae that could potentially serve as settlement substrate for corals. In contrast, feeding by *Sp. chrysopterum* rarely results in deep grazing scars as it primarily browses on macroalgae and long sediment-laden turfs that it tears from the reef. In addition, *Sp. viride* is a dominant member of the parrotfish assemblage on high relief reefs in St. Croix, which represent the locations where reef-building corals have historically thrived. In contrast, *Sp. chrysopterum* is relatively uncommon on these reefs.

Several lines of evidence suggest that the parrotfish fishery in St. Croix has had large impacts on parrotfish populations and cascading impacts on ecosystem function. First, like other heavily fished locations in the Caribbean, parrotfish assemblages in St. Croix are dominated by small species. Second, parrotfish biomass is much higher on shallow reefs within Buck Island National Marine Monument (BINMM) where parrotfish have been protected from fishing for more than a decade, compared to shallow locations outside of BINMM. In addition, parrotfish assemblages within BINMM have a higher proportion of relatively large parrotfish species, such as *Sp. viride* and *Sc. vetula*, compared to fishery accessible locations. Finally, monitoring data suggest that populations of *Sp. viride* declined outside of BINMM between 2003 and 2010 relative to inside the reserve, where abundance of *Sp. viride* remained unchanged.

Changes in the overall biomass, size structure, and species composition of parrotfish assemblages can drive major changes in ecological processes on reefs. For example, comparisons of areal grazing rates and bioerosion rates on randomly selected shallow 'pavement' inside and outside of BINMM indicate that areal grazing rates are ~ 2 times higher and bioerosion rates are ~ 3 times higher inside BINMM. These differences are driven almost entirely by the greater abundance of the two relatively large parrotfish species, *Sp. viride* and *Sc. vetula* inside the reserve.

Managing parrotfishes to increase grazing rates in locations most suitable for reef-building corals provides a tangible goal for fisheries management. To achieve this goal, managers must account for the fact that different species and size classes of parrotfishes have unique feeding behaviors and habitat preferences that result in different ecological impacts. For example, of the two major fishery targets in St. Croix (*Sp. viride* and *Sp. chrysopterum*), only *Sp viride* is predicted to be an important driver of overall grazing rates on most coral reefs in St.

Croix. The three parrotfish species that contribute the most to areal grazing rates in St. Croix are *Sc. taeniopterus*, *Sc. vetula* and *Sp. viride*, with the latter two species being especially important on high relief reefs where corals have historically thrived. In contrast, the two species that contribute most to the removal of macroalgae are *Sp. aurofrenatum* and *Sp. rubripinne*. Thus, efforts to increase areal grazing rates of parrotfish assemblages in St. Croix should focus on *Sc. taeniopterus*, *Sc. vetula* and *Sp. viride*, while efforts to increase consumption of macroalgae should focus on *Sp. aurofrenatum* and *Sp. rubripinne*.

Several strategies could be used to reduce fishing effort on *Sp. viride*, *Sc. vetula*, *Sc. taeniopterus*, *Sp. aurofrenatum* and *Sp. rubripinne* in order to increase their abundance on high-relief reefs where they are most likely to benefit reef-building corals. One possibility would be to prohibit the take of these species entirely. A second option would be to enact a spatial management plan prohibiting the take of parrotfishes on the high relief reefs that are deemed critical habitat for endangered corals. We believe that spatial management is likely to be the best option for simultaneously maximizing ecosystem-level and fishery goals. By prohibiting the take of parrotfishes on high-relief reefs, impacts of parrotfish fishing would be largely concentrated in lower-relief areas with less potential for direct and indirect negative impacts on endangered corals. In addition, to the extent that commercial parrotfish fishing in St. Croix already takes place in low relief areas, impacts on fishermen would be minimized.

In addition to commercial fishing, recreational fishing can strongly impact the biomass and size structure of fished populations. The extent of recreational fishing in St. Croix is currently unknown, but we suggest that recreational spearfishers may be an important source of parrotfish mortality on St. Croix and they may be disproportionately important on high-relief reefs. Unlike trap and net fishing, which can be most efficient in low-relief areas or along reef margins, spearfishing is likely to be most effective (and therefore practiced most often) on high-relief reefs where average fish densities tend to be highest. In addition, many parrotfish species are highly susceptible to night spearfishing, making it possible for a few spearfishers to quickly deplete a particular location of parrotfishes. For these reasons, we believe that fishery management plans need to consider potential impacts of recreational as well as commercial fishers on parrotfish assemblages in St. Croix. We believe that managers should consider bans on recreational spearfishing of parrotfishes, particularly at night.

The three largest species of parrotfishes in the Caribbean, *Sc. guacamaia*, *Sc. coelestinus*, and *Sc. coeruleus*, are ecologically extinct on St. Croix, and their take is currently prohibited. These prohibitions are appropriate and should stay in place, as these large parrotfish species have life history traits that make them especially vulnerable to overfishing. In addition, many of the ecological impacts of parrotfishes are size-dependent and some (e.g., bioerosion) can only be achieved by larger individuals and larger species. Thus, there is a need to conserve large species and large individuals. Minimum size limits have also been recently enacted for fished parrotfish species in St. Croix, an appropriate step that will help ensure that parrotfishes reach reproductive size before entering the fishery.

Regardless of the specific fisheries management actions taken, managers will need information from robust fisheries-dependent and independent monitoring programs in order to assess whether management goals are being achieved. NCRMP, TCRMP, DPNR, and TIP monitoring programs are critical tools for making these assessments, but these programs are not currently optimized to understand how changes in fishery management strategies affect species-specific catch and effort, or how changes in catch affect the size-structure, species composition, and ecological impacts of parrotfish assemblages. Thus, we suggest that monitoring programs are re-evaluated with these goals in mind.

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Background

On many coral reefs, including those in the U. S. Caribbean, parrotfishes are both important fishery species that support local economies and key grazers that facilitate the settlement, growth, and survivorship of reef-building corals (Adam et al. 2015a). With their beak-like jaws, parrotfish scrape and excavate algae from carbonate surfaces, eroding the reef framework while provisioning space for coral recruitment (Bruggemann et al. 1996, Hughes et al. 2007, Mumby et al. 2007b, Steneck et al. 2014). Some species of parrotfishes feed on large seaweeds that can inhibit the growth and survivorship of corals (Burkepile & Hay 2008), while others feed on the diminutive algal turfs and endolithic algae that live on and within the reef framework (Bruggemann et al. 1996). As the main drivers of bioerosion, sediment production, and algal consumption in many coral reef ecosystems, parrotfishes play a complex role in both the break-down and regeneration of reefs (Polunin 2001, Bellwood et al. 2012a, Burkepile et al. 2013, Bonaldo & Hay 2014, Jackson et al. 2014).

Many parrotfishes grow exceptionally fast and achieve high population densities in environments with very low standing crops of algae, and populations often increase rapidly following large coral-killing disturbances that liberate space for algal growth (Adam et al. 2011, Gilmour et al. 2013, Russ et al. 2015, Han et al. 2016). Rapid growth rates make parrotfish attractive fishery species, yet fisheries can reduce the abundance and alter the species composition and size structure of parrotfish assemblages (McClanahan 1994, Hawkins & Roberts 2003, Taylor et al. 2015), ultimately impacting the overall structure and function of coral reef ecosystems (Bellwood et al. 2012b, Humphries et al. 2014, Jackson et al. 2014, Bozec et al. 2016).

In addition to their important ecological role, parrotfishes are targeted in reef fish fisheries throughout much of the Caribbean, including the U.S. Virgin Islands and Puerto Rico (SERO-LAPP 2012). Correlational data from reefs experiencing a gradient in fishing pressure suggest that these fisheries can have strong negative impacts on the total biomass, species composition, and size structure of parrotfish assemblages (Hawkins & Roberts 2003, Comeros-Raynal et al. 2012, Vallès & Oxenford 2014). Observational and experimental evidence suggests that reductions in parrotfish density and size structure from fishing may lead to increases in algae, decreases in coral recruitment, and potentially declines in the overall resilience of the ecosystem (Mumby et al. 2007a, Mumby & Harborne 2010, Steneck et al. 2014; but see Kuempel & Altieri 2017). These observations have led some scientists to call for complete bans on the harvest of parrotfishes (e.g. Jackson et al. 2014). While bans have recently been enacted in some places (e.g., Belize, and Bonaire), parrotfish fishing is an economically and culturally significant activity in many locations, including parts of the U.S. Caribbean, which makes complete bans on fishing parrotfish undesirable or unachievable in these locations (SERO-LAPP 2012). Management plans that allow for fishing while preserving the wider ecological roles of parrotfishes provides an alternative to complete fishing bans (Mumby 2014, Adam et al. 2015a, Bozec et al. 2016), and have the potential to provide important fishery yields while maintaining key ecological services. However, development of such management plans requires detailed information about the specific ecological role of different parrotfish species, the levels of fishing that are sustainable, and a framework to integrate these disparate sources of information.

Parrotfish functional groups

Caribbean parrotfishes can be categorized into four functional groups based on their unique foraging behaviors, diets, and capacity for bioerosion (Adam et al. 2018a; Table 1): 1) macroalgal browsers: *Sparisoma chrysopterum*, *Sp. rubripinne*, and *Sp. aurofrenatum*, which feed on large seaweeds and long turfs, 2) excavating/bioeroding grazers: *Sp. viride*, *Scarus guacamaia*, and *Sc. coelestinus*, which feed on short epilithic algal turfs and endolithic algae, 3) scraping grazers: *Sc. vetula*, *Sc. taeniopterus* which feed by scraping and cropping diminutive algal turfs from the reef, and 4) the cropping grazer, *Sc. coeruleus*, which primarily crops long turfs from the reef without scraping the substrate. Each functional group is differentially responsible for carrying out key ecological processes including: 1) clearing space on the reef via the removal of turf algae, 2) removing macroalgae that can compete with established corals and also inhibit coral recruitment, and 3) bioerosion of existing dead coral framework. Despite these major differences between species, parrotfishes in the U. S. Caribbean are currently managed as a single species complex.

Table 1. Functional group classification of nine species of Caribbean parrotfishes based on field observations of foraging behavior, diet, and bite mechanics in the Florida Keys National Marine Sanctuary (Adam et al. 2018a). Browsers feed on significant amounts of macroalgae as well as filamentous turfs. In contrast to scrapers and excavators, browsers tend to feed on longer filamentous turfs which they tear from the reef. Unlike browsers, scrapers and excavators forage on short, sparse filamentous turfs and endolithic algae and CCA which they scrape or excavate from the reef framework.

	Primary bite type	**Grazing scars^A**	**Diet^B**	**Bite rate (b/m)^C**	**Foray size (bites)**
Browsers:					
*Sp. aurofrenatum**	Tearing	occasional	M, LT	low (<10)	median = 1, mean = 1.5
*Sp. chrysopterum**	Tearing	occasional	M, LT	low (<10)	median = 1, mean = 1.4
*Sp. rubripinne**	Tearing	occasional	M, LT	low (<10)	median = 1, mean = 1.3
Excavators:					
*Sp. viride**	scraping/excavating	usual	E, CCA, ST	low (<10)	median = 1, mean = 1.9
Sc. guacamaia	scraping/excavating	usual	E, CCA, ST	I (10-20)	median = 2, mean = 2.7
Sc. coelestinus	scraping/excavating	usual	E, CCA, ST	I (10-20)	median = 2, mean = 3.6
Scrapers:					
*Sc. vetula**	scraping/excavating	often	E, CCA, ST	high (>20)	median = 4, mean = 5.8
*Sc. taeniopterus**	scraping/excavating	often	E, CCA, ST	high (>20)	median =4, mean = 5.4
Croppers:					
Sc. coeruleus	Cropping	rare	LT, S	I (10-20)	median = 2, mean = 3.1

* Species studied in St. Croix

[A] usual > often > occasional > rare
[B] M = macroalgae, LT = Long turf algae, E = endolithic algae, CCA = crustose coralline algae, ST = short turf algae, S = Sand
[C] I = intermediate

<u>*Parrotfish fisheries in the U. S. Caribbean*</u>

The largest parrotfish fishery in the U. S. Caribbean is located on St. Croix (SERO-LAPP 2012). For many years, commercial landings of parrotfishes on St. Croix had approached or exceeded 400,000 lbs. annually (SERO-LAPP 2012). During this time, parrotfishes accounted for nearly one third of landings and 23% of the total fisheries revenue on St. Croix, which was more than any other fishery sector (Valdés-pizzini et al. 2010). While parrotfishes are targeted throughout the island, major fishing grounds are concentrated on the east end of St. Croix including Lang Bank, and on the southwest shore (Figure 1; Valdés-Pizzini et al. 2010). Fish are sold at local markets, with the vast majority of parrotfishes being eaten by residents. This contrasts with other important fishery species, which are sold to local restaurants and hotels that cater to tourists (Valdés-pizzini et al. 2010). Parrotfish are low value relative to other fishery species, such as grouper and snapper, and it is very likely that they have experienced increased fishing pressure in recent decades as stocks of these more commercially valuable species have declined (Rothenberger et al. 2008, Kadison et al. 2017).

Figure 1: Map of STX, showing fishing grounds on east and south shores

Managers have taken several actions in recent years to reduce fishing effort on parrotfishes and/or increase the sustainability of fishing practices on St. Croix in general. These include a moratorium on issuing new commercial fishing permits, the designation of the newly expanded Buck Island Reef National Monument as a fully protected marine reserve (effectively protecting ~ 7% of the St. Croix shelf area from fishing), a prohibition on the use of gill and trammel nets in federal and territorial waters, and a ban on the take of the three largest species of parrotfish in the Caribbean, *Scarus guacamaia*, *Scarus coelestinus*, and *Scarus coeruleus*, among other actions (See Table 2 for detailed timeline of key management actions). In addition, in 2010, annual catch limits (ACLs) of 240,000 lbs. were established for St. Croix, which represented a significant reduction from the estimated ~400,000 lbs taken annually from 2006 to 2008 (SERO-LAPP 2012). Unfortunately, like most small-scale tropical fisheries, parrotfish fisheries in St. Croix are relatively data poor, and fisheries managers lack both reliable fisheries-dependent data, fisheries-independent data, and key demographic information on parrotfishes that are needed to better estimate levels of fishing that are sustainable (SEDAR-26 2011).

Table 2. Timeline of management actions impacting St. Croix USVI

Management action	**Year**	**Area affected**
Establishment of no-take marine reserve around Buck Island Reserve National Monument (BIRNM)	1961	704 acres around Buck Island, St. Croix (259 acre no-take marine reserve)
Establishment of Salt River Marine Sanctuary and Wildlife Reserve; no fishery prohibitions	1995	Limited are amount of coral reef habitat on the north shore of St. Croix, adjacent to Salt River
Expansion of BIRNM and designation as a fully protected no-take marine reserve	2001	19,015 acres around Buck Island, St. Croix
Moratorium on issuing new commercial fishing permits	2001	St. Croix, St. John, and St. Thomas
Establishment of the East End Marine Park	2006	60 square miles (5 square miles of no-take marine reserves)
Annual catch limits (ACLs) for parrotfish (240,000 lbs)	2010	State and federal waters around St. Croix, St. John, and St. Thomas
Prohibition of the harvest of the three largest species of Caribbean parrotfishes (*Sc. coelestinus*, *Sc. guacamaia*, and *Sc. coeruleus*)	2012	State and federal waters around St. Croix, St. John, and St. Thomas

In addition, while sustainable fishing levels have traditionally been defined based on population metrics such as maximum sustainable yield, managers are increasingly tasked with taking an ecosystem-based approach to fisheries management (NOAA 2016). In the case of parrotfishes, this requires understanding not only how different harvest strategies will impact parrotfish populations, but also how changes in parrotfish assemblages resulting from fishing will impact the overall resilience of the coral reef ecosystem. An ecosystem based approach to fisheries management (EBAFM) must also consider the direct and indirect effects of fisheries on protected species (NOAA 2016). In the Caribbean, managers must consider the potential impacts of parrotfish fisheries on the ability of parrotfishes to provision critical habitat for corals species listed under the U.S. Endangered Species Act (ESA) (NOAA 2011). This is an exceedingly difficult task given that fisheries managers currently lack the data needed to estimate the impacts of the fishery on parrotfish populations, much less how these impacts will cascade to affect reef ecosystems and specific coral species through a series of nonlinear interactions in complex, spatially heterogeneous ecological communities. Here we summarize the results of a three year study funded by the NOAA Coral Reef Conservation Program to synthesize available information on parrotfish populations in St. Croix and to assess potential impacts of the parrotfish fishery on reef ecosystems. We conclude by highlighting knowledge gaps and by providing concrete recommendations to managers in the face of high levels of uncertainty.

Overall Project Findings

1. Patterns of Parrotfish Grazing in St. Croix

To estimate feeding impacts of parrotfishes on the reefs of St. Croix, we used field derived estimates of bite rate, bite area, bite volume, total algal consumption and proportion of diet comprised of macroalgae for each of 7 species that account for > 99% of the parrotfish biomass on reefs in St. Croix. We used these parameters to calculate key metrics of herbivory for each species of parrotfish, including the proportion of reef area scraped (referred to as ‘area scraped’), biomass of macroalgae removed, and bioerosion. We then combined these data on species and size-specific estimates of ecological impacts with survey data from NCRMP as well as survey data collected specifically for this project (Adam et al. 2018b) to summarize the contribution of each species to each ecological process in different habitats around St. Croix.

1.1 *Parrotfish foraging behavior in St. Croix*

In order to parameterize grazing models specific to St. Croix, we collected data on the feeding behavior of the following six species of parrotfishes, *Sc. taeniopterus*, *Sc. vetula*, *Sp. aurofrenatum*, *Sp. chrysopterum*, *Sp. rubripinne*, *Sp. viride*) at three locations (Long Reef, Cane Bay, and Buck Island) on the north shore of St. Croix during June and July 2015 (Adam et al. 2016) (Figure 2).

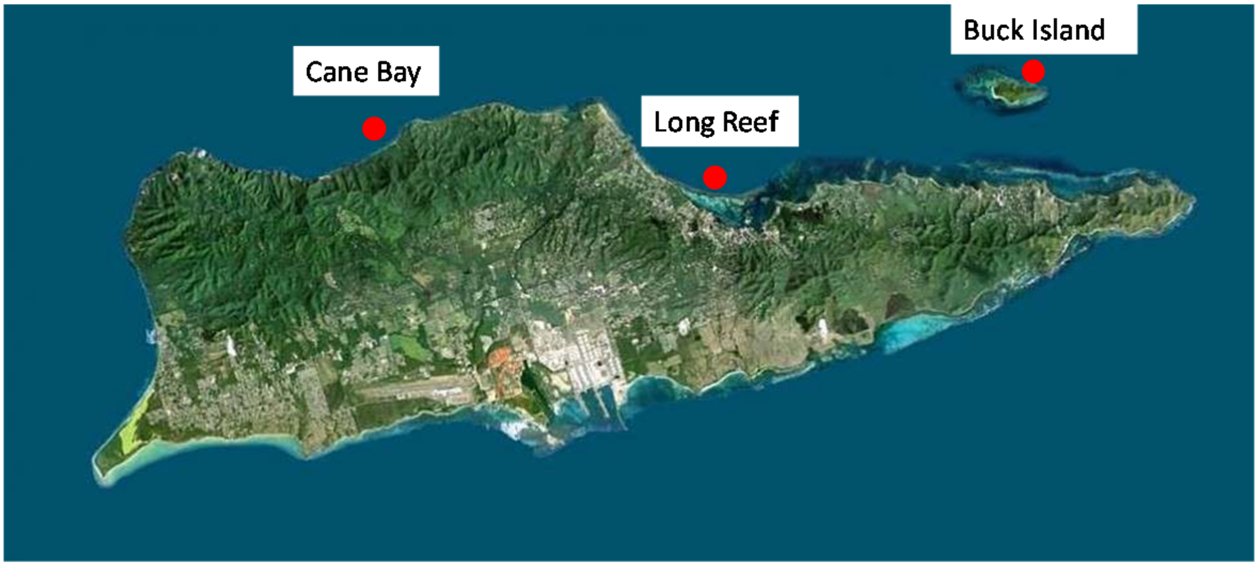

Figure 2. Satellite image of St. Croix, U. S. Virgin Islands showing locations of the three study sites.

To quantify parrotfish behavior, approximately six individuals of each species were observed per site for 20 min each. Foraging behavior was recorded by a SCUBA diver while towing a GPS receiver (Garmin GPS 72) attached to a surface float, which obtained position fixes of the focal fish at 15 second intervals. Fish were followed from a close distance (~ 2 m when possible), and food items were identified to the lowest taxonomic level possible, with macroalgae and coral usually identified to genus or species. We also recorded the type of substrate targeted during each foraging bout, categorizing each substrate as one of the following: (1) dead coral, (2) coral pavement, (3) boulder, (4) rubble, (5) ledge, or (6) sand. Dead coral included both convex and concave surfaces on the vertical and horizontal planes of three dimensional coral skeletons that were attached to reef substrate. Coral pavement was carbonate reef with little topographic complexity (i.e., flat limestone pavement). Boulder was large remnants of dead mounding corals not clearly attached to the bottom and often partially buried in sand. Coral rubble consisted of small dead coral fragments (generally < 10 cm in any dimension) that could be moved with minimal force. Ledges were dead coral substrates with a slope greater than 90 degrees. In order to quantify the relative abundance of different substrates and food types, we estimated the percent cover of algae, coral, and other sessile invertebrates on each of the six substrates commonly targeted by parrotfishes (dead coral, coral pavement, boulder, rubble, ledge, and sand) in 0.5 m x 0.5 m photoquadrats. Photographs were taken at 2.5 m intervals on 30 m transects, with a total of 10 haphazardly placed transects sampled at each site. Each photoquadrat was divided into sixteen 12 cm x 12 cm sections which were individually photographed, and percent cover was estimated from 9 stratified random points per section (N = 144 point per quadrat).

Foraging behavior and diets of parrotfishes in St. Croix were qualitatively similar to what has been reported in other locations in the Caribbean (Randall 1967, Lewis 1985, Bruggemann et al. 1994, McAfee & Morgan 1996, Cardoso et al. 2009, Adam et al. 2015c). In addition, quantitative comparisons of food preferences and foraging behavior for fishes in St. Croix and the Florida Keys indicated that fishes were behaving similarly in the two systems (Roycroft

2018; Figure 3). This confirms that the functional group framework we developed in the Florida Keys (Table 1) is robust and can be applied to fishes in St. Croix.

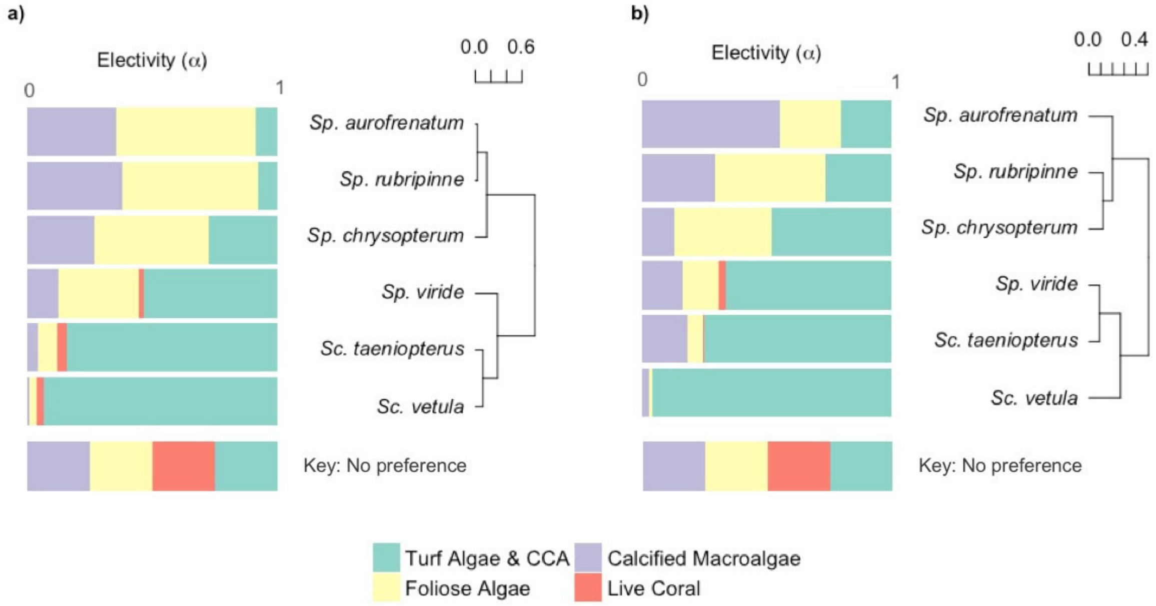

Figure 3. Species-averaged dendrograms using food preference data collected at a) FKNMS, and b) St. Croix. The bar labeled "Key: No preference" represents what the distribution would look like if a species were to exhibit no preference for a food item. Dendrograms for both FKNMS and St. Croix show that parrotfishes cluster into two groups based on their food preference. Bar charts show the mean electivity α, of each food group targeted (N = ~18 individuals per species).

1.2 Using behavioral data to estimate ecological impact

To estimate feeding impacts, we used estimates of bite rate, bite area, bite volume, total algal consumption and proportion of diet comprised of macroalgae for each of 7 species that account for > 99% of the parrotfish biomass on reefs in St. Croix. Species included: *Scarus iseri, Sc. taeniopterus, Sc. vetula, Sparisoma aurofrenatum, Sp. chrysopterum, Sp. rubripinne,* and *Sp. viride*. When possible, we used species-specific data from St. Croix (Table 3). We estimated bite rate and proportion of macroalgae in the diet of different sized fishes from behavioral observations made in St. Croix (Adam et al. 2016, described above). For species that were likely to graze the substrate, we analyzed photographs of haphazardly selected bites to examine the probability of leaving a grazing scar, the size of scars that were made, and the relationship between these responses and fish size (Adam et al. 2018a). From these data we derived parameters on bite rate and proportion of the diet comprised of different food items, and how food item selection varied with fish size. We used these parameters to calculate key metrics of herbivory for each species of parrotfish, including the proportion of reef area scraped (referred to as 'area scraped'), biomass of macroalgae removed, and bioerosion. Because previous work has shown that the bite rate, bite area and volume, and diet of different parrotfish species are dependent on size (Bruggemann et al. 1996, Lokrantz et al. 2008, Adam et al. 2018a), all parameters were size-specific.

Total algal consumption for each species of parrotfish was estimated using the following empirically-derived relationship between herbivore size and consumption (van Rooij et al. 1998):

$$C = 0.0342 \times W^{0.816} \qquad (1)$$

where C is the daily intake of organic carbon of an individual fish and W is the wet body mass of the fish. Estimated fish length from diver surveys was converted to body mass using published length-weight relationships (Table 3). To estimate the amount of macroalgae consumed by a fish we multiplied the mean proportion of bites that targeted macroalgae (Table 3) by total consumption. For three species of fish, *Sp. aurofrenatum*, *Sp. chrysopterum*, and *Sp. rubripinne*, macroalgal consumption was strongly size-dependent (Adam et al. 2018). For these species, we modeled the proportion of bites that targeted macroalgae using the following equation:

$$P = exp(Z+X*L)/(1+exp(Z+X*L)) \qquad (2)$$

Where P is the probability that a bite will be on macroalgae, L is the total length of a fish in cm, and Z and X are species specific scaling parameters estimated from logistic regression.

These calculations resulted in species-specific estimates of macroalgal consumption in units of grams of organic carbon per day. In addition to knowing the total amount of algae and macroalgae removed by parrotfishes, we also estimated areal grazing rates of scraping and excavating parrotfishes. Areal grazing rates provide an estimate of the area of the reef fish can keep free of algae and potentially make available for the settlement of coral larvae (Mumby 2006). Areal grazing rates were estimated by combining data on bite scar size, bite rate, and the probability that a bite would leave a grazing scar. Bite scar size was estimated according to the following equation (Bruggemann et al. 1994):

$$B = M \text{ x } L^2 \qquad (3)$$

where B is the area of the bite scar (in units of cm^2), M is a species-specific scaling parameter, and L is the total length of a fish in cm. We used empirically derived estimates of M for *Sc. vetula* and *Sp. viride* based on the work of Bruggemann and colleagues (1994) in Bonnaire. This assumes that bite scar size is constant among locations and that the relationship between bite scar size and total length is identical among species within the genus *Scarus*. Unlike previous models of parrotfish grazing (e.g., Mumby 2006) that also assume a constant relationship between bite scar size and total length within the genus *Sparisoma*, our observations suggest that *Sparisoma* species other than *Sp viride* generally do not scrape or excavate the substrate while foraging and only occasionally leave a visible grazing scar (Adam et al., 2018a; see also Cardoso et al. 2009). Thus, these species were not included in the calculation of areal grazing rates.

Bite rate was calculated using the following equation:

$$R = A \text{ x } L + B \qquad (4)$$

where R is bites per minute and A and B are species-specific parameters, estimated via least squares linear regression from the previously described behavioral observations of parrotfishes on the north shore of St. Croix (Adam et al. 2018b).

The proportion of bites that left a grazing scar were modeled with the following equation:

$$S = exp(C+D*L)/(1+exp(C+D*L) \qquad (5)$$

Where C and D are species specific scaling parameters estimated from logistic regression and L is the total length of a fish in cm.

In order to calculate the area of reef scraped per year by an individual fish we used the following calculation:

$$A = S_s \text{ X } B_s \times R_s \times 219{,}000 \qquad (6)$$

where A is the area scraped by an individual parrotfish in units cm^2 year^{-1}, B_s, R_s, and S_s are species-specific bite scar sizes and bite rates from equations (3), (4), and (5), and 219,000 is the estimated number of minutes a fish spends grazing per year (assuming constant grazing rates over a period of 10 hours per day). To estimate the total area of the reef scraped by an assemblage of parrotfish we used the following calculation:

$$TG = \sum_{S=1}^{S} A_s \qquad (7)$$

where S is the total number of species and A_s is the total area scraped per species from equation (5). This gives us on estimate of the area of the reef scraped by a parrotfish assemblage, and allows us to partition grazing among species and size classes. In order to aid interpretation, we then converted *TG* to a proportional rate to estimate the proportion of the reef scraped per year by each species. Note that this calculation does not account for the fact that the surface area of the reef will be greater than its footprint. We could correct for this using site-specific rugosities (e.g., Mumby 2006). However, we have chosen to focus on how parrotfish assemblage structure impacts areal grazing rates for a constant rugosity since we think this information is most relevant to management.

In addition to calculating macroalgal consumption and areal grazing rates, we also estimated bioerosion rates. We estimated the volume of carbonate removed per bite using the following equation

$$V = P \text{ x } L^3 \quad (8)$$

where V is the volume of the bite scar (in units of cm^3), P is a species-specific scaling parameter, and L is the total length of a fish in cm. Similar to our calculations of bite area, species-specific scaling parameters were obtained from Bruggemann and colleagues (1996) for *Sc. vetula* and *Sp. viride*, and extrapolated to other species. The volume of the material removed was then converted to mass based on published densities of reef carbonate (we assumed an average density of 1.5 g cm^{-3}). Bioerosion rates were then scaled up to the individual- and assemblage-level following the same logic as areal grazing rates.

Table 3. Herbivory parameter estimates, with variable names in parenthesis. In all cases, size of fish is total length (TL) in cm. Blank cells indicate that a given parameter does not apply. Parameters that include a size slope and intercept were not included for those species for which there was no relationship between size of the fish and that aspect of foraging. Superscripts indicate source of data.

Species	Proportion macroalgae	Proportion macroalgae size intercept (Z)	Proportion macroalgae size slope (X)	Bite scar coef. (M)	Bite rate slope (A)	Bite rate intercept (B)	Bite scar intercept (C)	Bite scar slope (D)	Volume coef. (P)	Length-weight (a)	Length-weight (b)
Scarus iseri	0.037[1]			4.01E-04[2a]	0.87[1]	39.4[1]	2.21[3]	0.035[3]	1.93E-07[4a]	0.017[5]	3.02[5]
Scarus taeniopterus	0.037[1]			- 4.01E-04[2a]	0.87[1]	39.4[1] -	2.21[3]	0.035[3]	1.93E-07[4a]	0.018[5]	3.0[5]
Scarus vetula	0.008[1]			4.01E-04[2] -	0.64[1]	34.9[1]	1.31[3]	0.035[3]	1.93E-07[4]	0.019[5]	3.045[5]
Sparisoma aurofrenatum		-2.65[1]	0.102[1]	-		- -				0.0047[5]	3.43[5]
Sparisoma chrysopterum		-7.97[1]	0.268[1]							0.0099[5]	3.17[5]
Sparisoma rubripinne		-4.42[1]	0.153[1]							0.019[5]	3.0[5]
Sparisoma viride	0.043[1]			5.84E-04[2]	0[1]	5.14[1]	1.17[3]	0.071[3]	1.30E-06[4]	0.025[5]	2.92[5]

1. This study
2. Bruggemann et al 1994; 2a. Values applied from *Sc. vetula*
3. Adam et al. in press
4. Bruggemann et al 1996; 4a. Values applied from *Sc. vetula*
5. Bohnsack and Harper 1994

1.3 Biogeography of parrotfish foraging impacts

In order to determine which parrotfish species are driving ecological processes on coral reefs in St. Croix, we combined data on parrotfish behavior with data on the density, size structure, and species composition of parrotfish assemblages from diver surveys conducted as part of the National Coral Reef Monitoring Program (NCRMP). The data we analyzed were collected by trained divers in 2015 through a collaboration between NOAA's Biogeography Branch, NOAA SEFSC, National Park Service, Virgin Islands Department of Planning and Natural Resources, the Nature Conservancy, the University of the Virgin Islands, and the University of Miami. Briefly, nearshore benthic habitat maps were used to inform a random stratified sampling design where survey locations were randomly chosen in different habitat types, depth strata, and regions in waters < 30 m deep around the entire island of St. Croix. At each location, divers counted all individual fish encountered on 25 m X 4 m wide belt transects and estimated their sizes by placing fish in 5 cm size bins. We used published length-weight relationships and species- and size-specific foraging parameters (Table 3) to estimate the biomass of different parrotfish species and to estimate their predicted ecological impacts in the different habitats. A total of 239 surveys were conducted in 5 different habitat types (Fig. 4).

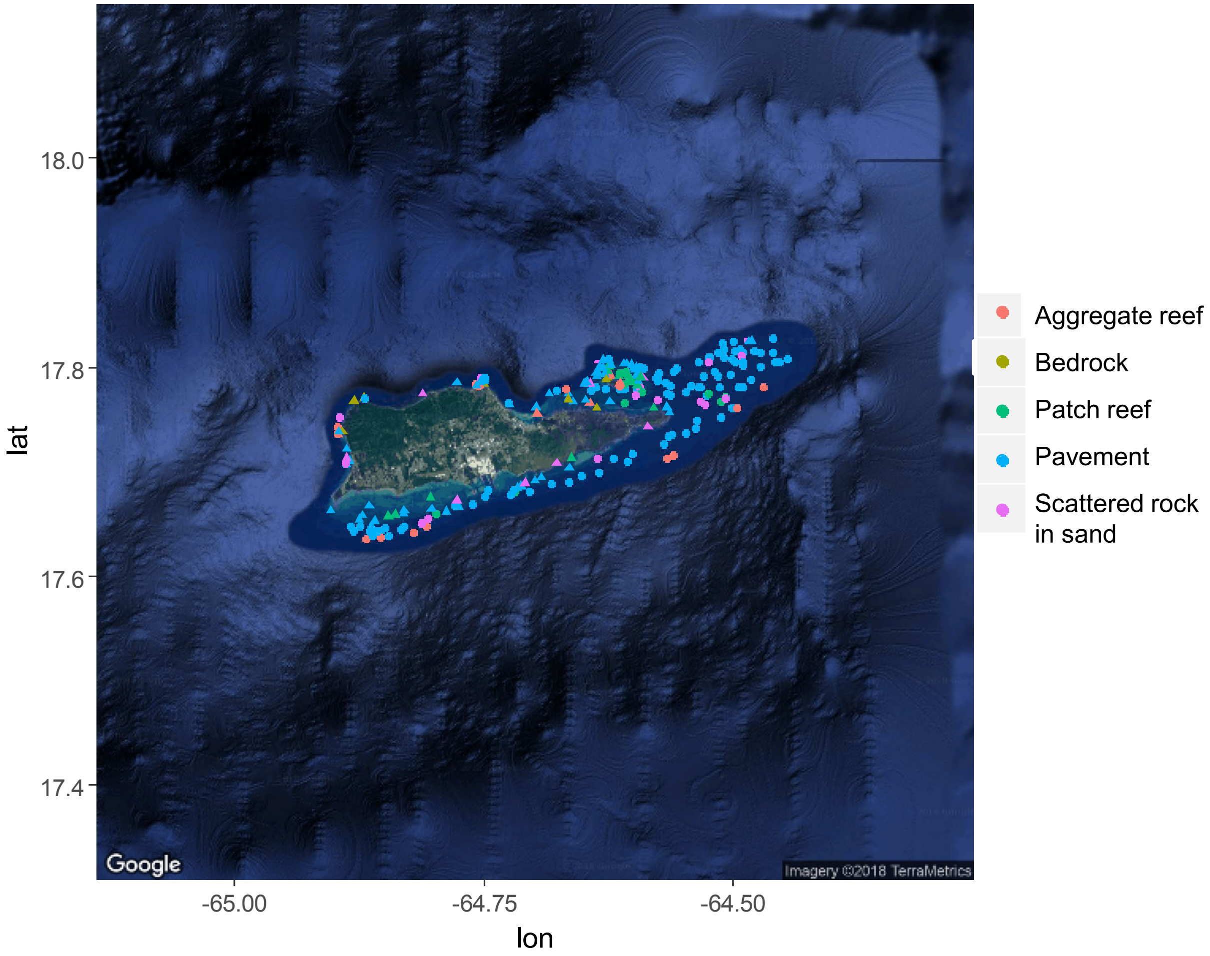

Figure 4. Locations of NCRMP sites surveyed in 2015 in five different habitat types (denoted by the different colored points). Reefs > 12 m depth ('deep reefs') are depicted as circles (aggregate reef, n = 15; bedrock, n = 0; patch reef, n = 12; pavement, n = 98, scattered rock in sand = 17) and reefs < 12 m depth ('shallow reefs') are depicted as triangles (aggregate reef, n = 8; bedrock, n = 8; patch reef, n = 14; pavement, n = 57, scattered rock in sand = 10).

Parrotfish biomass and predicted ecological impacts varied greatly among depths and habitat types (Figs. 5 and 6). On deep reefs, three species of parrotfish, *Sc. taeniopterus*, *Sp. aurofrenatum*, and *Sp. viride*, accounted for the majority of parrotfish biomass in all habitat types (Fig 5). Each of these three species belong to separate functional groups that are responsible for different ecological processes (Table 1). Biomass of all three species tended to be highest on architecturally complex reefs (i.e., aggregate reefs, patch reefs) relative to lower relief areas (i.e., pavement and scattered rock in sand). As a result, architecturally complex reefs had higher rates of macroalgae removal, areal grazing, and bioerosion, with different species driving each of these key processes (Fig. 5).

Shallow reefs tended to have a more diverse parrotfish assemblage compared to deep reefs, with larger differences in parrotfish biomass and species composition among habitat types. Architecturally complex reefs (i.e., aggregate reefs, patch reefs) had much higher parrotfish biomass and associated grazing and bioerosion rates compared to low relief areas (i.e., bedrock, pavement, scattered rock in sand) (Fig. 6). *Sp. aurofrenatum* and *Sp. rubripinne* were more abundant on high relief reefs, resulting in higher rates of macroalgae removal. *Sc. vetula* was also more abundant on high relief reefs, where it was a major driver of areal grazing rates, likely reflecting the affinity of this species for shallow high-relief habitats where they tend to feed on short, productive, sediment-free turfs (Adam et al. 2015b, Adam et al. 2018). Similar to deep reefs, bioerosion rates in all habitats were largely driven by the abundance of *Sp. viride*, which was much more abundant on high relief reefs compared to low relief areas. High relief reefs in shallow habitats experienced similar rates of macroalgae removal, but higher rates of areal grazing and bioerosion compared to deeper reefs, largely due to greater abundances of *Sc. vetula* and *Sp. viride.*

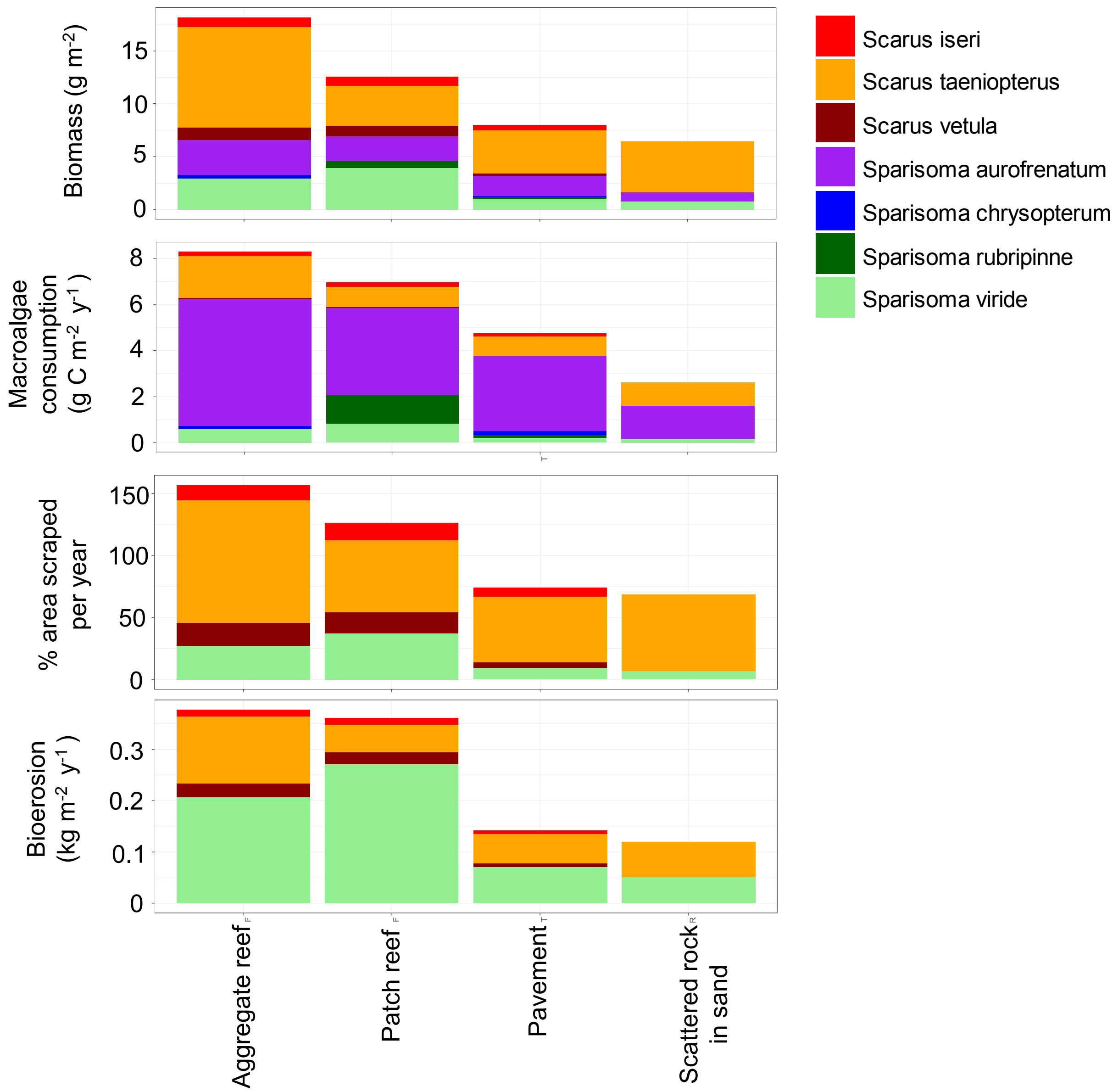

Figure 5. Mean (a) biomass, (b) macroalgal consumption, (c) areal grazing, and (d) bioerosion rates of 7 species of parrotfishes across 5 different habitat types on deep (> 12 m) reefs in St. Croix during 2015. Ecological processes were estimated based on species- and size-specific parameters based on behavioral observations of fishes in St. Croix and elsewhere (Table 3). See figure 5 for sample sizes.

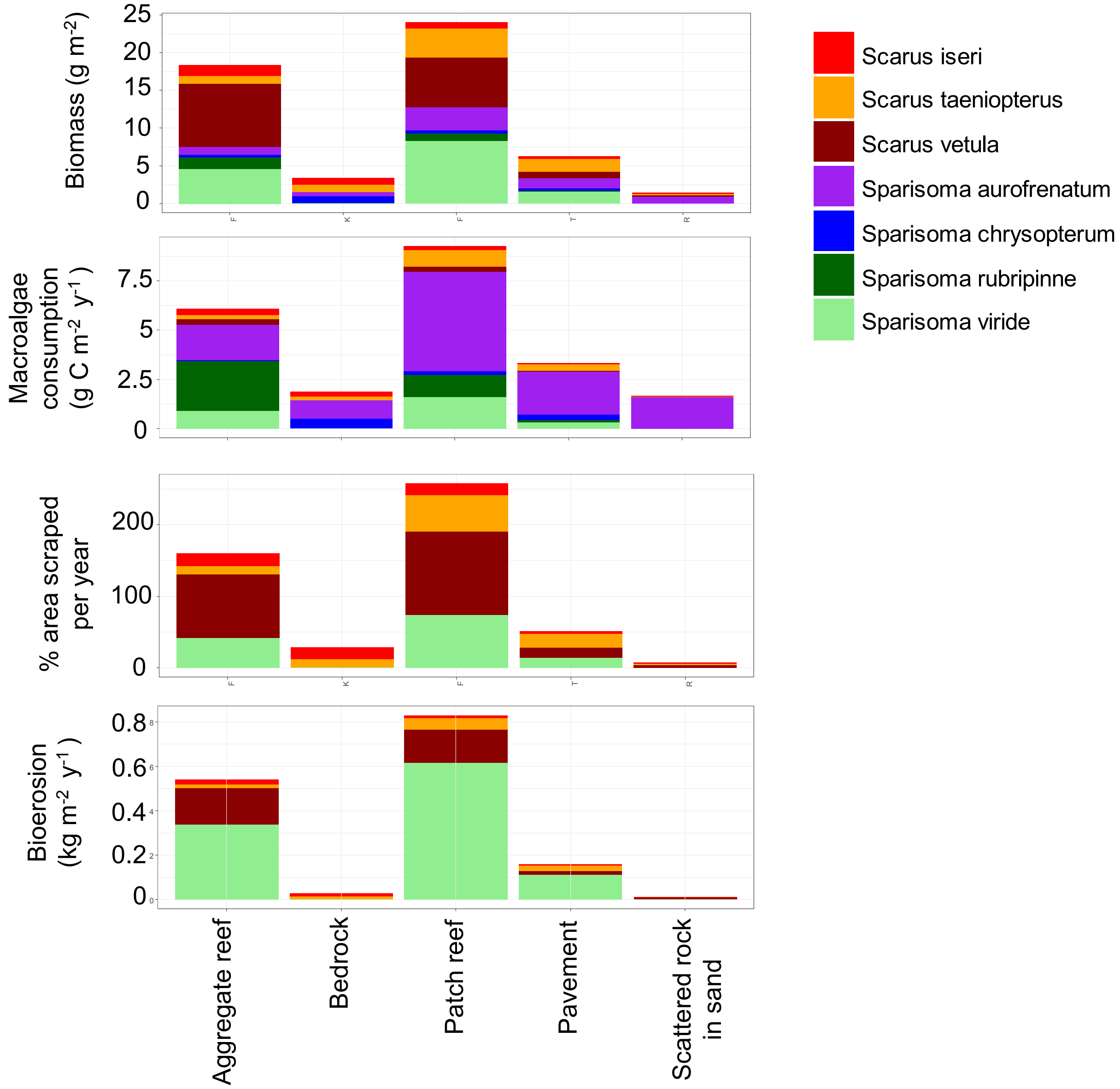

Figure 6. Mean (a) biomass, (b) macroalgal consumption, (c) areal grazing, and (d) bioerosion rates of 7 species of parrotfishes across 5 different habitat types on shallow (< 12 m) reefs in St. Croix during 2015. Ecological processes were estimated based on species- and size-specific parameters based on behavioral observations of fishes in St. Croix and elsewhere (Table 3). See figure 5 for sample sizes.

2. Fisheries Impacts on Parrotfish Populations and Ecosystem Function

Commercial, artisanal, and recreational fishing can strongly impact the species composition, size structure, and total biomass of fish assemblages (Hawkins & Roberts 2003, Jackson et al. 2014, Edwards et al. 2014). A recent global meta-analysis comparing coral reefs in remote locations with reefs that are accessible to fisheries suggests that fishing reduces the biomass of herbivorous fishes by approximately half, with even larger impacts on some functional groups (Edwards et al. 2014). However the magnitude of the fishing impact varies greatly among systems due to a variety of factors (e.g., variation in productivity, fishing intensity, management, etc.) that could potentially exacerbate or mitigate fishery impacts.

In addition to knowing the extent that fisheries reduce the biomass and alter the species composition and size structure of fishes, managers also need to know how these shifts impact overall ecosystem processes. Here we use several complementary approaches, using fishery-dependent and fishery independent data, to estimate fishing impacts on herbivorous parrotfishes and the ecosystem processes they perform in St. Croix, USVI.

2.1 Fisheries targets

Two different data sets were used to evaluate parrotfish fishery targets and fishing gears: 1) the National Marine Fisheries Service Southeast Fisheries Science Center's (SEFSC) Trip Interview Program (TIP) and 2) commercial landings data from the USVI Department of Planning and Natural Resources (DPNR) commercial catch record (CCR). TIP and CCR data were accessed in July 2018 from the SEFSC. TIP data are collected by port samplers who interview fishermen and measure their catch. CCR data are fishermen reported catch records that include landings by family (and more recently species) with information on the fishing trip, including the fishing gears used.

According to the fishermen reported CCR records, the parrotfish fishery peaked in 2007 at nearly 450,000 lbs and has since declined to less than 100,000 lbs (Fig. 7). The apparent decline coincided with a reduction in the ACL (Table 2). It is difficult to know the extent that the decline represents a reduction in effort, a decline in fishable biomass, or underreporting of catch by fishermen. Parrotfishes are primarily caught using nets or by spear or hand while diving (Fig. 7). In the past, parrotfishes were also landed in traps, but the trap fishery has declined in recent years and currently represents only a small fraction of the total parrotfish fishery (Fig. 7)

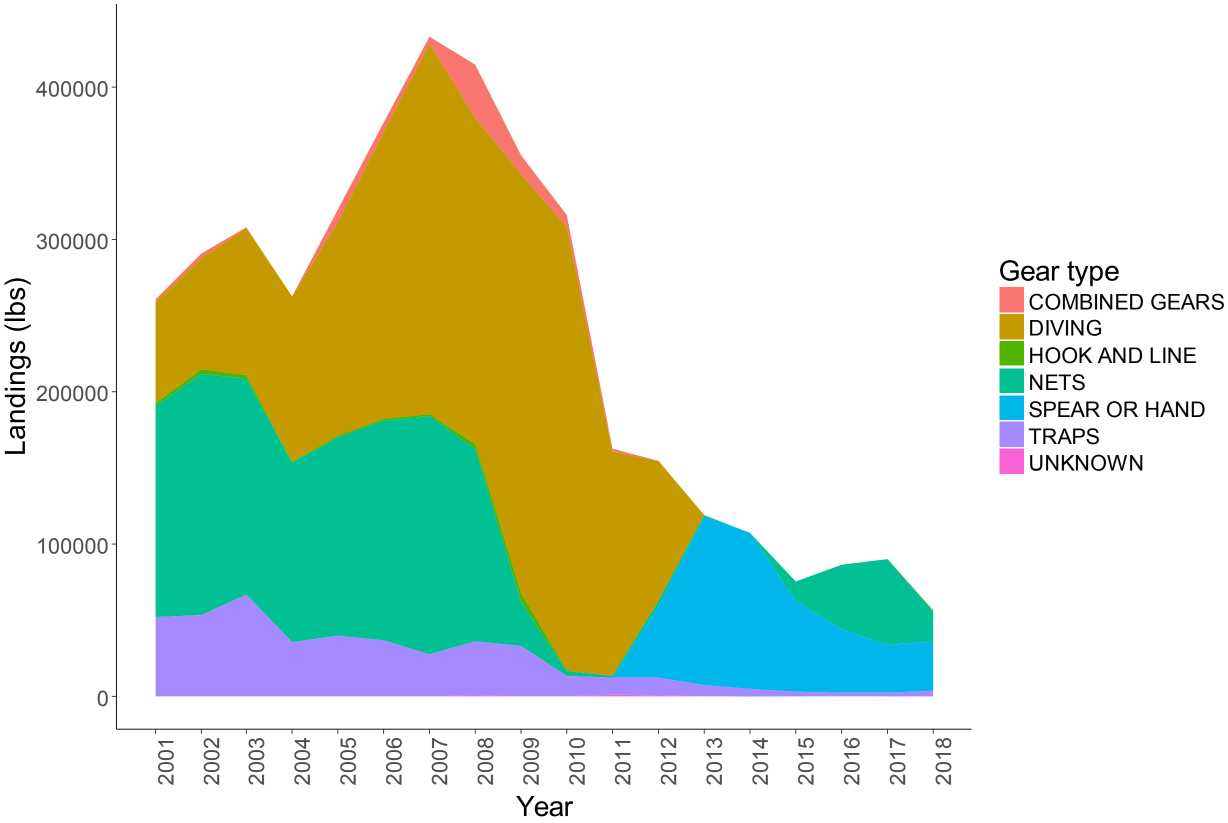

Figure 7. Annual parrotfish landings in St. Croix by gear type from 2001 to 2018 (source: CCR).

According to the TIP data, two species of parrotfishes, *Sparisoma chrysopterum* and *Sparisoma viride*, comprise over 85% of the catch, with *Sparisoma chrysopterum* alone accounting for nearly 50% of the catch (Figure 8). *Sp. chrysopterum* and *Sp. viride* belong to different functional groups (Table 1; Adam et al. 2018) and the two species have distinct ecological roles (Figs. 5 and 6). *Sp. viride* is an excavator that is the major driver of bioerosion on most reefs around St. Croix (Figs. 5 and 6) and elsewhere in the Caribbean. In addition to removing reef carbonate, the excavating feeding mode used by *Sp. viride* results in deep grazing scars denuded of algae that could potentially be colonized by coral larvae or CCA. In contrast, *Sp. chrysopterum* tends to browse on macroalgae and long sediment-laden turfs that it tears from the reef (Adam et al. 2018). In addition, *Sp. chrysopterum* is relatively uncommon on the hard-bottom habitat sampled by NCRMP (Figs. 5 and 6) and tends to be more abundant on low-relief pavement areas compared to high-relief reefs (Adam et al. 2015b, Mumby 2014). Further, when present on high-relief reefs, *Sp. chrysopterum* tends to feed on highly sedimented turfs growing on unstable coral rubble or low relief substrate that is likely to be poor settlement habitat for corals and other reef calcifiers (Adam et al. 2015b, Adam et al. 2018). Thus, *Sp. chrysopterum* and *Sp. viride* are likely to have fundamentally different impacts on reef ecosystems.

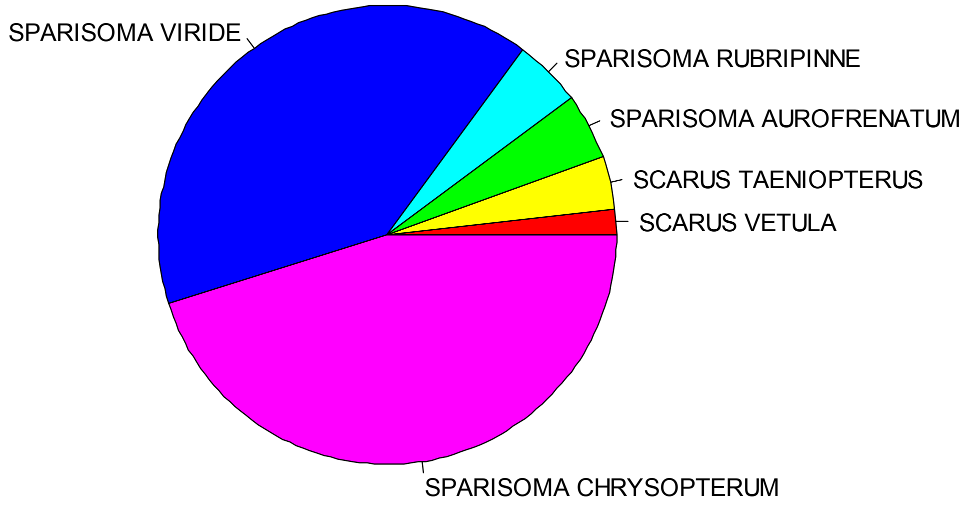

Figure 8. Species composition of parrotfish catch by weight (source: TIP).

2.2 Regional and historical context

Humans were exploiting near-shore environments of the Caribbean long before modern ecological studies (Jackson 1997). Thus, time series spanning the period before and after the development of fisheries generally do not exist, and ecologists are forced to use indirect methods to estimate fishery impacts. In regions where a gradient of fishing intensity exists, fishery impacts are often inferred by comparing across locations with different levels of fishing pressure (e.g.,Friedlander & DeMartini 2002, Hawkins & Roberts 2003, Sandin et al. 2008). Such indirect methods have the potential to confound natural spatial variability with fisheries impacts (Schmitt & Osenberg 1996), yet they can be useful when combined with other historical and ecological data. Here we compare the biomass, species composition, and size structure of parrotfish assemblages in St. Croix with several other locations in the Caribbean that experience different levels of fishing pressure, including fishery protected sites within St. Croix. We find that, like other heavily fished locations in the Caribbean, parrotfish assemblages in St. Croix are dominated by small species. Together with qualitative historical data, these observations suggest that fisheries in St. Croix have had pervasive impacts on the parrotfish assemblage.

According to NCRMP data, mean parrotfish biomass on different reef types in St. Croix varied between ~ 1 to 25 g m^{-2} (Figs. 5 and 6). This variation falls within the normal range for Caribbean reefs. For example, according to Jackson et al. (2014), median parrotfish biomass for Caribbean reefs from 2000 to 2012 was ~ 11 g m^{-2}. Further, Jackson et al. (2014) found that approximately a quarter of reefs surveyed had parrotfish biomass less than 6 g m^{-2}, while more than a quarter had parrotfish biomass greater than 20 g m^{-2}. Importantly, the NCRMP surveys include reefs inside and outside of a large marine reserve (BINMM) that has been well protected from fishing for more than a decade. Thus, to better understand the potential impacts of fisheries in St. Croix on parrotfish assemblages we compared parrotfish biomass, assemblage structure, and predicted ecological impacts inside and outside of BINMM.

Unfortunately, the two habitat types that had the highest biomass and diversity of parrotfishes on St. Croix, shallow aggregate reefs and shallow patch reefs, were only sampled four and five times, respectively, outside of BINMM, precluding a comparison of fishery accessible and unfished locations for these important habitat types. Therefore comparisons between BINMM and the rest of St. Croix can only be made for 'pavement', which tends to have low parrotfish biomass and diversity compared to high relief reefs (Figs. 5 and 6). These comparisons indicate that parrotfish biomass on shallow pavement is nearly 2-fold greater inside BINMM compared to the same habitat outside BINMM. Differences in parrotfish biomass were primarily driven by a greater abundance of the two large species, *Sp. viride* and *Sc. vetula*, within BINMM. As a result, areal grazing rates were > 2-fold greater and bioerosion rates were > 3-fold greater inside BINMM compared to outside BINMM on shallow pavement (Fig. 9). On deep pavement, parrotfish biomass and species assemblages were similar inside and outside of BINMM, although reefs outside BINMM had higher abundance of *Sc. taeniopterus*, and as a result had ~ 1.5-fold greater areal grazing rates and bioerosion rates compared to reefs inside BINMM (Fig. 9).

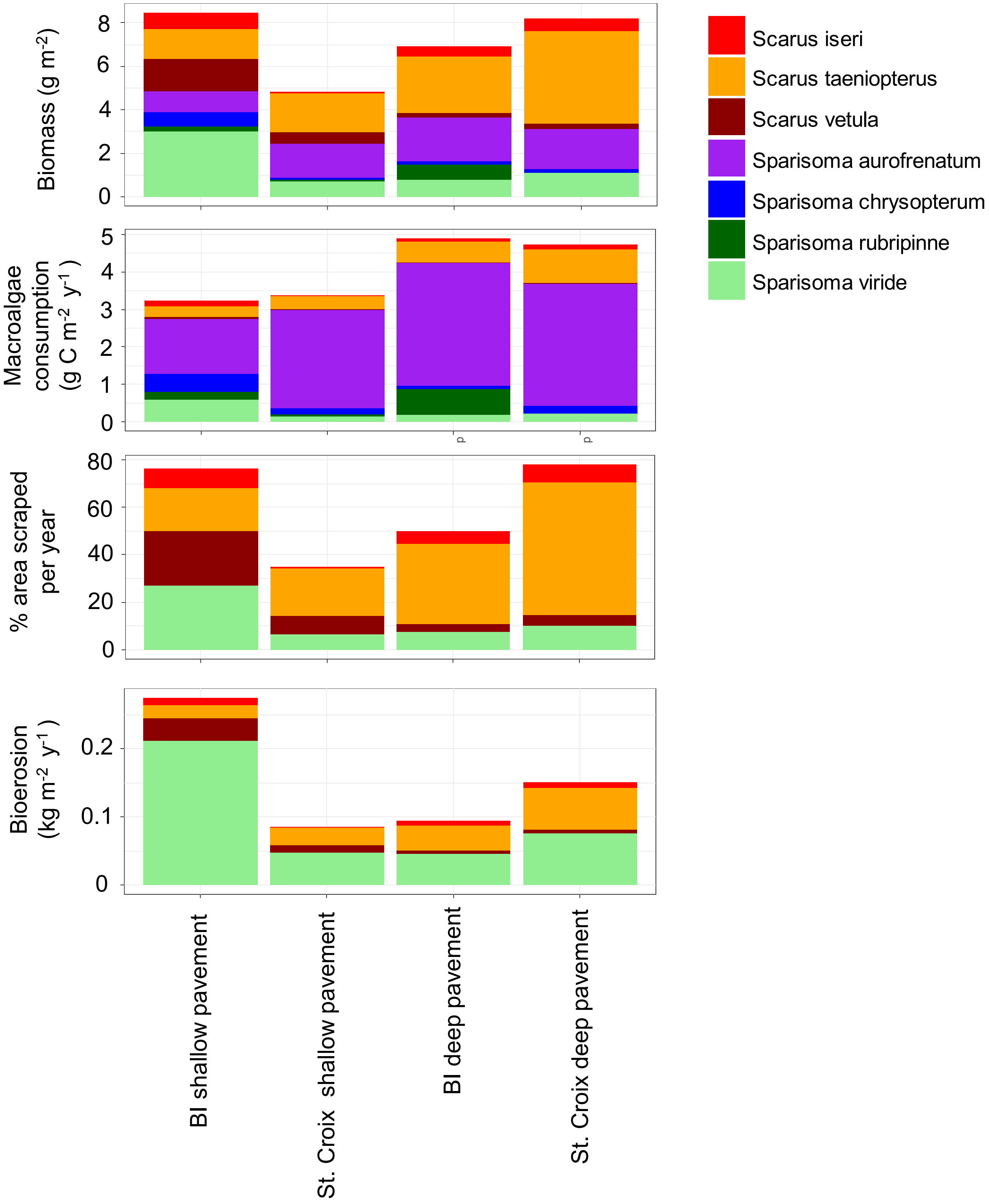

Figure 9. Mean (a) biomass, (b) macroalgal consumption, (c) areal grazing, and (d) bioerosion rates of 7 species of parrotfishes of 7 species of parrotfishes on shallow (< 12 m) and deep (>12 m) pavement habitat inside and outside of BINMM during 2015.

In addition to reducing total parrotfish biomass, intense fishing pressure should select for parrotfish species with life history traits that make them resilient to fishing (e.g., small size, fast growth rates, early onset of reproduction) (Taylor et al. 2014). Caribbean parrotfishes vary greatly in size and related life history traits. Thus, we would expect that variation in fishing intensity could be a major driver of parrotfish assemblage structure, with higher fishing intensity selecting for smaller, shorter lived species. To contextualize the parrotfish assemblage structure in St. Croix, we plotted the relative biomass of ten species of parrotfishes that vary by ~ 2 orders of magnitude in weight across reefs in St. Croix and other locations in the Caribbean.

Data from six locations were replotted from Hawkins and Roberts (2003) who argued that the differences in parrotfish assemblage structure across locations were driven by differences in fishing pressure. Data from the remaining 4 locations are from ongoing fishery-independent monitoring programs run by NOAA in the FKNMS and USVI (NCRMP data from the USVI plus RVC surveys in Florida led by the SEFSC). As described above, these data include counts from openly fished reefs in St. Croix as well as on reefs protected from fishing in BINMM. In addition, we also plot data from St. Thomas/St. John, which experiences lower levels of parrotfish fishing compared to St. Croix (NOAA 2012). Finally, we also included data from the FKNMS, which experiences extremely low levels of parrotfish fishing. To facilitate comparisons among locations, we restricted the NOAA data to shallow (< 12 m depth on St. Croix and St. John/St. Thomas; < 6 m in the FKNMS) low relief areas, since this was the only habitat type that was sampled sufficiently in all locations. In St. Croix and St. Thomas/St. John, this corresponded to the 'shallow pavement' strata, while in FKNMS data are from the 'shallow forereef'. In both St. Croix and St. Thomas/St. John, data are from NCRMP surveys conducted in 2015. Data for the FKNMS are aggregated from surveys conducted annually between 2003 and 2012.

The data from Hawkins and Roberts illustrate that parrotfish biomass in heavily fished locations, such as Jamaica, tends to be dominated by small species such as *Sp. aurofrenatum* and *Sc. taeniopterus* (Fig. 10). In contrast, in places with lower fishing pressure, such as Bonaire, parrotfish assemblages are often dominated by larger species such as *Sp. viride* and *Sc. vetula* (Fig. 10). The data from Hawkins and Roberts also illustrate that the largest species in the Caribbean, *Sc. guacamaia*, *Sc. coelestinus*, and *Sc. coeruleus*, are rare or absent on most reefs throughout the region. In fact, these species are currently found in high densities only on reefs that are very well protected from fishing (Debrot et al. 2008, Comeros-Raynal et al. 2012).

Similar to other heavily fished locations in the Caribbean, reefs in St. Croix tend to be dominated by small parrotfish species, such as *Sp. aurofrenatum* and *Sc. taeniopterus* (Fig. 10). In contrast, in BINMM, where a fishing ban has been effectively enforced for more than a decade, parrotfish assemblages are dominated by the larger species, *Sp. viride* and *Sc. vetula* (Fig. 10). On St. Thomas and St. John, where reefs are generally fishery accessible, but where there are lower levels of parrotfish fishing than St. Croix, the relative biomass of small and large species is intermediate between Buck Island and fishery accessible reefs in St. Croix (Fig 10). Importantly, it is only in FKNMS (where parrotfishes have historically been unfished) that the three largest species of parrotfishes are present. These large species are virtually absent from reefs in the Virgin Islands but were abundant enough in the 1960s that they were frequently caught in poison stations by Jack Randall, who described them as being moderately abundant at the time (Randall 1963, 1967).

Thus, with the exception of BINMM (which has been effectively protected from fishing for over a decade), the reefs around St. Croix are dominated by smaller parrotfish species. Comparison with heavily and lightly fished locations elsewhere in the Caribbean, as well as with a fishery protected site on St. Croix, suggest that this is a fishing effect. In addition, historical data suggest that the virtual absence of the three largest species in the Caribbean from the reefs of St. Croix is a recent phenomenon.

While these patterns are highly consistent with a fishing effect, it is important to point out that factors in addition to fishing mortality can structure parrotfish assemblages (Adam et al. 2015a). For example, different parrotfish species have unique habitat preferences (Adam et. al 2015b). We attempted to control for habitat differences by stratifying data by depth and reef type, such that similar depth ranges and broad habitat types were compared across reefs. Nonetheless, some systematic habitat differences may remain. For example, the reefs in BINMM are well-developed and highly architecturally complex. These habitat attributes could be one factor driving the differences in parrotfish assemblage structure. For example, *Sc vetula*, which was overrepresented at BINMM compared to reefs elsewhere in St. Croix, tends to be strongly associated with high relief reefs (Adam et al. 2015b). In contrast, the smallest species, *Sp. aurofrenatum*, which was underrepresented at BINMM, appears to be more of habitat generalist and is less strongly associated with shallow high-relief reefs (Adam et al. 2015b).

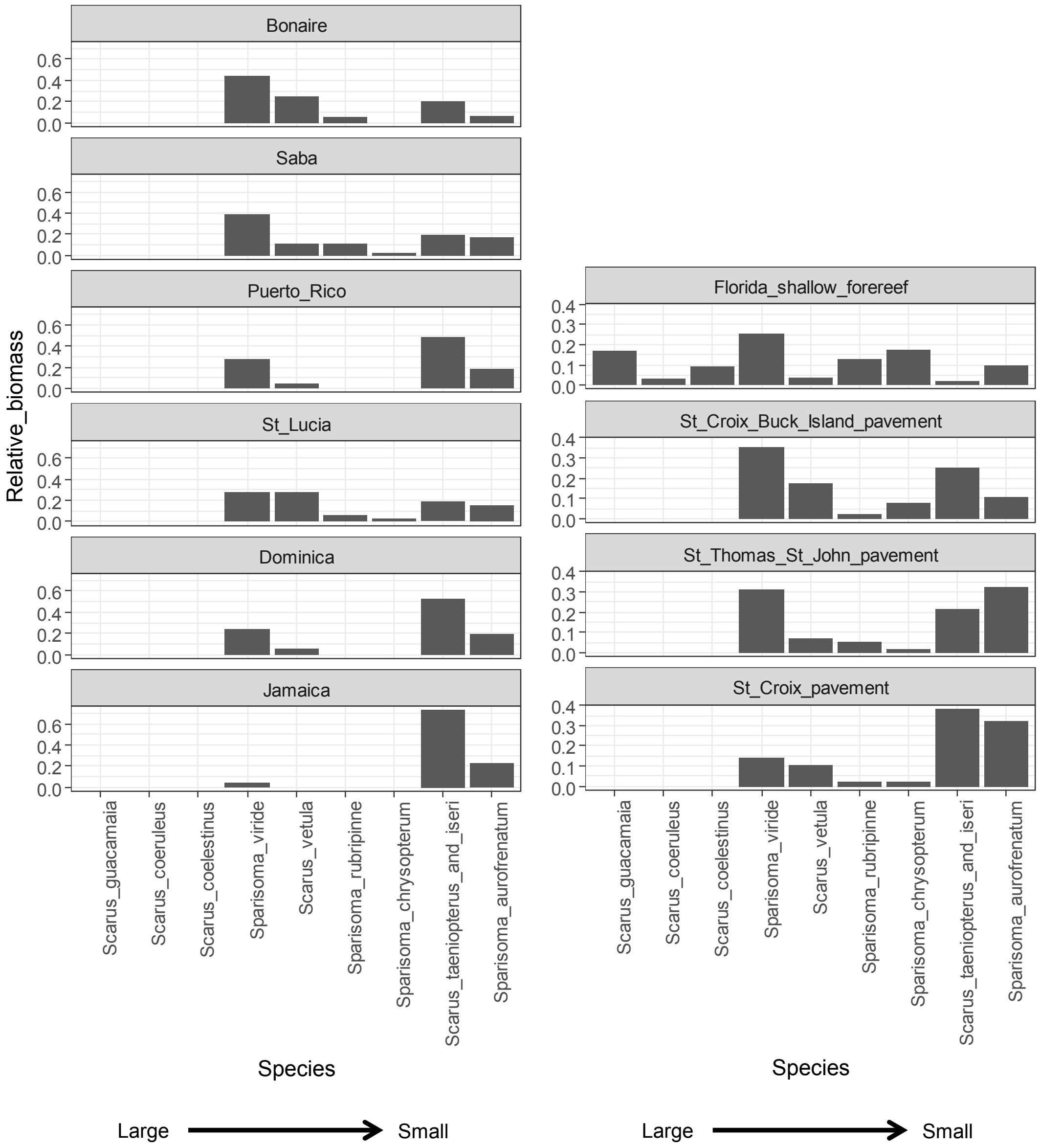

Figure 10. Mean relative biomass of parrotfishes per count, where species are arranged along the x-axis in order of decreasing size. The six panels on the left were redrawn from Hawkins and Roberts (2003) and are stacked in order of decreasing fishing pressure (top least, bottom most fished). Note that the relative abundance of large species declines with increasing fishing pressure. Panels on the right are from ongoing fishery-independent monitoring programs run by NOAA. Fishes were counted by trained divers in circular plots or on belt transects. Parrotfishes are unfished on reefs in Florida. In St. Croix, parrotfishes are protected from fishing on Buck Island where fishing is prohibited. Note that the relative biomass of large species decreases from Florida, where parrotfishes have been historically protected from fishing, to Buck Island where a fishing ban has been strongly enforced for over a decade, to the rest of St. Croix, where parrotfish are fished commercially and recreationally.

2.3 Parrotfish dynamics in relationship to recent management actions

In addition to comparing parrotfish biomass and assemblage structure inside and outside of BINMM, we also compared parrotfish population trajectories inside and outside of BINMM following the expansion of the reserve and enforcement as a 'no-take' marine reserve. For these analyses we used visual surveys conducted biannually in north eastern St. Croix by NOAA's Biogeography Branch of the Center for Coastal Monitoring and Assessment from 2003 to 2010. Locations of surveys were selected using a simplified random stratified design, which distinguished all 'hard bottom' habitats from 'soft bottom' habitats. Because we are interested in the impacts of parrotfish on coral reefs, we focus exclusively on hard bottom habitat. Between 2003 and 2010, approximately 1000 surveys were conducted with ~ 54% of surveyed reefs being inside BINMM, and the remaining reefs being outside the monument in the East End Marine Park (EEMP) (Fig. 11). A small number of sites were excluded from analyses because they were in deep water (> 100 feet) or did not have rugosity measurements (See Table 4 for sample sizes).

Table 4. Number of sites by year and management strata from 2003 to 2010 used in analyses.

	2003	2004	2005	2006	2007	2008	2009	2010
BINMM	79	45	77	95	50	83	39	41
EEMP	78	50	79	77	39	76	25	39

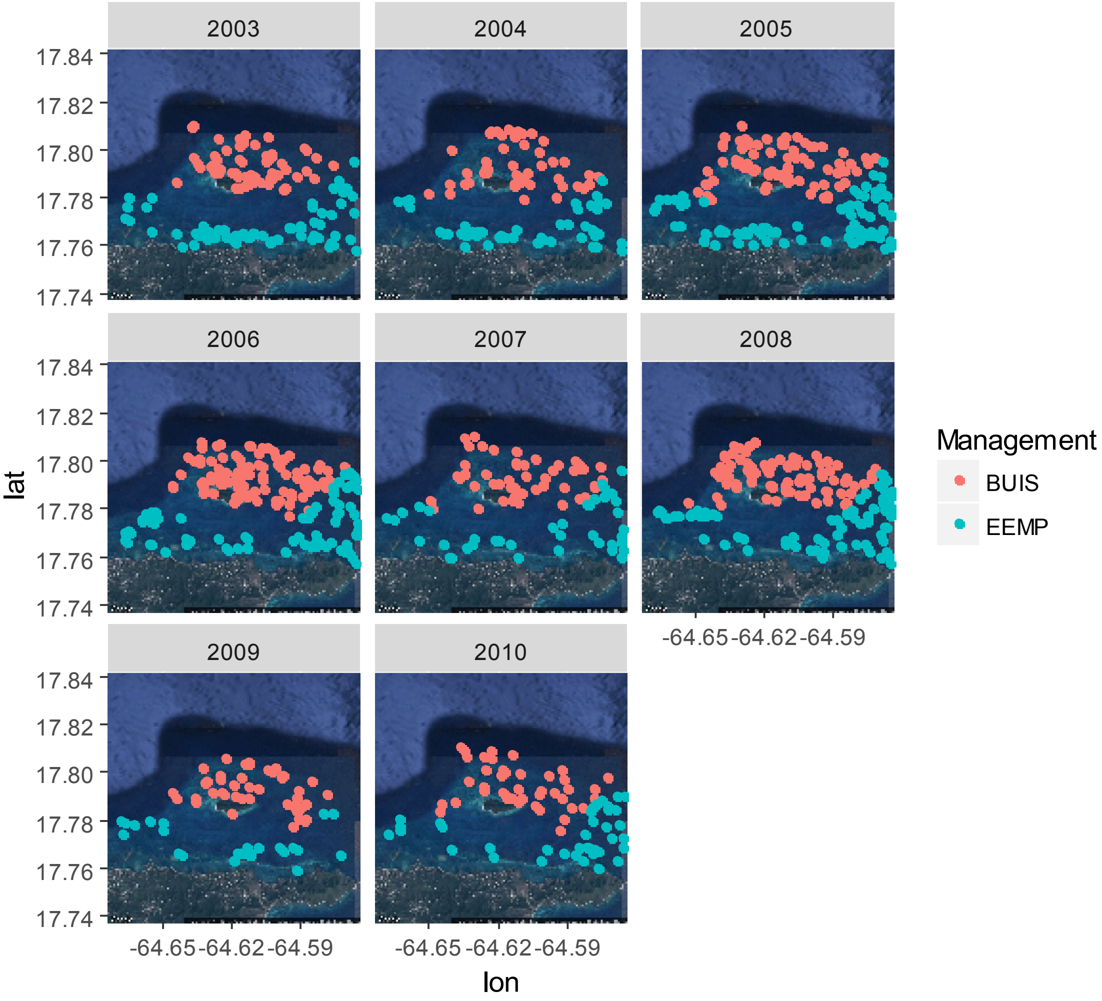

Figure 11. Satellite image of north eastern St. Croix showing locations of fish surveys conducted inside and outside of BNMM between 2003 and 2010. Enforcement of a fishing ban inside BNMM began in 2003, shortly after the expansion of the monument in 2001 (BUIS = Bucks Island National Marine Monument; EEMP = East End Marine Park).

Enforcement of BINMM as a no-take marine reserve, where fishing is prohibited, began in 2003 with compliance increasing through time (Pittman et al. 2008). Thus, if fishing were having a negative impact on parrotfish populations, we would expect an increase in parrotfish abundance inside of BINMM relative to sites outside of the reserve. In addition, we would expect heavily fished species to have a larger positive response to the reserve compared to lightly fished species. To test these hypotheses, we modeled parrotfish counts inside and outside of

BINMM using a generalized linear mixed model with a quasi-poisson distribution to account for overdispersion. Two separate analyses were conducted for the two most abundant species, *Sp. viride* and *Sp. aurofrenatum*. *Sp. viride* is the largest species of parrotfish regularly encountered on St. Croix (Fig. 10) and is a common fishery target (Fig. 8). In contrast, *Sp. aurofrenatum* is the smallest common species of parrotfish on St. Croix (Fig. 10) and contributes much less to the fishery (Fig. 8). We anticipated that the abundances of both species would be strongly impacted by habitat characteristics that covary spatially, and thus we used a mixed model framework to explicitly account for habitat variables (rugosity and depth) and spatial autocorrelation. Before running the statistical models, we first interpolated counts of *Sp. viride* and *Sp. aurofrenatum* for all years combined (2003 to 2010) using ordinary krigging as implemented by the R package 'krigging'(Olmedo 2014). While these interpolations do not account for any temporal trends, they are a useful tool for visualizing the spatial scales over which parrotfish abundances vary. The interpolations indicated that the abundance of both *Sp. viride* and *Sp. aurofrenatum* were highly patchy at scales of 100s of meters to several kilometers (Figs. 12 and 13).

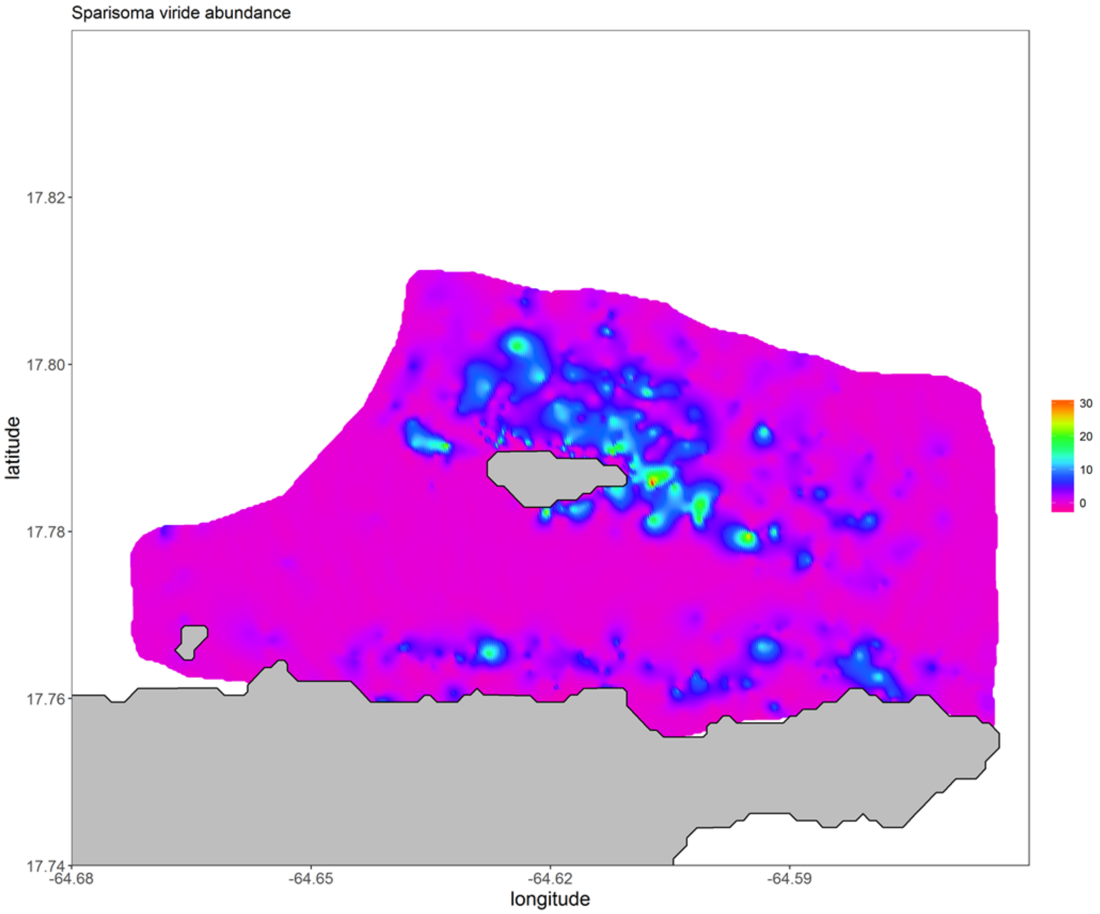

Figure 12. Interpolated abundance of *Sparisoma viride* based on 972 surveys of hard bottom habitat conducted between 2003 and 2010.

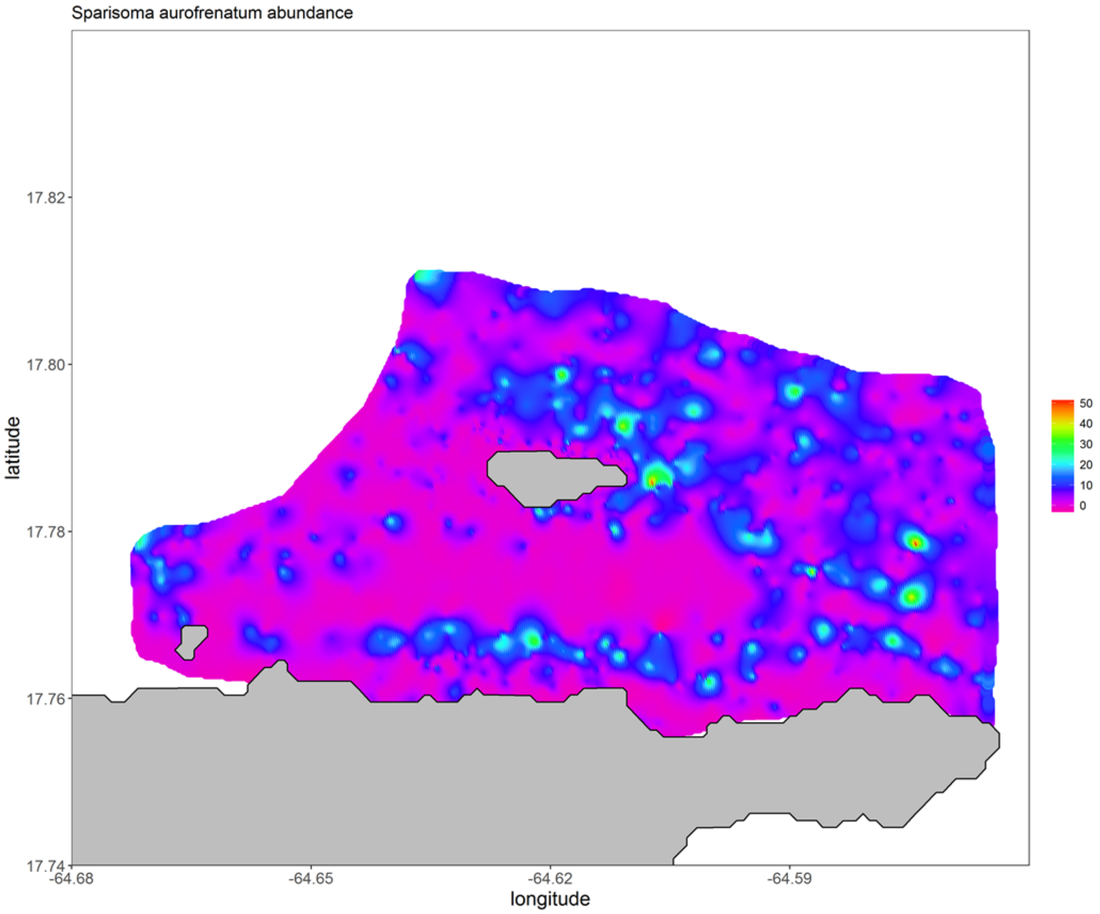

Figure 13. Interpolated abundance of *Sparisoma aurofrenatum* based on 972 surveys of hard bottom habitat conducted between 2003 and 2010.

Analysis of the dynamics of *Sp. viride* indicated a significant interaction between management zone and year (P = 0.03) with *Sp. viride* abundance tending to decline outside of BINMM while increasing slightly or remaining unchanged within BINMM (Fig. 14). In contrast, there was no significant interaction between management type and year for *Sp. aurofrenatum*, with *Sp. aurofrenatum* apparently exhibiting no temporal trends inside or outside of BINMM (Fig. 15). These results suggest a potential positive effect of protection from fishing within BINMM on the abundance of *Sp. viride*.

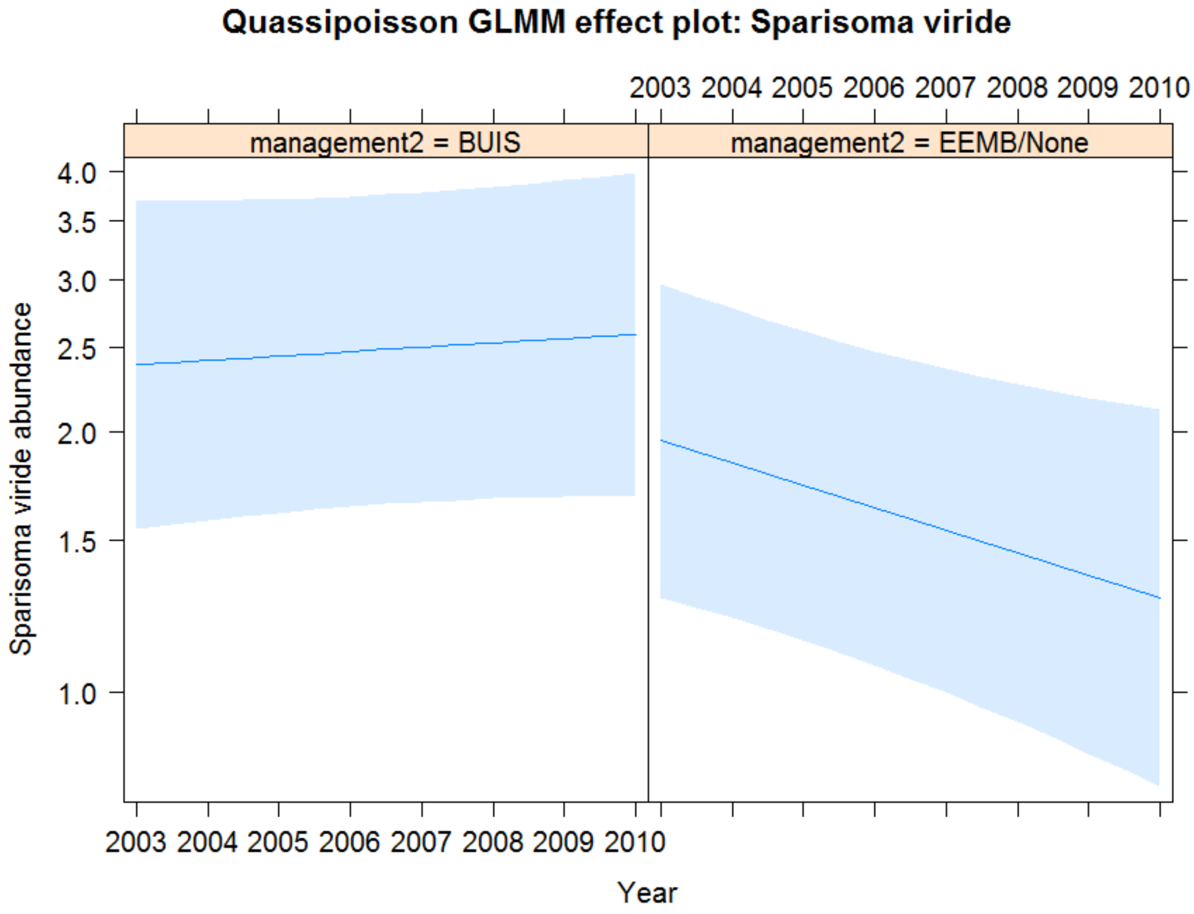

Figure 14 Effects plot from generalized linear mixed effect model showing that *Sp. Viride* abundance remained constant within BINMM (management2 = BUIS) while declining outside of BINMM (management2 = EEMB/None) between 2003 and 2010

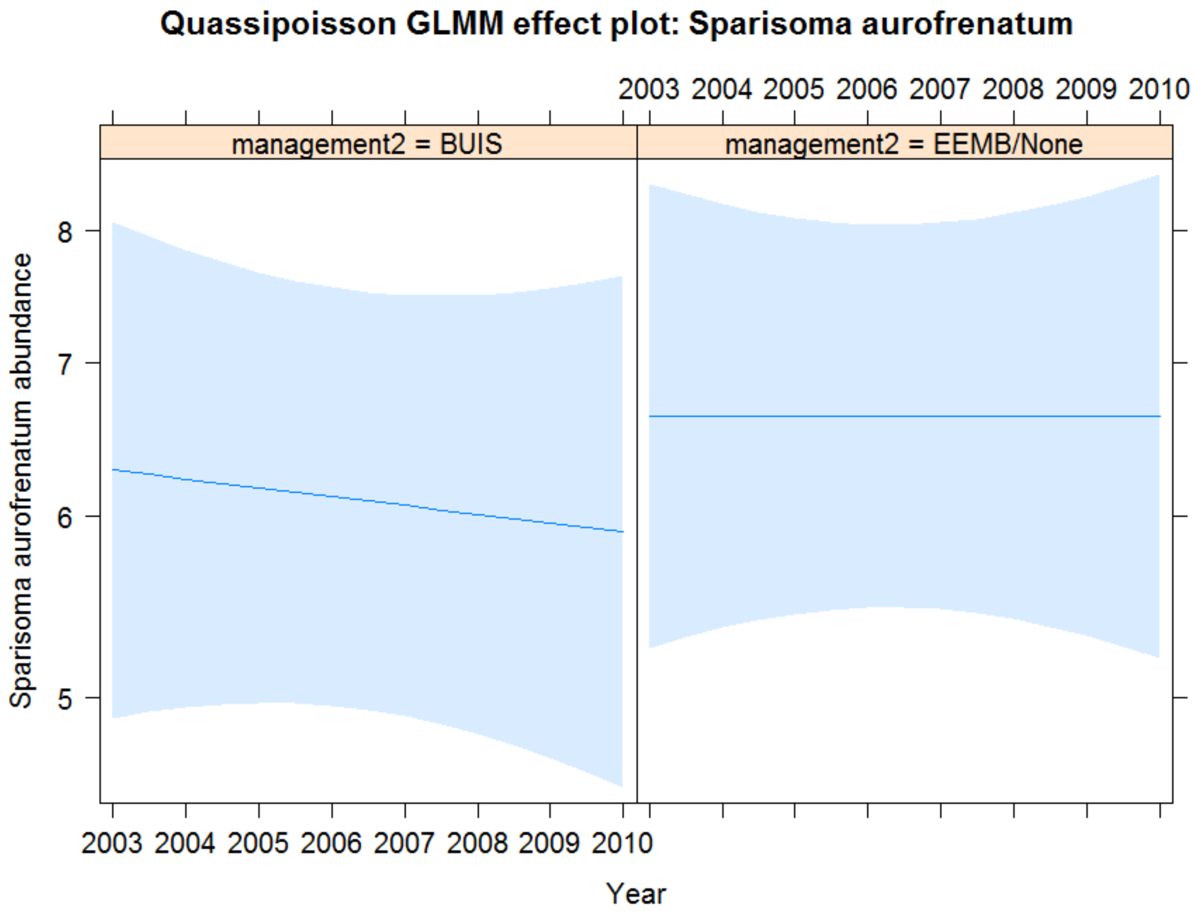

Figure 15. Effects plot from generalized linear mixed effect model showing no difference in the dynamics *Sp. aurofrenatum* inside (management2 = BUIS) vs outside of BINMM (management2 = EEMB/None).

2.4 Summary of parrotfish fishery impacts

The reefs of the USVI were considered overfished by some researchers as early as the 1950's (Randall 1963). Nevertheless, at that time, several large grouper and snapper species as well large parrotfish species, such as *Sc. coelestinus*, were relatively common (Randall 1967). Today, the largest parrotfish species, *Sc. guacamaia*, *Sc. coeruleus*, and *Sc. coelestinus*, are functionally extinct on St Croix as are many commercially important species of grouper and snapper that were previously abundant (Kadison et al. 2017). Parrotfishes—which historically have had little commercial value—are currently a major component of the reef fish fishery in St. Croix, comprising as much as one third of reported landings in recent years (Valdés-pizzini et al. 2010).

Several lines of evidence suggest that the parrotfish fishery in St. Croix has had large impacts on parrotfish populations and cascading impacts on ecosystem function. First, like other heavily fished locations in the Caribbean, parrotfish assemblages in St. Croix are dominated by small species. Second, parrotfish biomass is much higher on shallow reefs within BINMM, where parrotfish have been protected from fishing for more than a decade, compared to shallow locations outside of BINMM. In addition, parrotfish assemblages within BINMM have a higher proportion of relatively large parrotfish species, such as *Sp. viride* and *Sc. vetula*, compared to fishery accessible locations. Finally, monitoring data suggest that populations of *Sp. viride* declined outside of BINMM between 2003 and 2010 relative to inside the reserve, where abundance of *Sp. viride* remained unchanged.

Yet, despite these multiple lines of evidence, it is currently not possible to use monitoring data to quantitatively estimate the impact of the fishery on parrotfish populations or grazing impacts for a number of reasons. These include: 1) lack of historic data, 2) unknown levels of poaching inside BINMM, 3) low number of comparable reference sites outside of BINMM, 4) high levels of natural spatial variability in parrotfish abundance, and 5) insufficient protection time to allow recovery of larger longer lived species, such as *Sc. guacamaia*, *Sc. coelestinus*, and *Sc. coeruleus*. Nonetheless, comparisons of parrotfish biomass and grazing impacts inside and outside of BINMM are instructive. In shallow pavement areas inside BINMM, where grazing is dominated by the two large species, *Sp. viride* and *Sc. vetula*, areal grazing rates are > 2-fold greater, and bioerosion rates are > 3-fold greater compared to shallow pavement areas outside of BINMM (Fig. 9). In contrast, in deeper pavement areas, where grazing and bioerosion are dominated by the smaller species, *Sc. taeniopterus*, areal grazing rates and bioerosion rates are ~ 1.5 fold greater outside of BINMM than inside BINMM (Fig. 9). These comparisons illustrate that the impacts of the parrotfish fishery are likely to vary across habitats and depths due to differences in the species composition of the parrotfish assemblage and differences in the susceptibility of different parrotfish species to the fishery. Specifically, habitats where ecological processes are dominated by larger species (which tend to be more heavily fished and more susceptible to a given level of fishing pressure) are likely to be impacted more greatly by the fishery than other habitats. In St. Croix, large parrotfish species, such as *Sp. viride* and *Sc. vetula*, appear to be disproportionately important for areal grazing rates in shallow areas compared to deep areas. Grazing by these two species also appears to be disproportionately important in many high relief habitats, which represent the locations where reef-building corals have historically thrived. Similarly, the relatively large species, *Sp. rubripinne*, appears to be disproportionately important for the consumption of macroalgae in shallow, high-relief habitats. Protection of these species from fishing is therefore predicted to have positive effects on overall grazing rates in these important habitats.

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Appendix 1: Biogeography of parrotfish foraging impacts

Tom Adam

September 5, 2018

Data Sources

For this analysis we used the folowing data set: Hile, S. 2016. National Coral Reef Monitoring Program: Assessment of coral reef fish communities in St. Croix, U.S. Virgin Islands from 2015-06-08 to 2015-06-19 (NCEI Accession 0151727). NOAA National Centers for Environmental Information. Dataset. [[https://doi.org/10.7289/V5F769MM (https://doi.org/10.7289/V5F769MM)]

```
fish<-read.csv("NCRMP_STX2015_FishAbundance_FINAL.csv", header = T)
```

Data attributes

```
str(fish)
```

```
## 'data.frame':    7051 obs. of  29 variables:
##  $ X                    : int  1 2 3 4 5 6 7 8 9 10 ...
##  $ survey_index         : int  9360 9360 9360 9360 9360 9360 9360 9360 9360 9360 ...
##  $ region               : Factor w/ 1 level "STX": 1 1 1 1 1 1 1 1 1 1 ...
##  $ survey_year          : int  2015 2015 2015 2015 2015 2015 2015 2015 2015 2015 ...
##  $ survey_date          : Factor w/ 10 levels "6/10/2015","6/11/2015",..: 3 3 3 3 3 3 3 3 3 3
...
##  $ station_code         : Factor w/ 239 levels "B1","B10","B11",..: 2 2 2 2 2 2 2 2 2 2 ...
##  $ latitude             : num  17.8 17.8 17.8 17.8 17.8 ...
##  $ longitude            : num  -64.6 -64.6 -64.6 -64.6 -64.6 ...
##  $ biotope              : Factor w/ 4 levels "ESTX","LANG",..: 1 1 1 1 1 1 1 1 1 1 ...
##  $ admin                : Factor w/ 4 levels "BUIS","EEMP",..: 1 1 1 1 1 1 1 1 1 1 ...
##  $ habitat              : Factor w/ 5 levels "AGRF","BDRK",..: 3 3 3 3 3 3 3 3 3 3 ...
##  $ depth                : Factor w/ 2 levels "DEEP","SHLW": 1 1 1 1 1 1 1 1 1 1 ...
##  $ stratum              : Factor w/ 43 levels "ESTX_BUIS_AGRF_DEEP",..: 4 4 4 4 4 4 4 4 4 4
...
##  $ fish                 : int  1 1 1 1 1 1 1 1 1 1 ...
##  $ LPI                  : int  1 1 1 1 1 1 1 1 1 1 ...
##  $ demo                 : int  1 1 1 1 1 1 1 1 1 1 ...
##  $ N_cells_stratum      : int  641 641 641 641 641 641 641 641 641 641 ...
##  $ N_fish_cells_sampled : int  6 6 6 6 6 6 6 6 6 6 ...
##  $ fish_sampling_weights: num  107 107 107 107 107 ...
##  $ N_LPI_cells_sampled  : int  6 6 6 6 6 6 6 6 6 6 ...
##  $ LPI_sampling_weights : num  107 107 107 107 107 ...
##  $ N_demo_cells_sampled : Factor w/ 12 levels "1","10","13",..: 8 8 8 8 8 8 8 8 8 8 ...
##  $ demo_sampling_weights: Factor w/ 41 levels "102","1040.7",..: 4 4 4 4 4 4 4 4 4 4 ...
##  $ minDepth             : Factor w/ 88 levels "1","10","11",..: 33 33 33 33 33 33 33 33 33 33
...
##  $ maxDepth             : Factor w/ 85 levels "11","12","13",..: 29 29 29 29 29 29 29 29 29 2
9 ...
##  $ rugosity             : num  1.13 1.13 1.13 1.13 1.13 ...
##  $ species_name         : Factor w/ 165 levels "Abudefduf saxatilis",..: 6 7 8 8 8 21 27 27 3
2 39 ...
##  $ fish_length          : num  12.5 12.5 7.5 12.5 17.5 17.5 12.5 17.5 23 3 ...
##  $ abundance            : int  2 8 3 42 1 1 3 1 1 6 ...
```

```
unique_surveys<-fish[!duplicated(fish$survey_index),1:13]
table(unique_surveys$habitat, unique_surveys$depth)
```

```
##       
##         DEEP SHLW
##   AGRF   15    8
##   BDRK    0    8
##   PTRF   12   14
##   PVMT   98   57
##   SCR    17   10
```

Map of survey locations

```r
library(ggplot2)
library(ggmap)
map <- get_map(location = c(lon=-64.7, lat=17.73), zoom=10, maptype='satellite')
```

```
## Map from URL : http://maps.googleapis.com/maps/api/staticmap?center=17.73,-64.7&zoom=10&size=640x640&scale=2&maptype=satellite&language=en-EN&sensor=false
```

```r
Stcroix_map <- ggmap(map)
Stcroix_map +geom_point(aes(x = longitude, y = latitude, color = as.factor(habitat), shape = depth), size = 1, data = unique_surveys)
```

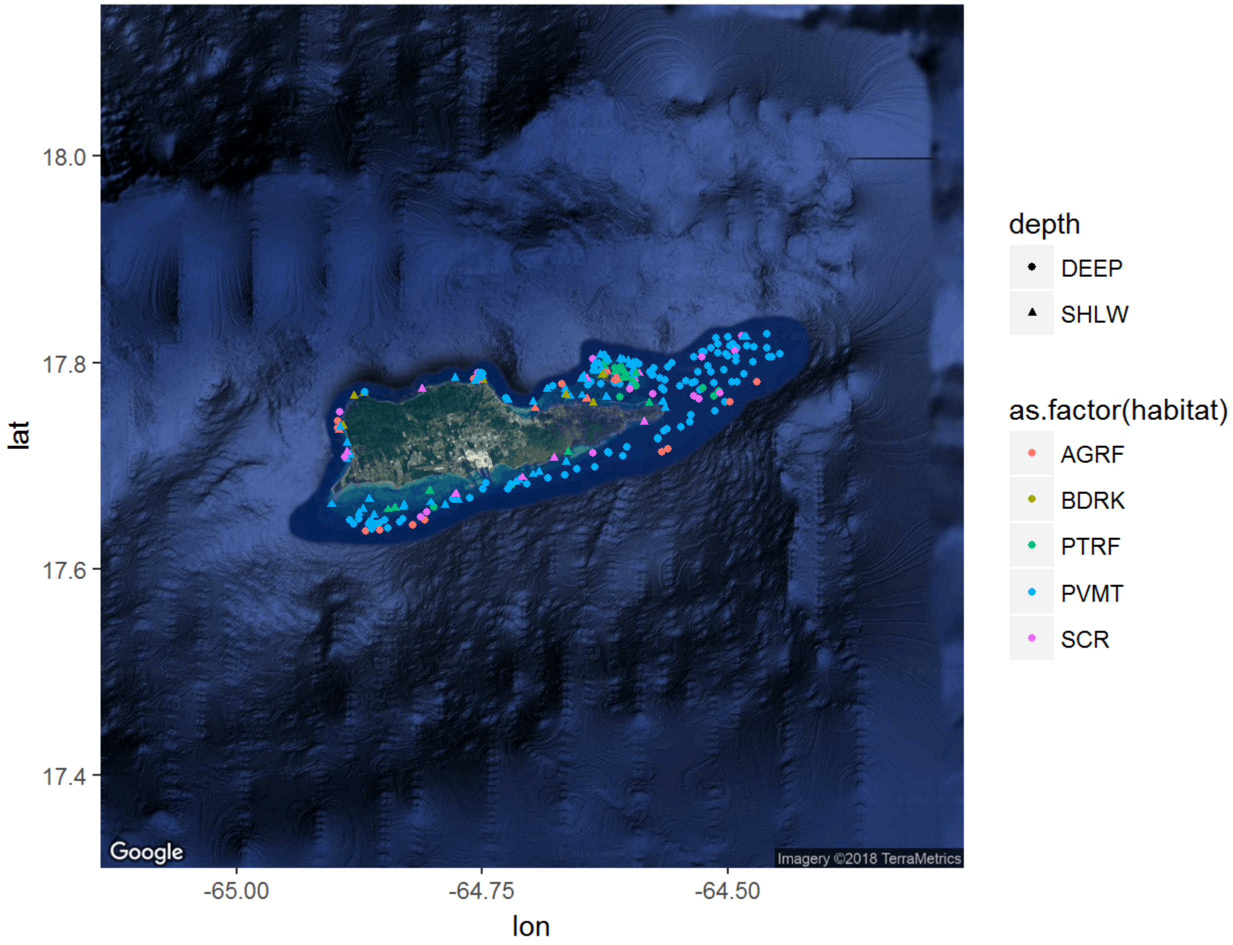


Table for estimating parrotfish grazing impacts (Table 3 in the main report)

```r
params<- read.csv("PF_params.csv", header = T)
params
```

```
##                   Species Prop_mac     Z     X        M     A     B     C
## 1           Scarus iseri    0.037    NA    NA 0.000401 -0.87 39.40 -2.21
## 2    Scarus taeniopterus    0.037    NA    NA 0.000401 -0.87 39.40 -2.21
## 3          Scarus vetula    0.008    NA    NA 0.000401 -0.64 34.90 -1.31
## 4 Sparisoma aurofrenatum       NA -2.65 0.102       NA    NA    NA    NA
## 5 Sparisoma chrysopterum       NA -7.97 0.268       NA    NA    NA    NA
## 6   Sparisoma rubripinne       NA -4.42 0.153       NA    NA    NA    NA
## 7       Sparisoma viride    0.043    NA    NA 0.000584  0.00  5.14 -1.17
##       D        P      a     b
## 1 0.035 1.93e-07 0.0170 3.020
## 2 0.035 1.93e-07 0.0180 3.000
## 3 0.035 1.93e-07 0.0190 3.045
## 4    NA       NA 0.0047 3.430
## 5    NA       NA 0.0099 3.170
## 6    NA       NA 0.0190 3.000
## 7 0.071 1.30e-06 0.0250 2.920
```

merge with survey data

```
fish2<-merge(fish, params, by.x = 'species_name', by.y = 'Species', all.x = T, all.y = T)
```

Calculate predicted grazing impacts based on equations in section 1.2 of the main report

```
weight<-fish2$a*fish2$fish_length^fish2$b
fish2<-cbind(fish2, weight)
total_weight<-fish2$weight*fish2$abundance
fish2<-cbind(fish2, total_weight)
consumption<-(0.0342*fish2$weight^0.816)*fish2$ abundance
fish2<-cbind(fish2, consumption)
macro_not_size_dep<-fish2$consumption*fish2$Prop_mac
fish2<-cbind(fish2, macro_not_size_dep)
macro_size_dep<-exp(fish2$Z+fish2$X.y*fish2$fish_length)/(1+exp(fish2$Z+fish2$X.y*fish2$fish_len
gth))*fish2$consumption
fish2<-cbind(fish2, macro_size_dep)
macro_all<-rowSums(fish2[,c("macro_not_size_dep", "macro_size_dep")], na.rm = T)
fish2<-cbind(fish2, macro_all)
bite_area<-fish2$M*fish2$fish_length^2
fish2<-cbind(fish2, bite_area)
bite_rate<-fish2$A*fish2$fish_length+fish2$B
fish2<-cbind(fish2, bite_rate)
bite_scar<- exp(fish2$C+fish2$D*fish2$fish_length)/(1+exp(fish2$C+fish2$D*fish2$fish_length))
fish2<-cbind(fish2, bite_scar)
bite_area_per_year<-fish2$bite_scar*fish2$bite_rate*fish2$bite_area*219000* fish2$abundance
fish2<-cbind(fish2, bite_area_per_year)
bite_mass<-1.5*fish2$P*fish2$fish_length^3
fish2<-cbind(fish2, bite_mass)
bite_mass_per_year<- fish2$bite_scar*fish2$bite_rate*fish2$bite_mass*219000* fish2$abundance
fish2<-cbind(fish2, bite_mass_per_year)
```

Summary of predicted grazing impacts by habitat strata on deep and shallow reefs

Shallow reefs

```
fish3<-subset(fish2, fish2$depth == "SHLW")
```

Summarize variables

Total Biomass

```
biomass<-aggregate(fish3$total_weight, by = list(fish3$survey_index, fish3$species_name), sum, na.rm = T, drop = F)
biomass_sub<-subset(biomass,
biomass$Group.2 == "Scarus iseri" | biomass$Group.2 == "Scarus taeniopterus"| biomass$Group.2 == "Scarus vetula"| biomass$Group.2 == "Sparisoma aurofrenatum"| biomass$Group.2 == "Sparisoma chrysopterum"| biomass$Group.2 == "Sparisoma rubripinne"| biomass$Group.2 == "Sparisoma viride")
colnames(biomass_sub)<-c("SurveyIndex", "Species", "Biomass")
```

Macroalgal consumption

```
macro_consumption<-aggregate(fish3$macro_all, by = list(fish3$survey_index, fish3$species_name), sum, na.rm = T, drop = F)
macro_consumption_sub<-subset(macro_consumption,
macro_consumption$Group.2 == "Scarus iseri" | macro_consumption$Group.2 == "Scarus taeniopterus" | macro_consumption$Group.2 == "Scarus vetula"| macro_consumption$Group.2 == "Sparisoma aurofrenatum"| macro_consumption$Group.2 == "Sparisoma chrysopterum"| macro_consumption$Group.2 == "Sparisoma rubripinne"| macro_consumption$Group.2 == "Sparisoma viride")
colnames(macro_consumption_sub)<-c("SurveyIndex", "Species", "Macroalgal_consumption")
```

Areal grazing

```
bite_area_per_year<-aggregate(fish3$bite_area_per_year, by = list(fish3$survey_index, fish3$species_name), sum, na.rm = T, drop = F)
bite_area_per_year_sub<-subset(bite_area_per_year,
bite_area_per_year$Group.2 == "Scarus iseri" | bite_area_per_year$Group.2 == "Scarus taeniopterus"| bite_area_per_year$Group.2 == "Scarus vetula"| bite_area_per_year$Group.2 == "Sparisoma aurofrenatum"| bite_area_per_year$Group.2 == "Sparisoma chrysopterum"| bite_area_per_year$Group.2 == "Sparisoma rubripinne"| bite_area_per_year$Group.2 == "Sparisoma viride")
colnames(bite_area_per_year_sub)<-c("SurveyIndex", "Species", "Area_scraped_per_year")
```

Bioerosion

```
bite_mass_per_year<-aggregate(fish3$bite_mass_per_year, by = list(fish3$survey_index, fish3$species_name), sum, na.rm = T, drop = F)
bite_mass_per_year_sub<-subset(bite_mass_per_year,
bite_mass_per_year$Group.2 == "Scarus iseri" | bite_mass_per_year$Group.2 == "Scarus taeniopterus"| bite_mass_per_year$Group.2 == "Scarus vetula"| bite_mass_per_year$Group.2 == "Sparisoma aurofrenatum"| bite_mass_per_year$Group.2 == "Sparisoma chrysopterum"| bite_mass_per_year$Group.2 == "Sparisoma rubripinne"| bite_mass_per_year$Group.2 == "Sparisoma viride")
colnames(bite_mass_per_year_sub)<-c("SurveyIndex", "Species", "Erosion_per_year")
```

Now Combine grazing metrics

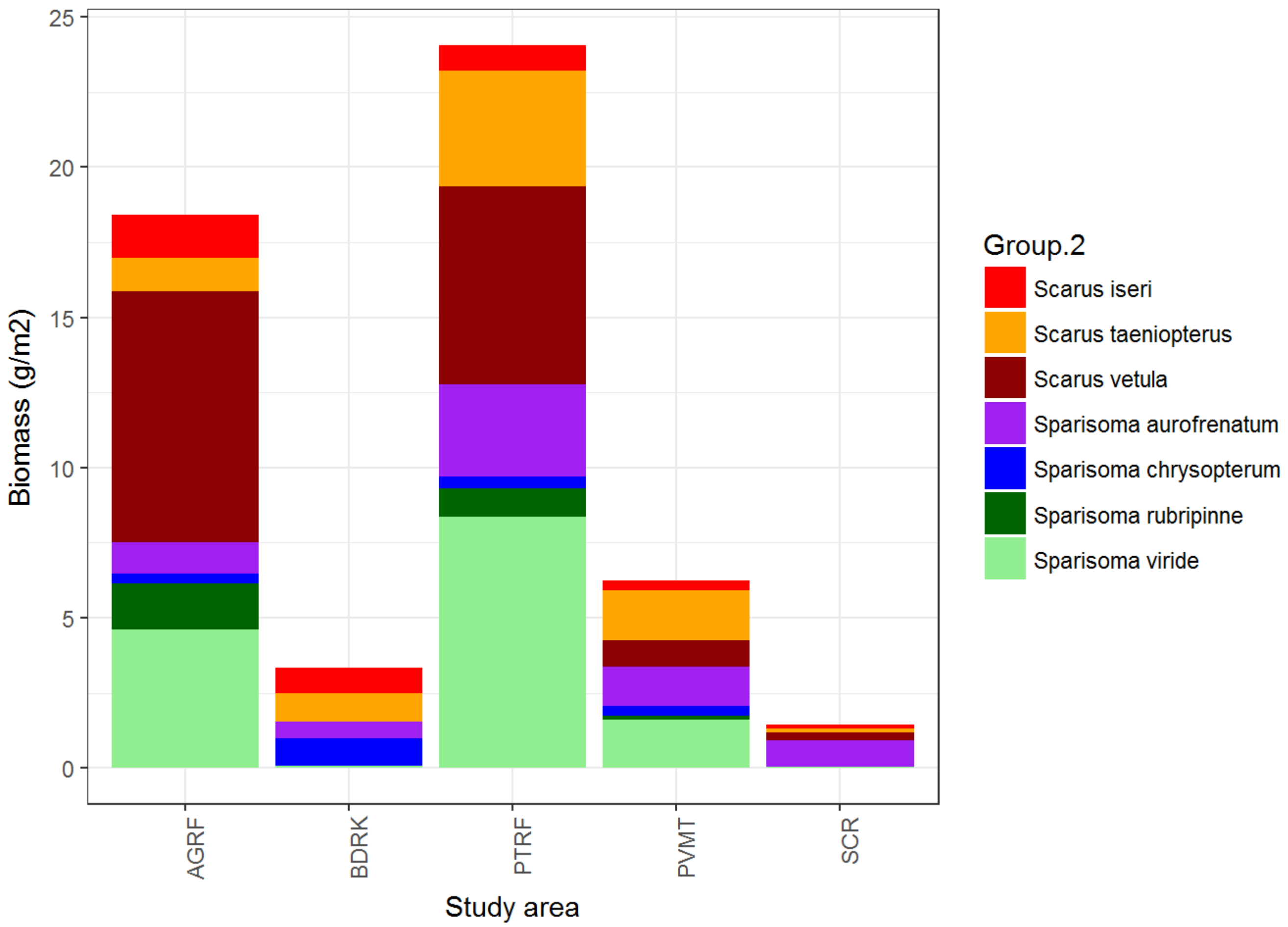
```
grazing_sum<-cbind(biomass_sub, macro_consumption_sub, bite_area_per_year_sub, bite_mass_per_year_sub)
grazing_sum<-grazing_sum[,c(1:3,6,9,12)]
grazing<-merge(grazing_sum, unique_surveys, by.x = "SurveyIndex", by.y = "survey_index", all.x = T)
```

And get summary for plotting data

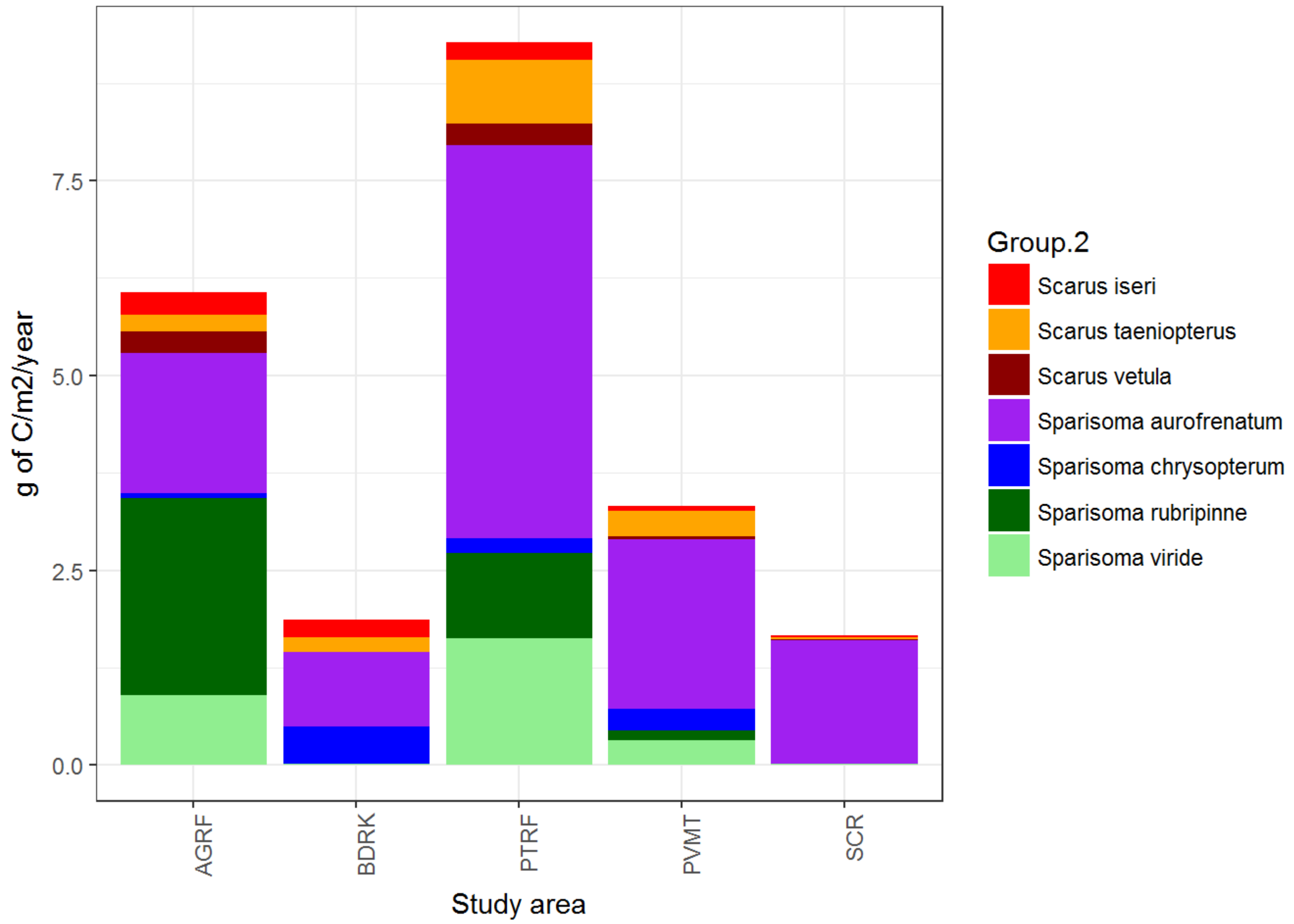
```
library(gdata)
grazing[is.na(grazing)]<-0
grazing_summary<-drop.levels(aggregate(grazing[,c(3:6)], by = list(grazing$habitat, grazing$Species), mean))
```

Graph data

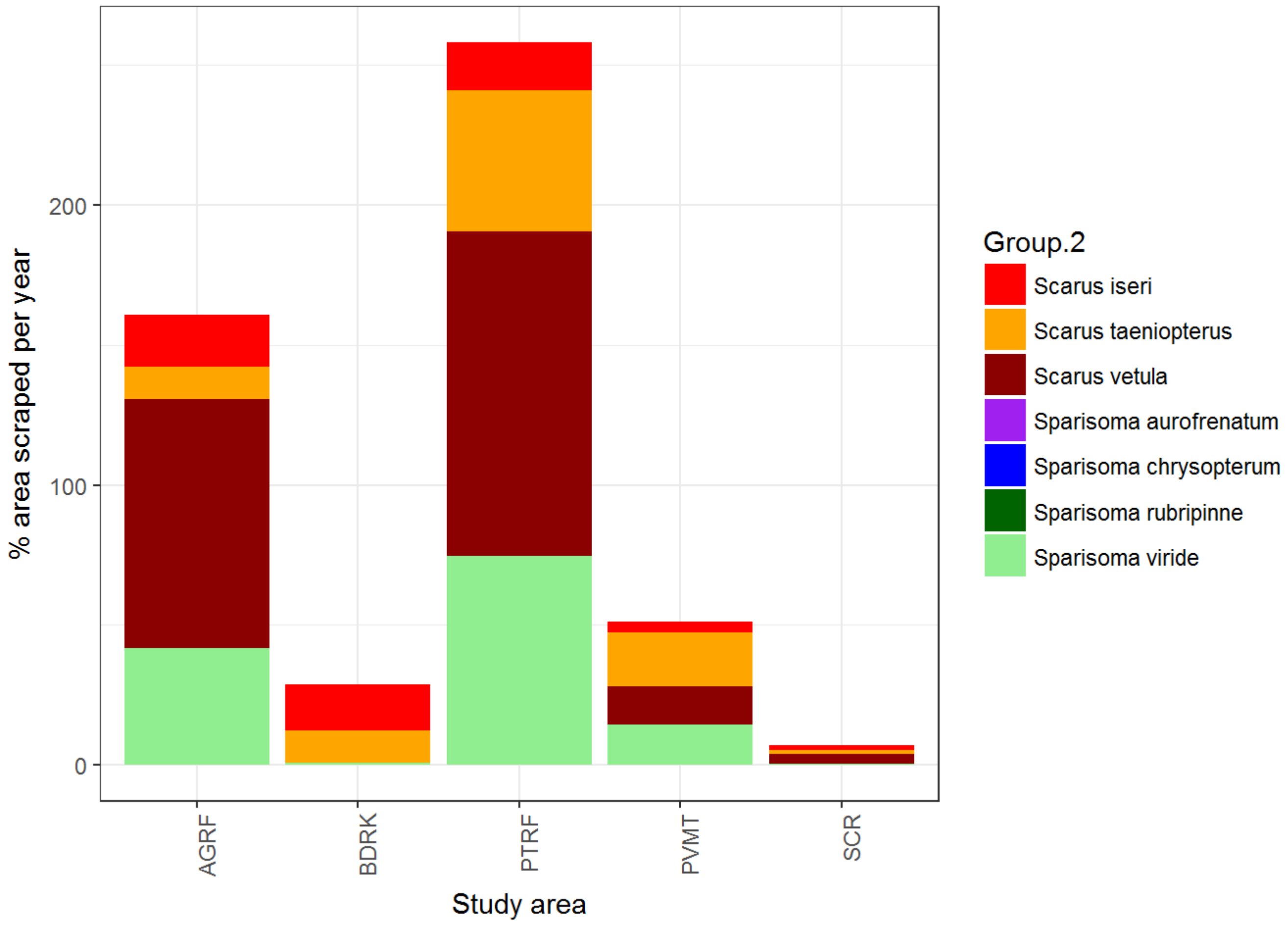
```
ggplot(grazing_summary)+geom_col(aes(x = Group.1, fill = Group.2, y = Biomass/100)) + theme_bw() + theme(axis.text.x=element_text(angle=90, hjust = 1)) + scale_fill_manual(values = c("red", "orange", "dark red", "purple", "blue", "dark green", "light green"))+ylab("Biomass (g/m2)") +xlab("Study area")
```



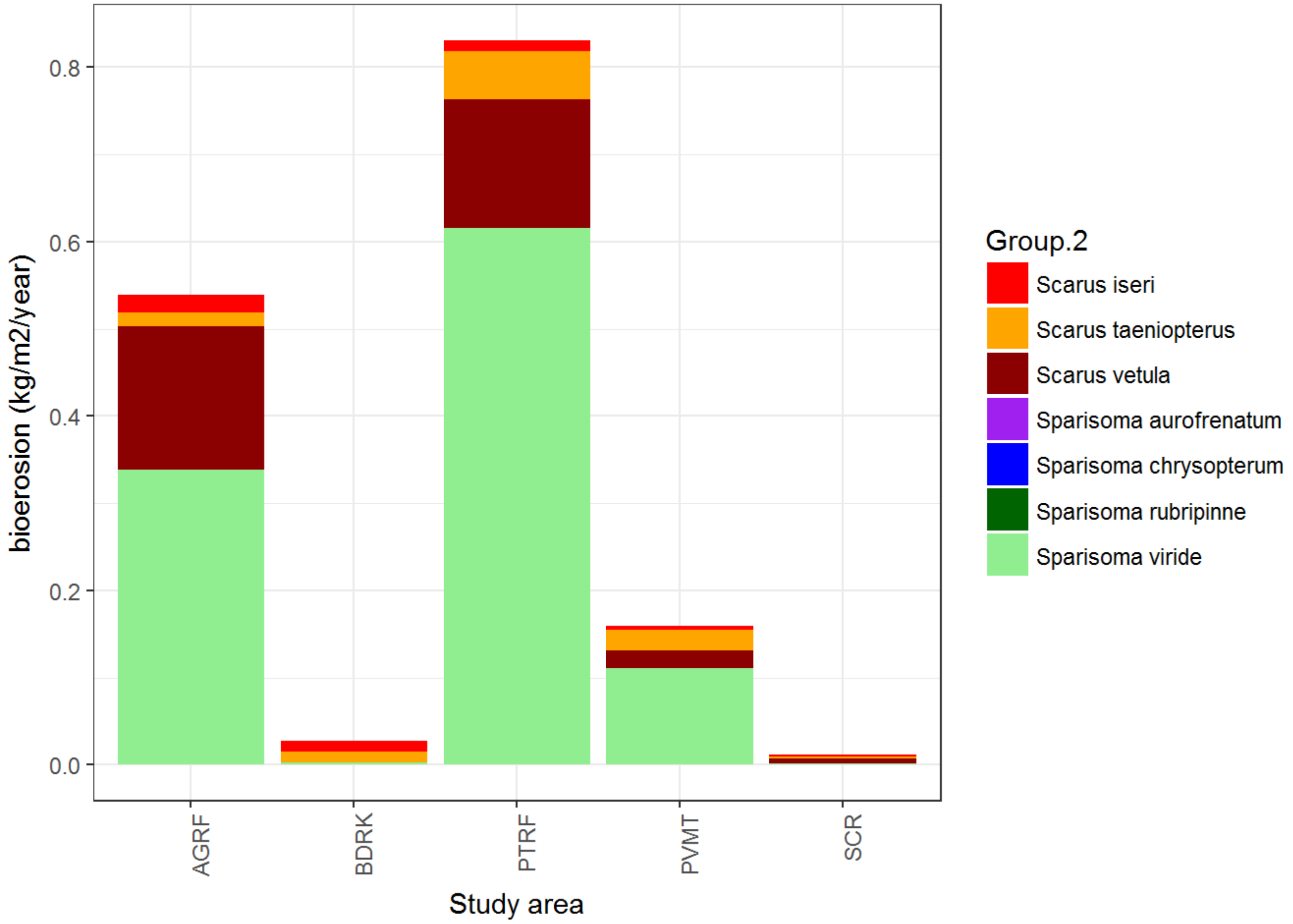
```
ggplot(grazing_summary)+geom_col(aes(x = Group.1, fill = Group.2, y = Macroalgal_consumption*365
/100)) + theme_bw() + theme(axis.text.x=element_text(angle=90, hjust = 1)) + scale_fill_manual(v
alues = c("red", "orange", "dark red", "purple", "blue", "dark green", "light green"))+ylab("g o
f C/m2/year") +xlab("Study area")
```



```
ggplot(grazing_summary)+geom_col(aes(x = Group.1, fill = Group.2, y = Area_scraped_per_year/1000
0)) + theme_bw() + theme(axis.text.x=element_text(angle=90, hjust = 1)) + scale_fill_manual(valu
es = c("red", "orange", "dark red", "purple", "blue", "dark green", "light green"))+ylab("% area
 scraped per year") +xlab("Study area")
```



```
ggplot(grazing_summary)+geom_col(aes(x = Group.1, fill = Group.2, y = Erosion_per_year/100000))
 + theme_bw() + theme(axis.text.x=element_text(angle=90, hjust = 1)) + scale_fill_manual(values
 = c("red", "orange", "dark red", "purple", "blue", "dark green", "light green"))+ylab("bioerosi
on (kg/m2/year)") +xlab("Study area")
```



Deep reefs

```
fish4<-subset(fish2, fish2$depth == "DEEP")
```

Summarize variables

Total Biomass

```
biomass<-aggregate(fish4$total_weight, by = list(fish4$survey_index, fish4$species_name), sum, n
a.rm = T, drop = F)
biomass_sub<-subset(biomass,
biomass$Group.2 == "Scarus iseri" | biomass$Group.2 == "Scarus taeniopterus"| biomass$Group.2 ==
 "Scarus vetula"| biomass$Group.2 == "Sparisoma aurofrenatum"| biomass$Group.2 == "Sparisoma chr
ysopterum"| biomass$Group.2 == "Sparisoma rubripinne"| biomass$Group.2 == "Sparisoma viride")
colnames(biomass_sub)<-c("SurveyIndex", "Species", "Biomass")
```

Macroalgal Consumption

```
macro_consumption<-aggregate(fish4$macro_all, by = list(fish4$survey_index, fish4$species_name), sum, na.rm = T, drop = F)
macro_consumption_sub<-subset(macro_consumption,
macro_consumption$Group.2 == "Scarus iseri" | macro_consumption$Group.2 == "Scarus taeniopterus" | macro_consumption$Group.2 == "Scarus vetula"| macro_consumption$Group.2 == "Sparisoma aurofrenatum"| macro_consumption$Group.2 == "Sparisoma chrysopterum"| macro_consumption$Group.2 == "Sparisoma rubripinne"| macro_consumption$Group.2 == "Sparisoma viride")
colnames(macro_consumption_sub)<-c("SurveyIndex", "Species", "Macroalgal_consumption")
```

Areal Grazing

```
bite_area_per_year<-aggregate(fish4$bite_area_per_year, by = list(fish4$survey_index, fish4$species_name), sum, na.rm = T, drop = F)
bite_area_per_year_sub<-subset(bite_area_per_year,
bite_area_per_year$Group.2 == "Scarus iseri" | bite_area_per_year$Group.2 == "Scarus taeniopterus"| bite_area_per_year$Group.2 == "Scarus vetula"| bite_area_per_year$Group.2 == "Sparisoma aurofrenatum"| bite_area_per_year$Group.2 == "Sparisoma chrysopterum"| bite_area_per_year$Group.2 == "Sparisoma rubripinne"| bite_area_per_year$Group.2 == "Sparisoma viride")
colnames(bite_area_per_year_sub)<-c("SurveyIndex", "Species", "Area_scraped_per_year")
```

Bioerosion

```
bite_mass_per_year<-aggregate(fish4$bite_mass_per_year, by = list(fish4$survey_index, fish4$species_name), sum, na.rm = T, drop = F)
bite_mass_per_year_sub<-subset(bite_mass_per_year,
bite_mass_per_year$Group.2 == "Scarus iseri" | bite_mass_per_year$Group.2 == "Scarus taeniopterus"| bite_mass_per_year$Group.2 == "Scarus vetula"| bite_mass_per_year$Group.2 == "Sparisoma aurofrenatum"| bite_mass_per_year$Group.2 == "Sparisoma chrysopterum"| bite_mass_per_year$Group.2 == "Sparisoma rubripinne"| bite_mass_per_year$Group.2 == "Sparisoma viride")
colnames(bite_mass_per_year_sub)<-c("SurveyIndex", "Species", "Erosion_per_year")
```

Now combine grazing metrics

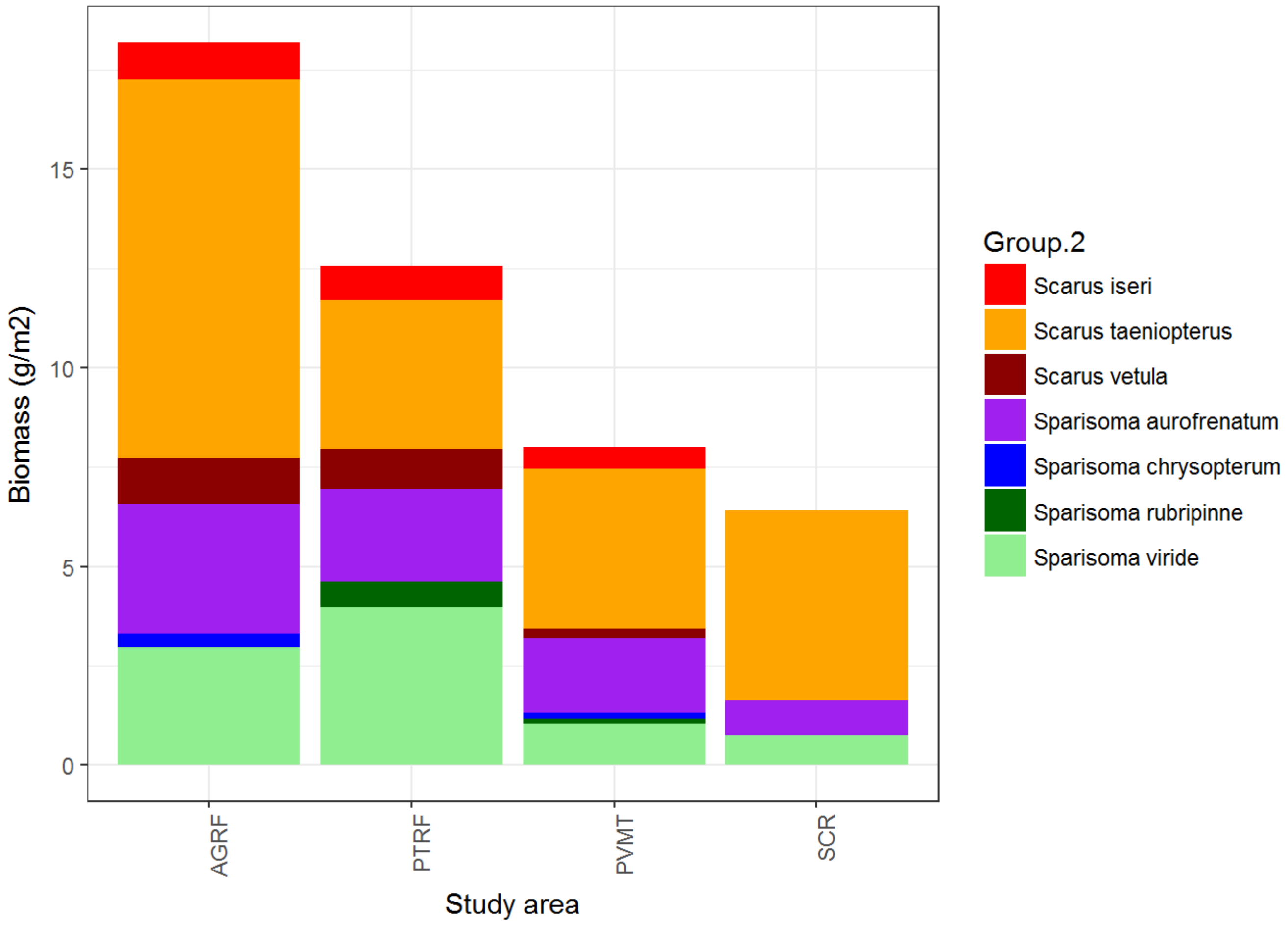
```
grazing_sum<-cbind(biomass_sub, macro_consumption_sub, bite_area_per_year_sub, bite_mass_per_year_sub)
grazing_sum<-grazing_sum[,c(1:3,6,9,12)]
grazing<-merge(grazing_sum, unique_surveys, by.x = "SurveyIndex", by.y = "survey_index", all.x = T)
```

And get summary for plotting data

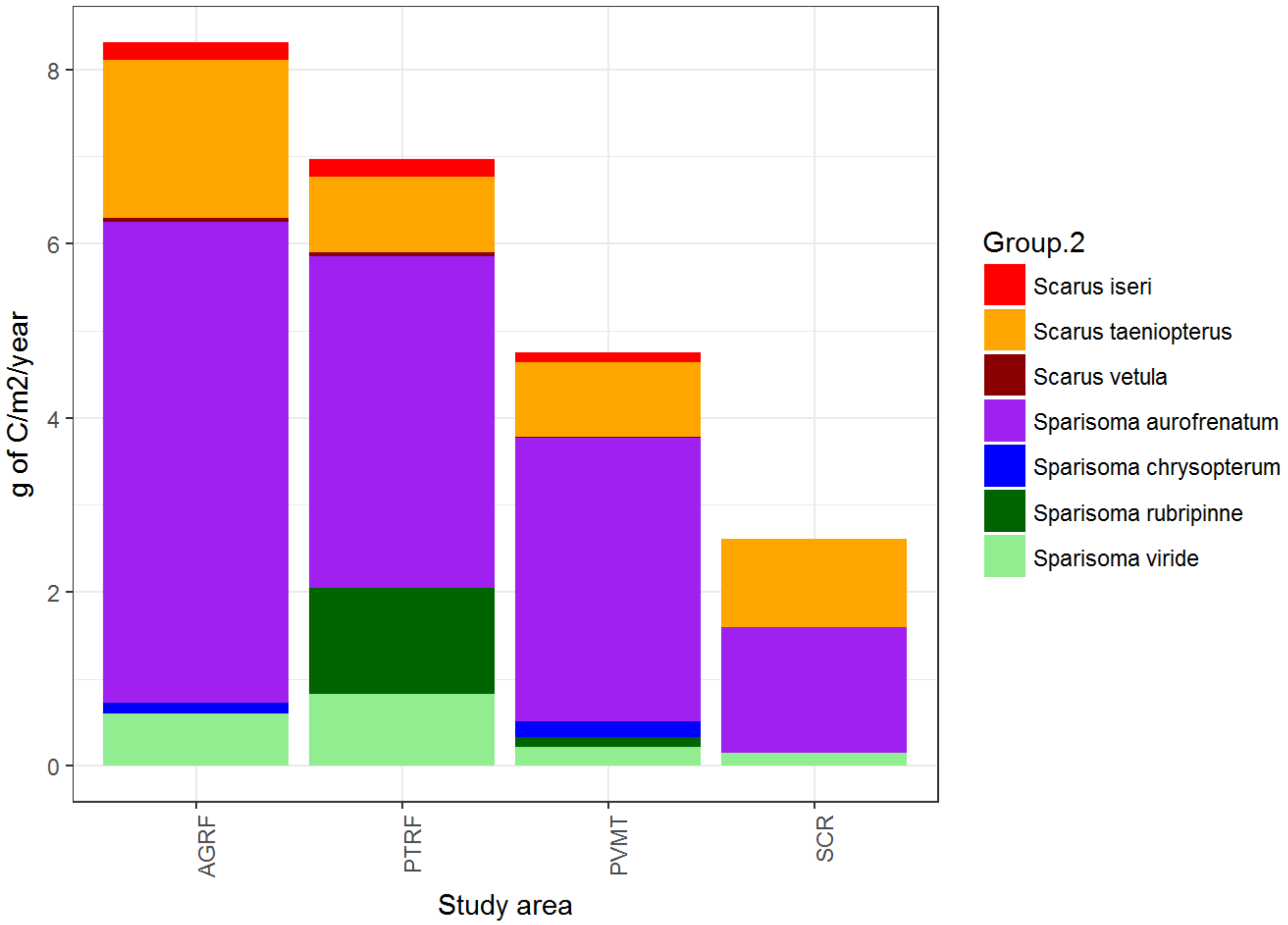
```
grazing[is.na(grazing)]<-0
grazing_summary<-drop.levels(aggregate(grazing[,c(3:6)], by = list(grazing$habitat, grazing$Species), mean))
```

Graph data

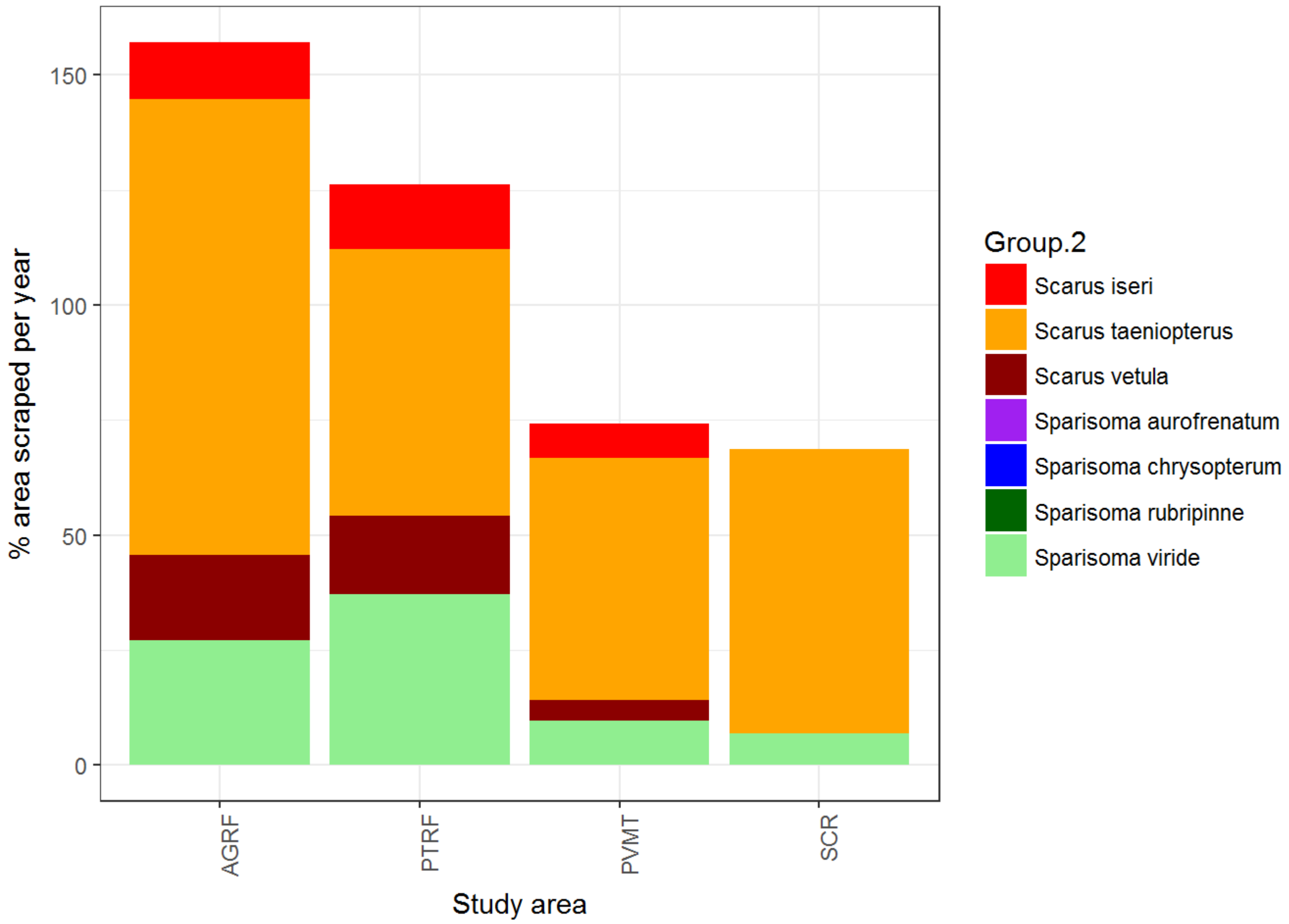
```
ggplot(grazing_summary)+geom_col(aes(x = Group.1, fill = Group.2, y = Biomass/100)) + theme_bw() + theme(axis.text.x=element_text(angle=90, hjust = 1)) + scale_fill_manual(values = c("red", "orange", "dark red", "purple", "blue", "dark green", "light green"))+ylab("Biomass (g/m2)") +xlab("Study area")
```



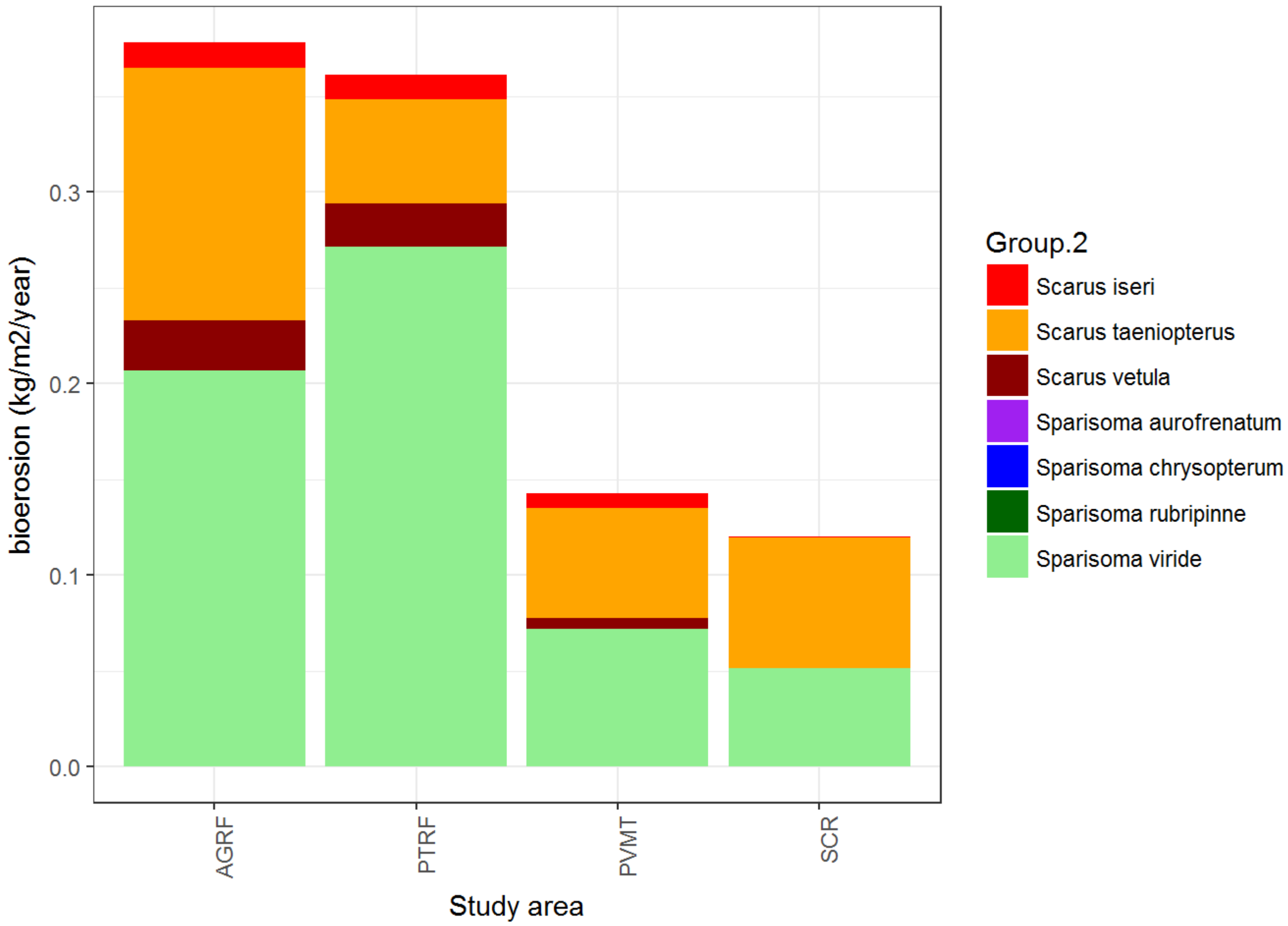
```
ggplot(grazing_summary)+geom_col(aes(x = Group.1, fill = Group.2, y = Macroalgal_consumption*365
/100)) + theme_bw() + theme(axis.text.x=element_text(angle=90, hjust = 1)) + scale_fill_manual(v
alues = c("red", "orange", "dark red", "purple", "blue", "dark green", "light green"))+ylab("g o
f C/m2/year") +xlab("Study area")
```



```
ggplot(grazing_summary)+geom_col(aes(x = Group.1, fill = Group.2, y = Area_scraped_per_year/1000
0)) + theme_bw() + theme(axis.text.x=element_text(angle=90, hjust = 1)) + scale_fill_manual(valu
es = c("red", "orange", "dark red", "purple", "blue", "dark green", "light green"))+ylab("% area
 scraped per year") +xlab("Study area")
```



```
ggplot(grazing_summary)+geom_col(aes(x = Group.1, fill = Group.2, y = Erosion_per_year/100000))
 + theme_bw() + theme(axis.text.x=element_text(angle=90, hjust = 1)) + scale_fill_manual(values
 = c("red", "orange", "dark red", "purple", "blue", "dark green", "light green"))+ylab("bioerosi
on (kg/m2/year)") +xlab("Study area")
```


bioerosion (kg/m2/year)
0.0
0.1
0.2
0.3
AGRF
PTRF
PVMT
SCR
Study area
Group.2
Scarus iseri
Scarus taeniopterus
Scarus vetula
Sparisoma aurofrenatum
Sparisoma chrysopterum
Sparisoma rubripinne
Sparisoma viride