

Red Mangrove (*Rhizophora mangle*) Reproduction and Seedling Colonization after Hurricane Charley: Comparisons of Charlotte Harbor and Tampa Bay

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ABSTRACT: Reproductive aspects of life history are known to be important in recovery following disturbance in many plant species although this has not been well studied in mangroves. Hurricane Charley devastated large areas of mangroves in Charlotte Harbor, Florida, in August 2004. We surveyed 6 forests in Charlotte Harbor (2002, 2003, and 2005) and 16 in Tampa Bay, Florida (2001, 2002, 2003, and 2005) for total numbers of reproducing trees and trees heterozygotic for albinism that produce both normal and albino propagules. Tree size (estimated height and diameter at breast height) was also recorded for sentinel heterozygotic trees. Total number of reproducing trees km⁻¹ was used as an index of reproductive output of the population, and deviation from the 3:1 (normal:albino propagules) ratio on heterozygotic trees expected with 100% selfing was used to estimate outcrossing. Numbers of *Rhizophora mangle* reproducing trees km⁻¹ of shoreline in Charlotte Harbor were reduced by an order of magnitude following Hurricane Charley, while numbers of reproducing trees in Tampa Bay were similar to those of previous years. Reduced reproduction in Charlotte Harbor was accompanied by fewer new recruits in plots on Sanibel and Captiva Islands. Numbers of new recruits after the storm also tended to be fewer in plots where canopy loss was greater. More new recruits occurred in sites that had higher densities of pre-storm *Rhizophora* seedlings and greater relative dominance by *Rhizophora*. Outcrossing of sentinel trees was 2.5 times greater in Charlotte Harbor (mean site⁻¹ = 33.6 ± 6.7%; with 17% of forest sites completely selfing) than in Tampa Bay (mean site⁻¹ = 13.4 ± 4.7%; with 40% of sites completely selfing), although the implications for seedling recruitment of this difference are not known.

Introduction

Powerful hurricanes cause extensive disturbance of mangrove canopies that affects recovery rates and succession patterns (Baldwin et al. 2001; Cahoon et al. 2003; Hensel and Proffitt 2003; Smith et al. 1994). Recovery following disturbance is influenced by the density and species composition of surviving trees, reproductive output, genetic ecology, dispersal, soil edaphic factors, and the suite of seedling predators in the area. Reproductive and genetic parameters are particularly important in plant colonization, growth, recovery following disturbance, and founding of new populations in any plant species (Silvertown 1987; Barnette and Husband 1990). The red mangrove, *Rhizophora mangle* L., is a major intertidal foundation species (Dayton 1972; Bruno and Bertness 2001) in the New World tropics even though the linkages between reproductive life history phenomena and resilience to perturbation are incompletely understood for this

species. Studies linking life history and ecological genetics of marine foundation species to disturbance are critical to an adequate understanding of hurricane effects, human development, and large scale forcing caused by a changing climate.

Unlike the situation in many terrestrial systems, in intertidal mangrove and salt marsh communities there is generally no persistent seed bank in the soil to allow rapid seedling recruitment after disturbance, instead recruitment in intertidal plant communities occurs by growth of already established seedlings (Sherman et al. 2000), colonization by new seedlings (Edwards et al. 2005; Proffitt and Devlin 2005), and vegetative growth of neighboring plants (Proffitt et al. 2003).

R. mangle (hereafter referred to as *Rhizophora*) is a shoreline dominant throughout most of south Florida and is also codominant with the other two mangrove species at low to mid tide levels. This viviparous species produces large seedling propagules (< 20 to > 30 cm long at maturity) that disperse by floating (Tomlinson 1986). *Rhizophora* propagules are much larger than those of the other two dominant mangrove species in Florida. The

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large size allows for more maternally provided energy reserves that enhance survival during dispersal via floating and promotes rapid establishment and early growth of seedlings.

Although epicormic sprouting is common in other mangrove species, *Rhizophora* has limited ability for regeneration from roots of downed trees or by coppicing from broken trunks. Also unlike the other two common mangrove species in Florida, *Rhizophora* is a pre-dominantly self-fertilizing (selfing) species (Teas and Handler 1979; Lowenfeld and Klekowski 1992; Proffitt and Travis 2005), although the degree of outcrossing varies substantially in different locations (Lowenfeld and Klekowski 1992; Proffitt and Travis 2005, Proffitt and Travis unpublished data).

High selfing rates coupled with strong selection pressures can purge a population of deleterious alleles (Goodwillie et al. 2005). Selfing also allows a tree that has colonized a remote site to reproduce in the absence of other trees and will increase the degree of carry-over of maternal genes to the next generation. High incidence of selfing also greatly reduces genetic diversity and can increase the deleterious effects of inbreeding depression. Even though *Rhizophora* appears well adapted for the low to mid intertidal habitat, the reduced genetic diversity caused by selfing may affect its ability to adapt to future changes (e.g., conditions in an urbanized estuary) or may influence the percent of seedlings able to survive following colonization of disturbed areas. Although this aspect of the genetic ecology of *Rhizophora* is not well understood, our knowledge of some salt marsh foundation plant species is more advanced. Selfing and crossing with closely related individuals greatly increases the rate of inbreeding depression in *Spartina alterniflora*, a dominant salt marsh plant (Travis et al. 2004). Mating system affects genetic ecology in terms of clonal growth rates of different genotypes (Proffitt et al. 2003), patterns of facilitation and dispersion of associated species (Proffitt et al. 2005), ecological functions (Seliskar et al. 2002), and seedling recruitment and genetic diversity of the populations during recovery from large scale die-off (Edwards et al. 2005).

The early growth of *Rhizophora* seedlings depends not only on the size of the propagule, but also on other maternal or genetic effects that operate independently of propagule size. Although propagule size is often cited as a defining factor in *Rhizophora* early seedling growth, recent results from a field experiment indicate that this only explains a very small proportion of the variation in seedling growth during the first year after planting, and that other differences in growth of seedlings from different maternal trees remain after the size

covariate is factored out (Proffitt and Travis unpublished data). Survival from parasitism by an obligate beetle also differs for seedlings from different maternal families of *Rhizophora* independently of propagule size (Sousa et al. 2003; Devlin 2004). These studies suggest important genetic and maternal effects in the propagules that likely affect recovery after hurricanes and other disturbances. Light regimes, nutrients, sulfide, and elevation also influence *Rhizophora* seedling growth (McKee 1993; Devlin 2004; Proffitt and Travis unpublished).

Our objectives are to address selected aspects of *Rhizophora* life history in terms of possible contributions to population recovery following massive devastation of mangroves in Charlotte Harbor by Hurricane Charley, a category 4 storm (Milbrandt et al. 2006). Different areas of these mangrove forests were dominated or codominated by *Rhizophora*, *Avicennia germinans* (L.) Stearn., and *Laguncularia racemosa* (L.) Gaertn. f. We present data on *Rhizophora* reproductive effort before and after Hurricane Charley in Charlotte Harbor, Florida, and compare with data from Tampa Bay, Florida. Because propagule dispersal is pre-dominantly local (Clarke and Kerrigan 2000; Sengupta et al. 2005), colonization rates can be strongly affected by changes in reproductive output of the population. We also provide ancillary information on the outcrossing rate in each stand. Although survival and growth comparisons of seedling produced by outcrossing and selfing have not been studied in this species, such information from salt marsh systems suggest that breeding system can affect seedling success (Travis et al. 2004; Edwards et al. 2005). We also show supporting data from an ongoing study (Milbrandt unpublished data) of seedling colonization from plots in heavily damaged and less affected areas in Charlotte Harbor.

Materials and Methods

RHIZOPHORA REPRODUCTION

We recorded numbers of reproducing trees km^{-1} of mangrove-dominated shoreline during the peak season of maturing propagules (July and August) from forested stands in Charlotte Harbor (2002, 2003, and 2005, $n = 6$ forests) and Tampa Bay (2001, 2002, 2003, and 2005, $n = 16$ forests). Reproductive data were gathered in association with surveys for albino mutation rates; data from some of the Tampa Bay sites are also reported in Proffitt and Travis (2005). Charlotte Harbor forests were Tarpon Bay, east Pine Island, Patricio Island, Part Island, Ding Darling, and northern Estero Bay. In Tampa Bay there were 10 sites along the eastern shoreline of the bay area from the Alafia River in the north to Terra Ceia Bay in the south, 4 sites

along the western shoreline of the Tampa Bay proper from upper Old Tampa Bay to Fort Desoto Park, and 2 sites in upper Boca Ceiga Bay.

The procedure for gathering data on reproductive output consisted of boating slowly along the shoreline and counting all trees that produced at least 10 propagules as reproducing and measuring the distance of mangrove-dominated shoreline surveyed. Density of reproducing trees was then calculated by dividing the number of reproducing trees by the length (km) of shoreline surveyed. Our survey generally incorporates trees within 10 m of open water. Tree size was measured by both visually estimating height and rank diameter at breast height (DBH) for sentinel trees as described in Proffitt and Travis (2005), and we used correlation analysis to determine if there was a relationship between the two size measures. The DBH ranking system was the same as that used by Proffitt and Travis (2005): 1 (< 5 cm DBH), 2 (5–10 cm DBH), 3 (> 10–15 cm DBH), 4 (> 15–20 cm DBH), or 5 (> 20 cm DBH). In Tampa Bay, DBHs were not recorded for sites surveyed in 2002.

Trees that are heterozygotic for albinism produce yellow or reddish propagules in addition to normal green propagules, and these trees were used as sentinels by which to estimate the degree of outcrossing in that forest. We used significant deviation (using Chi-square test) from an expected 3:1 ratio of green:albino propagules in sentinel trees found at sites surveyed to estimate the outcrossing rate (100% selfing produces propagules in a 3:1 ratio, see Lowenfeld and Klekowski [1992] and Proffitt and Travis [2005] for details). There were 41 sentinel trees recorded in Charlotte Harbor and 92 in Tampa Bay. Locations of each were recorded to facilitate use in future studies.

Data were grouped as follows for statistical analysis by one-way analysis of variance (ANOVA; Systat, Inc. 2002; GLM module) and Tukey a posteriori multiple comparisons with Bonferroni corrections: Charlotte Harbor pre-Charley (2002 and 2003) sites, Charlotte Harbor post-Charley (2005) sites, and Tampa Bay sites. For statistical analysis, we grouped the site in Tampa Bay surveyed in 2005 with the Tampa Bay sites from previous years because no major hurricane directly affected that site in the southeastern portion of the bay that year. Proportion of outcrossing was arcsin (square root) transformed prior to analysis to address lack of normality in the data distribution. Possible relationships among percent outcrossing, tree size, and numbers of reproducing trees km^{-1} were explored using either product-moment correlation or Spearman rank correlation analyses for both estuaries separately.

SEEDLING RECRUITMENT

A permanent quadrat was established in each of 24 circular study plots at 4 separate locations ($n = 3$ location $^{-1}$) in April 2005 on Sanibel Island at Ding Darling National Wildlife Refuge. All plots had open access to the bay and were located in relatively low elevation areas dominated by *Rhizophora*; actual elevations were not measured for this study. Randomly generated distance and bearing were used to determine the position of the quadrat from the center of a 6 m radius, circular plot. PVC was used to mark the corners of a 1 m square. Each *Rhizophora* seedling in the quadrat was tagged with a 15 cm cable tie, around the base of the propagule. Sites were revisited after the reproductive season (December 2005) to determine the number of new seedlings that had colonized and established in the permanent quadrats. The amount of canopy loss was calculated from measurements of living and felled or broken trees at the site (Milbrandt et al. 2006).

Results

Sampling effort per forest as indicated by length of shoreline surveyed was similar in the two estuaries except for the post-storm year (2005) in Charlotte Harbor, when far fewer reproducing trees could be found and much more shoreline had to be covered to obtain a reliable sample (Table 1). Total reproducing trees recorded per estuary were 4,108 (Charlotte Harbor) and 16,168 (Tampa Bay). Mean total reproducing trees per forest site ranged from 761.3 to 1,281.3. Tree heights were strongly correlated with the rank DBHs in the two estuaries (Spearman rank correlation = 0.959, $p < 0.0005$).

Tree size (DBH) analysis compared Tampa Bay, Charlotte Harbor pre-storm, and Charlotte Harbor post-storm. Trees were larger in Charlotte Harbor than in Tampa Bay (mean rank DBH \pm standard errors, number of forests: Charlotte Harbor 3.4 ± 0.36 , $n = 6$; Tampa Bay 2.0 ± 0.15 , $n = 9$), and sizes of sentinel trees did not differ before and after the storm in Charlotte Harbor (one-way ANOVA of DBH, $R^2 = 0.678$, $F_{2, 12} = 12.617$, $p < 0.001$, and Tukey multiple comparisons).

The density of reproducing *Rhizophora* shoreline trees in Charlotte Harbor decreased by an order of magnitude in post-Charley 2005 (one-way ANOVA $R^2 = 0.55$, $F_{2, 19} = 11.55$, $p < 0.001$; Fig. 1). The a posteriori Tukey test showed that Tampa Bay and Charlotte pre-Charley sites were not different from one another ($p < 0.207$), but that both were different from Charlotte post-Charley ($p < 0.001$ and $p < 0.023$, respectively). No such trend in reduced reproduction in 2005 was observed in Tampa Bay itself, but caution is in order for this

TABLE 1. Data from surveys of *Rhizophora mangle* reproduction in different years for Charlotte Harbor and Tampa Bay, including numbers of forests surveyed, kilometers of mangrove-dominated shoreline included in the surveys, total numbers of reproducing trees counted, and tree heights (m) and rank DBHs (diameter at breast height). Values are means (\pm one standard error). Tree Height and DBH were not recorded in 2001 (indicated by ND).

	Number of Forests	Kilometers Surveyed	Total Trees	Height	DBH	Percent Outcrossing
Charlotte Harbor						
2002	1	2.8	819	5.8	2.6	38.3
2003	3	3.2 (0.69)	873.8 (83.4)	8.6 (1.8)	3.7 (0.46)	41.1 (1.6)
2005	2	15.1 (11.6)	306.5 (97.5)	6.3 (0.25)	2.8 (0.05)	20.0 (20.0)
Tampa Bay						
2001	7	1.4 (0.24)	761.3 (115.7)	ND	ND	14.2 (8.2)
2002	6	2.8 (1.0)	1281.3 (192.5)	3.7 (0.54)	1.9 (0.18)	18.8 (7.8)
2003	2	2.9 (0.55)	1100.5 (55.5)	4.1 (1.7)	2.0 (0.50)	3.9 (3.9)
2005	1	1.5	950	3.5	2.3	0
2001–2005 mean and SE	16	2.1 (0.42)	1010.5 (103.6)	3.8 (0.46)	2.0 (0.15)	13.4 (4.7)
2001–2005 N	16	16	8	8	15	

interpretation since only one site was surveyed. Observations in Tampa Bay by Proffitt and Travis during field work to measure seedling growth in an unrelated field experiment suggested that high levels of reproduction were occurring in a number of locations in the estuary.

Percentage outcrossing was significantly greater in Charlotte Harbor relative to Tampa Bay. One-way ANOVA ($R^2 = 0.30$, $F_{2, 18} = 3.840$, $p < 0.041$) and Tukey multiple comparisons indicated that Charlotte Harbor pre-Charley (40.4% outcrossing) was different than Tampa Bay (13.4%; $p < 0.032$), but that Charlotte Harbor post-Charley (20.0% outcrossing) was not significantly different from Charlotte Harbor pre-Charley ($p = 0.381$) or Tampa Bay ($p = 0.830$).

In Tampa Bay, 56% of forest surveys had significant outcrossing while in Charlotte Harbor 83% of sites had some degree of outcrossing. One site in Tampa Bay was omitted from outcrossing analysis because there was only one albino tree at the site, and testing for deviation via Chi-square analysis was not possible.

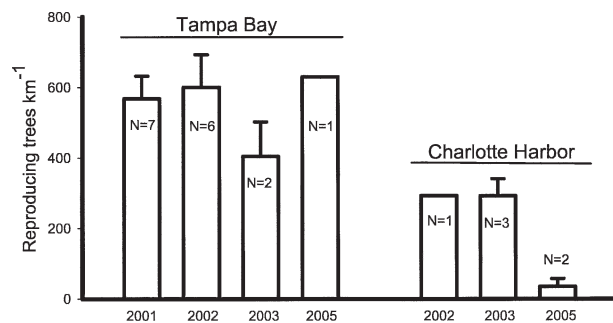


Fig. 1. Numbers of reproducing *Rhizophora mangle* trees km⁻¹ of shoreline in two Florida Gulf coast estuaries (TB = Tampa Bay, CH = Charlotte Harbor) from 2002 to 2005. Values are means \pm 1 standard error. N numbers are shown in association with the bars.

In Tampa Bay, the percent outcrossing was positively correlated with the density of reproducing trees km⁻¹ ($r = 0.72$, $p < 0.04$), but there was no correlation in Charlotte Harbor possibly because of the small number of sites (6) and the fact that with one exception (0% outcrossing) the surveys showed relatively high and consistent rates of outcrossing (38.3–42.7% outcrossing). There was no significant correlation of percent outcrossing at $p = 0.05$ with tree size in either estuary.

Many seedlings in Charlotte Harbor plots survived Hurricane Charley (Fig. 2, April 2005 data). New recruitment in the year after the storm (Fig. 2, December 2005 data) was minimal, likely in part as a result of the reduced reproduction. New recruitment declined with increasing canopy loss, but was greater in plots that had large numbers of pre-storm seedlings.

Discussion

Life history parameters may play an important role in initial recovery of populations of *Rhizophora* following a major hurricane. The importance of reproduction is emphasized by co-occurrence of peak seasons for hurricanes and mature *Rhizophora* propagules. Late summer storms result in the drop and dispersal of propagules, although major hurricanes may strand many propagules at elevations higher than they can survive. Spring and early summer major storms may damage or remove flowers, fruits, and young propagules, reducing the crop of potential recruits that same year. Winter storms may produce forest gaps available for colonization by the next summer's propagules, but the effect of winter storms on tree reproduction are unknown.

Our study provides a link between the density of reproducing trees and the extent of new colonizing *Rhizophora* seedlings the year following a major hurricane. This suggests that there is at least a 1-yr

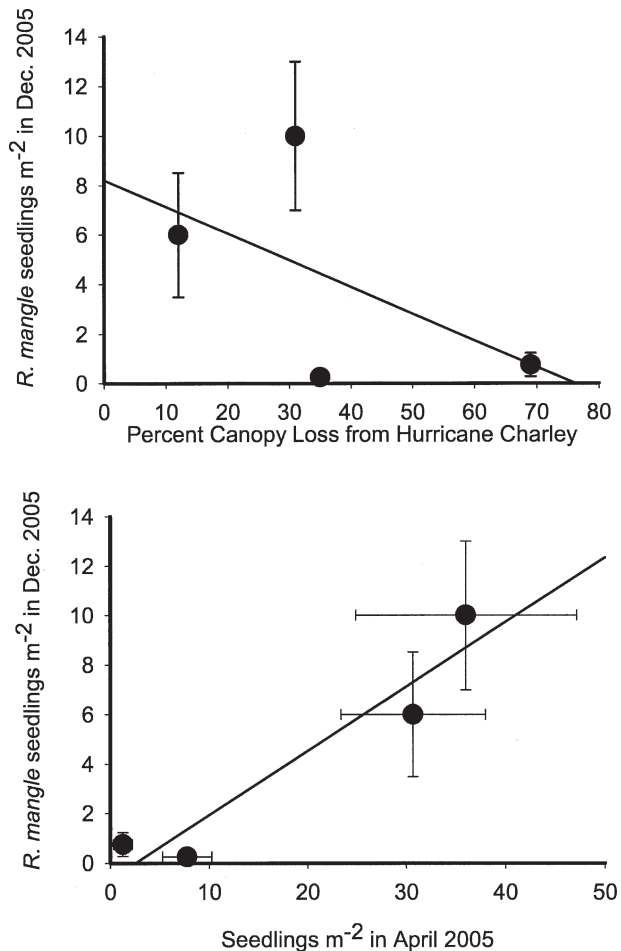


Fig. 2. The number of new seedling recruits m^{-2} relative to the percent canopy loss at four locations on Sanibel and Captiva Islands in Charlotte Harbor, Florida and in December 2005 relative to the number of seedlings in April 2005 (hurricane survivors). Values are means \pm 1 standard error. The trend lines were calculated via regression analysis. The regressions were not significant at $p = 0.05$ possibly because there are only four points, so regression statistics are not reported.

lag in significant reproduction by *Rhizophora* that could allow seedling survivors of the storm of any mangrove species to have an advantage in recovering a site where canopy has been totally or partially removed. Our data also show differences between two Florida estuaries in levels of outcrossing of this species, although whether or not this could be related to seedling survival and growth following colonization is not established.

The number of reproducing trees km^{-1} of shoreline in Charlotte Harbor was reduced by an order of magnitude following Hurricane Charley. Only a small portion of this reduced density of reproducing trees appears to be a result of actual tree mortality, because large numbers of trees survived along the shoreline (Proffitt and Milbrandt

field observations). We speculate that stress from leaf and branch removal and other damage may have resulted in the trees placing more effort into recovery and vegetative growth in the year following Charley. Loss of propagules floating at the time of Charley to upland areas because of wave and storm surge and damage of tree reproductive parts by Charley may have also contributed to low seedling recruitment.

Reduced reproduction by surviving trees was accompanied by low numbers of new recruits in permanent survey plots. Numbers of new recruits after the storm tended to be lower in plots where greater loss of the canopy occurred. A trend was seen of more new recruits to sites that had more pre-existing *Rhizophora* seedlings and greater dominance by *Rhizophora* prior to the storm. These data suggest that most of the new recruitment was from local trees within or near the plots and is consistent with the findings of limited dispersal noted in other studies (McGuinness 1997; Clarke and Kerrigan 2000; Sengupta et al. 2005). Initial regeneration in Charlotte Harbor forests will likely come from seedlings and saplings that survived Hurricane Charley as little reproduction and new recruitment was observed for the year following the storm. This interpretation must be viewed as tentative since data on elevation were not available at the time of this analysis although all plots had open access to the bay.

Those plots with large numbers of seedlings surviving the storm may regenerate a *Rhizophora*-dominated canopy quickly. Because of reduced reproduction and recruitment, plots with low numbers of surviving seedlings may be colonized by seedlings of other mangrove species. Eventual canopy dominance in these plots will then be determined by species-specific colonization rates (see similar outcomes in a Florida restoration site in nearby Naples Bay in Proffitt and Devlin 2005), effects of local physical and chemical parameters (Smith 1987; McKee et al. 1988; Ellison and Farnsworth 1993; McKee 1993, 1995; Feller et al. 2003), interactions with parasites (Sousa et al. 2003; Devlin 2004), effects of microhabitat generating fauna (Minchinton 2001), and competition with other mangroves (Proffitt and Devlin 2005). In the Naples Bay restoration site, *Rhizophora* did not significantly colonize most study plots, possibly because water access to the site was restricted to a single flushing channel and to periods of very high tides that topped a small berm surrounding much of the site on the seaward side, but both *A. germinans* and *L. racemosa* were able to colonize this site (Proffitt and Devlin 2005). This suggests that the much larger *Rhizophora* propagules have limited colonization potential from off-site areas when water avenues

are small or blocked, as can occur by vegetation downed by hurricanes.

Mortality of *Rhizophora* sentinel trees in Charlotte Harbor was not significantly size related (Charlotte Harbor (CH) pre-storm DBH = 3.7 ± 0.46 , $n = 4$, post-storm DBH = 2.8 ± 0.05 , $n = 2$), although our results may lack the statistical power to accurately assess size differences. Milbrandt et al. (2006) found that, overall, smaller trees suffered less damage than did larger ones. Our post-hurricane survey sites were not located in the area of severest disturbance, which may account for this difference.

Outcrossing rates of sentinel trees are 2.5 times greater in Charlotte Harbor than in Tampa Bay. Whether seedling survival and growth is enhanced by outcrossing remains unknown. No study has addressed the question of whether or not *Rhizophora* seedlings from outcrossing trees have greater survival and growth potential than seedlings from selfing trees. Field and greenhouse experiments have demonstrated that significant differences of substantial magnitude in growth occur among cohorts of seedlings from different maternal trees, even when the effects of propagule size is factored out as a covariate (Devlin 2004; Proffitt and Travis unpublished data). Although this is not a direct link to outcrossing, it is consistent with the possibility of genetic differences in seedling survival and growth. This might be a fruitful avenue for future research of red mangrove reproductive life history.

ACKNOWLEDGMENTS

The authors acknowledge funding from the U.S. Geological Survey Tampa Bay Project (C. E. Proffitt and S. E. Travis) and the Sanibel-Captiva Conservation Foundation's Core Research Program (E. C. Milbrandt) for portions of the work reported herein. C. E. Proffitt and S. E. Travis thank Carole McIvor, various staff of the U.S. Geological Survey for assistance with logistics and field work in Tampa Bay, and Ernie Estevez of Mote Marine Laboratory for assistance with 2003 surveys in Charlotte Harbor. E. C. Milbrandt thanks Brad Klement for assistance in the field. The authors also wish to thank J. N. "Ding" Darling National Wildlife Refuge for permission to establish and monitor forested study plots. The manuscript benefited substantially from comments from Donna Devlin, David Crewz, and two unidentified reviewers.

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Received, April 10, 2006
Revised, August 21, 2006
Accepted, August 27, 2006