RESISTANCE OF CORAL REEF FISHES IN BACK REEF AND LAGOON HABITATS TO A HURRICANE

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ABSTRACT

On 17 November 1999, hurricane Lenny passed 30 km south of St. Croix, U.S.V.I. Six sites on the east end of St. Croix (four north shore sites, two south shore sites) had been visually censused in June and October 1999, prior to hurricane Lenny, and were censused again in February, June, and October 2000, and in February 2001. The two south shore sites, where hurricane damage was greatest, were also censused in December 1999 to obtain measurements of short-term hurricane effects. Densities of *Stegastes leucostictus* (Müller and Troschel in Schomburgk, 1848), *Halichoeres bivittatus* (Bloch 1791), and all species combined of two different sizes (< and > 5 cm) and on different habitats at exposed (south shore) and protected (north shore) sites were examined for short-term and long-term hurricane effects. Despite extensive hurricane-associated damage to habitats at the two exposed sites, fishes seemed resistant to hurricane effects in the short-term: there were no detectable hurricane effects on fishes in any size class in any habitat examined. In the long-term, normal seasonal changes were most influential in determining densities of small fishes for all taxa examined, and large fishes showed little temporal variation. Given the frequency of hurricanes passing close to St. Croix, the resistance of coral reef fishes to a hurricane should not be surprising.

Hurricanes are common in the Caribbean, and may play an important role in the dynamics of coral reef communities. As resource managers begin to utilize marine protected areas as conservation and management tools, information on the effects of disturbances, such as hurricanes, and the response of fishes to such disturbances, will be a necessary component of design strategies. Despite documentation of hurricane effects on coral reefs and their associated biota, there is no consensus on the importance of these hurricanes to coral reef fishes. Physical damage to reefs, and thus loss of fish habitat, is patchy and unpredictable (Woodley et al., 1981; Edmunds and Witman, 1991; Hubbard et al., 1991; Bythell et al., 1993; Blair et al., 1994), and although some fishes may be redistributed due to hurricane-associated changes in habitat (Kaufman, 1983; Lassig, 1983; Aronson et al., 1993; Letourneur et al., 1993), other fishes appear to be either resilient to hurricane impacts (Walsh, 1983; Fenner 1991; Bouchon et al., 1994), or influenced more by non-hurricane processes (Letourneur et al., 1993; Adams, 2001). In light of the disparate findings on hurricane impacts on coral reef fishes, and the fortuitous nature of such "natural experiments", it is essential to document the responses of coral reef fishes to hurricanes to develop a better understanding of the importance of such disturbances.

As part of a study of habitat utilization by juvenile fishes in lagoons and back reefs of bank barrier reefs in the Caribbean, six sites on the east end of St. Croix, U.S. Virgin Islands (four sites on the north shore, two sites on the south shore) had been visually censused in June and October 1999. In November 1999, Hurricane Lenny followed an extended west–east track through the Caribbean, unprecedented in 113 yrs of records, and passed 30 km south of St. Croix on 17 November as a Category 4 hurricane, with strongest winds in the southeastern quadrant of the hurricane (Guiney, 1999; Fig. 1A). Since the hurricane passed to the south of St. Croix, and the strongest winds and seas

Bulletin of Marine Science

were on the south side of the island, we hypothesized that fishes at the two south shore sites would experience the greatest impact from the hurricane.

The passage of hurricane Lenny south of St. Croix, in the midst of a 2 yr study of fish habitat use in back reefs and lagoons of bank-barrier reefs, provided an opportunity to examine the impacts of a hurricane on fishes inhabiting these shallow nearshore habitats. In this paper, we (1) examine fish densities at the two south shore sites in 1999 for immediate post-hurricane effects, (2) examine densities of fishes at all six sites in 1999 to determine whether any short-term changes at the south shore sites differed from north shore sites (i.e., were within "normal" seasonal variation), and (3) for variables that had a significant temporal effect in 1999, compare seasonal changes at the south shore sites between 1999 (hurricane Lenny) and 2000 (no hurricane) to further examine whether hurricane Lenny impacted seasonal trends.

Materials and Methods

Sampling Methods and Locations.—We visually censused fishes along transects in lagoons and back reefs at four sites on the north shore and two sites on the south shore of St. Croix (Fig. 1B). Each site included a section of back reef and its associated lagoon, and all sites were similar in terms of bank-barrier reef orientation and lagoon area. The back reef is a shallow area composed mostly of highly intermixed calcareous pavement, patch reef (coral heads) and rubble, with smaller patches of sand, algal plain, or seagrass mixed in, and is contiguous with the rest of the bank-barrier reef. The lagoons begin at the shoreline, are bounded on the seaward side by the back reef of a bank-barrier reef, and are comprised of five habitat types: (1) "patch reef" is isolated, high-relief, calcareous structure (not part of the contiguous reef) with a vertical profile that often, but not always, contains live coral cover; (2) "rubble" is low-relief, calcareous structure composed primarily of conch shells or dead/dying coral fragments that are not attached to the substrate; (3) "seagrass" is monospecific, or nearly monospecific, stands of *Thalassia testudinum* Banks & Soland. ex Koenig, with varying densities of *Syringodium filiforme* Kütz. mixed in; (4) "sand" is bottom of open sand with no or very little (< 10% cover) plants or coralline material represented; and (5) "algal plain" is sand bottom dominated by *Halimeda* spp., *Penicillus* spp., and *Udotea* spp., which may include sparse stands of *S. filiforme* and *T. testudinum*.

In June and October 1999, February, June, and October 2000, and February 2001, fishes on each of the six study sites were visually censused on two non-consecutive days. The two study sites on the south side of St. Croix, Turner Hole, and Rod Bay, were also each censused from 9–12 December 1999, 3 wks after Hurricane Lenny passed the island, to provide estimates of short-term hurricane effects and qualitative assessments of hurricane damage. To ensure consistent counts, the same two divers did all censusing. All non-cryptic fishes (i.e., we excluded gobiids, apogonids, bleniids) within a 50 m long × 2 m wide × 2 m high transect were counted, and recorded in three size categories (< 3 cm, 3–5 cm, > 5 cm), with 20 lagoon transects and 14 back reef transects completed at a site on each day. Within lagoons, the locations and directions of transects were randomized (based on a grid with 10 × 10 m squares), and fishes were recorded in association with the habitat where they were observed. The lengths of transect tape crossing each habitat type were recorded to provide estimates of percent cover by habitat type and to allow calculation of fish densities by habitat type. Non-overlapping back reef transects were parallel to the longitudinal axis of the back reef, with no differentiation of habitat types due to the highly intermixed nature of the back reef habitats. The basic units of analysis for back reef and lagoon were the census data collected from a single site in a single day. Thus, for each census period, for each study site, there were two census days, each with a total of 1400 m^2 of back reef habitats and 2000 m^2 of lagoon habitats censused.

Hurricane Lenny.—On 17 November 1999, the eye of Category 4 hurricane Lenny passed 30 km south of St. Croix, with strongest winds (135 kts) in the southeast quadrant of the hurricane (Guiney, 1999; Fig. 1A). Maximum sustained winds on St. Croix were 60 kts and minimum

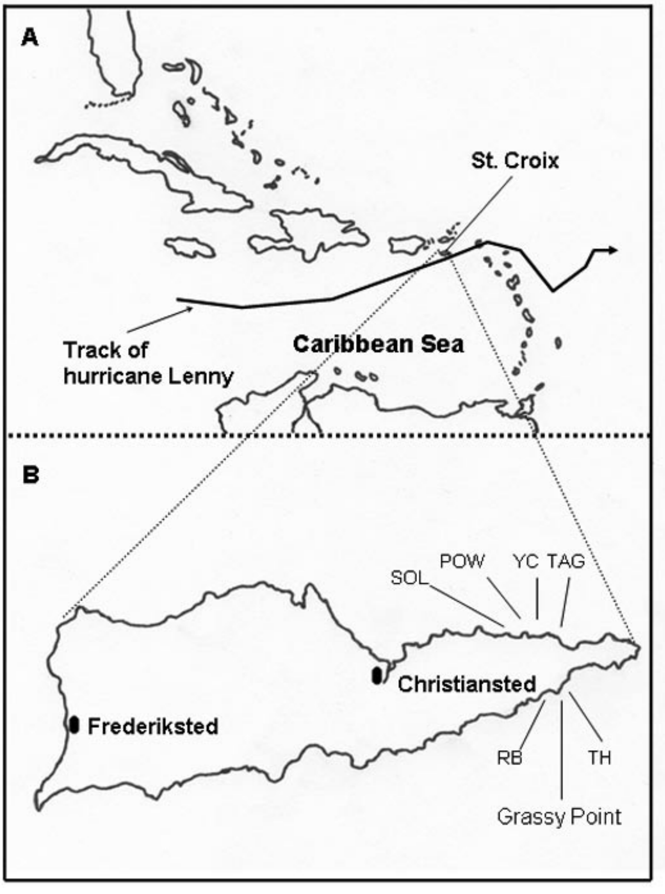

Figure 1. Locations of (A) St. Croix, and track of hurricane Lenny from 13 through 23 November 2000 (hurricane Lenny passed 30 km south of St. Croix on 17 November 2000); and (B) study sites on the eastern end of St. Croix. Abbreviations are: TH = Turner Hole, RB = Rod Bay, TAG = Tague Bay, YC = Yellowcliff Bay, POW = Pow Point, SOL = Solitude Bay.

pressure was 980 mb; the hurricane produced high seas (open ocean waves of 3–3.9 m on 17 November), high hurricane tides (0.9 m), and considerable coastal erosion along the south and west coasts, with much less impact on the north shore (Guiney, 1999). Therefore, we considered the two south shore sites to be potentially impacted by the hurricane and the four north shore sites to be relatively protected.

ANALYSES.—We combined the small (< 3 cm) and medium (3–5 cm) size classes into a single category to reduce the influence of temporal variation resulting from settlement pulses (in the small (< 3 cm) category; Adams and Ebersole, 2002), and condense most of each year class into a single size category. In addition, habitats differ in how much they are used by different species and life stages of fish (Nagelkerken et al., 2000a; Adams and Ebersole, 2002). Fish were either absent from or in extremely low density on sand, so this habitat was excluded from analysis. Therefore, we analyzed densities of the focal taxa in two size classes on five habitats. Since *Stegastes leucostictus* Müller and Troschel in Schombursk, 1848 would likely be impacted by a hurricane event due to its small size and territorial behavior (Kaufman, 1983), and it was in sufficiently high abundance (Adams and Ebersole, 2002), densities of this territorial pomacentrid were examined on back reef, patch reef, and rubble. *Halichoeres bivittatus* (Bloch, 1791), a small ubiquitous labrid, was the only species sufficiently abundant in all census periods on seagrass and algal plain for analysis. Densities of all species combined were examined on all habitats.

We examined the effects of hurricane Lenny on the fish assemblages in three ways. First, since the greatest effects of the hurricane were on the south shore of St. Croix (Guiney, 1999) we examined whether the fish assemblages of the two south shore sites (Turner Hole and Rod Bay) suffered measurable short-term impacts from the hurricane; i.e., were fish densities in December notably different from other months? For each size class (small, < 5 cm; and large, > 5 cm), we used repeated measures ANOVA (repeated by Month: June, October, December, February) with Site as the fixed factor, to analyze densities of: (a) *S. leucostictus* on back reef, patch reef, and rubble, (b) *H. bivittatus* on seagrass and algal plain, and (c) all species combined on all habitats. We used repeated measures ANOVA because we censused fish assemblages at the same sites repeatedly over time so the same individuals may have been counted in multiple months, and thus the measurements might not have been independent. The term of interest for this analysis was Month: a significant Month or Month × Site effect led to graphical examination to discover the nature of the month-to-month difference in fish density. Graphical examination was used since in many cases this approach is more revealing than additional statistical tests of significance (Cleveland, 1993). Significant effects were attributed to the hurricane if fish densities in December departed from the expected temporal trend, due to settlement, of highest densities of small fishes in June and October, with a steady decline to an annual minimum in February (Adams and Ebersole, 2002).

The second approach was to determine whether changes in fish densities from pre-hurricane (June and October) to post-hurricane (February) census periods were greater for south shore than north shore sites. This hypothesis was based on greater damage to the south shore sites from wave energy generated by hurricane Lenny as it passed to the south of St. Croix. To determine if Turner Hole and Rod Bay differed from the four north shore sites we included all six study sites in a repeated measures ANOVA on densities, as above, but using only the census periods during which all sites were censused (June, October, and February). The term of interest for this second set of analyses was the Month × Site interaction: if south shore sites were impacted differently by the hurricane, south and north shore sites that were similar prior to the hurricane would be different after the hurricane. Significant Month × Site interactions were examined graphically, as above.

Density data were log(x+1)-transformed prior to analyses, and we used the Huynh-Feldt adjusted probability when the model did not meet the sphericity assumption (Wilkinson et al., 1996). For each of these two analytical approaches (south shore sites only; north shore vs. south shore sites), probabilities were Bonferroni-adjusted to maintain an experiment-wise error rate of 0.05 (Sokal and Rohlf, 1995). One or more lagoon habitats were not run across by transects on a census day in some months for some north shore sites, resulting in multicolinearity due to too few values for a habitat-site interaction term. We replaced each missing cell (12 missing of 672 total cells) with the average for that habitat (pooled across north shore sites only) for that month. This provided a conservative estimate of the missing value; i.e., since the purpose of the ANOVA was to test for a difference between north shore and south shore sites, using habitat-specific values derived from other north shore sites provided a conservative estimate of temporal trends within the north shore sites.

Table 1. Percent change in densities of small (< 5 cm) and large (> 5 cm) *Stegastes leucostictus* on back-reef from October 1999–February 2000 (hurricane year) and from October 2000–February 2001 (non-hurricane year).

	Hurricane year		Non-hurricane year	
Site	Small fish	Large fish	Small fish	Large fish
Turner Hole*	–71	109	–64	–12
Rod Bay*	–63	138	0	–35
Tague Bay	–19	156	–38	–22
Yellowcliff Bay	–1	136	–65	8
Pow Point	–60	18	0	–35
Solitude Bay	–12	90	–5	–40

* = South Shore sites.

Finally, since there was a significant seasonal effect for both large and small *S. leucostictus* on back reef habitats in the year of hurricane Lenny, we calculated percent change in densities of small (< 5 cm) and large (> 5 cm) *S. leucostictus* from October 1999–February 2000 (year with hurricane Lenny) and October 2000–February 2001 (year with no hurricane) to determine the extent to which the hurricane affected this site-attached species.

Results

Hurricane Damage to Habitats.—Coastal erosion was evident at both Turner Hole and Rod Bay. Though the point of land (Grassy Point) separating the two south shore study lagoons normally provides protection from hurricanes to the eastern end of Rod Bay, the unique west–east track of hurricane Lenny produced greater impacts to habitat in Rod Bay, while Turner Hole received less wave energy, as it was somewhat sheltered by Grassy Point (Fig. 1B). Coral and coral rubble were lost from the back reef at Turner Hole; the western-most section of the back reef (protected by Grassy Point) remained intact with damage increasing towards the eastern end. Rubble was displaced into the lagoon, and moving sand scoured, undermined, or buried some seagrass beds (*Thalassia testudinum* Banks & Soland. ex Koenig and *Syringodium filiforme* Kütz.), leaving exposed and/or detached rhizomes and exposed tips of buried seagrass blades (AJA, pers. obs.). Coastal erosion was evident at both Turner Hole and Rod Bay. Damage to the Rod Bay back reef, exposed to hurricane seas on the west side of Grassy Point, was greater than at Turner Hole. The loss of Rod Bay lagoon seagrass and algal cover was even more impressive, with large-scale movement of sand, some seagrass loss due to covering by sand, and severe scouring of other seagrass beds (AJA, pers. obs.). Overall, total area of seagrass and algal plain habitats was reduced and total area of sand was increased at Turner Hole, and especially Rod Bay, after the hurricane (Table 2).

Hurricane Effects at South Shore Sites.—For all combinations of taxon, habitat, and size category, fish densities were similar for Turner Hole and Rod Bay. The term of interest, Month (a Month or Month × Site effect), was statistically non-significant ($P > 0.008$; Bonferroni adjustment) for five out of six habitat and size combinations, and was statistically significant in one instance for *Stegastes leucostictus*: the Month effect was significant for large (> 5 cm) *S. leucostictus* on back reef ($F = 15.943$, $P < 0.008$; Bonferroni adjustment; Fig. 2A). The significant Month effect for large fish on back reef was due to a gradual increase in density from June 1999 through February 2000.

Table 2. Estimated percent cover of lagoon habitats at the two south shore sites (Rod Bay and Turner Hole) exposed to hurricane Lenny before (October 1999) and after (December 1999) the hurricane. Values are means, with standard error in parentheses.

		Habitat				
Location	Month	Patch reef	Rubble	Seagrass	Sand	Algal plain
Turner Hole	October	1.1	0.31	48.46	28.83	21.3
		(0.95)	(0.21)	(13.62)	(17.23)	(4.35)
	December	0.15	0.71	34.18	42.12	22.84
		(0.03)	(0.44)	(3.04)	(5.17)	(1.66)
Rod Bay	October	1.56	0.74	15.79	28.15	53.76
		(0.64)	(0.37)	(9.89)	(3.45)	(5.44)
	December	0.03	0.2	10.16	64.89	24.73
		(0.03)	(0.14)	(0.86)	(2.35)	(3.38)

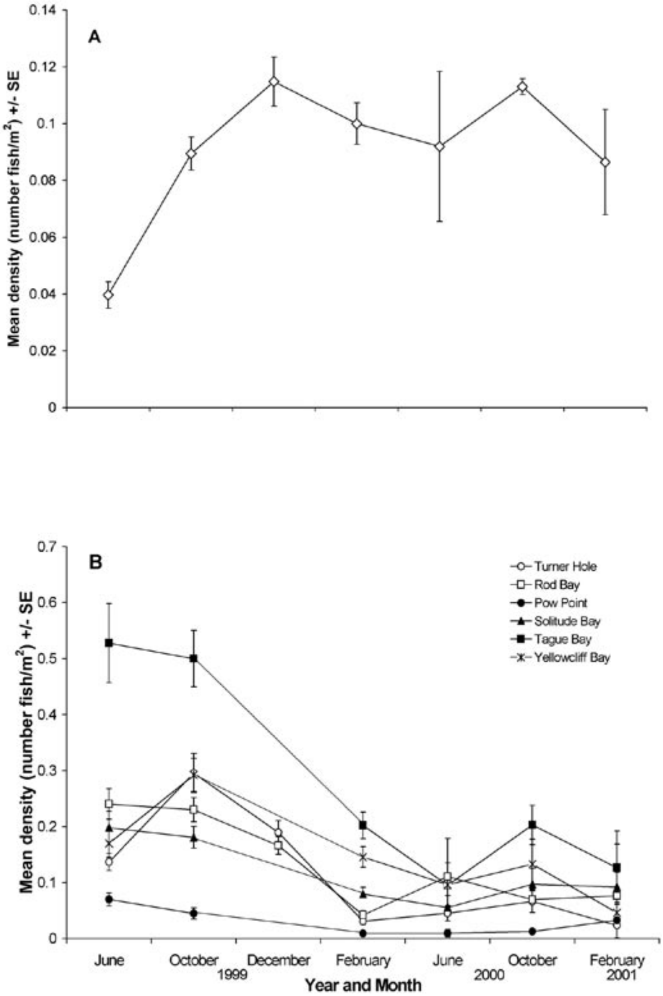

Figure 2. A) Temporal changes in densities of large *Stegastes leucostictus* in back reefs of the south shore sites, Turner Hole and Rod Bay (June 1999–February 2001). B) Temporal changes among north shore (solid symbols) and south shore (open symbols) sites for small *Stegastes leucostictus* in back reef habitat (June 1999–February 2001).

For *Halichoeres bivittatus* (Bloch, 1791), there was no significant Month or Month × Site effect for any habitat-size class combination ($P > 0.0125$; Bonferroni adjustment). Similarly, there was no significant Month or Month × Site effect for all species combined ($P > 0.005$; Bonferroni adjustment).

North vs South Shore Differences in Hurricane Effects.—Due to the passage of hurricane Lenny to the south of St. Croix, and highest winds and seas on the south shore (Guiney, 1999) we included fish densities for all sites in repeated measures ANOVA to determine whether there was a difference between the sheltered north ("normal" seasonal variation) vs. the exposed south (impacted by hurricane) shore. When all sites were included in analyses for *S. leucostictus*, the Month × Site interaction term was

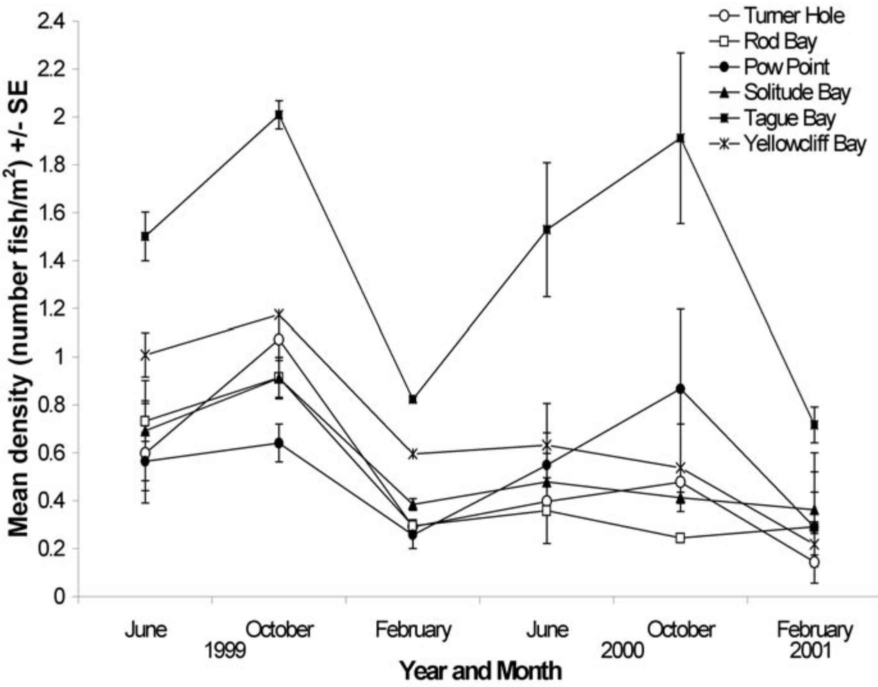

Figure 3. Temporal changes in total densities of small (< 5 cm) fishes by month for all species combined. Transect data were pooled across all habitats within a Site × Month for each of the six study sites (June 1999–February 2001).

significant only for small fish on the back reef (F = 8.948, P < 0.008; Bonferroni adjustment; Fig. 2B). Densities of small *S. leucostictus* at the south shore sites in February were near the low end of the range of densities for all sites in that month, and the slope of decline from October–February is steeper for these south shore sites than for the north shore sites, so it is arguable that this significant result is evidence for a hurricane effect. However, it might also be argued that the October–February decline is expected and similar among all sites, that the final winter density of small *S. leucostictus* at the south shore sites is within the range exhibited by the north shore sites, and that the significant Month × Site interaction may have been produced by two sites that showed increases, rather than decreases, in fish density from June–October.

When *H. bivittatus* densities at all six sites were examined, the Month × Site effect was not significant for any habitat – size-category combination (P > 0.0125; Bonferroni adjustment). Similarly, there was no significant Month × Site effect for either small or large fishes of all species combined (P > 0.005; Bonferroni adjustment).

Annual Comparisons of Seasonal Changes.—Despite the November hurricane, declines in densities of small *S. leucostictus* from October 1999–February 2000 were offset by increases in densities of large *S. leucostictus* (Table 1). In contrast, very little settlement and subsequently very little recruitment into the large size class occurred in the next year, resulting in a decline in densities of both small and large *S. leucostictus* from October 2000–February 2001, even though there was no hurricane. The pattern exhibited by small *S. leucostictus* was echoed by small fishes of all species combined (Fig.

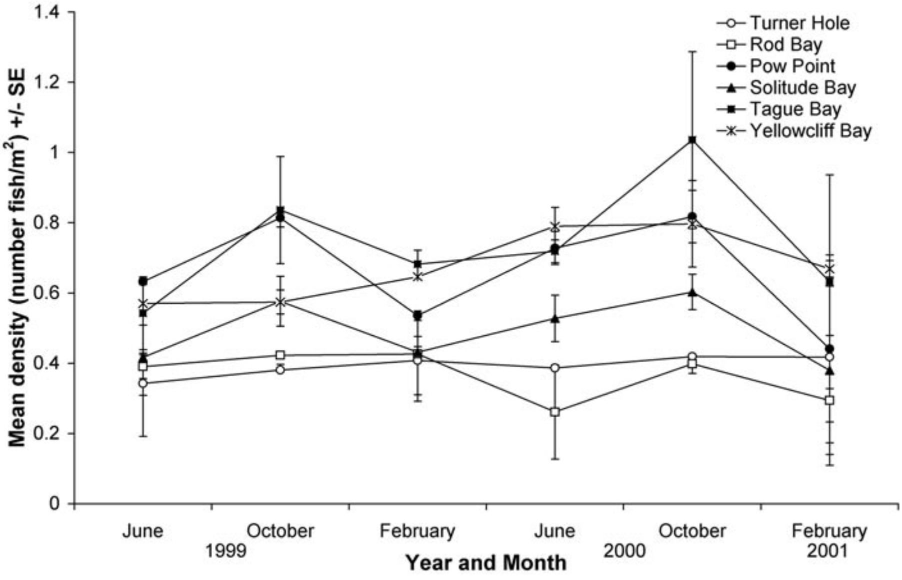

Figure 4. Temporal changes in total densities of large (> 5 cm) fishes by month for all species combined. Transect data were pooled across all habitats within a Site × Month for each of the six study sites (June 1999–February 2001).

3). During the hurricane year, which was also a year of high recruitment for all species, densities of small fishes were highest in October and lowest in February. In the following year, there was poor settlement at most sites, and densities of small fishes remained low throughout the year, with a minimum in February. Unlike large *S. leucostictus*, large fishes of all species combined remained relatively stable over time (Fig. 4), suggesting that adult populations did not suffer significant effects of hurricane Lenny – either directly or due to a loss of recruits.

Discussion

Hurricanes can impact fishes in two ways – directly or indirectly (Jones and Syms, 1998). Direct impacts are the result of strong currents and/or waves that sweep fishes from their habitats or injure them so they die or are more susceptible to predation (e.g., Woodley et al., 1981; Lassig, 1983). Given the time lag between the passage of hurricane Lenny and the post-hurricane census in December (22 d), we were unable to gather data on possible direct effects. However, since there was no detectable hurricane-associated decline in abundance in December, any direct effects were probably minimal.

More likely, and more frequently documented, are indirect effects, whereby habitat loss or degradation results in a decline in fish abundance or change in species composition (reviewed in Jones and Syms, 1998). The loss of habitat might cause greater predation or competition, and may give some species a greater advantage because of changes in habitats. The expected result is change in abundance and/or species composition of fishes. Thus, it is somewhat surprising that no hurricane effects on fishes were detected in this study despite the observed hurricane effects on habitats.

Our observations of hurricane-associated habitat degradation of back reef habitats contrast from those of Aronson (1993), who examined the effects of hurricane Hugo in 1989 on ophiuroid assemblages in back reef habitats in Rod Bay. He attributed the lack of a hurricane effect on ophiuroid assemblages to a lack of physical disturbance of back reef habitats, and hypothesized that the shallow reef crest absorbed much of the energy of the 6 m waves. Our observations imply that the reef crest was less effective at absorbing the waves from hurricane Lenny, possibly due to differences in direction of hurricane travel. Hurricane Hugo approached St. Croix from the southeast, as do most hurricanes, and under these conditions Rod Bay may receive some protection from Grassy Point (Fig. 1). In contrast, hurricane Lenny approached from the west, which exposed Rod Bay to the full brunt of hurricane waves. That we found greater evidence of hurricane damage in Rod Bay than Turner Hole supports this explanation. A second explanation is that frequent hurricanes that have impacted the south shore of St. Croix in recent years have degraded the integrity of the reef crest habitats and thus the wave-absorbing properties.

We propose that the apparent resistance of coral reef fishes of St. Croix to hurricane Lenny was due primarily to the high frequency of disturbances at this location. Although the track of hurricane Lenny was unprecedented in direction, the proximity of the hurricane's path to St. Croix was not; 28 hurricanes have passed within 75 nm of St. Croix in the past 113 yrs (National Hurricane Center), and the south shore has experienced repeated disturbance from these hurricanes (Hubbard et al., 1991), especially in recent years, beginning with hurricane Hugo in 1989.

The high frequency of disturbances on St. Croix may manifest itself in fish assemblages in three ways. First, hurricanes are frequent in the Caribbean, so one might expect that coral reefs and fish assemblages are adapted to these types of disturbances (Lugo et al., 2000). In addition, the hurricane damage of coral reef habitats is localized, and often does not affect the ability of reefs to provide food and shelter for fishes (Lugo et al., 2000). Many species are able to adapt to changes in habitat availability and either show no change or a rapid recovery in abundance (e.g., Kaufman, 1983; Walsh, 1983).

Second, frequent disturbances cause the coral reef communities to be in a persistent state of early succession (Witman, 1992; Done, 1999). Hurricanes may be frequent enough that the corals providing habitat for fishes are unable to re-colonize and grow (e.g., Riegl, 2001), so are always in an early state of succession. Therefore, rubble-associated fishes may be more common. This scenario implies that given sufficient time between disturbance events, coral and fish communities will follow a successional trajectory through increased diversity and, if no disturbances occur for an extended period, then eventually the decreased diversity of an equilibrium community (Connell, 1978).

Disturbances that are too frequent or too intense may induce a third scenario of a phase shift (Done, 1992; Jones and Syms, 1998). In this case, habitats have been so altered by frequent disturbances that the "traditional" successional trajectory is no longer viable. This is in contrast to reefs that have not lost their structural integrity and so are able to recover (Colgan, 1987). The shift to an alternate state may be the case on the south shore of St. Croix, which has suffered repeated intense disturbances since the 1980s, including the abovementioned hurricanes, coral disease, and *Diadema antillarum* (Philippi, 1845) die-off, as well as a reduction in abundance of herbivorous fishes from overfishing. Phase shifts can be induced by such a combination of events (Hughes, 1994), as well as with other disturbances (Syms and Jones, 2000; Ebersole, 2001). The fish assemblages at the south shore locations are dominated by species that can utilize the low-relief habitats, so are less likely impacted by hurricanes. Moreover, fishes that utilize the low-relief back reef and shallow seagrass habitats are likely already adapted to wave exposure and low topographical relief (Letourneur, 1996), so may be more likely to be resistant to hurricane disturbances.

Settlement of coral reef fishes in the Caribbean, and to St. Croix, occurs primarily in summer (Munro et al., 1973; Shulman, 1985a; Adams and Ebersole, 2002), and mortality is high during the time between settlement and ontogenetic migration (Shulman, 1985b). Thus, settlement, ontogenetic shifts, and mortality combine to create the normal temporal trend of highest densities of small fishes in October (the end of the settlement season) and lowest densities in February, as observed in this study. Letourneur et al. (1993) also concluded that seasonal change was more important than a hurricane in determining community structure of coral reef fishes at Reunion Island. This trend is exemplified in this study by *S. leucostictus*. In both years, densities of small *S. leucostictus* were highest in October and lowest in February after losses of small fishes due to mortality, growth, and possibly migration (McGehee, 1995). *Stegastes leucostictus* reach 5 cm (TL) ~200 d after settlement (McGehee, 1995), so individuals that settled during the previous summer would enter the large size class by the following February. From October 1999, a year with high recruitment, to February 2000, the substantial declines in densities of small *S. leucostictus* were accompanied by increases in densities of large *S. leucostictus*, regardless of site (i.e., south vs. north shore; Table 1). In contrast, in 2000, a year with low recruitment and no hurricane, declines in densities of small *S. leucostictus* in the back reef were not accompanied by increases in densities of large fishes, which indicates that mortality of large fishes was not offset by recruitment of new individuals into the large size class. Similar temporal patterns at all sites for *S. leucostictus* and for all species combined further suggest the strong influence of larger scale, longer-term phenomena that are not attributable to the hurricane.

In contrast to juveniles, densities of large (> 5 cm) fishes of all species combined showed little seasonal variation. The most parsimonious explanation for this is the storage effect (Warner and Chesson, 1985). In this scenario, the adult populations are dominated by a few strong year classes that result from years of high recruitment. This allows the population to remain stable, or to decline slowly over time, during periods of low recruitment. In such a scenario, the causes of low recruitment, and the resulting poor year classes, are variable, but as long as strong year classes occur with sufficient frequency, the average abundance of adults will remain relatively stable.

In conclusion, despite extensive hurricane damage to back reef and lagoon habitats at Turner Hole and Rod Bay, we found no evidence of significant short- or long-term hurricane effects on the associated fish assemblages. Damage to reef habitats by hurricane Lenny might not have been severe enough to induce changes in fish distribution similar to those seen in response to changes in reef structure after other hurricanes (Woodley et al., 1981; Kaufman, 1983; Lassig, 1983; Aronson et al., 1993; Letourneur et al., 1993), and reef fishes may simply be resistant to all but the most drastic changes in reef structure (Walsh, 1983). Alternatively, other, longer-term factors may be more influential to fish abundances (Letourneur et al., 1993; Adams, 2001). Based on the frequency of disturbances to St. Croix reefs, there are numerous reasons we might expect that these fishes would be adapted to hurricane-associated stresses (Karlson and Hurd, 1993), and that the impact of hurricanes on these fish assemblages would be relatively minor.

Acknowledgments

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