

# Characterising reef fish populations and habitats within and outside the US Virgin Islands Coral Reef National Monument: a lesson in marine protected area design

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**Abstract** Marine protected areas are an important tool for management of marine ecosystems. Despite their utility, ecological design criteria are often not considered or feasible to implement when establishing protected areas. In 2001, the Virgin Islands Coral Reef National Monument (VICRNM) in St John, US Virgin Islands was established by Executive Order. The VICRNM prohibits almost all extractive uses. Surveys of habitat and fishes inside and outside of the VICRNM were conducted in 2002–2004. Areas outside the VICRNM had significantly more hard corals, greater habitat complexity, and greater richness, abundance and biomass of reef fishes than areas within the VICRNM. The administrative process used to delineate the boundaries of the VICRNM did not include a robust ecological characterisation of the area. Because of reduced habitat complexity within the VICRNM, the enhancement of the marine ecosystem may not be fully realised or increases in economically important reef fishes may take longer to detect.

**KEYWORDS:** conservation, coral reefs, marine protected areas, marine reserves, reef fish, US Virgin Islands.

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## Introduction

Coral reef ecosystems are deteriorating around the world at an alarming rate (Wilkinson 2004), and those within the US Virgin Islands are no exception (Rogers & Beets 2001; Beets & Rogers 2002; Jeffrey, Anlauf, Beets, Caseau, Coles, Friedlander, Herzlieb, Hillis-

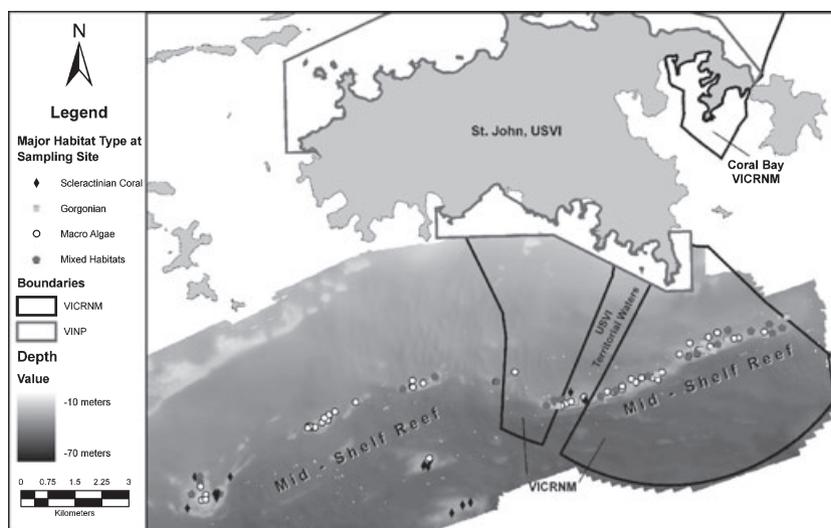
Starr, Kendall, Mayor, Miller, Nemeth, Rogers & Toller 2005). Intensive fishing has caused the loss of several spawning aggregations, as well as severe declines in size and abundance of important fish species (Beets & Friedlander 1999; Beets & Rogers 2002). In addition to the effects of fishing, habitat degradation in the form of coral and seagrass habitat

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loss due to hurricanes and coral diseases has led to an ecosystem that is now dominated by macroalgae (Rogers & Beets 2001; Beets & Rogers 2002). To help halt this degradation, federal, state and territorial government agencies have been working to establish marine protected areas (MPAs) and their more restrictive form, marine reserves (i.e. no extraction of resources) to protect marine ecosystems from the impacts of human uses.

A recently designated MPA is the Virgin Islands Coral Reef National Monument (VICRNM) established by US President Clinton on 17 January 2001 under the Antiquities Act of 1906 (34 Stat. 225, 16 U.S.C. 431). These submerged lands consist of about 51 km<sup>2</sup> of marine habitat off the island of St John, US Virgin Islands and are managed by the Secretary of the Interior through the National Park Service. The VICRNM was intended to enhance resources in the Virgin Islands and specifically in the Virgin Islands National Park, which was established by Congress in 1956 and expanded in 1962. This new Monument roughly doubles the area in and around St John now under the jurisdiction of the National Park Service. Provisions within the Presidential Proclamation prohibit all extractive uses with the exception of fishing for blue runner, *Caranx crysos*, south of St John and bait fishing in a small portion of the Coral Bay component of the VICRNM (Fig. 1). In addition, boat anchoring is prohibited in the VICRNM, except for emergency or authorised administrative purposes.

To be effective, MPAs should protect representative species and habitat types (Ballantine 1997; Murray, Ambrose, Bohnsack, Botsford, Carr, Davis, Dayton, Gotshall, Gunderson, Hixon, Lubchenco, Mangel, MacCall, McArdle, Ogden, Roughgarden, Starr, Tegner & Yoklavich 1999), and rare and vulnerable habitat types should be represented as completely as possible (Sladek Nowlis & Friedlander 2005). Because coral reef ecosystems only function properly when a mosaic of habitat types are present (Appeldoorn, Friedlander, Sladek Nowlis, Usseglio & Mitchell-Chui 2003; Christensen, Jeffrey, Caldow, Monaco, Kendall & Appeldoorn 2003), MPA networks should strive to include a range of habitat types in an interconnected manner. To assess the long-term effectiveness of the VICRNM, it is necessary to characterise the habitats and associated fauna within and outside the VICRNM to provide a baseline for future comparisons and to support adaptive management actions, such as modifications to the VICRNM boundaries. The National Park Service, the National Oceanic and Atmospheric Administration (NOAA) and the US Geological Survey initiated a joint project in 2002 to develop a baseline characterisation of species and their associated habitats within and outside the VICRNM to assess changes within the ecosystem. The purpose of this paper is to provide results from the baseline ecological characterisation to enable comparisons of fish assemblages and habitats within and outside the VICRNM, with the intended goal of providing better



**Figure 1.** Boundaries of Virgin Islands National Park (VINP) and Virgin Islands Coral Reef National Monument (VICRNM). Mid-shelf reef bathymetry data were derived from multibeam sonar data acquired in 2004 and 2005. Symbols represent survey locations and major habitat types defined at each location.

scientific guidance for the management of the VICRNM and Virgin Islands National Park (VINP).

## Materials and methods

The focus of this investigation was on the southern component of the VICRNM, specifically the mid-shelf reef area of the Monument (Fig. 1). The mid-shelf reef is unique for St John, because of its relatively deep (17–35 m) coral reef ecosystem and relatively high per cent live coral cover and topographic complexity. Not all of the mid-shelf reef area is contained within the VICRNM, because the MPA was delineated based on legal parameters of the Antiquities Act that defined federal waters. As a result, the VICRNM is bisected by a wedge that extends out from shore adjacent to privately held lands that are not included in the VICRNM. Additionally, the mid-shelf reef extends to the west of St John and south of St Thomas. This baseline assessment of the VICRNM occurs along the length of the mid-shelf reef both within and outside the VICRNM.

Sampling sites were randomly selected inside and outside of VICRNM along the coral reef habitat of the mid-shelf reef using the random point generator in ArcView 3.3 software. Modelled bathymetry derived from NOAA depth soundings was used as a surrogate to identify areas of potential coral reef habitats (viz. areas of scleractinian and gorgonian corals). Relatively rapid changes in topographic complexity of the bottom corresponded with the presence of hard and soft corals along the mid-shelf reef. Thus, all selected sites from a broad-scale perspective were considered coral reef sites comprising either hard or soft corals. Additional bathymetry data for water depths ranging from 20 to 100 m for the area south of St John (Fig. 1) were provided from multibeam surveys (2004–2005) off the NOAA ship Nancy Foster and processed by the NOAA Biogeography Team (see: [http://ccma.nos.noaa.gov/ecosystems/coralreef/usvi\\_nps.html](http://ccma.nos.noaa.gov/ecosystems/coralreef/usvi_nps.html)). Fish populations were surveyed and coral habitats were characterised based on the NOAA US Caribbean habitat classification system (Kendall, Kruer, Buja, Christensen, Finkbeiner & Monaco 2001). Fish surveys were conducted over 2-week periods in July 2002, 2003 and 2004 and associated fine-scale habitat data were obtained over the same 2-week periods in 2003 and 2004. Groupers aggregate to spawn during the winter months in the Virgin Islands (Beets & Friedlander 1999), while other taxa, such as surgeonfishes, *Acanthurus* spp., and parrotfishes, *Scarus* spp. and *Sparisoma* spp., have been reported to spawn year round (Domeier & Colin 1997). Thus, the summer

season was selected so results would not be influenced by seasonal spawning aggregations. SCUBA divers surveyed a total of 119 sites over 3 years at depths shallower than 33 m because of depth restrictions imposed by the use of Nitrox 36.

## Fish survey methods

Fish assemblages at each location were assessed using standard underwater visual belt transect survey methods (Brock 1954, 1982). The accuracy of belt transects is increased by conducting a greater number of short (25 m) transects rather than a few longer transects (100 m) because of the larger variance associated with the larger survey area (Brock 1982). In this study, a diver swam a single 25 × 4 m transect at a relatively constant speed and identified to the lowest possible taxon all fishes visible within 2 m to either side of the centreline (100 m<sup>2</sup> transect area). Survey time along the transect varied from 12 to 15 min depending on habitat complexity and fish abundance. The number of individuals by species was tallied in 5-cm size classes. The fish assemblage characteristics derived were species richness, density and biomass. Species richness was the number of species present per 25 × 4 m (100 m<sup>2</sup>) transect. Density was individuals 100 m<sup>-2</sup>, and biomass was kg 100 m<sup>-2</sup>.

Biomass estimates were calculated from live wet weight ( $W$ ) values derived from the visually estimated mean fork length (FL) for each size class for each species using the relation  $W = a(\text{FL})^b$ . Values of the parameters  $a$  and  $b$  for each species were derived from Bohnsack, Sutherland, Brown, Harper & McClellan (1986) and FishBase (<http://www.fishbase.org/>). For species not in these databases, estimates from available literature on the species or congeners were used. Biomasses of all fishes recorded in all surveys were obtained by multiplying the mean live wet weight for each size class for each species by the total number of individuals observed in that size class. Species were assigned to the following feeding groups based on Randall (1967), FishBase and the authors' experiences: herbivores, benthic invertebrate feeders (invertivores), planktivores and piscivores.

## Habitat characterisation

As a result of limited dive time at depth, a second diver conducted an assessment of fine-scale habitat quality and complexity within a 15-m diameter sampling area. The minimum and maximum depth of the hard substrate within the sampling area was recorded. Rugosity, an indicator of habitat complexity, was

given a value of 1–3 based on the height of the tallest hard structure: 1 if <0.5 m above the seafloor; 2 if 0.5- to 1.5-m tall; or 3 if > 1.5-m tall. The percentage of area covered by abiotic substrates including hard-bottom, sand and rubble was visually estimated along with the percentage of benthic cover including scleractinian coral (hard coral), gorgonians (soft coral), sponges, macroalgae and uncolonised hard substrate. Uncolonised hard substrate was defined as areas of hard substrate that contained <10% of scleractinian or gorgonian corals. The major habitat type was then determined based on the most prevalent biotic cover occurring within the 15-m sampling area.

### Statistical analyses

Comparisons of benthic habitat and fish assemblage characteristics (except for fish family biomass) within and outside VICRNM were conducted using Student's *t*-tests (Zar 1984). Benthic percentage data were arcsine square-root transformed for all analyses (Zar 1984). Density and biomass of fishes were  $\ln(x + 1)$  transformed for analyses to conform to the assumptions of all parametric tests. All analyses of numerical abundance and biomass excluded the masked goby, *Coryphopterus personatus* (Jordan & Thompson), because they were ubiquitous and their large numbers in samples (>1000) confounded trends in the rest of the fish assemblage. The masked goby was included in calculations of species richness.

A two-way ANOVA was used to compare biomass of trophic guilds between management strata. For the two-way ANOVA, unplanned multiple comparisons were tested using Tukey HSD multiple comparison procedures ( $\alpha = 0.05$ ). Fish family biomass was compared between management strata using a Wilcoxon Rank Sum (Mann–Whitney) Test (*Z*), because data did not conform to the assumptions of parametric statistics

(viz. homogeneity of variances and normal distributions) despite transformation.

## Results

### Habitat and fish assemblage comparisons

Although there was no significant difference in depth between management strata, other habitat variables differed between inside and outside the VICRNM (Table 1). Rugosity and live coral cover were greater outside the VICRNM compared with inside the VICRNM. The extent of hard bottom area outside the VICRNM was significantly greater than inside the VICRNM, whereas the opposite was true for sand. Inside the VICRNM, no sites were classified as primarily comprised of hard corals.

A total of 129 fish species were observed in the study area, and the prevalent economically important species are listed in Table 2. Fish species richness, density and biomass were all significantly greater outside the VICRNM (Table 3).

Two-way analysis of variance detected a significant interaction ( $F_{1,3} = 3.92$ ,  $P = 0.009$ ) between management strata and trophic guilds. Pooled biomass across management strata revealed that invertivores were the most important feeding guild by weight (43.2%), followed by herbivores (23.9%), planktivores (20.7%) and piscivores (13.2%) (Fig. 2). Planktivores showed the most striking difference in biomass between management strata with biomass nearly an order of magnitude greater outside of the VICRNM.

### Family and species comparisons

Parrotfishes and wrasses were the two most prevalent families by weight, with each comprising approxi-

**Table 1.** Mean (SD) benthic habitat characteristics inside and outside the Virgin Islands Coral Reef National Monument (VICRNM) along the mid-shelf reef south of St John, 2003–2004. *P* is the probability of a significant difference between inside and outside the VICRNM

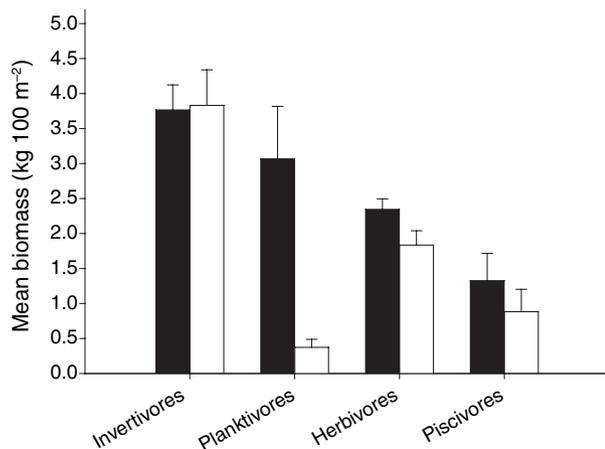
Habitat characteristic	Outside VICRNM ( <i>n</i> = 52)	Inside VICRNM ( <i>n</i> = 47)	% difference	<i>P</i> -value
<b>Abiotic</b>				
Depth (m)	26.03 (2.59)	26.90 (3.43)	3	0.160
Rugosity	2.00 (0.56)	1.47 (0.63)	27	<0.001
Hard bottom (%)	83.25 (11.01)	71.30 (29.72)	14	0.009
Sand (%)	12.19 (19.34)	20.43 (22.04)	40	0.017
Rubble (%)	4.56 (4.51)	8.26 (16.68)	45	0.378
<b>Biotic</b>				
Live coral cover (%)	25.36 (22.71)	8.00 (11.02)	65	<0.001
Gorgonian cover (%)	12.15 (9.13)	16.17 (16.09)	25	0.493
Macroalgal cover (%)	41.50 (19.93)	37.25 (23.64)	10	0.254

**Table 2.** Prevalent economically important species observed inside and outside Virgin Islands Coral Reef National Monument

Family	Scientific name	Common name
Serranidae groupers	<i>Cephalopholis cruentata</i> (Lacepède)	Graysby
	<i>Cephalopholis fulva</i> (Linnaeus)	Coney
	<i>Epinephelus guttatus</i> (Linnaeus)	Red hind
	<i>Mycteroperca tigris</i> (Valenciennes)	Tiger grouper
Carangidae jacks	<i>Caranx crysos</i> (Mitchell)	Blue runner
Lutjanidae snappers	<i>Lutjanus analis</i> (Cuvier)	Mutton snapper
	<i>Lutjanus apodus</i> (Walbaum)	Schoolmaster snapper
	<i>Lutjanus jocu</i> (Bloch & Schneider)	Dog snapper
	<i>Lutjanus mahogoni</i> (Cuvier)	Mahogany snapper
	<i>Ocyurus chrysurus</i> (Bloch)	Yellowtail snapper
Haemulidae grunts	<i>Anisotremus virginicus</i> (Linnaeus)	Porkfish
	<i>Haemulon album</i> Cuvier	Margate
	<i>Haemulon aurolineatum</i> Cuvier	Tomtate
	<i>Haemulon carbonarium</i> Poey	Caesar grunt
	<i>Haemulon flavolineatum</i> (Desmarest)	French grunt
	<i>Haemulon plumieri</i> (Lacepède)	White grunt
	<i>Haemulon sciurus</i> (Shaw)	Bluestriped grunt
Scaridae parrotfishes	<i>Sparisoma aurofrenatum</i> (Valenciennes)	Redband parrotfish
	<i>Sparisoma viride</i> (Bonnaterre)	Stoplight parrotfish
	<i>Sparisoma chrysopterus</i> Bloch & Schneider	Redtail parrotfish
	<i>Scarus vetula</i> (Bloch & Schneider)	Queen parrotfish
	<i>Scarus taeniopterus</i> Desmarest	Princess parrotfish
	<i>Scarus iseri</i> (Bloch)	Striped parrotfish
Balistidae triggerfishes	<i>Balistes vetula</i> Linnaeus	Queen triggerfish

**Table 3.** Comparison of mean (SD) fish assemblage characteristics inside and outside the Virgin Islands Coral Reef National Monument (VICRNM) along the mid-shelf reef south of St John (2002–04). *P* is the probability of a significant difference between inside and outside of the VICRNM

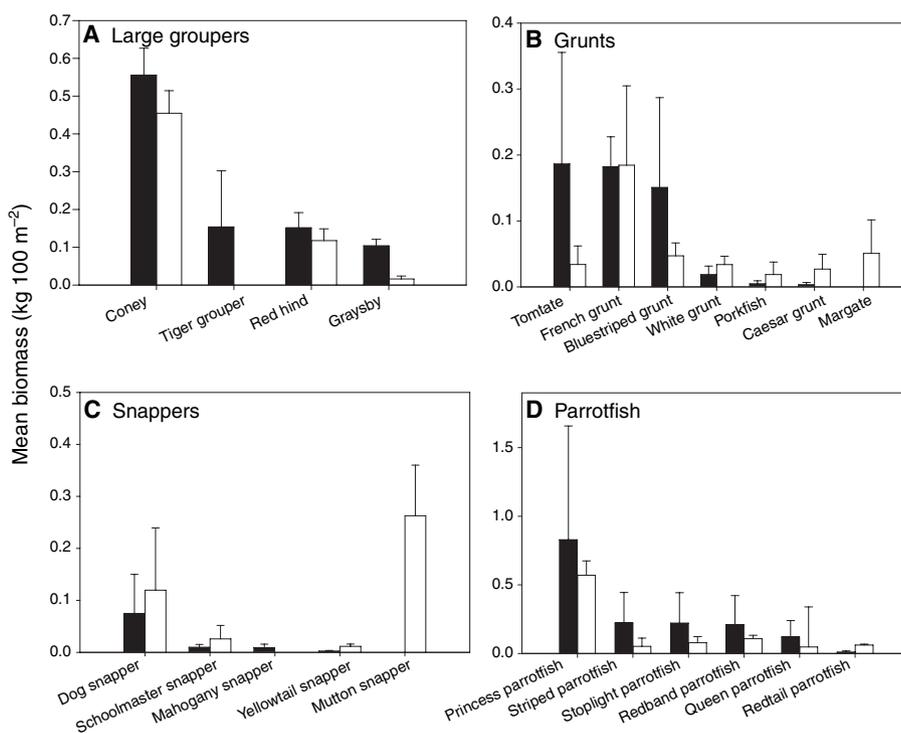
Fish assemblage characteristic	Outside VICRNM ( <i>n</i> = 62)	Inside VICRNM ( <i>n</i> = 57)	% difference	<i>P</i> -value
Species richness	26.50 (5.82)	22.61 (5.32)	15	< 0.001
Density (individuals 100 m <sup>-2</sup> )	283.48 (212.92)	212.30 (169.07)	25	0.028
Biomass (kg 100 m <sup>-2</sup> )	10.50 (8.46)	6.92 (5.88)	34	0.002

**Figure 2.** Biomass of trophic guilds inside (white bar) and outside (black bar) the Virgin Island Coral Reef National Monument (VICRNM). Error bars represent standard error of the mean.

mately 14% of the total fish biomass (Table 4). Total parrotfish biomass was 43% higher outside than inside the VICRNM, and pooled biomass of economically important parrotfish species (redband parrotfish, stoplight parrotfish, redtail parrotfish, queen parrotfish, princess parrotfish, striped parrotfish) was also greater outside the VICRNM ( $Z = 4.39$ ,  $P < 0.001$ , Fig. 3). Wrasses accounted for 20% of the biomass outside the VICRNM but were only 4% of total biomass inside the VICRNM. This difference resulted from the large abundance of creole wrasse, *Clepticus parrae* (Bloch & Schneider), outside the VICRNM, which constituted 78% of total wrasse biomass within the entire study area. Triggerfishes ranked third overall in biomass and were dominated by a single economically important species, queen triggerfish, which comprised 89% of the biomass in this family.

**Table 4.** Biomass of prevalent fish families outside and inside Virgin Island Coral Reef National Monument (VICRNM). *P* is the probability of a significant difference in biomass inside and outside VICRNM

Common name	Family	% total biomass	Outside VICRNM ( <i>n</i> = 62)		Inside VICRNM ( <i>n</i> = 57)		<i>P</i> -value
			Mean (SD) biomass (kg 100 m <sup>-2</sup> )	% biomass	Mean (SD) biomass (kg 100 m <sup>-2</sup> )	% biomass	
Parrotfish	Scaridae	14.65	1.62 (0.94)	15.38	0.93 (0.90)	13.44	< 0.001
Wrasses	Labridae	14.28	2.14 (4.59)	20.33	0.30 (0.42)	4.31	< 0.001
Triggerfishes	Balistidae	11.32	0.93 (1.39)	8.90	1.06 (1.51)	15.33	0.690
Groupers	Serranidae	9.44	1.00 (1.35)	9.54	0.64 (0.58)	9.26	0.025
Surgeonfishes	Acanthuridae	7.46	0.49 (0.47)	4.67	0.83 (0.94)	12.05	0.041
Squirrelfishes	Holocentridae	7.28	0.69 (1.02)	6.59	0.58 (0.70)	8.41	0.482
Grunts	Haemulidae	5.41	0.55 (1.74)	5.21	0.40 (1.39)	5.76	0.064

**Figure 3.** Mean biomass of economically important fish families inside (white bar) and outside (black bar) Virgin Islands Coral Reef National Monument. Error bars represent standard error of the mean. (a) Large groupers, (b) Grunts, (c) Snappers, (d) Parrotfish.

Larger economically important groupers had 44% greater biomass outside the VICRNM. All four economically important grouper species (graysby, coney, red hind and tiger grouper) had greater biomass outside the VICRNM (Fig. 3). Two tiger groupers accounted for 15% of the large grouper biomass outside the VICRNM and 10% of the total large grouper biomass for the entire survey area. These results reflect the overall low number of groupers and grouper biomass found throughout the study area (Beets & Friedlander 1999; Beets & Rogers 2002).

Grunt biomass was 27% greater outside the VICRNM compared with inside, although this difference was not significant (Table 4). Although tomtate was the most important grunt species by weight outside the VICRNM (Fig. 3), it only occurred in 5% of the surveys in this stratum. French grunt, was the most frequently encountered grunt, occurring in 35% of the total surveys, and represented the greatest grunt biomass inside VICRNM with biomass comparable with tomtate outside of the VICRNM.

Snappers were not abundant in either management stratum and only represented 3% of total fish biomass along the mid-shelf reef. Ten mutton snapper observed inside VICRNM accounted for 51% of the total snapper biomass pooled across management strata and resulted in a significantly greater snapper biomass inside the VICRNM (Fig. 3).

## Discussion

Marine protected areas are increasingly being used as a management tool to protect coral reef ecosystems, but there is debate on whether MPAs should be used to protect and increase biodiversity, as a fisheries management tool or to serve both purposes. Regardless of the objective of the implementation of an MPA, its success may hinge on proper location relative to critical habitats that support living marine resources. The absence of a full complement of habitats and structural complexity within a marine reserve may limit the potential of reef fish populations to increase in abundance (Sladek Nowlis & Friedlander 2004).

The VICRNM boundaries were primarily defined based on the legal parameters of the Antiquities Act. Thus, it was not feasible to integrate ecological design criteria into the process to delineate the boundaries of the VICRNM. The administrative process to define the boundaries of the VICRNM resulted in no protection for areas of the St John mid-shelf reef that contained relatively large areas of hard coral and high bathymetric complexity. Based on this study along the mid-shelf reef, many areas proximal to, but outside, the VICRNM are populated by hard corals including stands of living staghorn coral, *Acropora cervicornis* (Lamarck), which was recently listed as a threatened species. Conversely, the benthic habitat found at many of the sampling sites within VICRNM was primarily comprised of gorgonian-covered hard pavement (Kendall *et al.* 2001) (Fig. 1).

The mid-shelf reef is an important habitat because of its high bathymetric complexity, high percentage of live coral substrate and location in relatively deep water. The mosaic of habitats of the mid-shelf reef, and especially the areas outside the VICRNM, appear to support more complex hard coral habitats and greater richness, biomass and abundance of reef fishes compared with the VICRNM. Because of the relatively low number of economically exploited species currently throughout the study area (i.e. groupers, snappers, grunts) (Rogers & Beets 2001) and limited habitat and structural complexity within the VICRNM, the potential for reef fish species to increase in numbers and biomass may be diminished. Nevertheless, enforcement

of no extraction of marine species within the VICRNM is an important step in protecting and conserving marine resources around the island of St John. In an effort to avoid future management mistakes, most reserve designs will prove beneficial even if they are only first steps towards an ideal design (Sladek Nowlis & Friedlander 2004).

Based in part on the data generated during this investigation, discussions are underway between the US Department of the Interior and the US Virgin Island government to address the issue of the current wedge of US Virgin Island territorial waters that bisects the VICRNM (Fig. 1). The wedge makes it difficult for enforcement officers and fishers to determine accurately if they are operating inside or outside the VICRNM. Thus, discussions are being held on potential modification of VICRNM boundaries to minimise the confusion relative to exact location of VICRNM boundaries and to protect high-quality habitats and reef fish assemblages of the mid-shelf reef. If the wedge can be protected from extractive uses, the potential to enhance the VICRNM may increase because of the quality of the existing habitats and associated reef fish communities.

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## References

- Appeldoorn R.S., Friedlander A., Sladek Nowlis J., Usseglio P. & Mitchell-Chui A. (2003) Habitat connectivity in reef fish communities and marine reserve design in Old Providence–Santa Catalina, Colombia. *Gulf and Caribbean Research* **14**, 61–78.
- Ballantine W.J. (1997) *Design Principles for Systems of “No-take” Marine Reserves*. Workshop on the Design and Monitoring of Marine Reserves, February 18–20. Vancouver, Canada: Fisheries Centre, University of British Columbia, 20 pp.
- Beets J. & Friedlander A. (1999) Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. *Environmental Biology of Fishes* **55**, 91–98.

- Beets J. & Rogers C. (2002) Changes in fishery resources and reef fish assemblages in a marine protected area in the U.S. Virgin Islands: the need for a no take marine reserve. In: M.K. Kasim Moosa, S. Soemodihardjo, A. Nontji, A. Soegiarto, K. Romimoharto, Sukarno & Suharsono (eds) *Proceedings of the 9th International Coral Reef Symposium*. Bali, Indonesia: Ministry of Environment, Indonesian Institute of Sciences and the International Society for Reef Studies, pp. 449–454.
- Bohnsack J.A., Sutherland D.L., Brown A., Harper D.E. & McClellan D.B. (1986) *An Analysis of the Caribbean Biostatistical Database for 1985*. NOAA/NMFS/Southeast Fisheries Center, Coastal Resources Division, Contribution No. 86/87–10 35pp.
- Brock V.E. (1954) A preliminary report on a method of estimating reef fish populations. *Journal of Wildlife Management* **18**, 297–308.
- Brock R.E. (1982) A critique of the visual census method for assessing coral reef fish populations. *Bulletin of Marine Science* **32**, 269–276.
- Christensen J.D., Jeffrey C.F.G., Caldow C., Monaco M.E., Kendall M.S. & Appeldoorn R.S. (2003) Cross-shelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. *Gulf and Caribbean Research* **14**, 9–28.
- Domeier M.L. & Colin P.L. (1997) Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* **60**, 698–726.
- Jeffrey C.F.G., Anlauf U., Beets J., Caseau S., Coles W., Friedlander A.M., Herzlieb S., Hillis-Starr Z., Kendall M., Mayor V., Miller J., Nemeth R., Rogers C. & Toller W. (2005) The state of coral reef ecosystems of the U.S. Virgin Islands. In: J. Waddell (ed.) *The State of Coral Reef Ecosystems of the United States and the Pacific Freely Associated States: 2005*. Silver Spring, USA: NOAA Technical Memorandum NOS NCCOS 11. NOAA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team, pp. 45–90.
- Kendall M.S., Kruer C.R., Buja K.R., Christensen J.D., Finkbeiner M. & Monaco M. E. (2001) *Methods Used to Map the Benthic Habitats of Puerto Rico and the U.S. Virgin Islands*. Silver Spring, MD: National Oceanic and Atmospheric Administration. 45pp. Available from the World Wide Web: <http://biogeo.nos.noaa.gov/projects/mapping/caribbean/startup.html>.
- Murray S.N., Ambrose R.F., Bohnsack J.A., Botsford L.W., Carr M.H., Davis G.E., Dayton P.K., Gotshall D., Gunderson D.R., Hixon M.A., Lubchenco J., Mangel M., MacCall A., McArdle D.A., Ogden J.C., Roughgarden J., Starr R.M., Tegner M.J. & Yoklavich M.M. (1999) No-take reserve networks: protection for fishery populations and marine ecosystems. *Fisheries* **24**, 11–25.
- Randall J.E. (1967) Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* **5**, 665–847.
- Rogers C. & Beets J. (2001) Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the U.S. Virgin Islands. *Environmental Conservation* **28**, 312–322.
- Sladek Nowlis J. & Friedlander A. M. (2004) Marine reserve design and designation process. In: J. Sobel & C. Dahlgren (eds) *Marine Reserves: Their Science, Design and Use*. Washington, USA: Island Press, pp. 128–163.
- Sladek Nowlis J. & Friedlander A.M. (2005) Marine reserve design and function for fisheries management. In: E.A. Norse & L.B. Crowder (eds) *Marine Conservation Biology: the Science of Maintaining the Sea's Biodiversity*. Washington, USA: Island Press, pp. 280–301.
- Wilkinson C. (ed.) (2004) *Status of Coral Reefs of the World: 2004*, Vol. 1. Townsville, Australia: Australian Institute of Marine Science, 301 pp.
- Zar J.H. (1984) *Biostatistical Analysis*. Englewood Cliffs, USA: Prentice-Hall, 718 pp.