

Temporal Trends in Reef Fish Assemblages inside Virgin Islands National Park and around St. John, U.S. Virgin Islands, 1988-2006



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Executive Summary

This report is a result of long-term fish monitoring studies supported by the National Park Service (NPS) at the Virgin Islands National Park since 1988 and is now a joint NPS and NOAA collaboration. Reef fish monitoring data collected from 1988 to 2006 within Virgin Islands National Park (VINP) and adjacent reefs around St. John, U.S. Virgin Islands (USVI) were analyzed to provide information on the status of reef fishes during the monitoring period. Monitoring projects were initiated by the National Park Service (NPS) in the 1980s to provide useful data for evaluation of resources and for development of a long-term monitoring program.

Monthly monitoring was conducted at two reef sites (Yawzi Point and Cocoloba Cay) starting in November 1988 for 2.5 years to document the monthly/seasonal variability in reef fish assemblages. Hurricane Hugo (a powerful Category 4 storm) struck the USVI in September 1989 resulting in considerable damage to the reefs around St. John. Abundance of fishes was lower at both sites following the storm, however, a greater effect was observed at Yawzi Point, which experienced a more direct impact from the hurricane. The storm affected species differently, with some showing only small, short-term declines in abundance, and others, such as the numerically abundant blue chromis (*Chromis cyanea*), a planktivorous damselfish, exhibiting a larger and longer recovery period.

This report provides: 1) an evaluation of sampling methods, sample size, and methods used during the sampling period, 2) an evaluation of the spatial and temporal variability in reef fish assemblages at selected reef sites inside and outside of VINP, and 3) an evaluation of trends over 17 years of monitoring at the four reference sites. Comparisons of methods were conducted to standardize assessments among years. Several methods were used to evaluate sample size requirements for reef fish monitoring and the results provided a statistically robust justification for sample allocation.

An annual reef fish monitoring project was established in 1989 with 18 reef sites monitored until 1994. Variations in species richness ($CV = 12.7$), number of individuals ($CV = 27.8$), and biomass ($CV = 37.6$) among the monitoring sites emphasized the heterogeneity of habitats found around St. John. Comparisons of assemblage metrics inside and outside VINP showed no statistical difference in species richness or biomass, suggesting that the park is not functioning effectively as a protected area for reef fish assemblages. Analyses from this large sample of reefs were used to identify locations with high fish diversity to focus further long-term monitoring effort.

In 1995, a change in methodology was adopted and annual monitoring was restricted to four reference sites that were identified for their high biodiversity and conservation value. With the establishment of the NPS Inventory and Monitoring Program and selection of VINP as a Prototype Park in 1995, greater emphasis was given to development of sound and statically robust monitoring protocols. This need has since grown with the establishment of Virgin Islands Coral Reef National Monument (VICRNM) adjacent to Virgin Islands National Park, the expansion of Buck Island Coral Reef National Monument (BICRNM), and emphasis on monitoring within other NPS units.

Number of individual fishes and biomass were low, relative to subsequent years, immediately following Hurricane Hugo but increased rapidly, within one to three years, and then began to decline again afterwards. Hurricane Marilyn (a Category 3 storm) struck in 1995, which again depressed numerical abundance and biomass. A similar trend of rapid increase, followed by a somewhat slower decline, occurred for both assemblage metrics after this second disturbance event.

These analyses demonstrated that the most apparent factor influencing reef fish assemblages around St. John is large storm events. Storms had differential effects among reefs and species depending on exposure and reef type. It is imperative that these results be viewed with the knowledge that large changes in the entire ecosystem occurred prior to the establishment of monitoring. Large predators (e.g., groupers and snappers) are now in low abundances compared with documented investigations in the 1950-60s. The decline of predators can have profound cascading effects throughout the entire ecosystem, and has fundamentally altered the coral reefs of the Virgin Islands as it has elsewhere throughout the Caribbean.

The analysis of reef fish data included in this report provides evidence for two alarming conditions, both of which are important for resource management in VINP. **1) Reef fish assemblages within Virgin Islands National Park are not significantly different than assemblages outside park boundaries. 2) Several species, including some of the most abundant species, demonstrated substantial declines in abundance and frequency of occurrence over the past decade.** Some species, such as groupers and snappers (preferred in the local fishery), have documented declines throughout the U.S. Virgin Islands and have fared no better within VINP. Other species may have declined due to the combined effects of habitat change, from both natural and anthropogenic influences, and exploitation. Regardless of causes, we must conclude that the existing management strategies are not adequately protecting resources within the park and are in need of revision.

This work is one of the longest running research projects in the Caribbean for reef fishes and provides a strong basis for understanding the natural and anthropogenic factors which have affected reef fish assemblages around the island of St. John over the past three decades. The importance of long-term monitoring programs like this one cannot be overstated owing to the dramatic changes that have occurred in the past half century with the USVI and the danger of the “shifting baseline” where expectations are based solely on the current level of knowledge. Continuation of this work will provide the National Park Service, the Virgin Islands Government, and other management agencies and stakeholders with the information necessary to make informed decisions on the future of reef fish resources and coral reef ecosystem health in the U.S. Virgin Islands, with implications for the broader Caribbean, and tropical ecosystems worldwide.

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INTRODUCTION

Worldwide, coral reef ecosystems are declining at an alarming rate (Wilkinson 2004, Bellwood *et al.* 2004, Pandolfi *et al.* 2005) and the U.S. Virgin Islands (USVI) is no exception (Rogers and Beets 2001, Beets and Rogers 1997, Jeffrey *et al.* 2005, Rogers *et al.* 2008). The collapse of many Caribbean coral reefs has been attributed to dwindling fish stocks, increased eutrophication, and sediment runoff (Hughes 1994, Jackson *et al.* 2001, Mumby *et al.* 2006, Newman *et al.* 2006). Fishing is one of the most pervasive and direct impacts to coral reefs with a focus first on the larger more desirable species and a progressive shift towards smaller less desirable ones as time goes on and resources decline (Koslow *et al.* 1988, Russ and Alcala 1996, Jennings and Polunin 1997, Jennings and Kaiser 1998). With the removal of top predators in much of the Caribbean, overharvesting of herbivorous fishes such as parrotfishes and surgeonfishes has contributed to the increase in macroalgae and the decline in live coral throughout the region (Munro 1983, Hughes 1994, Rogers *et al.* 1997, Jackson *et al.* 2001, Newman *et al.* 2006, Mora 2008).

The effects of intensive fishing pressure have been felt throughout the USVI (Beets 1997, Beets and Friedlander 1999, Beets and Rogers 1997). About 180 species of reef fishes are harvested in the USVI (Caribbean Fisheries Management Council 1985) with the primary fishing gear being traps, followed by hook and line, and nets. Fishery resources throughout the USVI (Fig. 1), including those within Virgin Islands National Park (VINP), have declined dramatically over the last 30-40 years in spite of federal and territorial government regulations designed to protect them (Beets 1997, Beets and Rogers 1997). As far back at the late 1950s, Randall (1963) noted that the limited fringing reef area around the USVI received nearly all of the fishing effort, and as a consequence the effects of overfishing were evident. Large predatory fishes such as groupers and snappers are now far less abundant, the relative abundance of herbivorous fishes has increased, individuals of many fish species are smaller, and some spawning aggregations have been decimated (Beets and Friedlander 1992, 1999, Beets 1997, Beets and Rogers 1997).

In the 1960s, groupers and snappers dominated the landings in the USVI fishery but following the increased demand for fish with the tourism boom and technological changes in the fishery (larger boats, engines, and improved gear), fishers began to set more traps and target species like groupers and snappers, especially their spawning aggregations (Olsen and LaPlace 1979, Beets and Friedlander 1992). Nassau grouper, *Epinephelus striatus*, forms spawning aggregations around the full moon during winter months and was one of the dominant species in the fishery until the 1970s when the aggregation off St. Thomas was fished to collapse (Olsen and LaPlace 1979, Beets and Friedlander 1992). Following the decline of Nassau grouper and other large grouper species, fishers targeted smaller groupers such as red hind (*Epinephelus guttatus*) and coney (*Cephalopholis fulva*), which began to decline in landings as well over time (Beets and Friedlander 1992, Beets *et al.* 1994, Beets and Friedlander 1999).

The level of fishing effort varies greatly among locations in the USVI, with some fishers using a limited amount of gear nearshore and others setting long trap lines on the insular shelf, including within VINP boundaries (Garrison *et al.* 1998). VINP was established in 1956 and consists of 2,947 ha of land (approximately 56% of the 48 km² island) with marine portions added in 1962

(2,287 ha of surrounding waters). Although commercial fishing is prohibited, VINP's enabling legislation allows for the "customary uses of or access" to park waters for fishing, including the use of traps of "conventional Virgin Islands design". When the park was first established, fishers usually set only a few, smaller traps but with the advent of outboard motors, line hauls, and larger fiberglass boats, fishermen now fish further offshore with a larger number of traps (Beets 1997, Garrison *et al.* 1998).

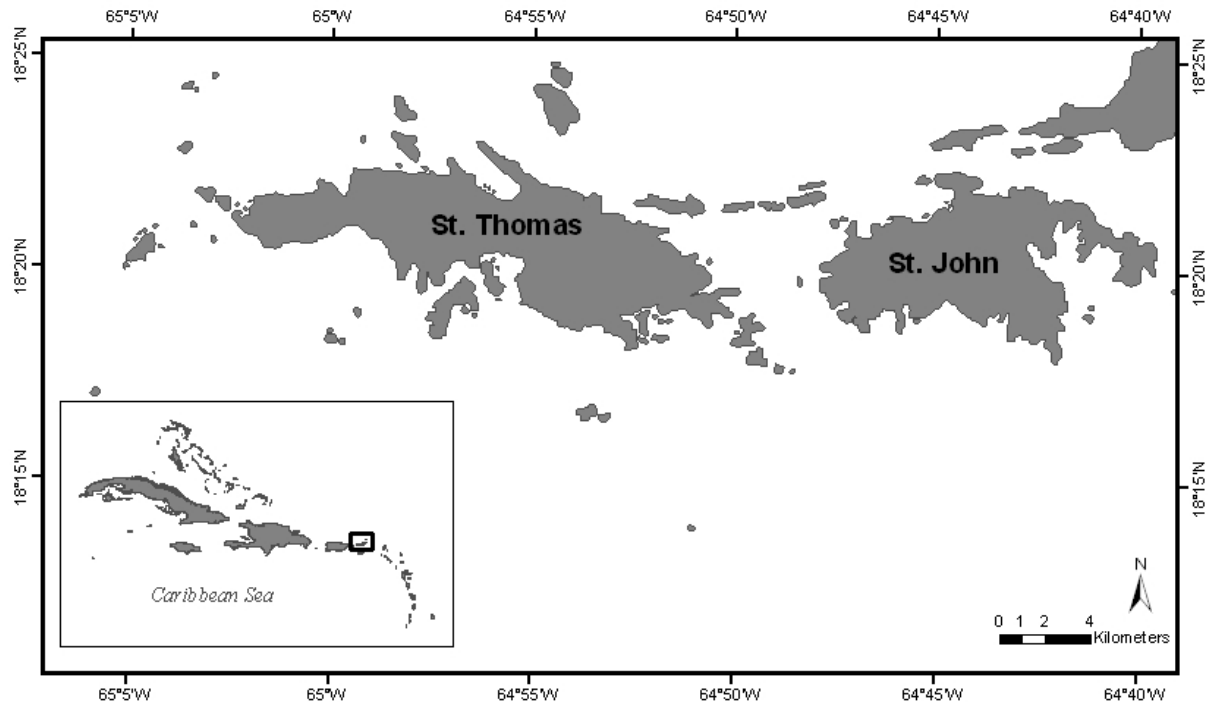


Figure 1. St. Thomas and St. John, U.S. Virgin Islands.

Fisheries landings within the boundaries of the national parks are not recorded separately from the remainder of the territory. Annual visual sampling of traps from 1992 to 1994 provided minimum catch estimates of >5,000 kg/yr inside VINP (Garrison *et al.* 1998). Landings by St. John fishers are as high as 78,634 kg/yr (Beets 1996) but do not include catch from around St. John by fishers from surrounding islands.

Comparison of fish trap catches at Yawzi Point, St. John between 1982–1983 and 1993–1994 showed substantial changes among the top 10 families, with an average decrease in numbers caught of -75.5% among these families (Fig. 2, Beets 1997). Boxfishes [Ostraciidae] (-328%) and porgies [Sparidae] (-297%) showed the largest declines, while grunts [Haemulidae] (-118%), groupers [Serranidae] (-97%), and snappers [Lutjanidae] (-59%) also exhibiting large declines over this time period (Fig. 2). Parrotfishes [Scaridae] (+61%), squirrelfishes [Holocentridae] (+42%), and surgeonfishes [Acanthuridae] (+39%) all increased in trap abundance between 1982-83 and 1993-4.

The proportional catch by family also changed dramatically during this time (Fig. 3). The proportion of boxfishes declined by -76% but their contribution in 1982-83 was small (2.5%). The proportional catch of important resource families such as porgies declined by -65%, while

grunts (-51%), groupers (-47%), goatfishes (-34%), and snappers (-32%) all showed substantial declines in proportional abundance. The largest proportional increase was for parrotfishes (+185%) and squirrelfishes (+170%), followed by surgeonfishes (+76%) and angelfishes (+100%). Among the top 11 taxa, the average decline in numbers caught was -97%, with the largest declines observed for blueshape grunt [*Haemulon sciurus*] (-346%), pooled porgies [*Calamus spp.*] (-296%), schoolmaster snappers [*Lutjanus apodus*] (-215%), and lane snappers [*Lutjanus synagris*] (-150%) (Fig. 4). The mean length of the top eight numerically dominant species captured in fish traps at Yawzi Point, St. John between 1982-3 and 1993-4 decreased by -23%, on average (Fig. 5). Schoolmaster snappers (-33%), blueshape grunts (-29%), and doctorfish (-26%) showed the largest declines over the sampling period.

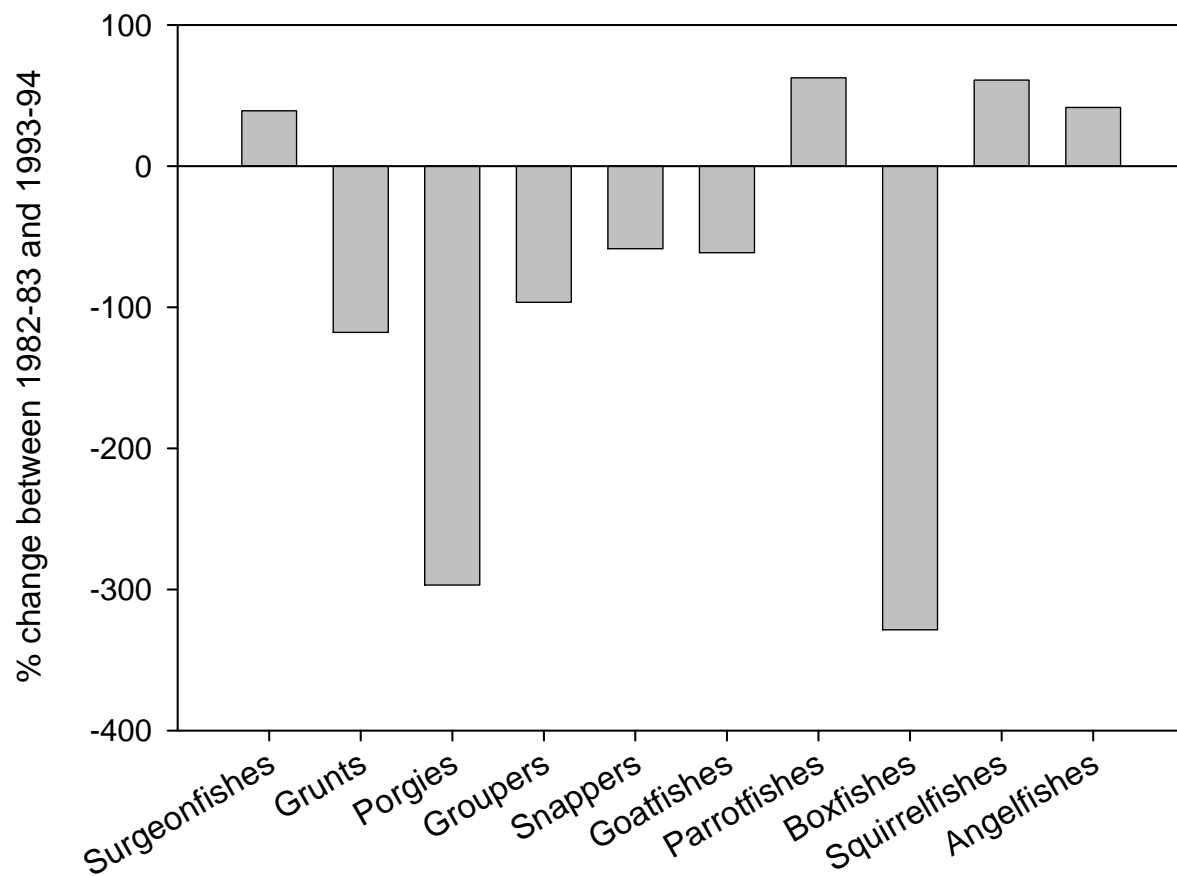


Figure 2. Percent change in number of individuals captured in fish traps at Yawzi Point, St. John between 1982-3 and 1993-4 for each of the top ten families (adapted from Beets 1997).

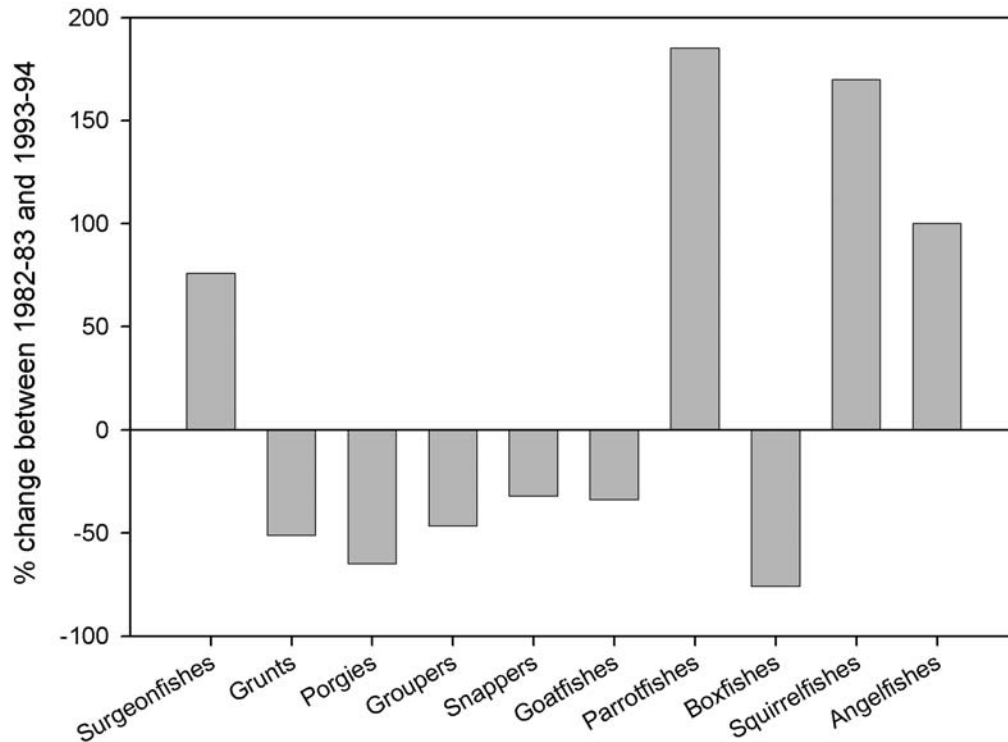


Figure 3. Percent change in numerical proportion of each of the top ten families captured in fish traps at Yawzi Point, St. John between 1982-3 and 1993-4 (adapted from Beets 1997).

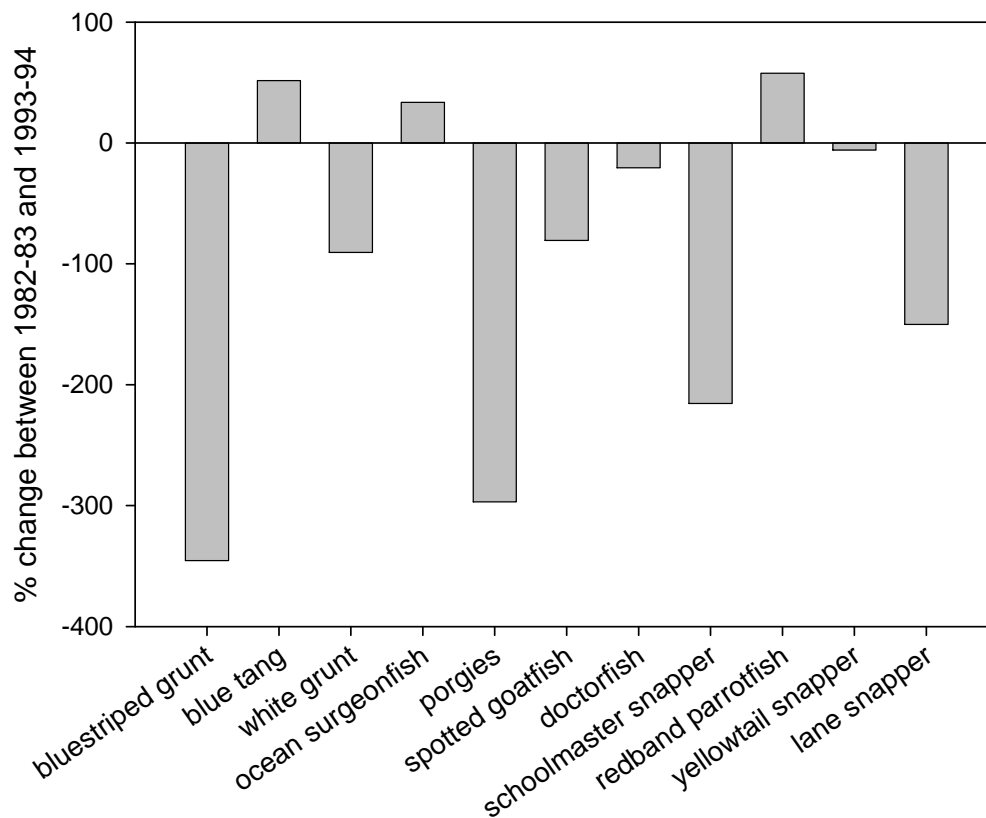


Figure 4. Percent change in numerical abundance of the top 11 taxa captured in fish traps at Yawzi Point, St. John between 1982-3 and 1993-4 (adapted from Beets 1997).

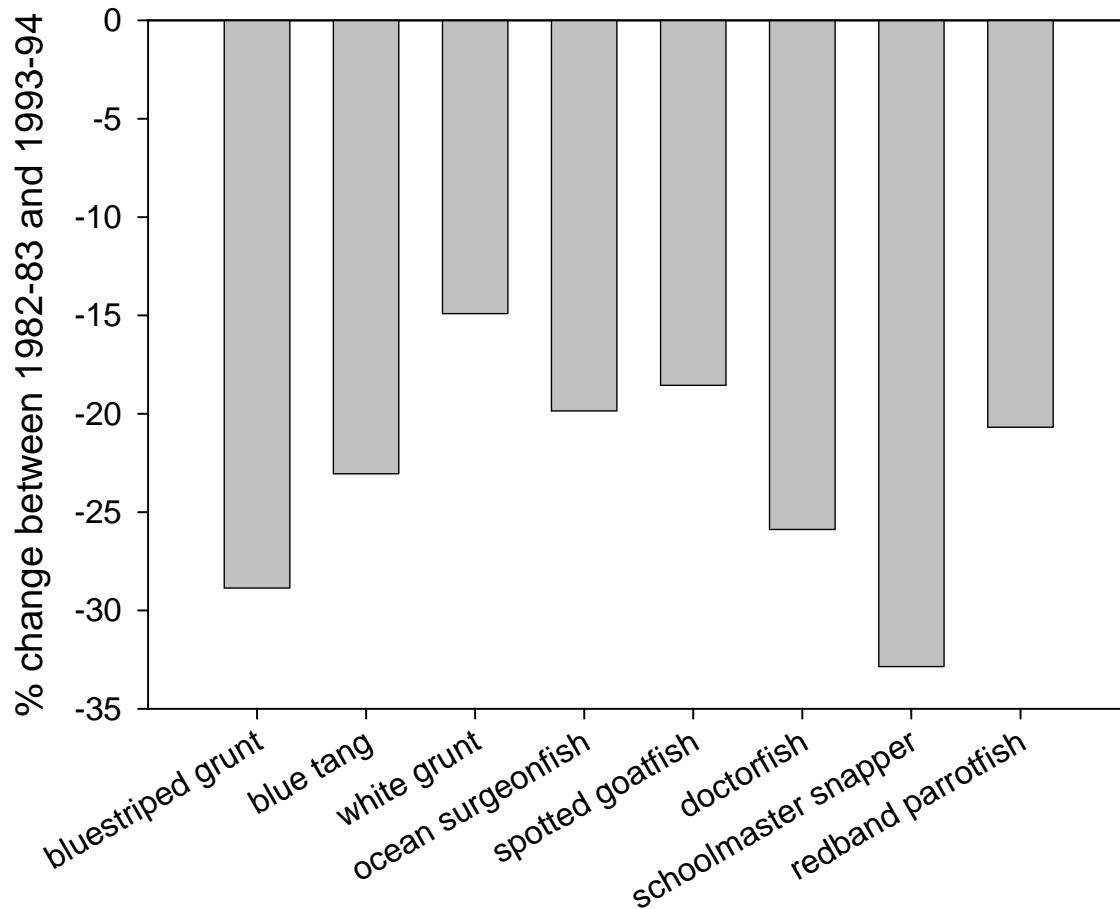


Figure 5. Percent change in mean length (FL cm) of the top eight numerically dominant species captured in fish traps at Yawzi Point, St. John between 1982-3 and 1993-4 (adapted from Beets 1997).

Reef Fish Research in Virgin Islands National Park

The National Park Service has supported reef fish research starting with the seminal work by John Randall from 1958-1961 which included: fisheries resources (Idyll and Randall 1959), fish tagging (Randall 1962), population structure (Randall 1963), fish grazing (1965), food habits (Randall 1967), and taxonomy (1968). The Tektite Program in 1969 and 1970 involved scientists living in a saturation diving habitat at a depth of 17 m in Lameshur Bay, St. John for weeks at a time. Nine studies dealing with various aspects of the ecology of coral-reef fishes were carried out during Tektite I and II and examined activity patterns, behavior, bio-acoustics, and herbivory (Collette and Earle, 1972).

In 1983, the Virgin Islands Resource Management Cooperative, supported primarily by the National Park Service and under the direction of Island Resources Foundation, produced a series of reports from 1986-1988 that provided maps and data that are the basis of many ongoing projects in VINP. Subsequent investigations of fish resources and fisheries investigations have been conducted around St. John, ranging from fisheries assessments, reef fish monitoring, hurricane impacts, and declining resources (Table 1).

Table 1. Partial list of reef fish and fisheries research conducted around St. John and Virgin Islands National Park and Biosphere Reserve (VINP/BR).

Topic	Author(s)
Marine community maps of bays within the VINP/BR	Beets <i>et al.</i> 1985
Fisheries habitat important to VINP/BR	Boulon 1986a
Map of fishery habitats within the VINP/BR	Boulon 1986b
Basis for long-term monitoring of fish and shellfish in VINP	Boulon 1987
Utilization of the VINP/BR by artisanal fishermen	Boulon and Clavijo 1986
Long-term monitoring of fisheries in VINP/BR	Boulon 1987
Assessment of fish and shellfish stocks in VINP/BR	Dammann 1986
Socioeconomic and cultural role of fishing in the VINP/BR	Koester 1986
Long-term monitoring of fisheries in VINP: Impact of Hurricane Hugo	Beets and Friedlander 1990
Long-term monitoring of fisheries in VINP: 1988-1992	Beets 1993
Queen conch populations in VI from 1981-1990	Friedlander <i>et al.</i> 1994
The effects of fishing and fish traps on fish assemblages within VINP and Buck Island National Monument.	Beets 1996
Can coral reef fish be sustained as fishing intensity increases	Beets 1997
Queen conch populations in VI from 1981-1996: management recommendations for VINP	Friedlander 1997
Groupers, snappers, queen conch and spiny lobster in VINP	Beets <i>et al.</i> 1996
Hurricanes and herbivory	Rogers <i>et al.</i> 1997
Reef fishes, overfishing and fish traps in St. John	Garrison <i>et al.</i> 1998
Spiny lobster evaluation within VINP	Wolff 1998
Evaluation of a Visual Census Method for Reef Fishes in VINP: Determination of Optimal Sample Size	Friedlander <i>et al.</i> 1999
Decline of fishery resources in the U.S. Virgin Islands	Rogers and Beets 2001
Fish recruitment on a fringing coral reef in VINP	Miller <i>et al.</i> 2001
Decline of fishery resources in the U.S. Virgin Islands	Beets and Rogers 1997
Decline of fishery resources in the U.S. Virgin Islands	Beets and Rogers 1997
Long-term trends in fish assemblage structure	Beets and Friedlander 2003
Movement patterns of reef fishes in VINP	Beets <i>et al.</i> 2003
Fish monitoring in VINP	Beets and Friedlander 2006
Fish monitoring in NPS South Florida/Caribbean	Menza <i>et al.</i> 2006
Fish populations inside/outside VI National Monument	Monaco <i>et al.</i> 2007
NOAA Biogeography Reef fish database http://www8.nos.noaa.gov/biogeography_public/query_main.aspx	Monaco <i>et al.</i> 2007

These investigations have provided valuable information, including information on the changes in fish assemblages around St. John that have occurred over the past several decades. Large changes, especially declines in exploited species inside and outside of VINP, have been noted by many of these studies in recent years.

Initiation of long-term monitoring

One of the greatest justifications for consistent monitoring is to document the effects of natural events, such as the impact of hurricanes, and to attempt to differentiate natural fluctuations from human stresses such as overfishing. The magnitude and periodicity of disturbances greatly affect the spatio-temporal patterns observed on coral reefs (Done *et al.* 1991, Connell 1997). The trajectories of these trends are determined by the synergistic effects of local and regional processes (Connell 1997, Bythell *et al.* 2000) and monitoring needs to be conducted over time scales commensurate with the periodicity of these disturbance events.

Numerous storms affected the community structure of reefs around St. John during the monitoring period covered in this report, with some storms having large effects (Rogers and Beets 2001, Fig. 6). The two largest storms passing St. John, Hurricane Hugo (1989) and Hurricane Marilyn (1995), devastated some reefs and had less influence on others (Rogers *et al.* 1991, 1997). Long-term and consistent monitoring data allowed for more critical assessment of these large disturbances and the differential effects that storms had on fish assemblage structure in addition to the impacts from fishing and other anthropogenic stressors.

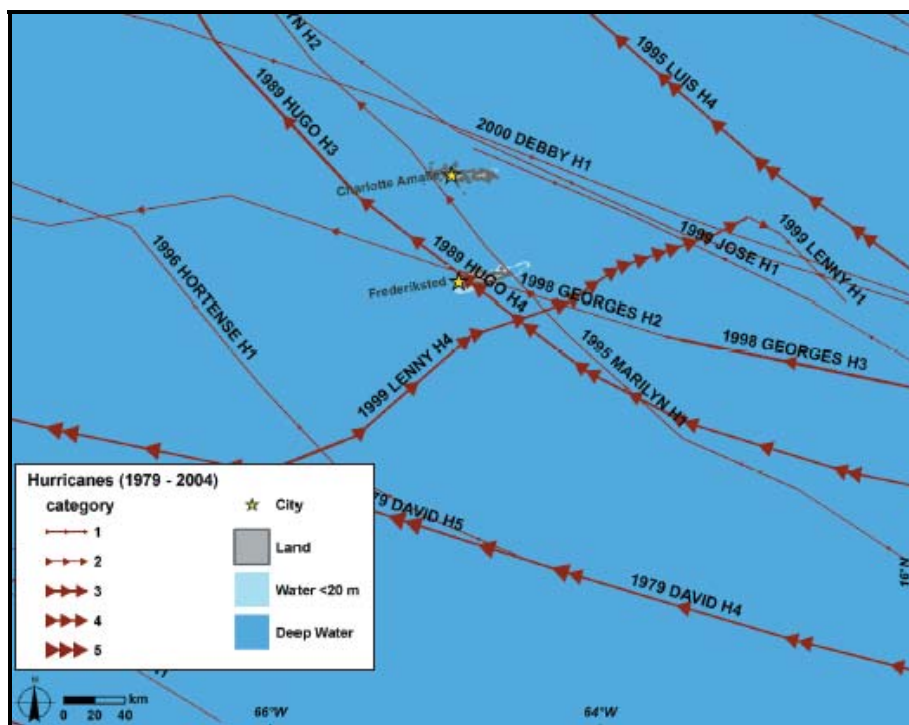


Figure 6. Tracks of major storms influencing marine habitats of the U.S. Virgin Islands, 1979-2004.

Consistent monitoring efforts of reef fishes commenced in November 1988 with an investigation to study the monthly variation in reef fish assemblages at two locations (Yawzi Point Reef and Cocoloba Reef) on the south shore of St. John in VINP and continued through May 1991 (Fig. 7, Beets and Friedlander 1990, Beets 1993). Following Hurricane Hugo in 1989, 18 reef sites were selected to monitor hurricane impacts on the fish assemblages around St. John, which included

the original two monthly sampling sites (Fig. 7). Except for a few monitoring sites that were replaced with new sites, all sites were sampled annually through 1994.

From 1995 to 2006, sampling was continued at four of the previous monitoring sites that had been surveyed since 1991 (Tektite, Yawzi Point, Haulover West, and Newfound, Fig. 8). The goals of this monitoring project were to: 1) establish a baseline of information on reef fish assemblages around St. John; 2) conduct sustained monitoring on representative high-diversity reefs; 3) collect data on reefs with known and potential environmental degradation; 4) compare fish assemblages among selected reefs; and 5) determine trends in reef fish assemblages over time. This report represents analyses of reef fish data collected using visual census methods around St. John, U.S. Virgin Islands from 1988 to 2006 and addresses the goals and objectives stated above.

METHODS

Description of habitats sampled

A diversity of habitat types are found around St. John, and these have been classified, described, and mapped (Beets *et al.* 1985, Kendall *et al.* 2001). Reef fish monitoring in this study between 1988 and 2006 in VINP was restricted to reef habitat only (Figs. 7 and 8). Monitoring sites were similar in live coral cover (usually 10-30%) and physical structure. Most sampling sites were located on the lower forereef of fringing reefs, which gradually sloped to sand, and were dominated by the lobed star coral, *Montastrea annularis* or mixed corals. Portions of this habitat are spatially complex with higher coral cover than surrounding gorgonian-dominated colonized pavement and have the greatest species richness and numerical abundance of fishes of all habitats around the island of St. John. Monitoring sites were located on these high-diversity portions of reef. Sampling was stratified in the lower forereef zone between two subzones (edge - a steep slope which extends from the forereef-sand interface to change in slope; platform - the gradual slope from the edge or the sand interface to the next shallower zone, e.g., upper forereef [*Acropora* zone]).

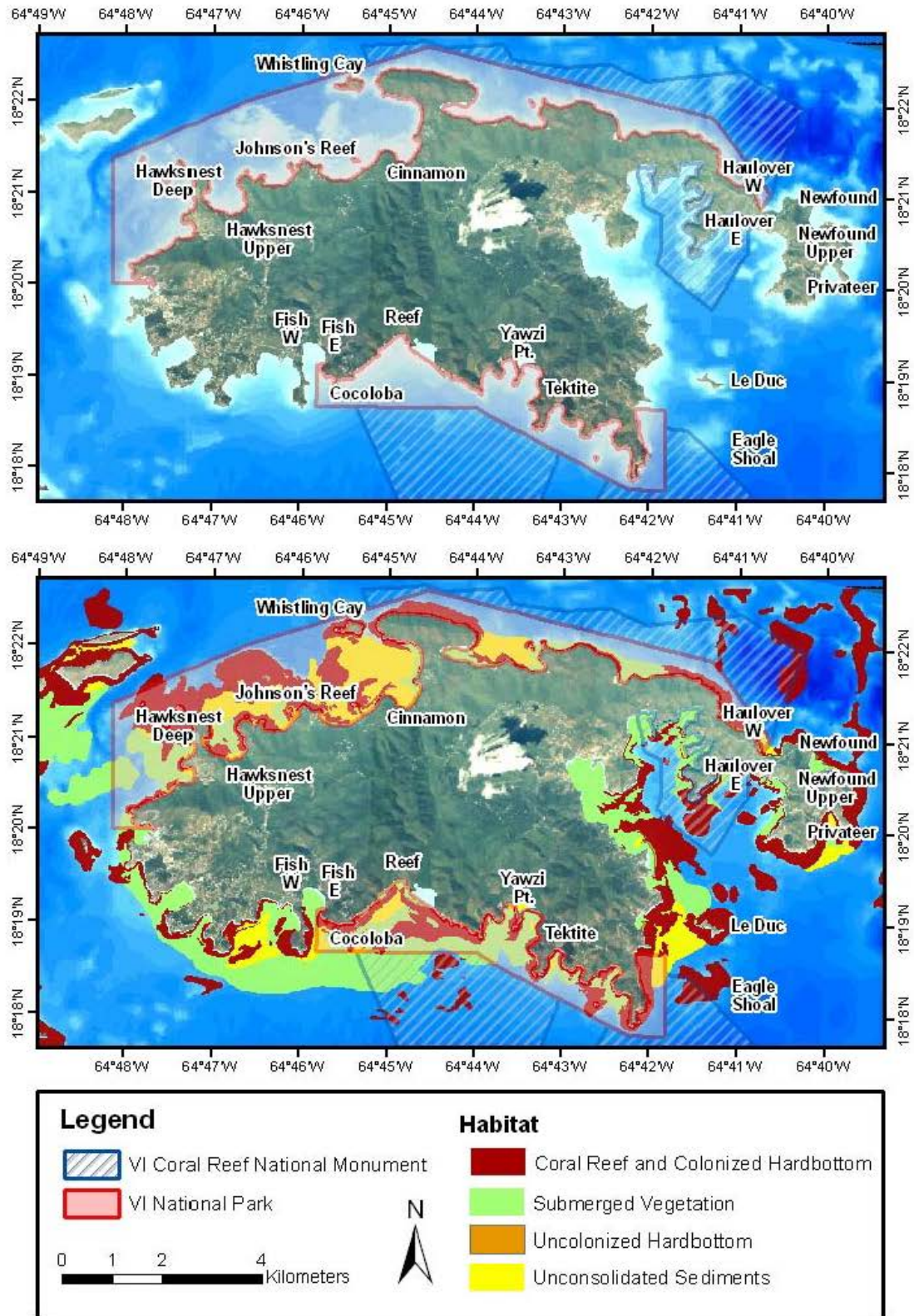


Figure 7. Location of fish sampling locations conducted around St. John, USVI between 1988 and 2006. Benthic habitat map source: Kendall *et al.* 2001.

Visual census methods

The primary reef fish monitoring method used at Yawzi Point Reef and Coccoloba Reef (Fig. 9), 1988-1991, and the four permanent monitoring reefs, 1995-2000, was the stationary visual census technique described by Bohnsack and Bannerot (1986). A single sample was conducted by a diver, who settles just above the reef substrate at a haphazardly selected point. During the point count, all fish species observed were listed within a 7.5 m radius cylinder (area: 176.7 m²) for 5 minutes. Numbers and sizes of fishes of each species (estimated fork length placed in separate size classes) were added following the 5 minute listing period. Habitat within the cylinder was briefly described, including substrate type, estimated coral cover, dominant benthic organisms, relative topographic complexity, depth, and location on the reef.

The modified visual census technique, developed for fish monitoring in Dry Tortugas National Park (Kimmel 1992), was used in VINP from 1989 to 1994. This modification used a 5 m radius cylinder (area: 78.5 m²) and 15 minute time interval with the last 5 minutes of the 15 minute total used to search and enumerate species and individuals by swimming throughout the cylinder. At the request of the National Park Service, a change back to the standard stationary visual census technique (Bohnsack and Bannerot 1986) in 1995 from the modified technique was done to standardize with investigators working elsewhere in the Caribbean and in the Florida Keys National Marine Sanctuary and Dry Tortugas National Park. For both methods, sampling was restricted to reef habitat. Sampling was not conducted if the cylinder occupied less than 50% hard substrate and/or reef (greater than 50% sand).

Statistical analyses

Standard reef fish assemblage parameters were included in the analyses: species richness (mean number of species per sample), numerical abundance (mean number of individuals per sample), and biomass (estimated live wet weight of individuals per sample). All analyses of numerical abundance and biomass excluded the masked goby (*Coryphopterus personatus*) because they were ubiquitous and their large numbers in samples (1,000's) obscured trends in the rest of the fish assemblage. The masked goby was included in calculations of species richness. Masked gobies are most abundant in reef structure with high topographic complexity and may be an important indicator of reef condition in the Virgin Islands, but this species contributes negligibly to biomass estimates because of its small size (< 3 cm).

Trophic groups used in the analyses were defined as herbivores, planktivores, piscivores (dominated by groupers and snappers), and secondary consumers (other predators represented by numerous families). Herbivores were further broken down into benthic herbivores (dominated by damselfishes) and mobile herbivores (dominated by parrotfishes and surgeonfishes). Biomass estimates were derived from calculated live wet weight. Live wet weight (W) was derived from the visually estimated mean fork length (FL) for each size class for each species using the relation $W = a(FL)^b$. Values of the fitting parameters a and b for each species were derived from Bohnsack *et al.* (1986) and the FishBase web site (<http://fishbase.org/>). For species not in these databases, estimates from available literature on the species or congeners were used. Biomass of all fishes recorded in all censuses was 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.

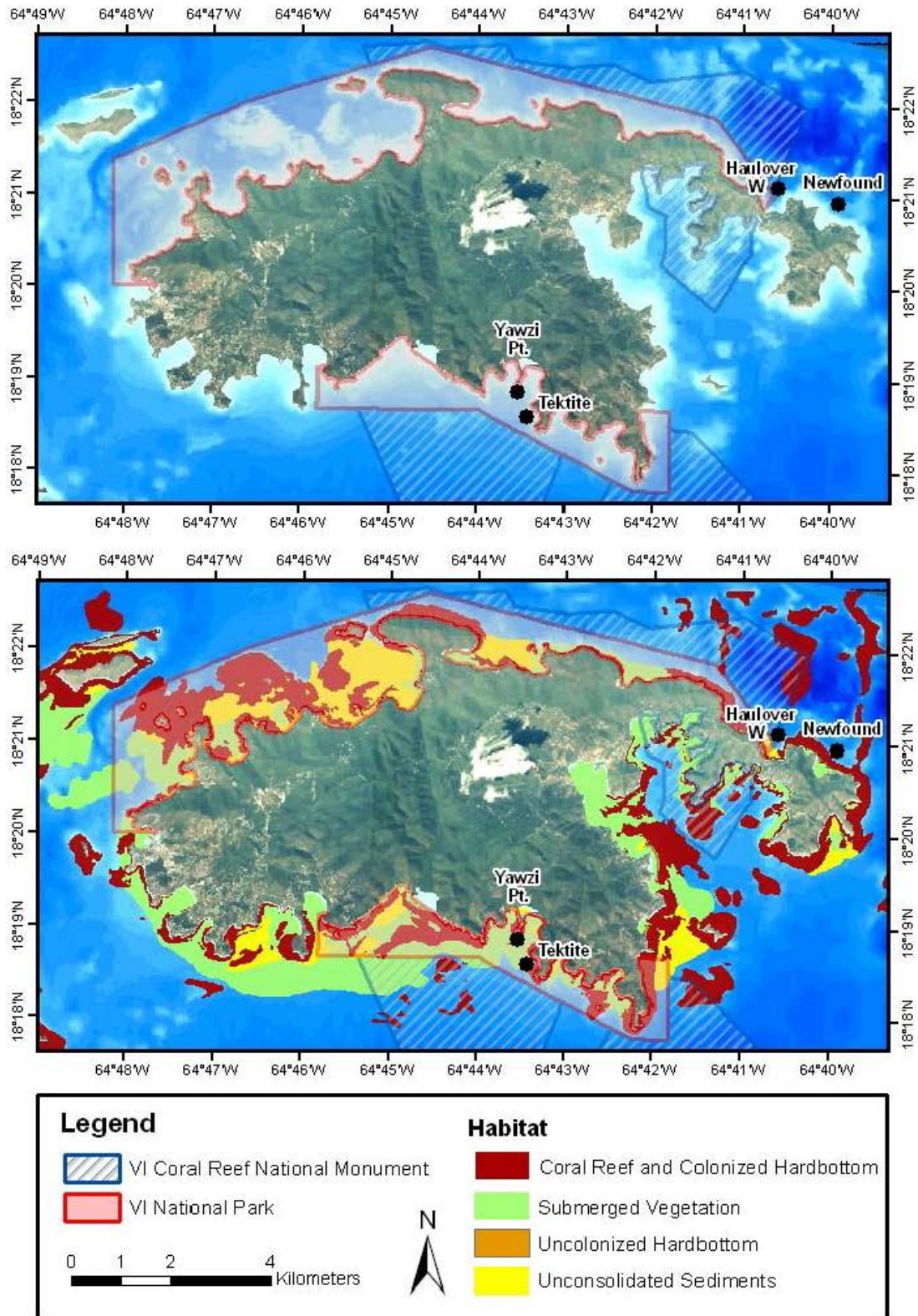


Figure 8. Benthic habitat map and locations of four permanent monitoring sites sampled from 1991 to 2006. Map source: Kendall *et al.* 2001.

Differences in species richness and numerical abundance between monthly sampling locations (Yawzi Pt. and Cocoloba Cay) were tested using a Student's t-test (t). Normality was tested using a Shapiro-Wilks W test ($P < 0.05$) while a Bartlett's test ($P < 0.05$) was used to examine homogeneity of variance. Comparisons of fish assemblage characteristics inside and outside of Virgin Islands National Park were also conducted using Student's t-test. Number of individuals did not meet the parametric assumption of homogeneity of variances despite transformation and a Mann-Whitney Rank Sum Test (U) was used in place of the parametric alternative. Table-wise Bonferroni corrections ($p = 0.05/m$), where m is the number of comparisons within the table, were employed to reduce Type I errors.

Non-metric Multi Dimensional Scaling (nMDS) analysis using PRIMER v6 (Clarke and Gorley 2001) was conducted to examine fish assemblage structure in ordination space among years. The data matrix consisted of mean fish numerical abundance by species for each year within each location. A Bray-Curtis Similarity matrix was created from the $\ln(x+1)$ transformed mean fish biomass matrix prior to conducting the nMDS. Differences in fish assemblage structure among years for each location were examined using a permutation-based hypothesis testing analysis of similarities (ANOSIM in PRIMER 6.0 [Primer-E Ltd., Plymouth, UK]) (Clarke and Gorley 2001, Clarke and Warwick 2001). This procedure generates an R statistic on a scale from 0 or negative value (identical assemblages) to 1 (completely dissimilar assemblages). The resulting P value indicates the probability that the two assemblages come from a similar distribution (Clarke and Warwick 2001).

Temporal data were fit to linear or 2nd order polynomial models with model selection based on best fit (R^2). Time periods for statistical analyses were: a) post Hurricane Hugo (1989-1994), b) post Hurricane Marilyn (1996-2000), and c) time since 2001.

Methods comparison study

A methods comparison was conducted on July 16, 1992 on Tektite Reef, the monitoring site with the consistently greatest species richness and fish abundance. Five plots on the reef of similar topographic complexity, coral cover, and depth were selected and marked for sampling. Each plot was located between 10-12 m water depth, approximately 25 m apart. Transect lines (15 m) were laid within each plot. Four experienced fish counters conducted one sample using each method within each plot. Method, site, and time were randomly assigned. This sampling design allowed for paired comparisons between methods for each diver at a given location. Species richness was the only assemblage characteristic or trophic group that showed a significant difference between methods and was therefore not included in any temporal analyses (Table 2). For all other assemblage metrics, methods were pooled among years.

Sample size analysis

Since 1995, the primary reef fish monitoring method used at the four permanent stations was the standard Bohnsack-Bannerot (1986) stationary visual census technique. Sample size had been set at a minimum of 18 samples per reef station per sampling date, based on earlier analysis of data

collected using the modified method (10 m/15 minutes). In July 1999, an oversampling effort ($n = 58$ samples) was conducted on Tektite Reef (approximately $13,500 \text{ m}^2$) in order to: 1) conduct a sample size analysis using the optimization technique and power analysis, 2) evaluate the advantages of random vs. haphazard sampling, and 3) provide a complete coverage for one reef among microhabitats and depths. Analyses of these data were previously reported (Friedlander *et al.* 1999).

Table 2. Comparison of A) assemblage characteristics, and B) trophic groups between two visual census methods (15 m/5 minutes and 10 m/15 minutes) conducted at Tektite Reef, VINP, St. John, on July 16, 1992. Values are means with one standard deviation in parentheses. The numerically abundant masked goby, *Coryphopterus personatus*, was excluded from these analyses. $N = 20$ for each method. Statistical comparisons conducted using paired t-tests = t. Bonferroni correction ($p = 0.05/m$), where m is the number of comparisons within the table.

A. Assemblage characteristics. Biomass $\ln(x)$ transformed for statistical analysis. $m = 3$; $p_{\text{crit}} = 0.05/3 = 0.0167$; ns = $p > 0.0167$; * = $p < 0.0167$; ** = $p < 0.001$; *** = $p < 0.0001$.

Assemblage characteristics	15 m (\pm SD)	10 m (\pm SD)	Percent difference from 15m	t	P	Bonferroni correction ($p = 0.05/3$)
Species richness	22.35 (± 3.17)	28.90 (± 3.77)	29.31	5.96	<0.0001	***
Number of individuals	181.45 (± 74.91)	200.00 (± 46.20)	10.22	0.91	0.37	ns
Biomass (kg)	0.62 (± 0.49)	0.69 (± 0.41)	11.29	0.55	0.59	ns

B. Number of individuals by trophic groups. All values except for benthic herbivores $\ln(x)$ transformed for statistical analysis. $m = 4$; $p_{\text{crit}} = 0.05/4 = 0.0125$; ns = $p > 0.0125$.

Trophic group	15m (\pm SD)	10m (\pm SD)	Percent difference from 15m	t	P	Bonferroni correction ($p = 0.05/4$)
Benthic herbivores	34.00 (± 14.87)	47.25 (± 20.36)	38.97	2.35	0.02	ns
Mobile herbivores	17.50 (± 13.52)	22.85 (± 9.13)	30.57	2.21	0.03	ns
Secondary carnivores	127.95 (± 68.81)	126.75 (± 45.19)	-0.94	0.26	0.80	ns
Top carnivores	3.00 (± 4.46)	4.05 (± 2.78)	35.00	1.78	0.08	ns

A species cumulation curve of the samples collected at Tektite Reef in 1999 showed that the cumulative number of species reached an asymptote at 22 samples (Fig. 9; Friedlander *et al.* 1999). The minimum sample size ($n = 18$) accounted for 96% of the total number of species

sampled at Tektite Reef. Optimization analysis of the Tektite Reef data suggested that approximately 11-16 samples were needed to sufficiently decrease the variation around the standard error of the mean (SE; Bros and Cowell 1987) for number of species and number of individuals (Fig. 10; Friedlander *et al.* 1999). Biomass showed little variation in mean SE but greater variation in high SE, with a larger number of samples ($n = 15-20$) required to substantially decrease variation around the SE+. This suggested that biomass should be analyzed with caution when smaller sample sizes are used and when sampling designs require this data type.

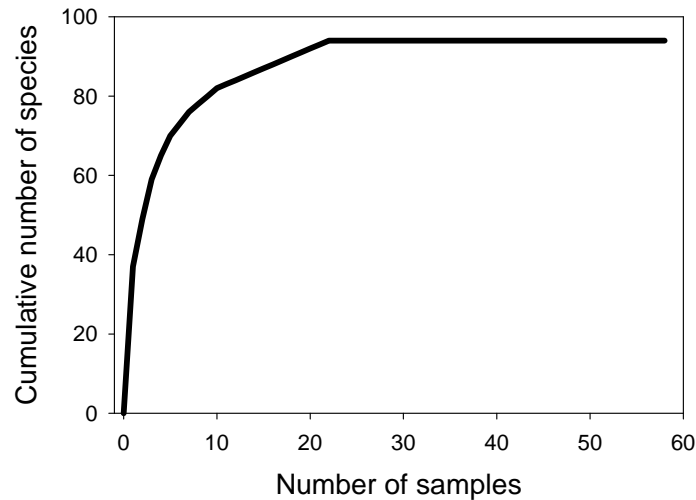


Figure 9. Cumulation curve showing the relationship between the cumulative number of species and the number of samples at Tektite Reef. From Friedlander *et al.* 1999.

The relationship of sample size with accuracy of the mean was examined for assemblage characteristics using data from the sample size study conducted at Tektite Reef (Fig. 11, $n = 58$ samples, Friedlander *et al.* 1999). Sample means were compared to a theoretical population mean using the t-distribution:

$$t - \text{value} = \frac{\text{sample mean} - \text{population mean}}{\sqrt{\text{sample variance} / \text{sample size}}} \quad (1)$$

(Eckblad 1991). The denominator of the above equation is the SEM. If the numerator is replaced with accuracy x sample mean, the equation can be rearranged to solve for sample size, for a specified relative accuracy in describing the theoretical population mean:

$$\text{Sample size} \approx (t\text{-value})^2 (\text{sample variance}) / (\text{accuracy} \times \text{sample mean})^2 \quad (2)$$

A type-I error rate (concluding that there is an effect when in fact none exists) of 0.10 was chosen to be more responsive to changes that may be occurring in the system before more serious changes occurred. This is a precautionary approach to management as mandated by the Magnuson-Stevens Fishery Conservation and Management Act. At a Type I error rate of 0.1, less than two samples were required to detect a 20% change in number of species, whereas, 12.8 were required to detect a 20% change in number of individuals and approximately 140 samples needed to detect a 20% change for biomass.

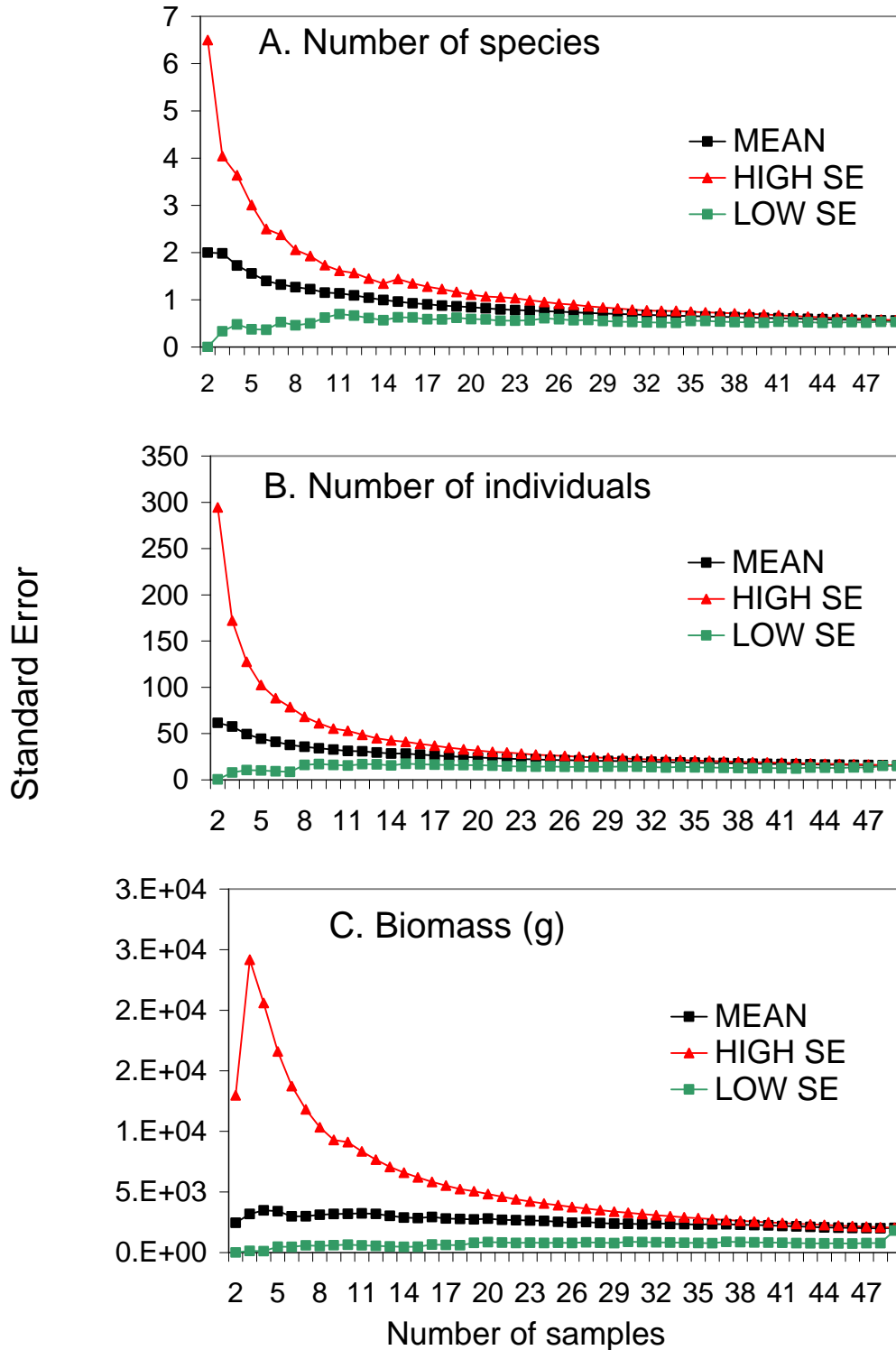


Figure 10. Sample size optimization of data from sample size analysis project at Tektite Reef, July 1999, for number of species, number of individuals, and biomass. Relationship between standard error of the mean (SE) and sample size. Monte Carlo simulation procedure for sample size optimization described by Bros and Cowell (1987). From Friedlander *et al.* 1999.

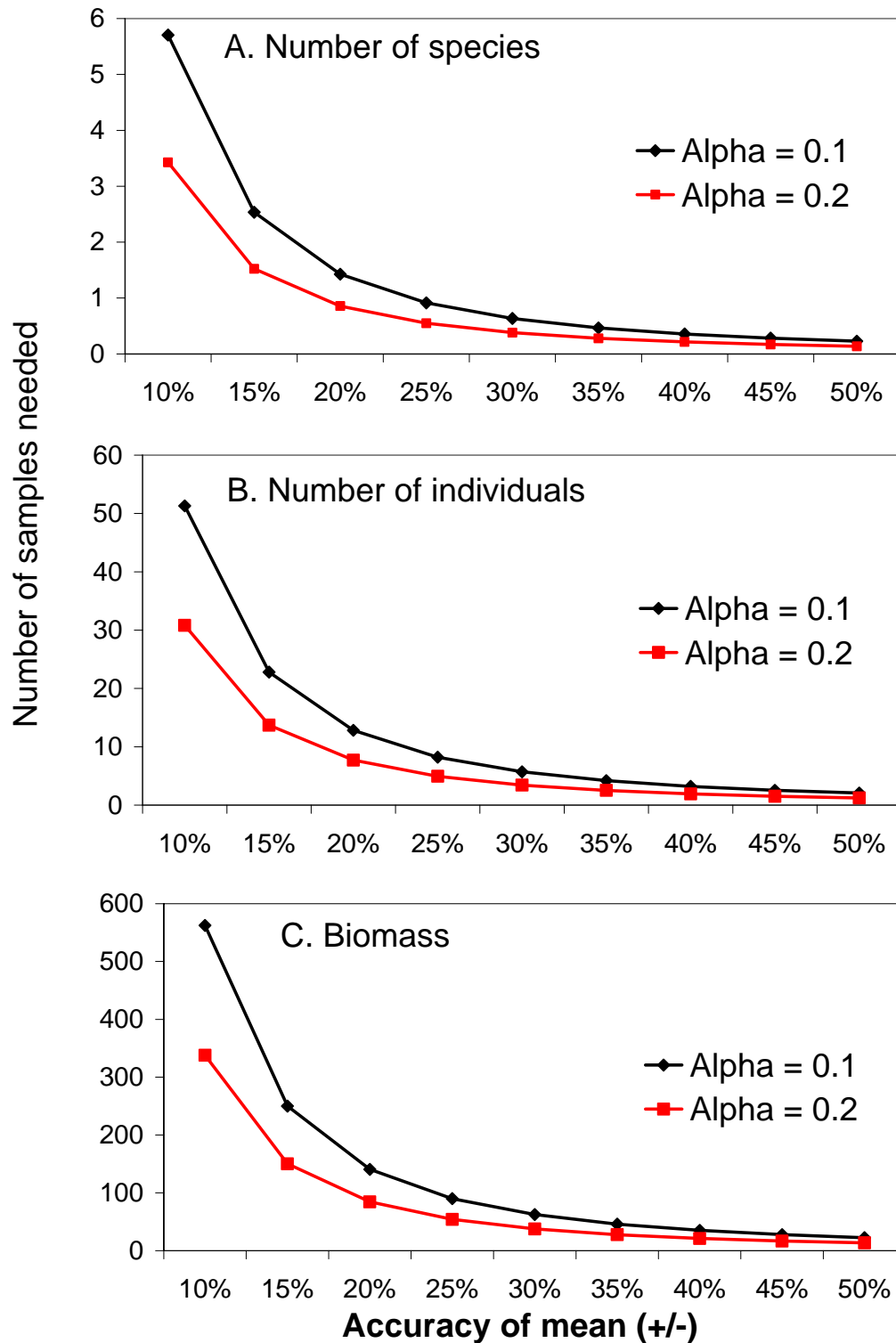


Figure 11. Estimated number of samples needed to detect changes in the mean of data from sample size analysis project at Tektite Reef, July 1999: A) number of species, B) number of individuals, and C) biomass. $N = 58$, $\alpha = 0.10$ and 0.20 . From Friedlander *et al.* 1999.

Fine-scale temporal reef fish dynamics

Understanding short-term temporal variability provides the critical context for interpreting the variability observed over longer time periods. An investigation to study the monthly variation in reef fish assemblages was initiated in November, 1988 and continued through May 1991 (Beets and Friedlander 1990, Beets 1993) using the stationary visual census technique developed by Bohnsack and Bannerot (1986). Starting in November, 1988, two reef sites, Yawzi Point and Cocoloba Cay, were sampled monthly until May, 1991 (Fig. 12). The two sites differed significantly ($t = 2.6$, $P = 0.01$) in average number of species per sample (Yawzi - $\bar{X} = 19.8 \pm 2.2$ SD, Cocoloba - $\bar{X} = 18.1 \pm 2.0$ SD) but were indistinguishable ($t = 0.38$, $P = 0.7$) in average numerical abundance of all individuals (Yawzi - $\bar{X} = 90.6 \pm 22.4$ SD, Cocoloba - $\bar{X} = 93.2 \pm 27.6$ SD).

Species richness and numerical abundance varied differently between the two sampling sites over the 2.5 year time period, although the variability among samples was similar at both sites (Fig. 12). Just prior to the initiation of sampling, tropical storm Gilbert (later a Category 4 hurricane), passed south of St. John. Fish assemblage characteristics appeared to increase during the first few months of sampling, particularly at Yawzi Point, and may have been a response to changes resulting from Gilbert. In September 1989, Hurricane Hugo (a Category 4 hurricane) struck the Virgin Islands. This large storm devastated local marine habitats, especially shallow coral reef and seagrass beds, and clearly influenced fish assemblages.

Numerical abundance and species richness were both lower at the two sites following Hurricane Hugo. However, the magnitude of this change was more pronounced at Yawzi Point compared to Cocoloba Cay. Yawzi Point was more exposed to the full force of Hugo and suffered extensive loss of benthic cover and structure. Prior to the storm, the reef at Yawzi had relatively high coral cover (~25%) dominated by *Montastrea annularis* (Beets *et al.* 1985, Rogers *et al.* 1991). Afterwards, coral cover dropped to <15% and habitat complexity was greatly reduced. In contrast, Cocoloba Cay had lower live coral cover (also dominated by *M. annularis*) and less reef structure than Yawzi Point prior to Hugo. This reef is protected to the southwest by Ditliff Point and did not suffer the same extent of storm damage and the response by the fish assemblage was not as dramatic as it was at Yawzi Point.

The storm differentially affected species, with some showing only short term declines in abundance, and others, such as the numerically abundant blue chromis (*Chromis cyanea*), a planktivorous damselfish, exhibiting a longer recovery period (Fig. 12). This was true for both locations despite the higher number of blue chromis at Yawzi Point ($\bar{X} = 11.0 \pm 9.2$ SD) compared to Cocoloba Cay ($\bar{X} = 8.9 \pm 5.6$ SD). Although the number of blue chromis was not significantly different between the two sites ($P = 0.06$), the variability in abundance was larger at Yawzi Point (COV = 83%) compared to Cocoloba Cay (COV = 63%) and presumably reflects the greater disturbance associated with this site.

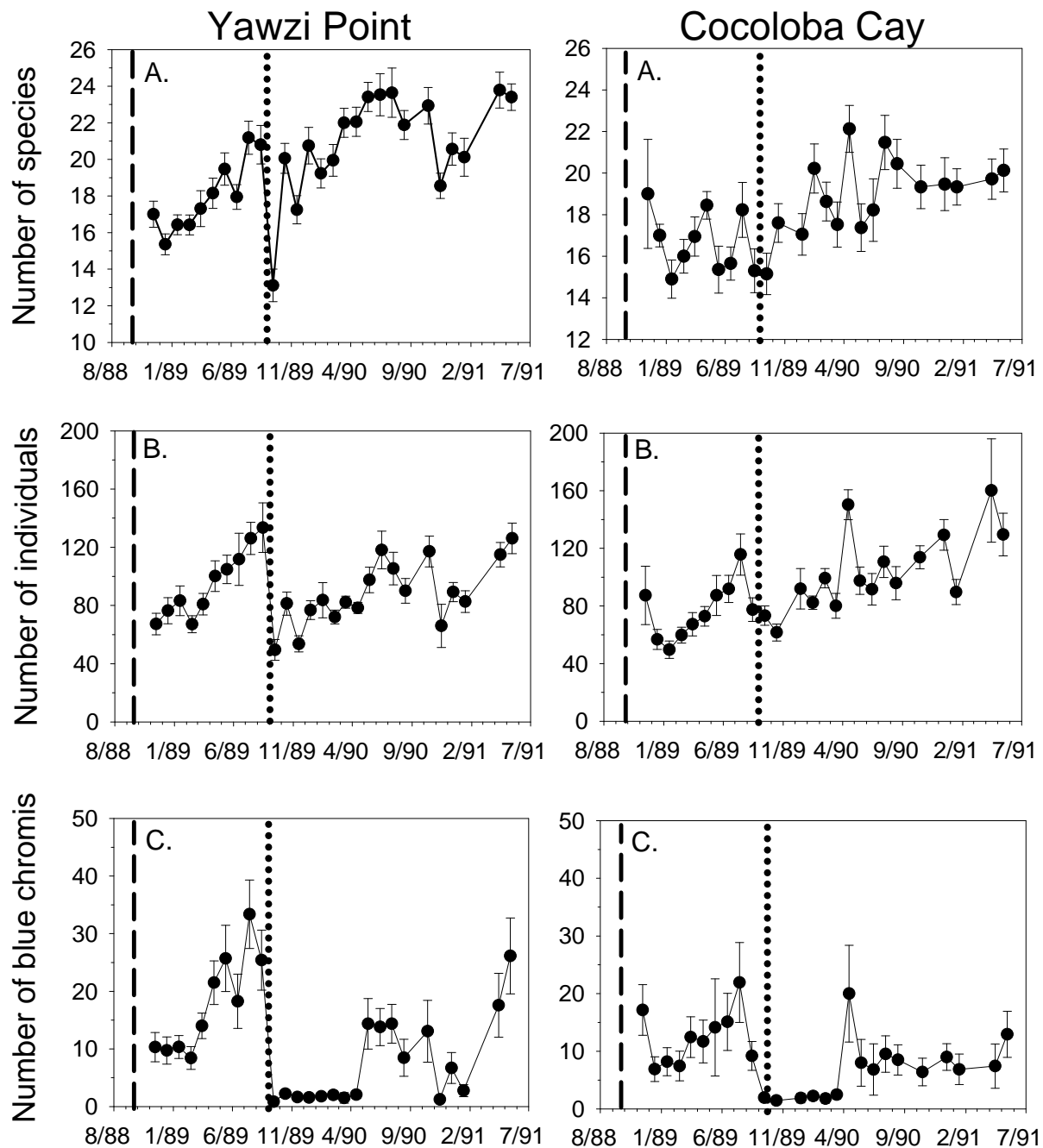


Figure 12. Mean monthly trends in: A) species richness, B) numerical abundance, and C) abundance of blue chromis (*Chromis cyanea*) at Yawzi Point and Cocoloba Cay monitoring sites, Nov 1988 – May 1991. Error bars are standard error of the mean. A large tropical storm, later Hurricane Gilbert, affected the southern coast of St. John in Sept. 1988 and is marked by the dashed lines. Dotted lines denotes the passing of Hurricane Hugo, Sept. 1989. (From Beets and Friedlander 2003)

Post disturbance assemblage dynamics

Following Hurricane Hugo in September 1989, NPS initiated reef fish sampling at a number of reef sites ($n = 18$) around St. John in addition to the monthly sampling at the two sites in the southern portion of VINP. Monitoring at the sites established in 1989 (originally 18 reef sites were selected with a few omitted and added among years) continued once per year during June/July, using the modified census method, until 1994.

Assemblage structure varied greatly among the 18 reef sites due to numerous factors, such as physical structure (topographic complexity, reef type, morphology), hydrodynamics, community dynamics, recruitment variability, connectivity with other habitats, etc. Analysis of monitoring data from the 18 reef sites around St. John, sampled 1989-1994, showed the variability in assemblage characteristics among reefs (Fig. 13). Mean species richness among reefs was 23.6 (± 4.7 SD) and ranged from a low of 15.3 (± 1.5 SD) at Whistling Cay, an offshore cay with low coral cover and low habitat complexity, to a high of 29.3 (± 5.5 SD) at Tektite Reef, a reef in Lameshur Bay on the south shore of St. John with high coral cover and high habitat complexity (Fig. 14). Yawzi Point ($\bar{X} = 27.3 \pm 4.9$ SD), also in Lameshur Bay, and Newfound Bay ($\bar{X} = 25.8 \pm 5.8$ SD) had the second and third highest species richness, respectively, among all reefs sampled.

Numerical abundance (Fig. 15) averaged 152.6 (± 163.4 SD) individuals per sample and was also highest at Tektite ($\bar{X} = 251.2 \pm 114.4$ SD) and dominated by planktivorous damselfishes (primarily blue [*Chromis cyanea*] and brown chromis [*C. multilineatus*]). Whistling Cay had the lowest average numerical abundance ($\bar{X} = 54.0 \pm 8.9$ SD) due again to the low overall habitat quality. Numerical abundance at the next lowest reef (Reef Bay - $\bar{X} = 116.3 \pm 76.4$ SD) was more than twice as high as Whistling Cay. Average biomass (kg) was 6.7 (± 7.9 SD) among reefs with the highest biomass observed at Newfound Bay Upper ($\bar{X} = 11.2 \pm 4.5$ SD), a dead, shallow *Acropora* zone with extremely high habitat complexity (Fig. 16). This reef area was dominated by schooling surgeonfishes, snappers, and grunts. Privateer Bay on the east end of the island had the lowest biomass ($\bar{X} = 3.4 \pm 7.8$ SD) and also had low coral cover and habitat complexity.

The four permanent monitoring reefs (Tektite, Yawzi Point, Newfound Bay, and Haulover West) ranked 1, 2, 3, and 6, respectively in average species richness among all sampling reefs. Tektite Reef also ranked first in numerical abundance, while Haulover West was in the upper quantile, and Yawzi Point and Newfound Bay were above the median. Tektite and Yawzi Point ranked 4th and 6th, respectively, in overall biomass with Newfound and Haulover above the median. These findings contributed to the selection of these reefs for permanent long-term monitoring sites since the National Park Service was most interested in biodiversity hotspots that had high conservation value.

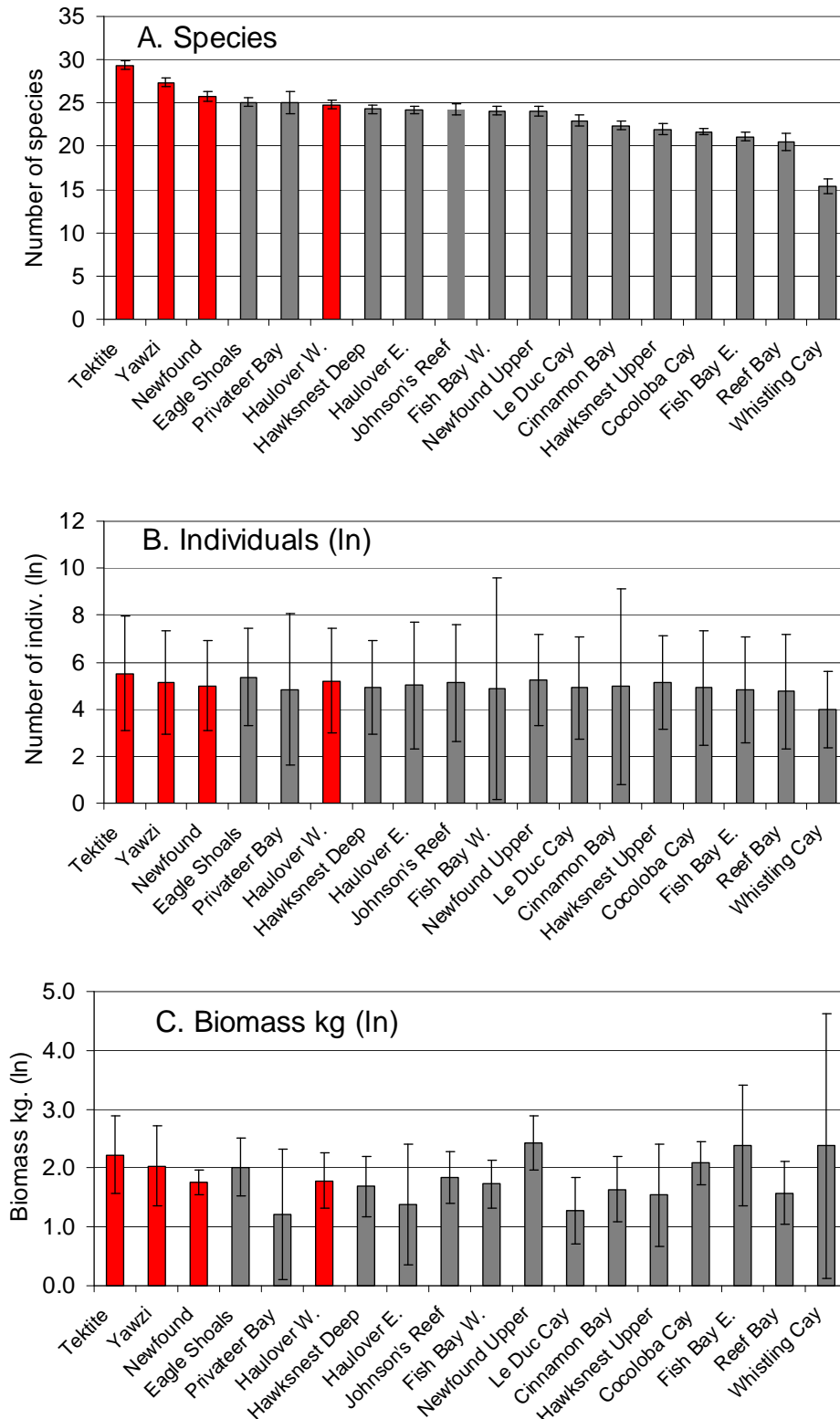


Figure 13. Assemblage characteristics among all locations surveyed between 1989 and 1995 (N = 18). Red bars indicate long-term monitoring locations. Values are means \pm se for 5 m radius cylinder (area: 78.5 m²) and 15 minute time interval.

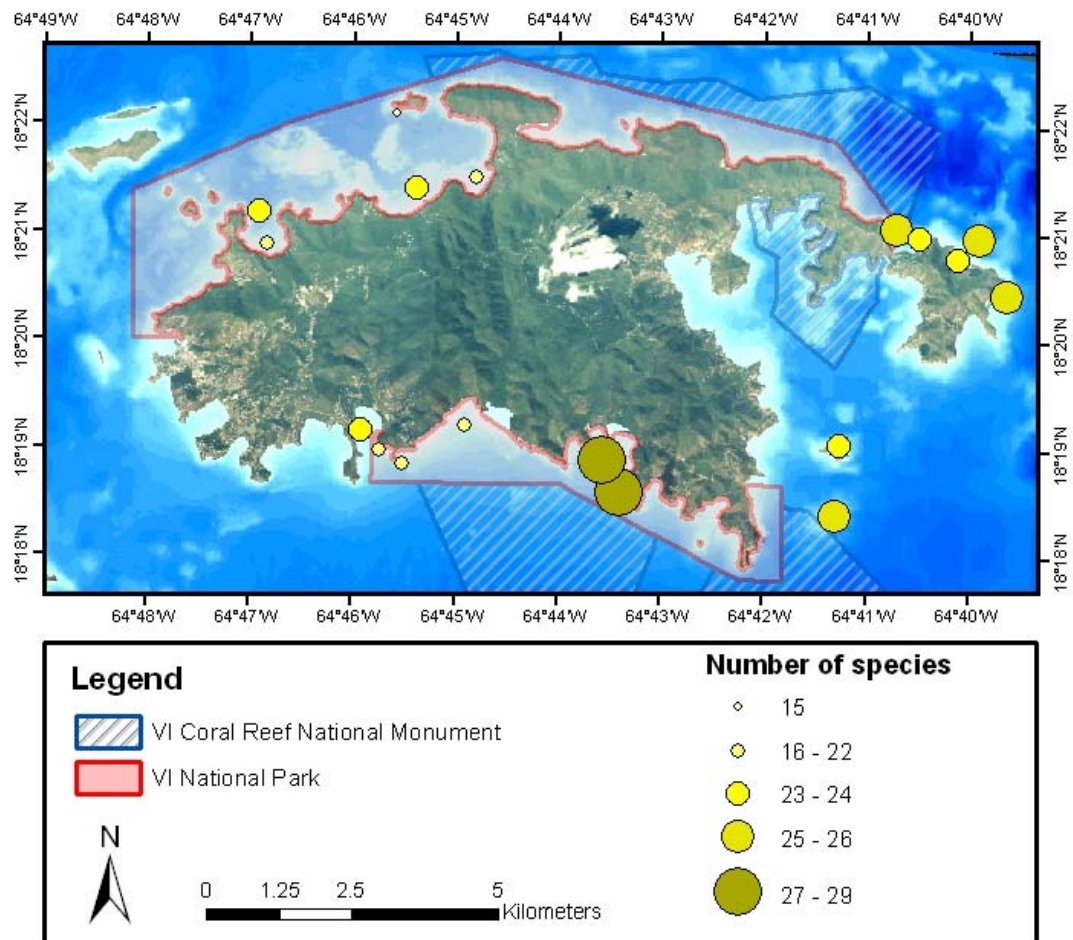


Figure 14. Mean number of species per sample among all locations surveyed between 1989 and 1995 (N = 18). Values are means for 5 m radius cylinder (area: 78.5 m²) and 15 minute time interval.

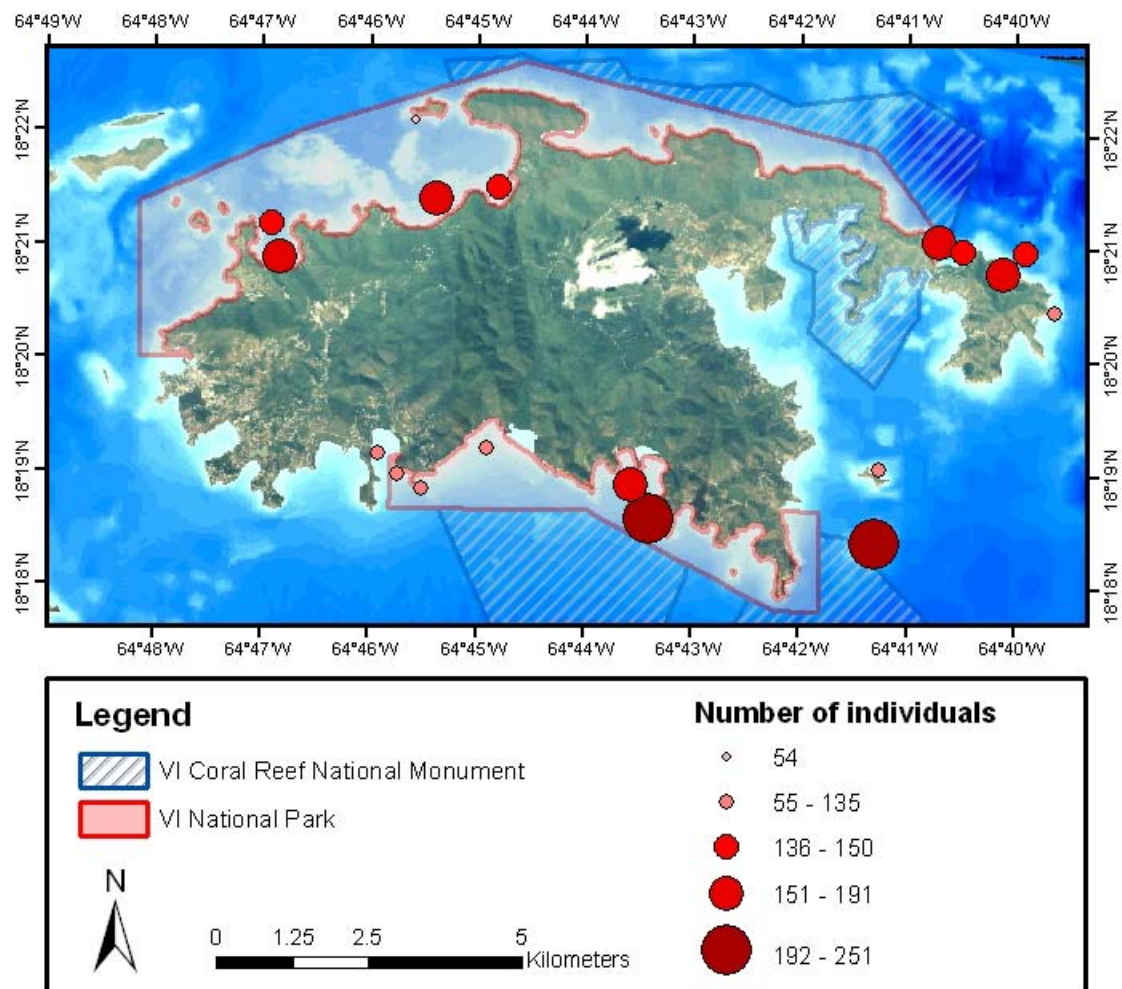


Figure 15. Mean number of individuals per sample among all locations surveyed between 1989 and 1995 (N = 18). Values are means for 5 m radius cylinder (area: 78.5 m²) and 15 minute time interval.

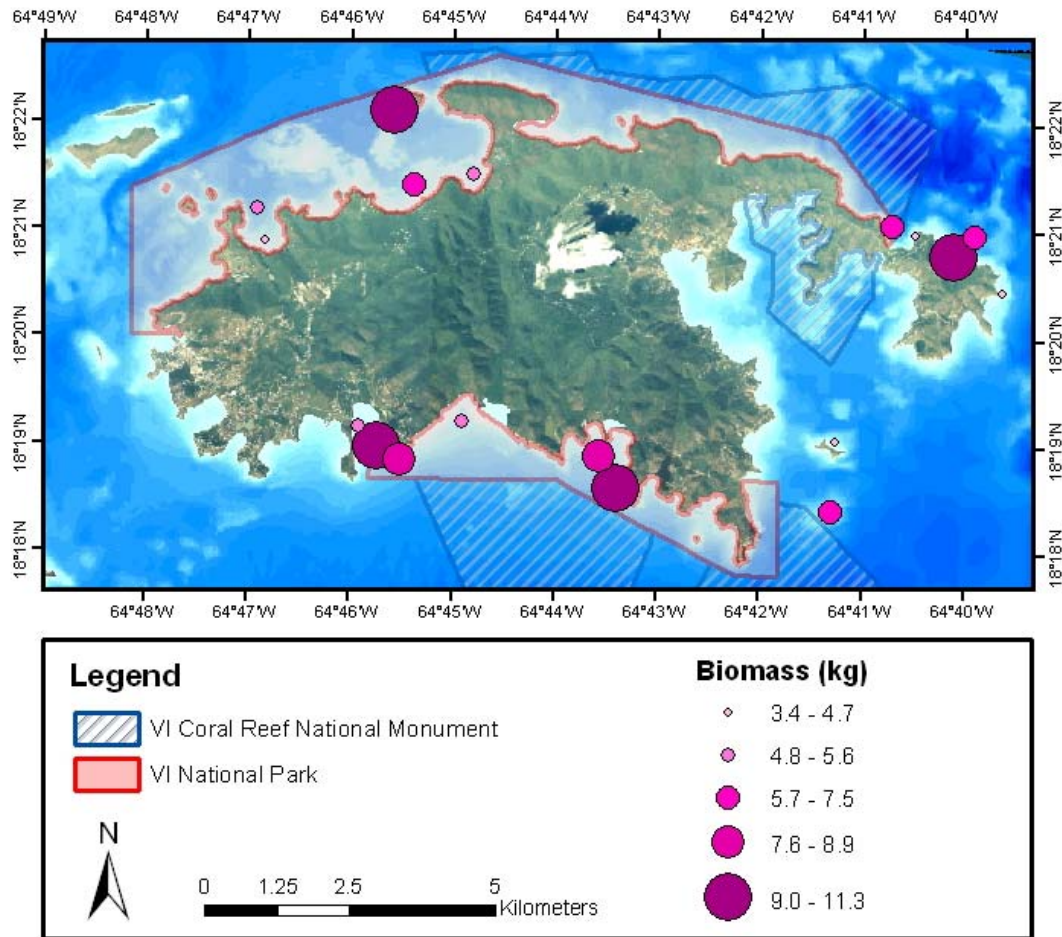


Figure 16. Mean biomass (kg) per sample among all locations surveyed between 1989 and 1995 (N = 18). Values are means for 5 m radius cylinder (area: 78.5 m²) and 15 minute time interval.

Conditions inside and outside of Virgin Islands National Park

To compare fish assemblage characteristics inside and outside Virgin Islands National Park, we analyzed data from the period during which numerous reef sites were monitored (n = 18, 1989-1994). These selected sites were in reef habitat with greater topographic complexity than surrounding colonized pavement. Sites that did not have an analog reef either inside or outside the park were excluded from this analysis. Reef sites located inside the park that were used in analyses included Hawksnest Bay Upper, Haulover Bay West, Fish Bay East, Yawzi Point Reef, and Tektite Reef (Fig. 7). Reef sites outside the park included Haulover Bay East, Newfound Bay West, Newfound Bay Upper, and Fish Bay West. There were no significant differences in number of species ($P > 0.05$) or fish biomass ($P > 0.05$) between sites inside and outside the park (Table 3). The total number of individuals was significantly greater ($P = 0.002$) at sites inside VINP compared with sites outside VINP, likely owing to the greater proportion of 'edge habitat', with greater topographic complexity, sampled inside the park (Haulover West, Yawzi Point, and Tektite Reef) and the associated presence of large schools of planktivores at these sites.

These analyses suggest that the park is not functioning effectively as a protected area for reef fish assemblages. The species richness of reef fishes and reef fish biomass was not significantly different between reefs located inside and outside of the park. Although reef fish abundance was significantly greater within the park, this was probably due to the greater number of reefs sampled within the park with sharp slopes and greater spatial complexity that support large numbers of planktivorous fishes. Numerous investigations have documented the negative status of the reef fish assemblages in the U.S. Virgin Islands, and specifically for VINP (Appeldoorn *et al.* 1992, Beets 1996, 1997, Rogers and Beets 2001, Beets and Rogers 1997). The results of this report provide additional evidence of the depressed condition of reef fishes in VINP. Similar conditions have been documented for queen conch (Friedlander *et al.* 1994, Friedlander 1997) and spiny lobster (Wolff 1998).

Table 3. Comparisons of fish assemblage characteristics inside and outside of Virgin Islands National Park using 15 m/5 minute point count data from 1989 to 1994. Values in parentheses are standard error of the mean using pooled variances. Number of individuals did not meet the parametric assumption of homogeneity of variances and a Mann-Whitney Rank Sum Test was in place of the parametric Student's t-test. Statistical values of pooled data: t = Student's t-test, U = Mann-Whitney Rank Sum test.

Assemblage Characteristic	Inside VINP	Outside VINP	Statistical value	P
Species	30.9 (± 0.70)	30.2 (± 0.80)	t = 0.714	0.476
Number of individuals	228.6 (± 7.5)	188.2 (± 8.6)	U = 9.51	0.002
Biomass (kg)	9.2 (± 0.7)	8.1 (± 0.6)	t = 1.12	0.23

Temporal trends in assemblage characteristics from 1989 to 2006

Trends in reef fish assemblage characteristics in VINP over the past 17 years have been dominated primarily by storm effects. Fish monitoring at the four reference sites (Yawzi Point, Haulover Bay, Tektite Reef, and Newfound Bay) was initiated following Hurricane Hugo in 1989, the largest storm to pass the Virgin Islands in decades, which had a large impact on reef substrate, encrusting organisms (especially corals) (Rogers *et al.* 1991, Rogers 1993), as well as reef fishes (Beets and Friedlander 1990, Beets 1993). Similar impacts were documented following the second largest storm that passed the Virgin Islands during the past 20+ years, Hurricane Marilyn (1995). Although these large storms damaged reef structure and decreased coral cover in shallow water, reef fish abundance and species richness recovered within 3-5 years following these impacts (Fig. 17).

Both number of individuals and biomass were low, relative to subsequent years, immediately following Hurricane Hugo. Both metrics increased rapidly, within one to

three years, and then began to decline. Hurricane Marilyn struck in 1995, which again depressed numerical abundance and biomass. A similar trend of rapid increase, followed by a somewhat slower decline occurred for both measures although the trend for biomass was not significant. A second order polynomial model fit provided the best fit for these data, possibly due to some type of intermediate disturbance response (Rogers 1993).

Temporal trends among reefs from 1989 to 2006

The four reefs responded somewhat differently to these disturbance events (Fig. 18). Yawzi Point was the most exposed to the full force of Hurricane Hugo (Rogers *et al.* 1991) and suffered extensive loss of benthic cover and structure. This reef had the lowest numerical abundance and biomass of the four following Hugo and also showed the largest intermediate disturbance response to this event. Tektite Reef is sheltered from the southeast (the direction of wave energy from Hugo) by Cabrite Horn Point and this reef showed the least damage from this storm. It also had the highest values for numbers and biomass following the hurricane and showed the least intermediate response to this event.

Following Hurricane Marilyn, Yawzi Point again showed the largest decline in both assemblage metrics, while Tektite showed the least. These responses are likely related to the continual deterioration of Yawzi Point and the relatively healthy state of Tektite Reef until a major bleaching event occurred in 2005 (Miller *et al.* 2006). Tektite Reef had some of the highest remaining coral cover around St. John and this bleaching event resulted in a decline in coral cover and an associated drop in the numerical abundance of fishes at this reef. Coral cover also declined at Newfound Bay which similarly showed a decline in number of individuals observed. The coral cover at Yawzi Point and Haulover Bay was already low and this bleaching event did not have the same relative impact on these reefs. Consequently, numerical abundance and biomass did not change appreciably at these sites.

Yawzi Point and Tektite Reef had overall higher biomass compared with Haulover and Newfound Bays. The presence of seagrass beds in Lameshur Bay results in a greater abundance of grunts and snappers, which utilize this habitat for nocturnal foraging (Beets *et al.* 2003). Biomass showed a trend similar to numerical abundance following storm events but the magnitude of the response was not as pronounced owing to the general lack of large and medium-sized fishes present.

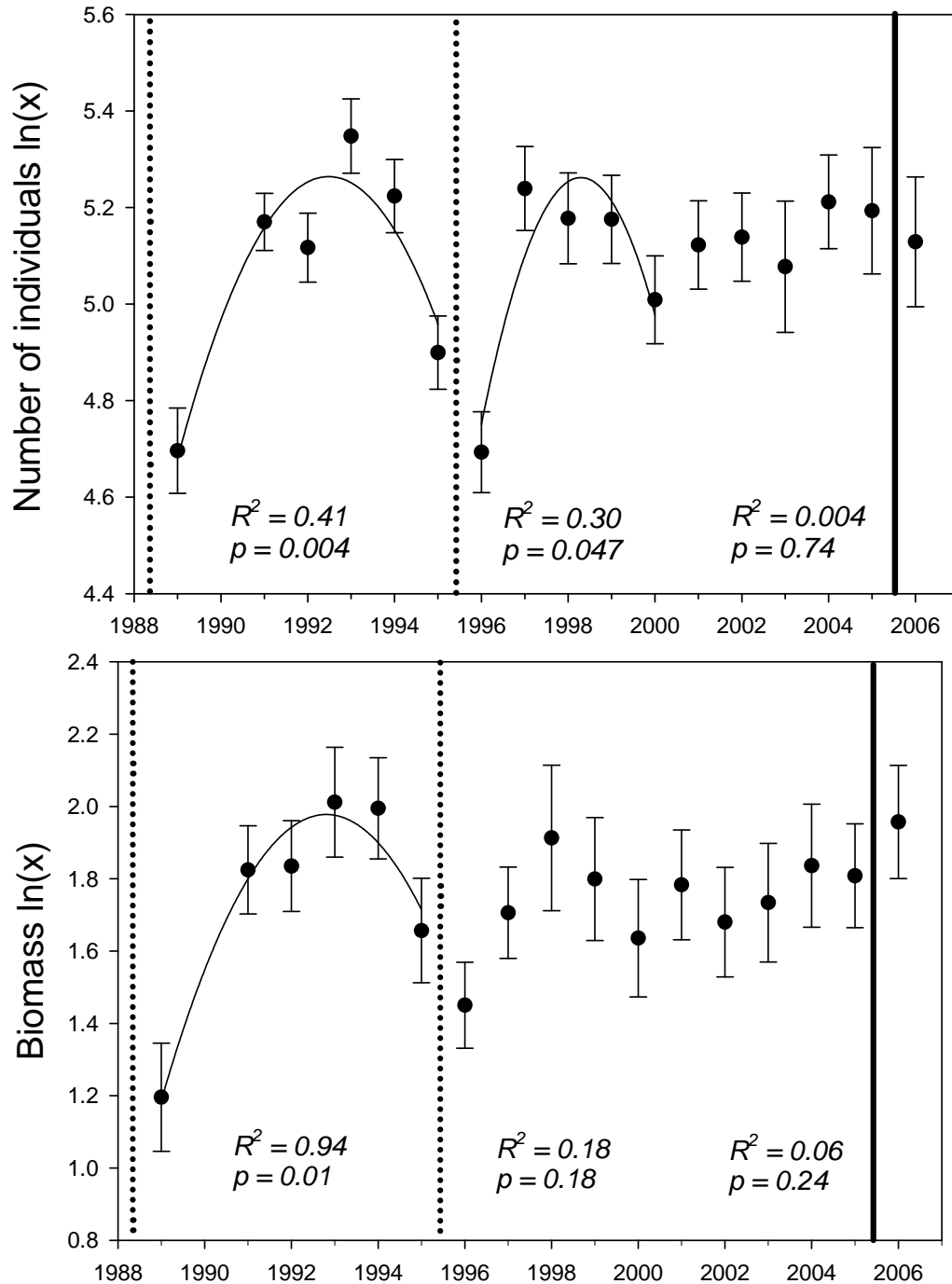


Figure 17. Time-series of numerical and biomass densities from 1989 to 2006 for four long-term reefs around St. John, U.S. Virgin Islands. Values are grand mean ($\ln[x]$, \pm standard error) for the mean densities among reefs ($N = 4$). Time periods for statistical analyses are, a: post Hurricane Hugo (1989-1994), b: post Hurricane Marilyn (1996-2000), and c: time since 2001. Time periods fit to linear and 2nd order polynomial models. R^2 and P values are for the best fit model (see Table 8 for model type). Vertical dotted lines denote periods of major hurricanes and the solid lines mark a major bleaching event.

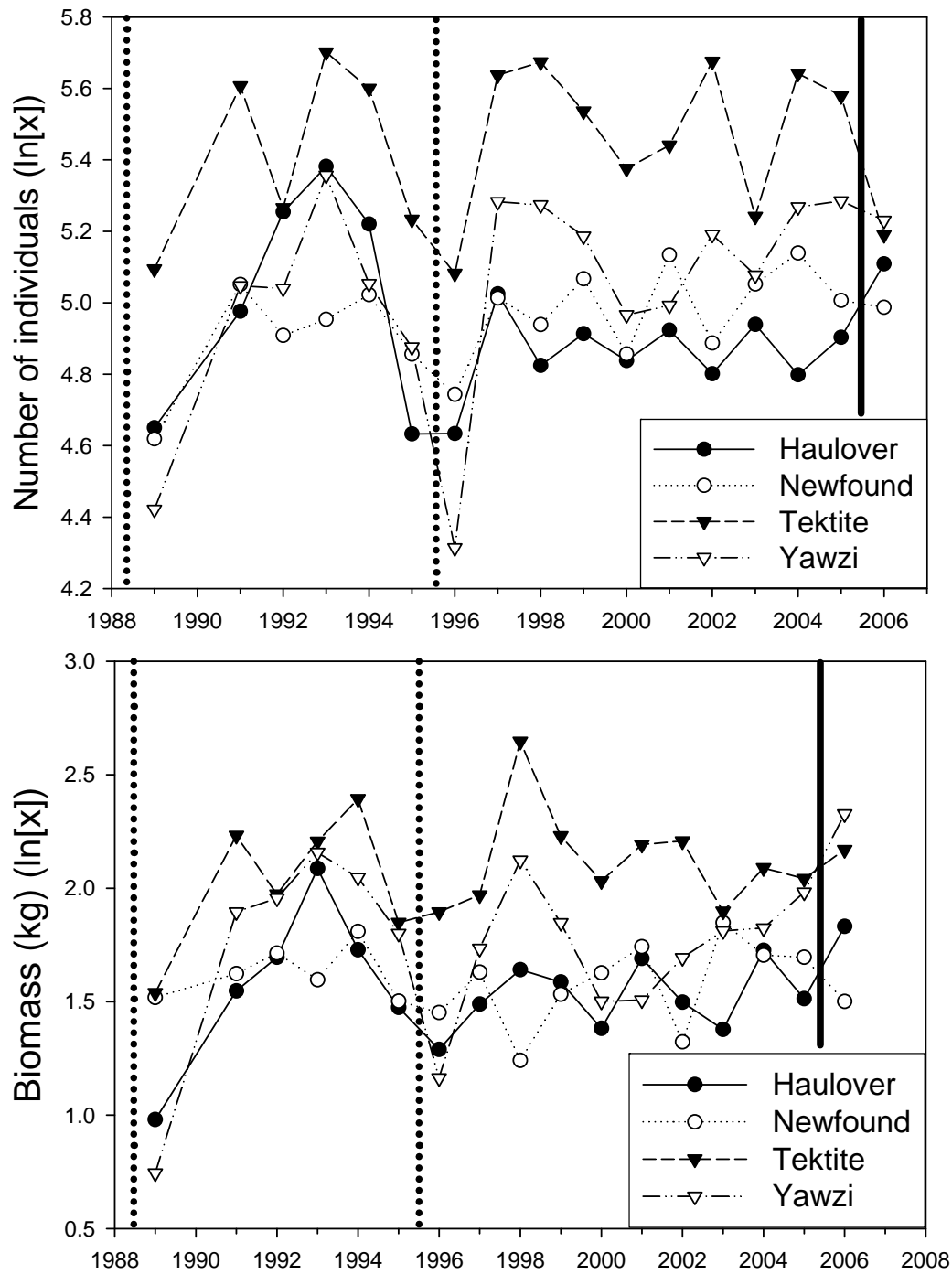


Figure 18. Time-series of numerical and biomass densities from 1989 to 2006 for each of four long-term reefs around St. John, U.S. Virgin Islands. Values are mean ($\ln[x]$) for each reef. The mean number of samples per reef per year was $19.34 (\pm 0.18 \text{ SD, min.} = 12, \text{ max.} = 32)$. Vertical dotted lines denote periods of major hurricanes and the solid lines mark a major bleaching event.

Temporal fish assemblage dynamics within reefs

Fish assemblage structure within reefs varied considerably among years. Much of this variation was driven by disturbance events and their direct impacts to the reef fish assemblages, as well as indirect effects associated with short and long-term habitat changes that occurred as a result of these storms. The responses to these disturbance events differed greatly among reefs depending on the degree of disturbance, the fish assemblage at the time of the event, and the response of the individual species to these events.

Yawzi Point was the most severely impacted by Hurricane Hugo among the four permanent reference reefs and showed the most dramatic change in fish assemblage structure as a result. The fish assemblage in 1989, following Hugo, was an extreme outlier in ordination space (Fig. 19) and well separated (>0.75), or clearly different ($R > 0.5$) from all other sampling years except 1996, which was the year following Hurricane Marilyn (Table 4). There was high concordance among samples for the remainder of the other sampling years. Following the bleaching event of 2005, the assemblage showed a large shift in ordination space.

Tektite Reef, although in close proximity to Tektite (< 1 km) and within the same bay complex, was not nearly as affected by Hurricane Hugo owing to the shelter from the southeast provided by Cabrite Horn Point. The assemblage in 1989 was well separated (>0.75) from the 1997 sample and clearly different from several other sampling years (1992, 1998, 2002, 2004). Following Hugo, the fish assemblage proceeded along a series of steps in ordination space until Hurricane Marilyn changed the assemblage structure once again (Fig. 20, Table 5). Following Marilyn, there was relatively high concordance in assemblage structure among the remaining sampling years.

The reef at Newfound Bay, on the northeastern portion of St. John, also experienced storm impacts from Hurricane Hugo. The fish assemblage immediately following Hugo was anomalous compared with the remaining sampling years but the Analysis of Similarities (ANOSIM) did not show large differences (Fig. 21, Table 6). There was relatively high concordance among all other survey years and the effects of Hurricane Marilyn and the 2005 bleaching event did not appear to affect the fish assemblage structure at Newfound to the degree that it did at Yawzi Point or Tektite Reef.

Haulover West was modestly affected by Hurricane Hugo and Hurricane Marilyn (Fig. 22, Table 7). The overall fish assemblage showed the least amount of variation among the four permanent reference reefs over the study period. The large change in assemblage ordination between 1994 and 1995 resulted from a change in sampling methodology from the smaller radius (5 m) to the larger radius (7.5 m) point count. For the former method, abundance of benthic damselfishes was higher relative to the latter method owing to the diver's ability to move throughout the cylinder and enumerate fishes during the count. Benthic damselfishes (primarily threespot [*Stegastes planifrons*]) dominated numerically at this reef site and the change in ordination likely does not reflect a true change in assemblage structure. A large change in assemblage structure was observed between 2005 and 2006 and may be related to the 2005 bleaching event.

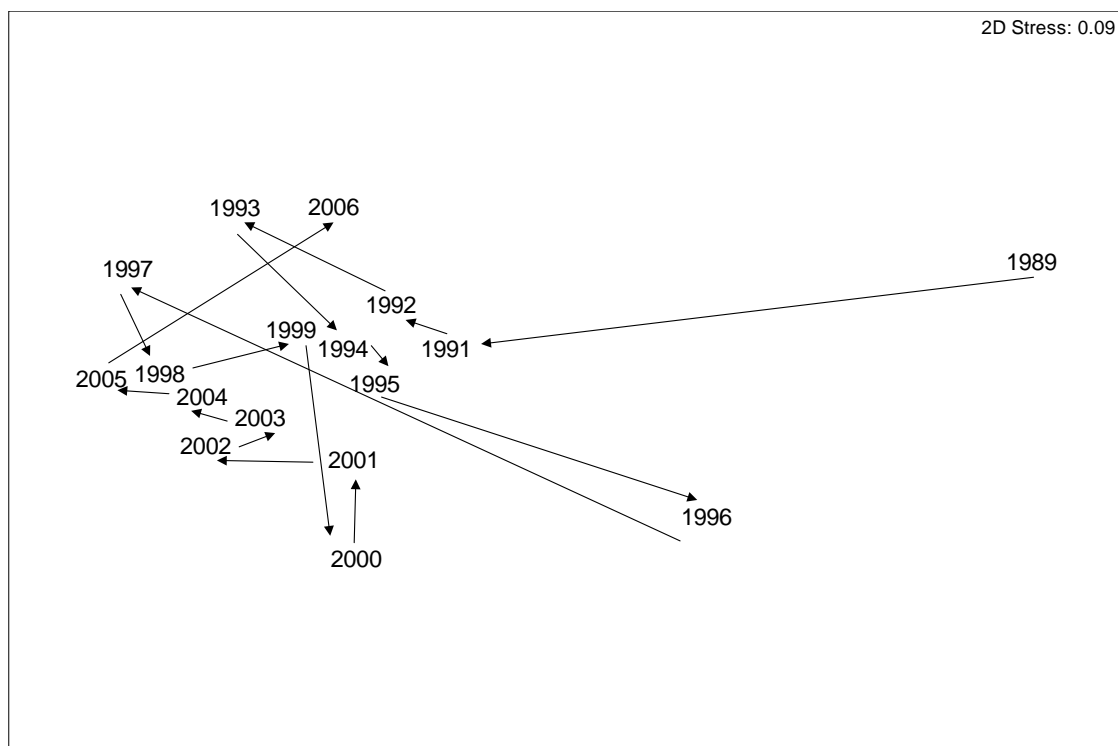


Figure 19. Nonmetric multidimensional scaling plot of mean fish numerical abundance by species for Yawzi Point among sample years from 1989 to 2006.

Table 4. Pairwise ANOSIM test comparisons between the sample years for Yawzi Point. The R statistic represents pairs of years that are well separated ($R > 0.75$) (yellow), overlapping but clearly different ($R > 0.5$) (grey), or barely separable at all ($R < 0.25$).

Yr.	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06
89	0.6	0.6	0.7	0.7	0.5	0.4	0.8	0.7	0.7	0.6	0.6	0.7	0.6	0.8	0.8	0.8
91		0.0	0.1	0.1	0.1	0.3	0.5	0.3	0.2	0.3	0.1	0.3	0.2	0.3	0.4	0.3
92			0.1	0.1	0.1	0.3	0.2	0.2	0.1	0.3	0.1	0.2	0.1	0.1	0.2	0.2
93				0.1	0.1	0.4	0.1	0.1	0.1	0.4	0.2	0.2	0.2	0.1	0.2	0.1
94					0.0	0.3	0.4	0.3	0.2	0.4	0.2	0.3	0.2	0.2	0.3	0.2
95						0.2	0.2	0.1	0.1	0.3	0.1	0.1	0.1	0.2	0.2	0.2
96							0.4	0.4	0.3	0.4	0.3	0.4	0.3	0.4	0.4	0.5
97								0.1	0.2	0.6	0.5	0.3	0.3	0.2	0.2	0.4
98									0.0	0.3	0.2	0.0	0.1	0.1	0.1	0.3
99										0.2	0.1	0.1	0.1	0.1	0.1	0.2
00											0.1	0.2	0.2	0.4	0.4	0.5
01												0.1	0.1	0.3	0.3	0.2
02													0.1	0.1	0.1	0.3
03														0.1	0.1	0.2
04															0.1	0.2
05																0.2

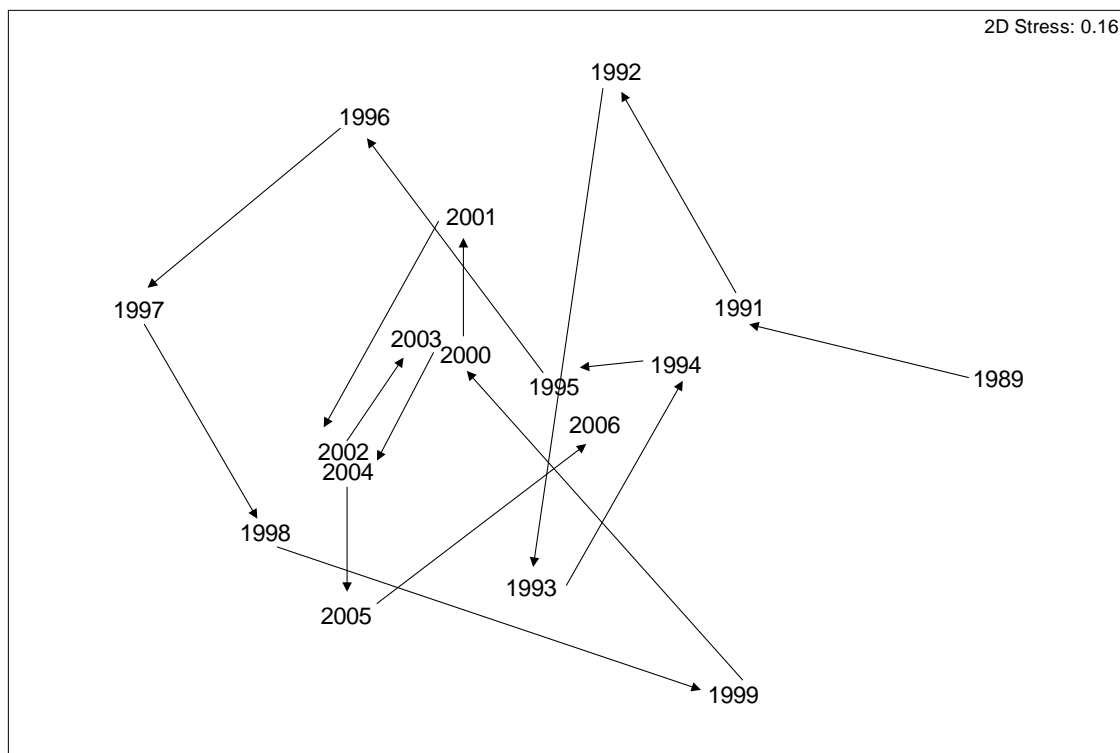


Figure 20. Nonmetric multidimensional scaling plot of mean fish numerical abundance by species for Tektite Reef among sample years from 1989 to 2006.

Table 5. Pairwise ANOSIM test comparisons between the sample years for Tektite Reef. The R statistic represents pairs of years that are well separated ($R > 0.75$) (yellow), overlapping but clearly different ($R > 0.5$) (grey), or barely separable at all ($R < 0.25$).

Yr.	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06
89	0.3	0.5	0.4	0.2	0.3	0.3	0.8	0.6	0.2	0.4	0.4	0.5	0.4	0.5	0.4	0.2
91		0.2	0.1	0.1	0.2	0.2	0.5	0.3	0.3	0.2	0.3	0.3	0.2	0.2	0.3	0.1
92			0.2	0.2	0.2	0.1	0.2	0.3	0.4	0.2	0.3	0.3	0.2	0.2	0.3	0.3
93				0.1	0.2	0.3	0.3	0.2	0.3	0.1	0.3	0.1	0.2	0.1	0.2	0.1
94					0.1	0.1	0.5	0.2	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.0
95						0.1	0.3	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.2	0.1
96							0.1	0.1	0.2	0.1	0.1	0.2	0.1	0.1	0.2	0.2
97								0.1	0.4	0.3	0.3	0.2	0.2	0.2	0.2	0.4
98									0.2	0.1	0.1	0.0	0.1	0.0	0.0	0.2
99										0.2	0.2	0.2	0.2	0.2	0.2	0.1
00											0.0	0.1	0.1	0.2	0.1	0.1
01												0.1	0.1	0.2	0.1	0.2
02													0.0	0.0	0.0	0.1
03														0.0	0.1	0.1
04															0.0	0.1
05																0.1

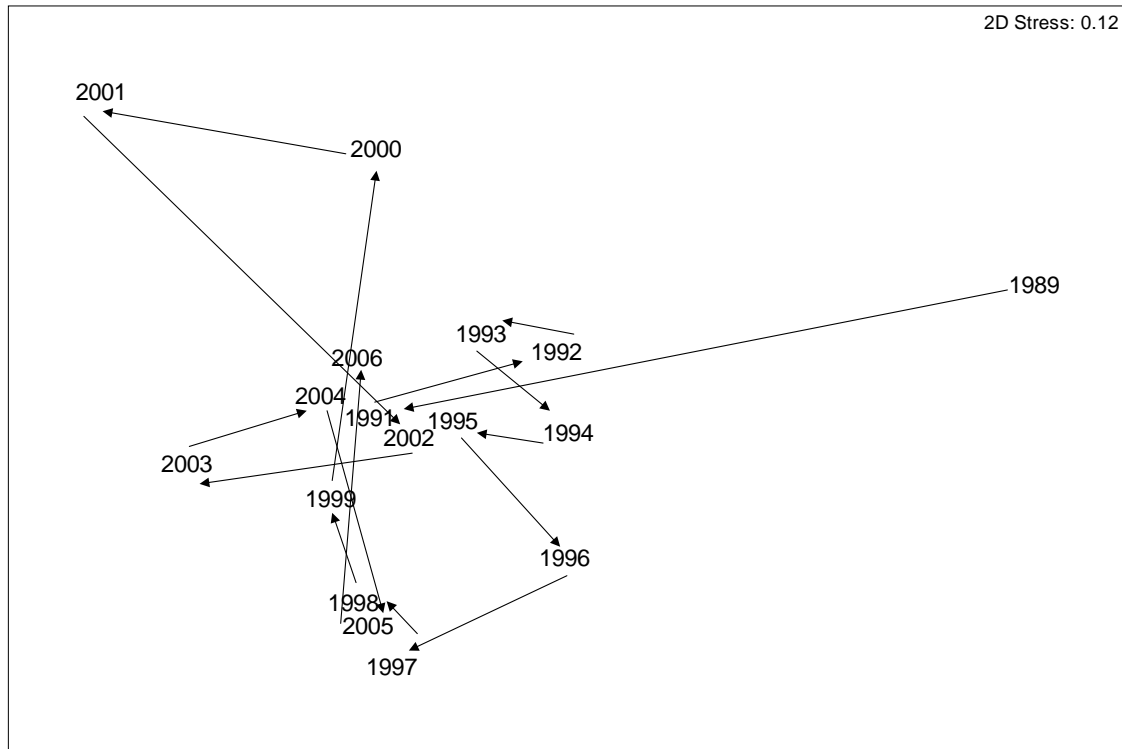


Figure 21. Nonmetric multidimensional scaling plot of mean fish numerical abundance by species for Newfound Reef among sample years from 1989 to 2006.

Table 6. Pairwise ANOSIM test comparisons between the sample years for Newfound Reef. The R statistic represents pairs of years that are well separated ($R > 0.75$) (yellow), overlapping but clearly different ($R > 0.5$) (grey), or barely separable at all ($R < 0.25$).

Year	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06
89	0.3	0.2	0.3	0.3	0.3	0.3	0.4	0.3	0.4	0.4	0.3	0.3	0.2	0.3	0.4	0.5
91		0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.2	0.1	0.0	0.1	0.1	0.1	0.2
92			0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.0	0.1	0.1
93				0.1	0.1	0.1	0.1	0.1	0.1	0.3	0.3	0.2	0.2	0.1	0.2	0.2
94					0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.2	0.1	0.1	0.1
95						0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.1	0.1	0.0	0.0
96							0.0	0.0	0.1	0.2	0.2	0.1	0.1	0.1	0.1	0.1
97								0.0	0.1	0.3	0.2	0.1	0.1	0.1	0.0	0.2
98									0.0	0.3	0.2	0.1	0.1	0.1	0.0	0.1
99										0.2	0.1	0.1	0.1	0.1	0.1	0.0
00											0.0	0.1	0.1	0.1	0.2	0.2
01												0.1	0.1	0.1	0.2	0.1
02													0.0	0.1	0.0	0.0
03														0.0	0.0	0.1
04															0.1	0.1
05																0.2

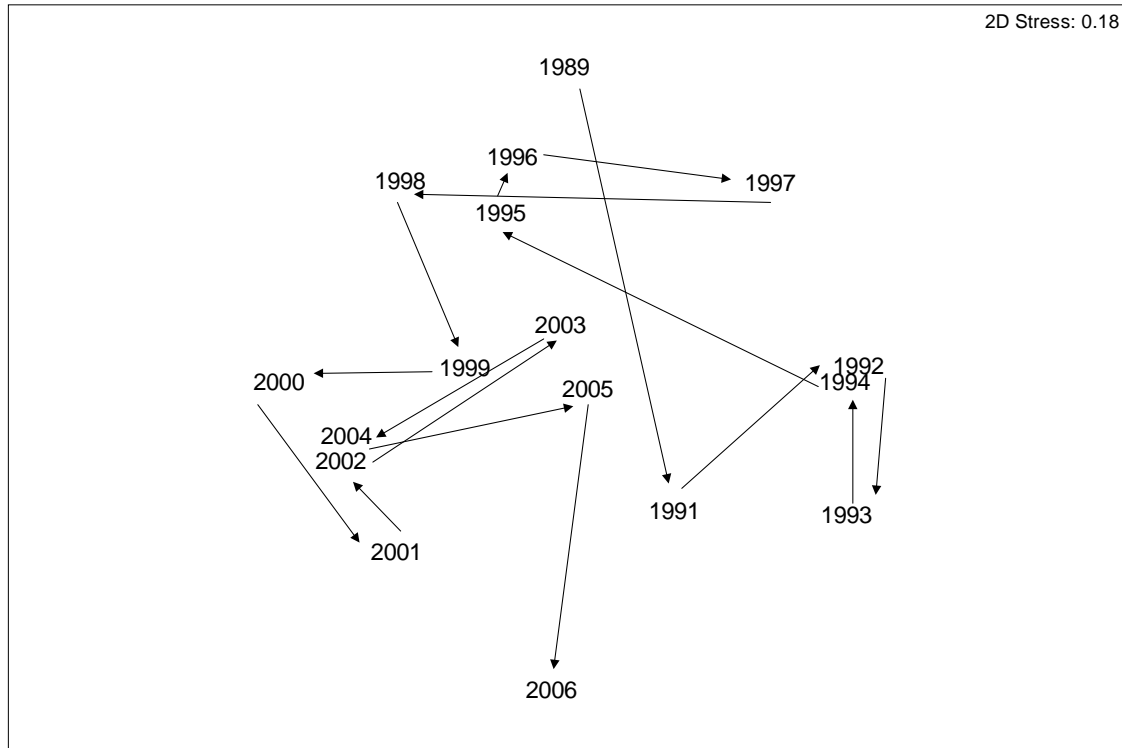


Figure 22. Nonmetric multidimensional scaling plot of mean fish numerical abundance by species for Haulover West Reef among sample years from 1989 to 2006.

Table 7. Pairwise ANOSIM test comparisons between the sample years for Haulover West Reef. The R statistic represents pairs of years that are well separated ($R > 0.75$) (yellow), overlapping but clearly different ($R > 0.5$) (grey), or barely separable at all ($R < 0.25$).

Yr.	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06
89	-0	0.2	0.4	0.2	0.1	0.1	0.1	0.1	0.2	0.2	0.2	0.2	0.1	0.2	0.2	0.2
91		0.1	0.1	0	0	0.1	0.2	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.2
92			0.1	0	0.3	0.3	0.1	0.2	0.2	0.3	0.3	0.4	0.2	0.3	0.2	0.2
93				0.1	0.4	0.4	0.3	0.4	0.4	0.4	0.5	0.5	0.4	0.4	0.3	0.3
94					0.2	0.3	0.1	0.2	0.2	0.2	0.3	0.2	0.2	0.2	0.2	0.1
95						0	0.2	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.2	0.3
96							0.2	0.1	0.2	0.2	0.3	0.1	0.1	0.2	0.2	0.3
97								0.1	0.1	0.2	0.2	0.2	0.1	0.2	0.1	0.1
98									0	0.1	0.1	0.1	-0	0.1	0	0.1
99										0	0	0.1	0	0	-0	0
00											0.1	0	0.1	0	0.1	0.1
01												0	0.1	0.1	0.1	0
02													0.1	0	0.1	0.1
03														0.1	-0	0.1
04															0	0.1
05																0

Temporal trophic dynamics

Herbivores, followed by planktivores and secondary consumers, were the most important trophic guilds by numerical abundance among the four permanent reefs (Fig. 23). Following Hurricane Hugo, all trophic groups except piscivores increased in numerical abundance but began to decline approximately five years after this storm. Herbivores and planktivores declined further following Hurricane Marilyn but quickly rebounded, with planktivores showing the most dramatic increase in numerical abundance. Herbivores continued to increase in abundance, while planktivores increased and declined twice during this time period. Secondary consumers fluctuated without trend and piscivores have remained at low levels over the entire time series.

The massive coral bleaching event in 2005, apparently had a large effect on trophic structure, with a decline in planktivorous fishes and increases in herbivorous fishes on all four reference reefs. General trends in herbivore abundance (Fig. 24) are confounded by the variable responses associated with different guilds within this feeding group. Numerical abundance increases were noted for small benthic herbivores (benthic damselfishes) and large mobile herbivores (parrotfishes and surgeonfishes) (Fig. 25). These increases in herbivore abundance are likely correlated with the increase in macroalgae cover as a result of this bleaching event.

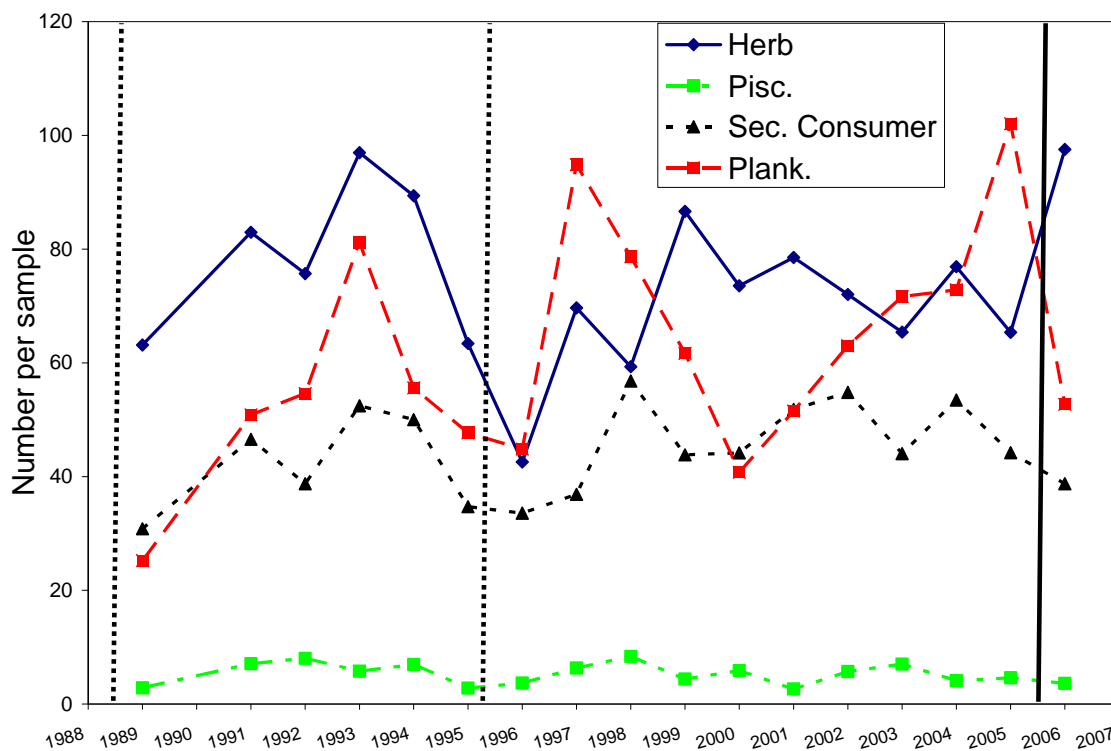


Figure 23. Mean number of individuals for each major trophic grouping: herbivores – herb., piscivores – Pisc., secondary consumer – Sec. Consumer, and planktivores – Plank. Vertical dotted lines denote periods of major hurricanes and solid line marks period of major bleaching event.

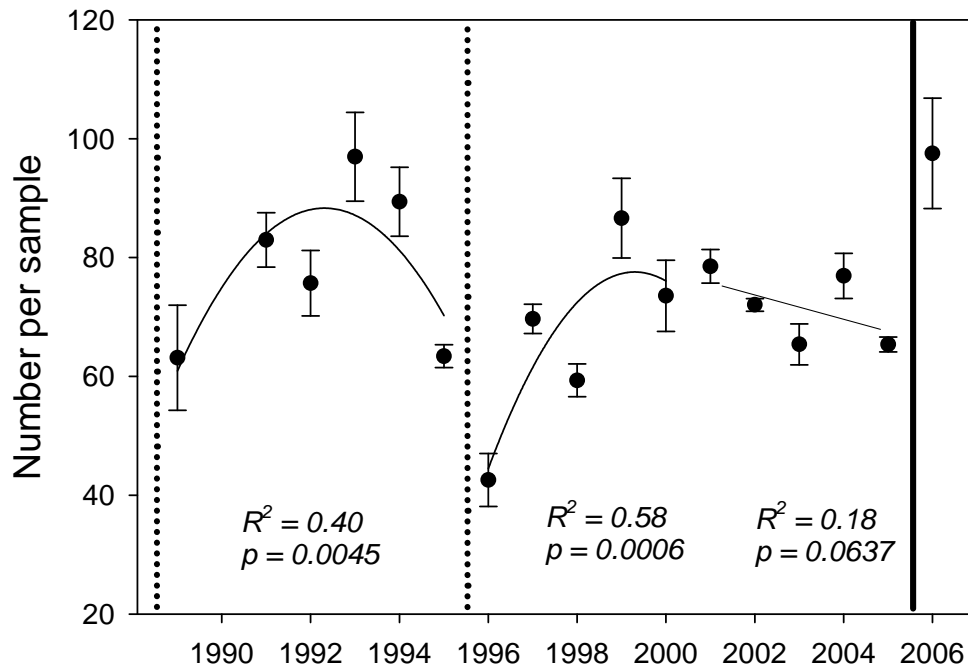


Figure 24. Mean number of herbivores per year for the four reference reefs pooled. Vertical dotted lines denote periods of major hurricanes and solid line marks period of major bleaching event.

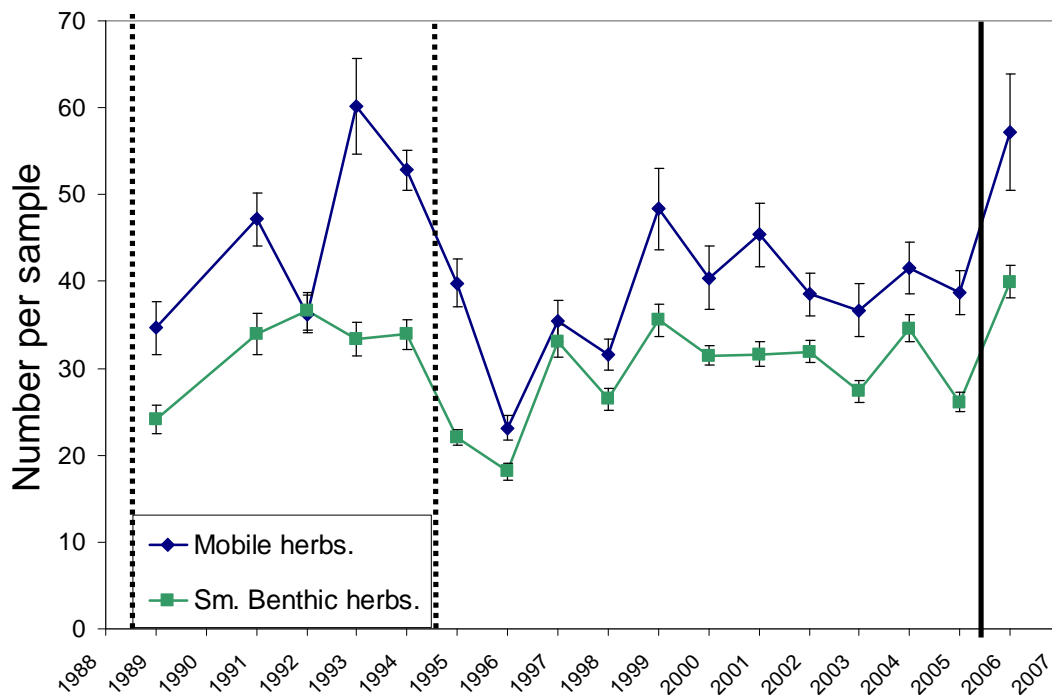


Figure 25. Mean number of mobile (surgeonfishes and parrotfishes) and small benthic herbivores (resident herbivorous damselfishes) for the four reference reefs pooled. Values are means and \pm se.

Numerical abundance of planktivores was low after Hurricane Hugo but increased to a high in 1993 followed by a gradual decline (Fig. 26). A similar trend occurred following Hurricane Marilyn, but from 2001 to 2005 a monotonic increase in numbers was observed. After the 2005 bleaching event, planktivore numbers declined rapidly to those levels observed in 2001. These trends were driven primarily by blue chromis and to a lesser degree, brown chromis.

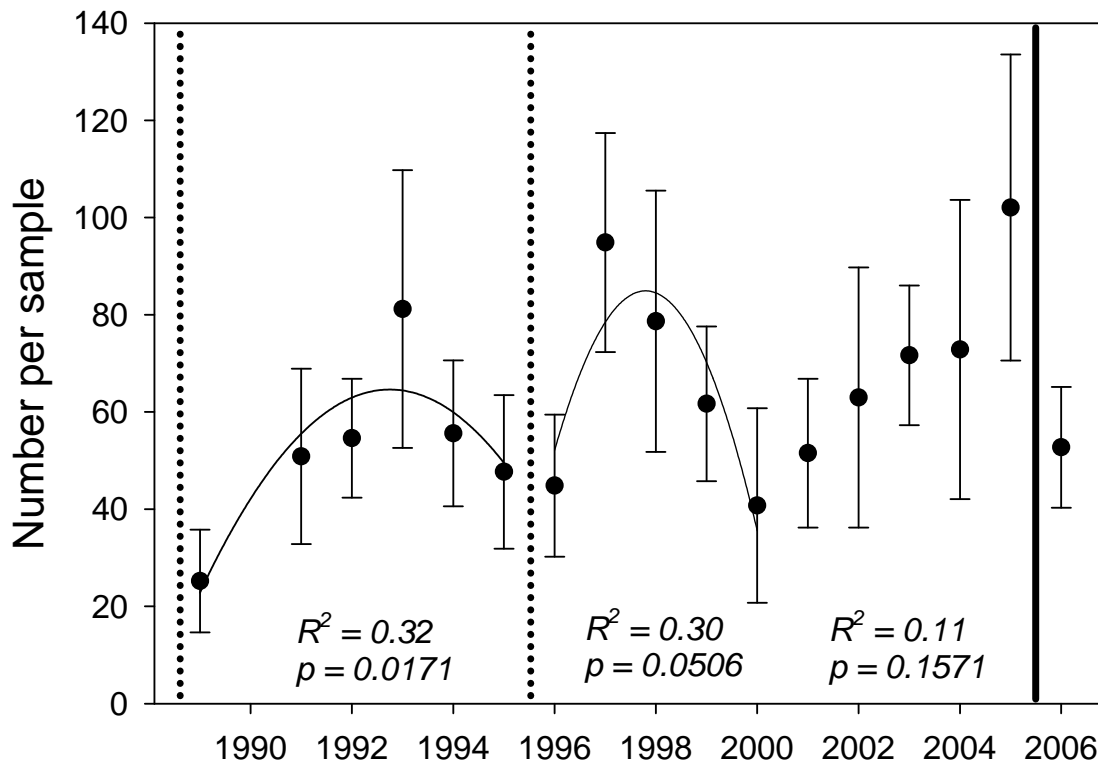


Figure 26. Mean number of planktivores per year for the four reference reefs pooled. Vertical dotted lines denote periods of major hurricanes and solid line marks period of major bleaching event.

Trends in the number of secondary consumers were less apparent but still showed a similar pattern to the other trophic groups following Hurricane Hugo with increasing numbers for four years then declining prior the Hurricane Marilyn (Fig. 27). After Mayilyn, the number of secondary consumers continued to increase for approximately seven years followed by a downward trend. This trend was accentuated by the bleaching event of 2005.

Despite low numbers of piscivores overall, the temporal patterns observed for the other trophic groups were still very similar (Fig. 28). Piscivores showed increases in numerical abundance for a three year period after Hugo, followed by a gradual decline and another three year increase after Marilyn with a rapid decline the next year. Piscivore numbers have remained low since 1999 and dropped even lower after the 2005 bleaching event.

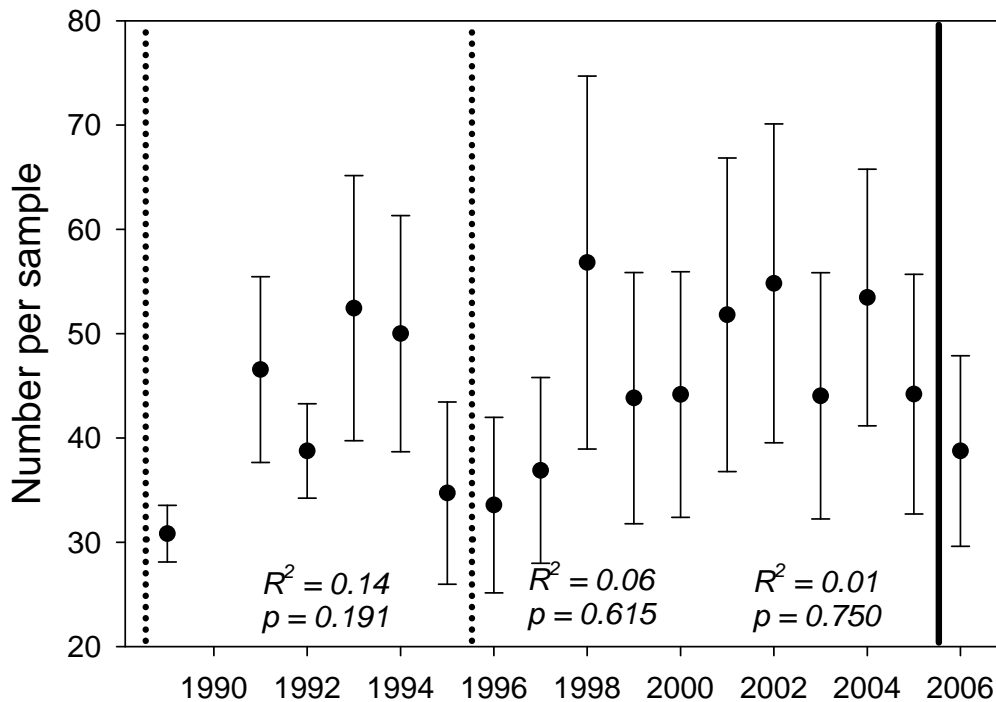


Figure 27. Mean number of secondary consumers per year for the four reference reefs pooled. Vertical dotted lines denote periods of major hurricanes and solid line marks period of major bleaching event.

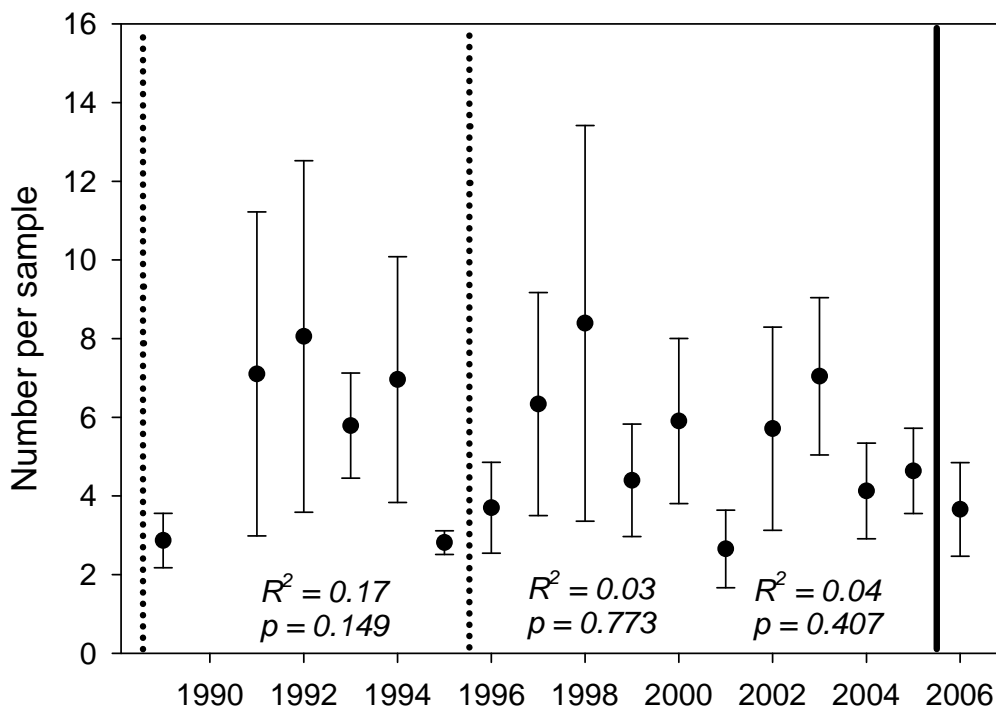


Figure 28. Mean number of piscivores per year for the four reference reefs pooled. Vertical dotted lines denote periods of major hurricanes and solid line marks period of major bleaching event.

Temporal family dynamics

All the major families showed a similar increasing then decreasing trend in numerical abundance following Hurricane Hugo (Fig. 29). Damselfishes (Pomacentridae) were the most abundant family numerically and were dominated by blue chromis (*Chromis cyanea* – 48% of total), followed by the threespot damselfish (*Stegastes planifrons* – 21%), and brown chromis (*C. multilineatus* – 12%). This family showed a humped response in abundance following Hugo with a large increase and then a gradual decline in numbers. A year after Marilyn, there was a large jump in numerical abundance of this family, mostly driven by an increase in the two planktivorous species (blue and brown chromis). Another decline ensued five years after Marilyn and then climbed to higher levels for the remainder of the study period.

Parrotfishes (Scaridae) and wrasses (Labridae) were the next more numerically important family among the reference reefs. Striped parrotfishes (*Scarus iserti*) made up nearly 62% of the numerical abundance of parrotfishes, followed by redband (*S. aurofrenatum* – 19%), stoplight (*S. viride* – 11%), and princess (*S. taeniopterus* – 3%). Tomtate (*H. aurolineatum*) comprised 55% of the grunts, with French (*H. flavolineatum*) contributing 26%, and bluestripe (*H. sciurus*) and white (*H. plumieri*) each providing an additional 7% to the total number of grunts. These families varied without any distinct trends over the study period.

Surgeonfishes (Acanthuridae) showed consistent and level numerical abundance between hurricanes Hugo and Marilyn but have shown a notable decline in numbers since 1996. Blue tang (*Acanthurus coeruleus*) made up 55% of the surgeonfish individuals, followed by ocean surgeonfish (*A. bahianus* – 39%), and doctorfish (*A. chirurgus* – 6%). Fewer schools of blue tang in recent years have caused this downward trend in overall surgeonfish numerical abundance. Groupers (Serranidae) have increased in numbers over time but this trend is driven almost exclusively by the increase in small hamlets (*Hypoplectrus* spp.) that made up more than 74% of numerical abundance in this family.

Parrotfishes and grunts (Haemulidae) were the dominant families by weight among the reference sites and, as with numbers, did not show discernable trends over the study period (Fig. 30). Snappers (Lutjanidae), dominated by lane (*Lutjanus synagris* – 40%), schoolmaster (*L. apodus* – 19%), and mutton (*L. analis* – 11%), were the third most important family by weight. Although damselfishes have increased in number over the past several years, they have declined in biomass as a result of size of the two chromis species. Jacks (Carangidae) have increased in biomass since 2001 with bar jacks (*Caranx ruber*) accounting for more than 84% of the total biomass in this family.

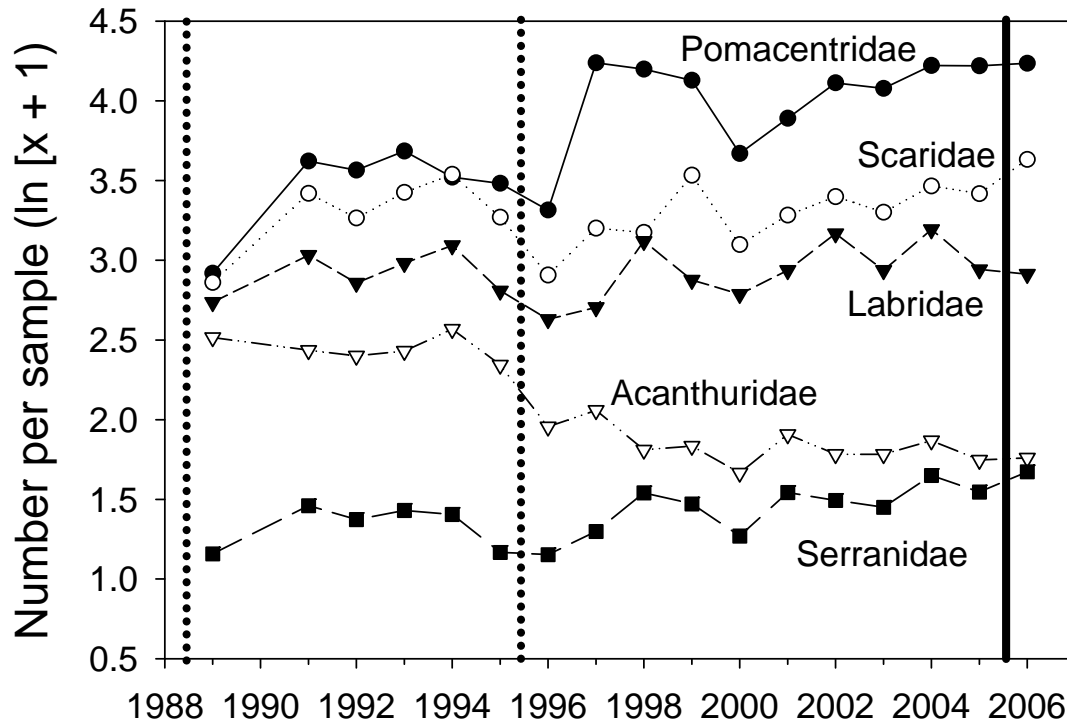


Figure 29. Mean number of individuals ($\ln[x+1]$) of the five most abundant families from 1989 to 2006.

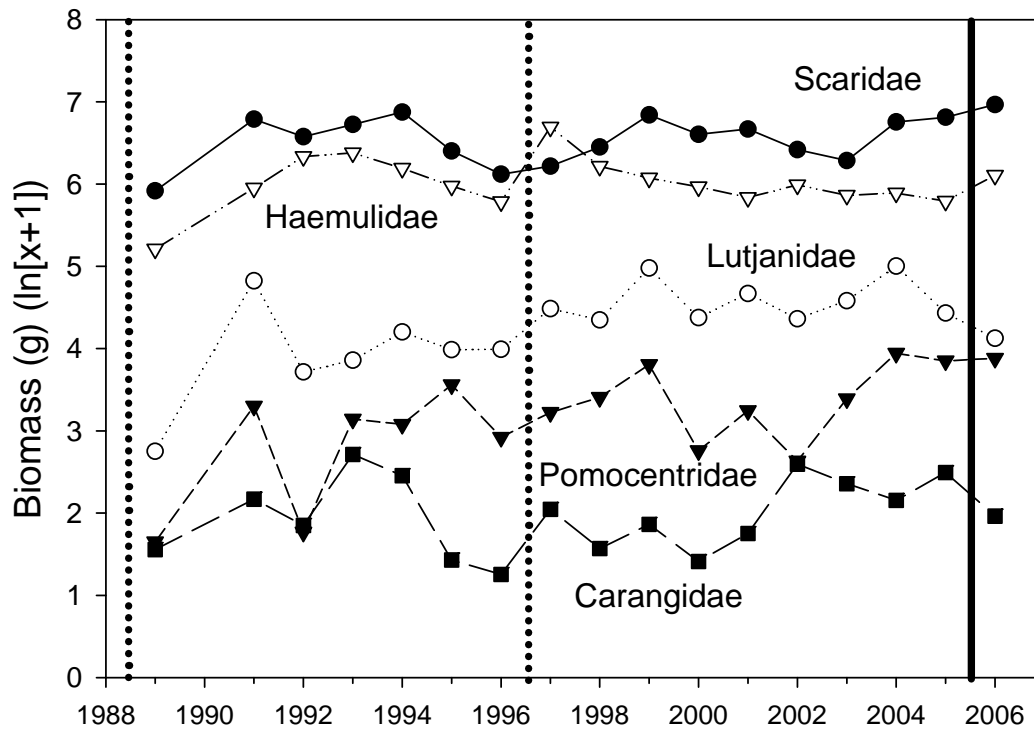


Figure 30. Mean biomass (g) ($\ln[x+1]$) of the five most abundant families based on weight from 1989 to 2006.

Temporal grouper dynamics

Epinepheline groupers (Serranidae) were once the most important component of the trap fishery in the U.S. Virgin Islands but due to overfishing and the collapse of several spawning aggregations, larger groupers are now rare in VINP and around St. John. Frequency of occurrence of larger groupers (Nassau – *Epinephelus straitus*, red - *E. morio*, tiger – *Mycteroperca tigris*, yellowfin – *M. venenosa*, and yellowmouth - *M. interstitialis*) has declined since 1991, but even then only two larger groupers on average were seen per every ten samples (Fig. 31). A complimentary study of the mid-shelf reef conducted between 2002 and 2004 found only two tiger groupers and no other larger grouper over 119 sampling locations (Monaco *et al.* 2007). A mid-sized grouper, red hind (*Epinephelus guttatus*), has shown an increase during recent years, likely in response to the spawning aggregation closure enacted in 1990 (Beets and Friedlander 1999). Small groupers have increased during recent years, probably due to ecological release in response to sustained low numbers of larger groupers.

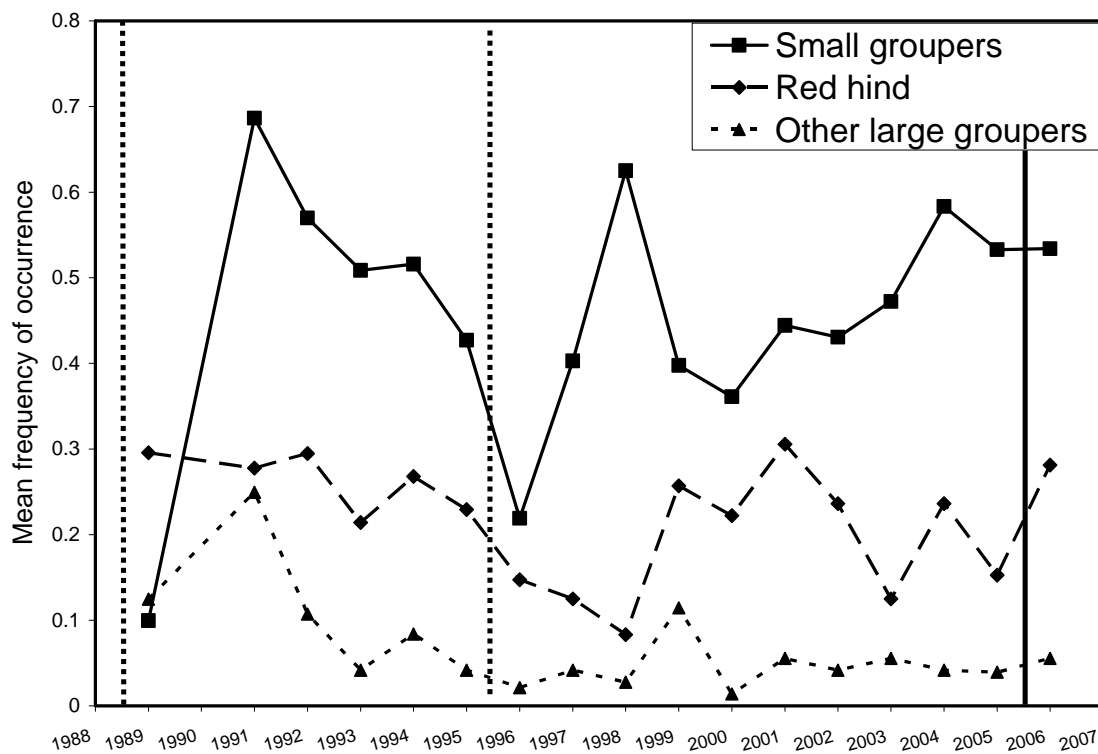


Figure 31. Mean frequency of occurrence of groupers. See text for definitions of groups.

Temporal dynamics of top species

The top five species by numerical abundance were blue chromis (*Chromis cyanea*), striped parrotfish (*Scarus iserti*), threespot damselfish (*Stegastes planifrons*), bluehead wrasse (*Thalassoma bifasciatum*), and brown chromis (*C. multilineatus*) (Fig. 32). Blue chromis have fluctuated in response to disturbance events while striped parrotfishes and threespot damselfish have increased in abundance over time (Table 8). The average size of striped parrotfish was 8.8 cm (± 13.1 SD), meaning that the increase in this species was related to schools of juveniles. The increase in these two species may reflect a change in substrate associated with disturbance events that created suitable habitat for these fishes. This includes the loss of coral cover, increase in macroalage, and the increase in reef rubble.

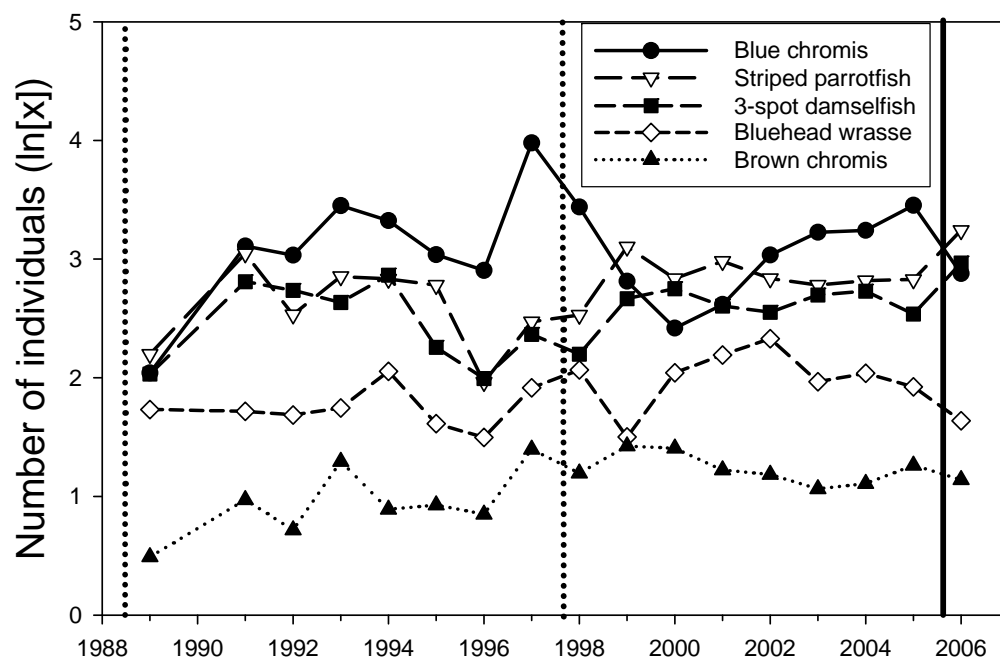


Figure 32. Mean numerical abundance ($\ln[x+1]$) for the five most abundant species.

Trends in length for important resource species over time

The average length for major resource species was examined over the 18-year study period by calculating the average length (\bar{L} , in length) of animals in the exploited part of the population for each species at or above the length at first capture (L_c) for each six year time period (1989-1994, 1995-2000, and 2001-2006) (Table 9). For the ten species examined, all declined in average size between 1989-1994 and 2001-2006. The largest declines were observed for graysby (-7.3%), followed by gray snapper (-6.6%), French grunt (-6.4%), and Spanish hogfish (-6.2%). Nearly all of these species showed notable declines in maximum size observed since the first sampling period. Red hind declined in maximum size by 28.3%, graysby by 25.7%, and Spanish hogfish by 25.0%. For a number of other resource species, there were insufficient numbers among sampling periods to make comparisons.

Table 8. Trends in numerical abundance of the top five species within each of three time periods. Results of best fit model between linear and 2nd order polynomial models.

	1989-95			1996-2000			2000-06		
	Model type	R ²	P	Model type	R ²	P	Model type	R ²	P
<i>Chromis cyanea</i>	2nd order Polynomial	0.37	0.008	2nd order Polynomial	0.35	0.024	Linear	0.03	0.41
<i>Scarus iserti</i>	2nd order Polynomial	0.1	0.31	2nd order Polynomial	0.39	0.01	2nd order Polynomial	0.24	0.05
<i>Stegastes planifrons</i>	2nd order Polynomial	0.09	0.38	Linear	0.22	0.05	2nd order Polynomial	0.07	0.53
<i>Thalassoma bifasciatum</i>	Linear	0.02	0.76	Linear	0.14	0.53	Linear	0.82	0.02
<i>Chromis multilineatus</i>	Linear	0.32	0.24	Linear	0.54	0.16	2nd order Polynomial	0.21	0.71

Table 9. Average length (FL cm) for important resource species between 1989 and 2006. Average length (\bar{L}) of animals in the exploited part of the population was calculated for each species at or above the length at first capture (L_c). L_{max} is the maximum size observed in each sampling period.

		1989-1994		1995-2000		2001-2006			
	L _c (cm)	\bar{L}	L _{max}	\bar{L}	L _{max}	\bar{L}	L _{max}	% diff. 89-94 & 95-00	% diff. 89-94 & 01-06
Species									
Groupers (Serranidae)									
Red hind (<i>Epinephelus guttatus</i>)	21	27.3 (6.8)	60.0	27.1 (6.0)	60.0	26.8 (5.4)	43.0	-0.73	-1.83
Graysby (<i>Cephalopholis cruentata</i>)	20	23.3 (3.9)	35.0	22.0 (2.4)	30.0	21.6 (1.8)	26.0	-5.58	-7.30
Coney (<i>C. fulva</i>)	20	22.0 (0.7)	30.0	21.8 (2.4)	26.0	21.9 (2.21)	26.0	-0.91	-0.45
Snappers (Lutjanidae)									
Gray snapper (<i>Lutjanus griseus</i>)	23	29.0 (7.0)	45.5	26.5 (5.8)	35.0	27.1 (7.5)	38.0	-8.62	-6.55
Schoolmaster (<i>L. apodus</i>)	22	26.2 (7.1)	45.0	25.7 (3.4)	40.0	25.7 (5.6)	40.0	-1.91	-1.91
Mahogany snapper (<i>L. mahogani</i>)	23	25.6 (2.1)	40.0	26.0 (2.2)	30.0	24.8 (5.3)	34.0	+1.56	-3.13
Grunts (Haemulidae)									
Bluestriped grunt (<i>Haemulon. sciurus</i>)	19	24.2 (4.7)	35.0	24.2 (5.2)	38.0	23.8 (5.3)	35.0	0.00	-1.65
White grunt (<i>H. plumieri</i>)	17	23.6 (10.0)	40.0	22.1 (5.4)	33.0	23.5 (6.7)	40.0	-6.36	-0.42
French grunt (<i>H. flavolineatum</i>)	16	18.6 (5.1)	22.5	17.2 (2.3)	25.0	17.4 (2.0)	22.0	-7.53	-6.45
Wrasses (Labridae)									
Spanish hogfish (<i>Bodianus rufus</i>)	20	27.5 (3.6)	40.0	25.5 (2.4)	35.0	25.8 (2.6)	30.0	-7.27	-6.18

DISCUSSION

Our study represents one of the longest extant research projects in the Caribbean and provides a good insight in the natural and anthropogenic factors which have affected reef fish assemblages around the island of St. John over the past three decades. By systematically examining the spatial and temporal dynamics of the reef fish assemblages around St. John, we were able develop a statistically robust monitoring program that focused on reefs with high diversity. Monitoring focusing on high biodiversity areas reduces the variability that is inherent in any reef fish monitoring program. In addition, these locations have high biodiversity and conservation value and are therefore of great importance to resource management agencies such as the National Park Service, whose mission is "*...to promote and regulate the use of the...national parks...which purpose is to conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations.*" (National Park Service Organic Act, 16 U.S.C.1.)

Trends in reef fish assemblage characteristics in VINP over the past 17 years have been dominated primarily by storm effects. Fish monitoring of four reference sites (Yawzi Point, Haulover Bay, Tektite reef, and Newfound Bay) was initiated following Hurricane Hugo in 1989, the largest storm to pass the Virgin Islands in decades, which had a large impact on reef substrate, encrusting organisms (especially corals), as well as reef fishes. Similar impacts were documented following the second largest storm that passed the Virgin Islands during the past 20+ years, Hurricane Marilyn in 1995. Although these large storms damaged reef structure and decreased coral cover in shallow water, reef fish abundance and species richness recovered within 3-5 years following these impacts.

During the past several years, the most profound changes in the reef fish assemblage have been shifts in trophic structure. Since 2000, the abundance of planktivorous fishes has increased, along with their proportion of total abundance, with the plantivorous damelfishes (*Chromis* spp.) being the dominant species responsible for this increase. Numerous factors may contribute to this shift, but the changes in benthic cover (the large decrease in coral cover and subsequent increase in algal cover) are probably large contributors. Additionally, reduction in habitat complexity associated with these biotic changes has likely affected the distribution and abundance of many reef fish taxa.

The massive coral bleaching event in 2005, apparently had an effect on trophic structure, with a decline in planktivorous fishes and increases in herbivorous fishes on all four reference reefs. Abundance increases were noted for small benthic herbivores (benthic damselfishes) and large mobile herbivores (parrotfishes and surgeonfishes). These increases in herbivore abundance are likely correlated with the increase in macroalgae cover as a result of this bleaching.

Comparisons of assemblage metrics inside and outside VINP showed no difference in species richness or biomass, suggesting that the park is not functioning effectively as a protected area for reef fish assemblages. Overfishing throughout the USVI has had profound effects on the resources within the national parks. The reef fish assemblage in the U.S. Virgin Islands has suffered the loss of large predators and a decline in abundance across all trophic levels resulting from years, if not decades, of overfishing. This release from top-down control has likely increased the importance of bottom-up processes, such as disturbance events and habitat loss.

Predatory fishes have been documented to provide strong regulatory effects in reef systems (Hixon 1991, Bascompte *et al.* 2005) and have experienced large changes in abundance over decades throughout the Caribbean (Jackson *et al.* 2001, Pandolfi *et al.* 2005). Large fishes, particularly the intensively harvested grouper and snappers, experienced declines in the Virgin Islands prior to the establishment of NPS monitoring programs (Beets and Rogers 1997, Beets and Friedlander in prep). During the 17-year monitoring period, the frequency of occurrence of large groupers in samples has declined and remained very low since 2000. A mid-sized grouper, red hind (*Epinephelus guttatus*), has shown an increase during recent years, likely in response to the spawning aggregation closure enacted in 1990. Small groupers have increased during recent years, probably due to ecological release in response to sustained low numbers of larger groupers.

Although this report provides a valuable perspective on reef fish monitoring, we cannot over-emphasize that the period of analysis is a short-term view of fish assemblages that have changed greatly during the past several decades. Monitoring must be framed in the context of these changes. Several publications have presented information and data comparisons on the changes in reef fish populations and assemblages around St. John and throughout the Virgin Islands (Appeldoorn *et al.* 1992, Beets 1996, 1997, Beets and Rogers 1997). For several species, such as large groupers and snappers, we are currently monitoring variations in very low abundances relative to historical abundances. Some species, such as the well-documented case of Nassau grouper (*E. striatus*), are even approaching local extinction (Beets and Rogers 1997; unpubl. data). Many species declines are due to overfishing, which has great effects on reef fish assemblage and coral community structure (e.g., 'phase shifts', see Hughes 1994). Numerous species, especially large predators, are less abundant, less frequent in samples, and have lower average lengths than recorded in previous decades (Beets 1997). Spawning aggregations have been extirpated and herbivorous fishes have increased proportionally in samples as higher-order predators have declined. Much of this change is due to fishing effort, which has continued in Virgin Islands National Park, and is compounded by the increases in coastal development, storm damage, and other natural biological factors (coral diseases, coral bleaching).

This analysis provides additional support to the evidence that resource conditions inside VINP are similar to the degraded conditions outside of the park, which has been presented in previous publications. Overfishing has had obvious and documented effects on reef fishes. Although additional information is needed on the resources, and specifically on exploited species and the level of fishing effort in park waters, there is a

urgent need for stricter management regulations within Virgin Islands National Park. The lack of evidence of protection of reef fishes suggests that conditions within the park are as poor as outside park boundaries and that stricter regulations are warranted.

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