

Bird Colonies Cause Seagrass Enrichment in a Subtropical Estuary: Observational and Experimental Evidence

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Colonies/roosts of piscivorous birds in Florida Bay, a subtropical estuary, concentrate nutrients by feeding away from their colonies/roosts and returning with food for young and to defaecate. Seagrass beds surrounding the colony islands were markedly different from those around similar islands that did not contain colonies. Seagrass standing crop was enhanced up to 200 m from bird colony islands compared with islands without colonies. The species of seagrass were also different at colonies, where *Halodule wrightii* and *Ruppia maritima* predominated in zones close to the colony islands. Around islands without colonies, only *Thalassia testudinum* was present.

Experimental bird perches placed to stimulate concentrated bird presence produced changes in adjacent seagrass meadows that were similar to differences between islands with colonies and those without. Over 5 years, seagrass standing crop increased around the experimental perches, and species dominance shifted from *T. testudinum* to *H. wrightii*. No similar changes occurred at control locations. These experimental results indicate that the bird concentrations are responsible for the observed differences in seagrass communities surrounding islands that contain colonies.

These enriched areas are significant to the seagrass ecosystem because many seagrasses in Florida Bay appear to be nutrient-limited. Demersal fish and invertebrate density and species richness have been shown to be a function of the seagrass standing crop and species composition, so the changes in seagrasses stimulated by localized bird concentrations have the capacity to alter the entire community structure.

Introduction

Historically, the southernmost tip of the Florida peninsula supported large populations of birds that roosted and nested colonially in Florida Bay and the adjacent coastal wetlands. While those bird populations have been drastically reduced (Frederick & Collopy, 1988), remnant populations show similar distribution patterns. These piscivorous birds forage

primarily in the Atlantic Ocean and adjacent Florida Bay or in the euryhaline habitats of the Everglades mangrove ecotone directly to the north or east of Florida Bay. They nest and/or roost colonially on mangrove islands. Defaecation by adults and nestlings concentrates nutrients at colony sites. Benthic communities in proximity to these colonies may be influenced by these nutrient additions.

Vertebrates have been implicated in the translocation and concentration of nutrients in many ecosystems. Reef-dwelling fish transport organic carbon, nitrogen, phosphorus and trace minerals from feeding areas to their resting sites on the reefs in both temperate and tropical environments (Bray *et al.*, 1981; Meyer *et al.*, 1983; Geesey *et al.*, 1984). The concentration and deposition of nutrients by colonial seabirds is responsible for the formation of guano deposits that have long been exploited by man for fertilizer. Bird colonies increase nutrient concentrations and phytoplankton productivity in the Barents Sea (Golovkin, 1967; Golovkin & Garkavaya, 1975), the productivity of mangrove trees in Florida (Onuf *et al.*, 1977), and intertidal benthic macroalgal production in the Baltic Sea and South Africa (Ganning & Wulff, 1969; Bosman *et al.*, 1986). Piscivorous seabird colonies also can affect terrestrial habitats: Lindeboom (1984) concluded that penguin excrement was the primary source of nitrogen for the Marion Island ecosystem, and Allaway and Ashford (1984) reported that seabirds were responsible for depositing about $0.7 \text{ kg dry weight m}^{-2} \text{ year}^{-1}$ of nutrient-rich excrement onto coral islands on the Great Barrier Reef, maintaining the forest that provides nesting sites for the colony.

Enhanced development of primary producers around bird colonies can have higher-level effects. The structures of the algal, invertebrate and avian communities on the shores of seabird islands are significantly altered by the presence of guano-producing seabirds (Bosman & Hockey, 1986, 1988). Leaves of mangrove trees on islands that support bird colonies are grazed at higher rates than leaves from nearby unenriched mangroves, presumably in response to greater nutritive value in the leaves from enriched areas (Onuf *et al.*, 1977).

The shallow water marine benthos surrounding many of the existing bird colonies in south Florida are dominated by seagrasses. Recent studies indicate that some subtropical seagrass meadows are nutrient-limited (Short *et al.*, 1985; Powell *et al.*, 1989). Because of the nutrient-limited nature of these subtropical inshore environments, the potential for the impact of nutrients from bird colonies is high. Densities of demersal invertebrates and fishes that inhabit seagrass meadows are positively correlated with seagrass density (Stoner, 1983; Sogard *et al.*, 1987), therefore nutrient inputs from bird colonies may be responsible for stimulating secondary production in seagrass systems.

In this study the impact of bird colonies on surrounding macrophytes was examined using two methods: (1) comparison of macrophyte communities adjacent to islands containing bird colonies with nearby islands that did not have colonies to test the hypothesis that there was increased macrophyte development due to bird colonies; and (2) experimental determination of the impact of birds on the benthic vegetation by creating bird roosting sites and quantifying the response of surrounding macrophytes during a 4-year period. This resultant experimental macrophyte community was compared to those associated with bird colonies.

Study area

Florida Bay is a large, roughly triangular, shallow embayment bordered on the north by the Florida mainland, on the south-east by the main line of Florida Keys, and on the west

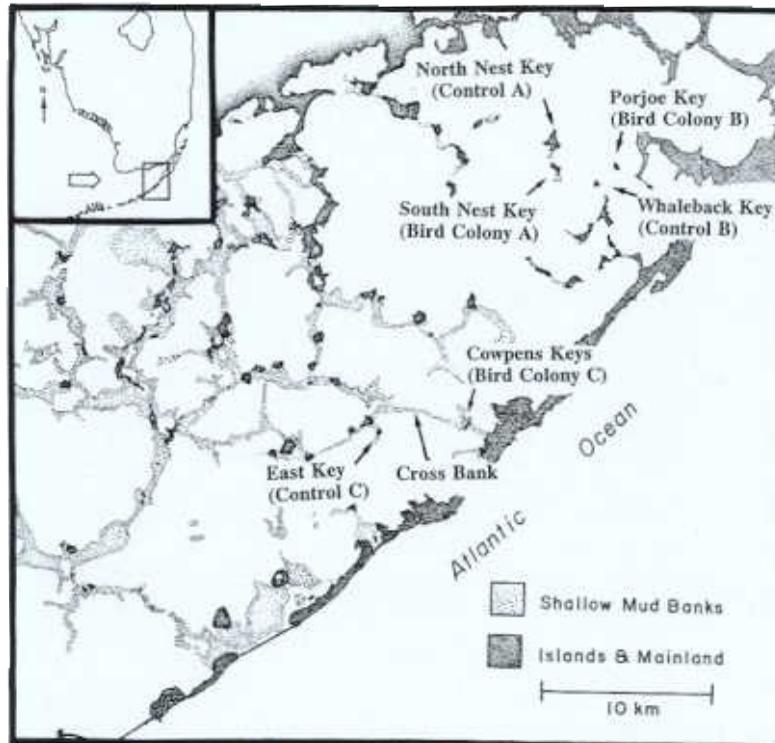


Figure 1. Map of eastern Florida Bay showing locations referred to in paper. Cross Bank was the site of experimental bird perch experiments.

by the Gulf of Mexico (Figure 1). The bottom of Florida Bay is generally covered by seagrass meadows that are dominated by *Thalassia testudinum*, intermixed with *Halodule wrightii* and local patches of *Syringodium filiforme* (Zieman *et al.*, 1989). The standing crop of seagrass decreases from the south-west to the north-east. This decrease follows a pattern of increasing isolation and variability caused by the restriction of water exchange due to a series of shallow anastomosing carbonate mud flats. The north-eastern portion of the bay has a depauperate seagrass flora which consists almost exclusively of *T. testudinum* (Zieman *et al.*, 1989). On the shallow banks of eastern Florida Bay, seagrass biomass has been shown to be nutrient-limited (Powell *et al.*, 1989).

The combined population of the principal piscivorous birds that roost or nest on Florida Bay mangrove islands is estimated to be between 35 000 and 40 000 (Table 1). In addition, an estimated 1500 to 2000 frugivorous white-crowned pigeons, *Columba leucocephala*, forage in upland hammocks and nest on mangrove islands in north-east Florida Bay (Reed Bowman, pers. comm.).

Methods

Comparison of bird and non-bird islands

Relatively large breeding bird colonies exist on three islands in north-eastern Florida Bay; numerous additional islands are used by smaller numbers of nesting birds and as communal roosts. Two of the colony islands, South Nest and Porjoe Keys, and one small

TABLE 1. Piscivorous bird populations that nest or roost on Florida Bay mangrove islands. Data from pers. obs. (G.V.N.P.) and pers. comm. (Alexander Sprunt IV)

Species	Population estimate
American white pelican (<i>Pelicanus erythrorhynchos</i>)	3000
Brown pelican (<i>Pelecanus occidentalis</i>)	2500
Double-crested cormorant (<i>Phalacrocorax auritus</i>)	6000
Magnificent frigatebird (<i>Fregata magnificens</i>)	500
Wading birds	
Great blue/white heron (<i>Ardea herodias</i>)	2000
Great egret (<i>Casmerodius albus</i>)	3000
Small waders (<i>Egretta</i> spp.)	4000
White ibis (<i>Eudocimus albus</i>)	6000
Roseate spoonbill (<i>Ajaia ajaja</i>)	1200
Gulls and terns (<i>Laridae</i>)	8000

TABLE 2. Population estimates of species using the three bird colony islands. Estimates from pers. obs. (G.V.N.P.) and counts (*) from Bjork and Powell (unpubl. data). See Table 1 for scientific names

Colony island	Species	Population estimate (individuals)
Bird colony island A	Magnificent frigatebird	50
	Brown pelican	135
	Roseate spoonbill	60*
Bird colony island B	Double-crested cormorant	200
	Magnificent frigatebird	50
	Roseate spoonbill	160*
	Small waders	600*
	White ibis	200*
Bird colony island C	Brown pelican	75
	Magnificent frigatebird	70
	Brown pelican	25

roost island, a mangrove clump in the Cowpens Keys, were chosen for analysis of the surrounding benthic vegetation (Figure 1). For clarity, these islands will be referred to as bird colony islands A, B, and C, respectively, for the remainder of this paper. Bird colony islands A and B are heavily used by magnificent frigatebirds (*Fregata magnificens*), double-crested cormorants (*Phalacrocorax auritus*), brown pelicans (*Pelecanus occidentalis*), and wading birds, while bird colony island C is used as a roost by frigatebirds and pelicans (Table 2). Each of these islands is vegetated by mangroves (*Rhizophora mangle* and *Avicennia germinans*) growing over largely submerged lands.

The benthic vegetation surrounding the nearest mangrove island of similar size and physiognomy to each of the three bird islands, but without a bird colony, was surveyed as a control site. The islands chosen as controls were North Nest Key, Whaleback Key, and a small, unnamed islet next to East Key (Figure 1). These islands will be referred to as control islands A, B, and C, respectively, for the rest of this paper.

The benthic vegetation near each island was surveyed along transects set up perpendicular to the shoreline. For each island, three transects were placed randomly in a 100-m stretch of shoreline near the maximum concentration of nests on the bird colony islands, and at the equivalent location on each of the control islands. Samples were taken every 10 m along the transects using a 15-cm core tube inserted about 35 cm into the sediment or to the bedrock if the sediment was shallower than 35 cm. Water and sediment depth were measured at each core location. Core samples were washed free of sediment, the above-ground macrophyte tissues separated by species, and the shoots of each seagrass species counted. All plant samples were acid-washed in dilute (10% v/v) HCl to remove carbonates and epiphytes, oven-dried (< 100 °C) to constant weight, and weighed.

Bird perch experiments

Field observations indicated that aquatic birds made regular use of any available perches on the shallow banks of Florida Bay. While roosting, these birds defaecated into the water below releasing large quantities of nitrogen and phosphorus per unit area (Powell *et al.*, 1989). To test the effects of bird faeces on seagrass distribution and density, perches were placed in shallow water where no alternative roosts were available. Five experimental perches, consisting of blocks of wood (5 cm × 10 cm × 10 cm) attached to 1.2-cm PVC pipe were placed at 600-m intervals along Cross Bank, a shallow (5 to 20 cm deep) seagrass-stabilized carbonate mud flat which runs between Cowpens Key (bird colony island C) and East Key (control island C; Figure 1). The size of the wooden blocks allowed only a single bird to perch at each site. A pointed 1.2-cm PVC pipe which could not be used as a perch by birds was placed 10 m from each of the five experimental perches as control stakes that provided the same presence of the stake in the water as the experimental perch. Bird use of the perches was determined by 29 surveys (20 during daylight and nine at night) performed in March–April, July–August and October–November 1984. Surveys were made from a boat with the aid of a spotlight at night. The species roosting on each stake was identified and recorded.

At the start of these experiments in the fall of 1983, four permanent 10 cm × 10 cm quadrats for non-destructive plant sampling were placed at the perch and control stakes at each of the five experimental stations. The quadrats were placed 20 cm and 40 cm from the stake along a line parallel to the direction of water flow across the bank. Seagrass standing crop and short shoot density were also sampled from four replicate 10 cm × 10 cm quadrats at the bird perch and control stake at three of the five stations. Only three of the five stations were sampled due to the observed homogeneity of the bank top. All of the above-ground plant tissue within these standing crop quadrats was harvested, separated by species, acid-washed in dilute HCl and oven-dried. Measurements of short shoot density and seagrass standing crop at each of the five stations were repeated in late October/early November in 1984 and 1987.

Results

Comparison of bird and non-bird islands

Mud banks and islands in Florida Bay are sediment accumulations on an almost flat bedrock platform (Zieman *et al.*, 1989). Mean water level was about 2 m over this bedrock platform at all of the islands studied in this paper. Sediment profiles sloped from up to 2 m thick at the edge of the islands to 30 cm or less between 40 and 150 m from the islands. Islands with bird colonies tended to have less steep slopes than control islands (Figure 2).

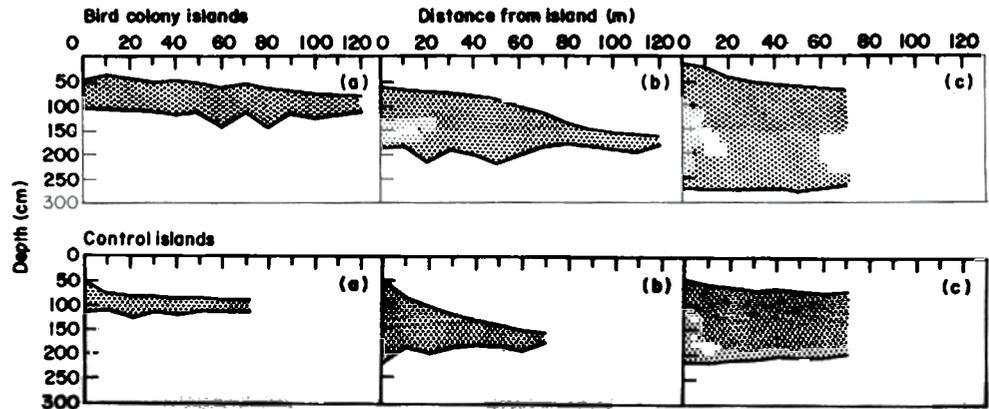


Figure 2. Comparison of sediment accumulation and water depth (—) at bird colony and control islands. The shaded area in each graph represents sediment accumulation over limestone bedrock.

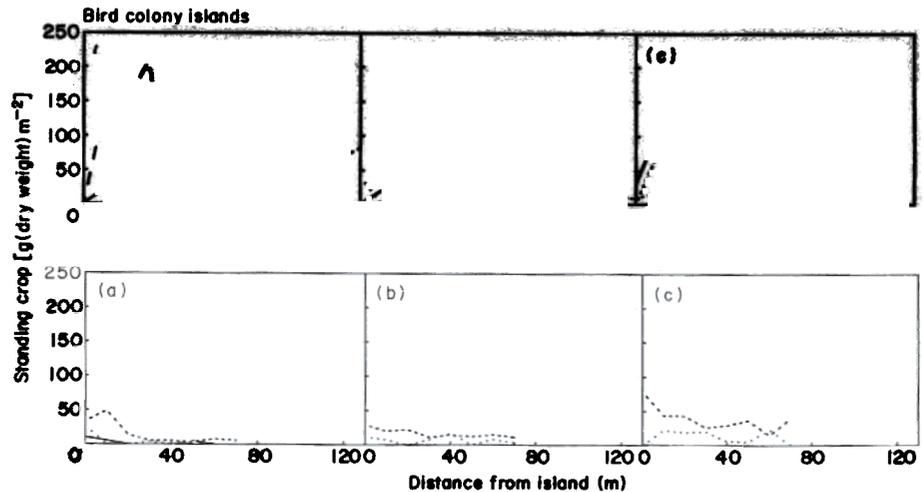


Figure 3. Comparison of standing crop of the seagrasses and macroalgae at bird colony and control islands. Each point is the mean of three cores. ... Macroalgae; --- *Ruppia*; — *Halodule*; ---- *Thalassia*.

Seagrass meadows adjacent to the three bird colony islands differed markedly from the meadows surrounding control islands both in species composition and total standing crop of macrophytes. At the two largest bird colony islands (A and B), there was an area extending 10–20 m from the islands devoid of seagrasses. Beyond that void, seagrass standing crop at all three bird colony islands was at least an order of magnitude greater than the control islands. Standing crop at bird colony islands was enhanced over controls up to 40 m from the small colony islet and up to 200 m from the big colony islands (Figure 3). Beyond these outer limits of enhancement, sediment depth was very shallow (Figure 2). Lack of sufficient sediment for seagrass development may limit the outer edge of the enhanced zone.

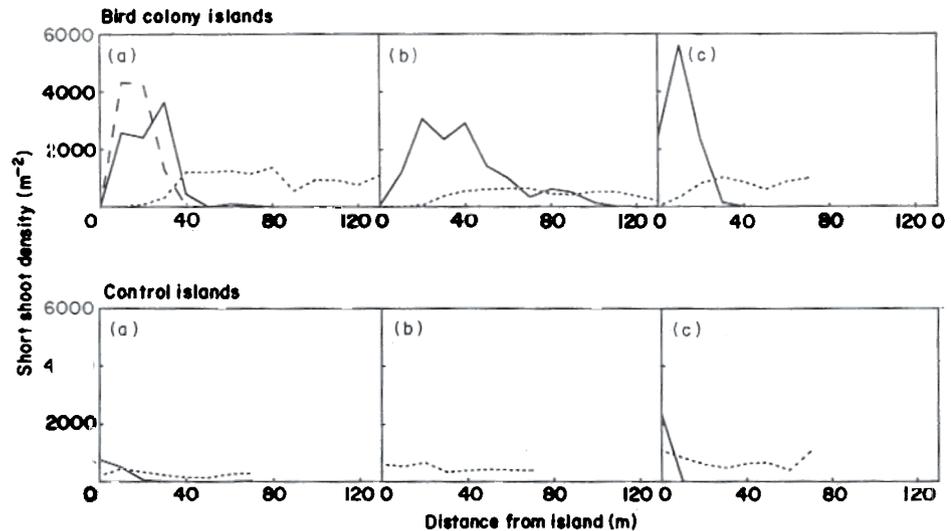


Figure 4. Comparison of short shoot density of the seagrasses at bird colony and control islands. Each point is the mean of three cores. --- *Ruppia*; — *Halodule*; ··· *Thalassia*.

Species composition of seagrass communities surrounding all of the control islands was limited to *T. testudinum* with occasional small ($<0.5 \text{ m}^{-2}$) low-density patches of *H. wrightii* located directly adjacent to the island under the overhanging mangroves. In contrast, the bird islands showed strong zonation of seagrass species (Figure 3). At bird colony island A (Figure 3), a 15- to 20-m wide band of *Ruppia maritima* was present adjacent to and seaward of the 10–20-m wide bare area. *R. maritima* was also observed in a similar location at bird colony island B, but not within the randomly selected transects due to its patchy distribution. Extensive surveys of the seagrasses of Florida Bay show that *R. maritima* is historically restricted in distribution to the less saline northern fringe of the bay (Zieman *et al.*, 1989) and only three additional sites, all of which are bird colonies (Cowpens south island, Arsnicker Key and Buoy Key) in central Florida Bay. *H. wrightii* was dominant in a 10–20-m wide band immediately beyond the bare area at bird colony island B and a similarly broad band beyond the *R. maritima* at bird colony island A. At bird colony island C, there was no bare area and the 10–20-m wide band of *H. wrightii* extended from the edge of the island.

A comparison of the density of seagrass short shoots at bird colony and control islands showed a similar pattern of much greater *H. wrightii*, and where present, *R. maritima*, density at bird colony island than control islands (Figure 4). At bird colony island A, the density of *T. testudinum* short shoots was substantially greater than at the control island A, but at the other two bird colony/control pairs there was no difference in *T. testudinum* density. In contrast to *H. wrightii*, the increase in *T. testudinum* standing crop around bird colony islands appears to be due to the presence of more robust short shoots rather than more short shoots.

Bird perch experiments

Single birds consistently roosted on the experimental perches both day and night. During 20 daylight surveys, roost stakes were occupied 81% of the time, primarily by two species,

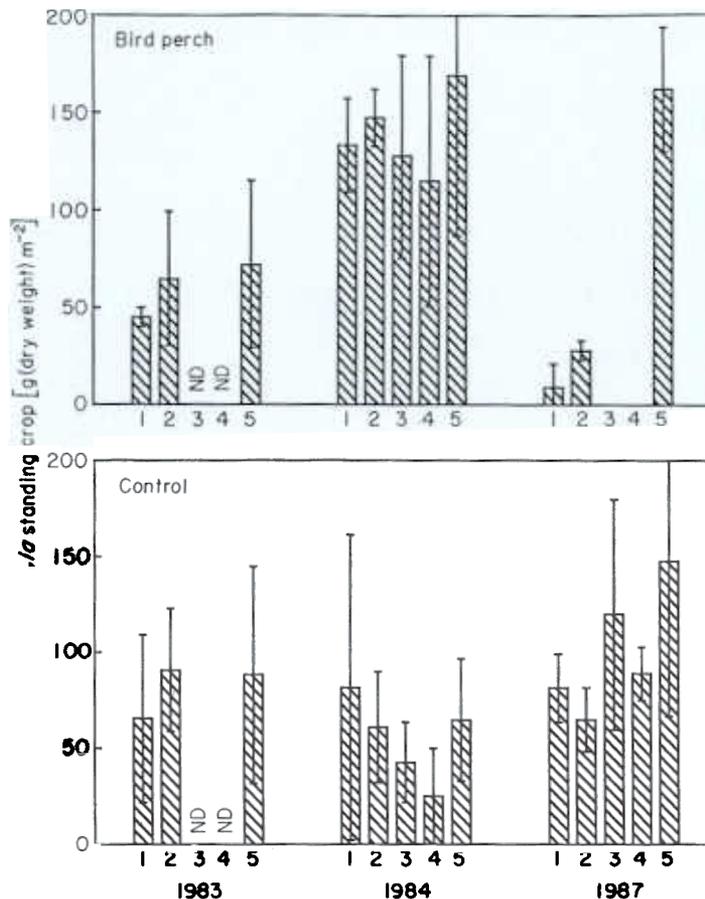


Figure 5. Standing crop of *Thalassia testudinum* at the experimental bird perches and control stakes in 1983, 1984 and 1987. Data from five stations in each year. Error bars indicate 95% confidence interval.

royal tern (*Sterna maxima*) and double-crested cormorant. After dark, birds (primarily royal terns) were present on the experimental stakes 87% of the time. No birds roosted on the control stakes.

Seagrass standing crop and short shoot (ss) density at the start of these experiments indicated that the top of Cross Bank was covered by a homogeneous *T. testudinum* meadow. This meadow had a standing crop of 73.8 ± 2.5 g (dry weight) m^{-2} (\pm SE, $n = 6$; Figure 5) with an average of 610 ± 50 ss m^{-2} ($n = 10$). There was very little *H. wrightii* present and there was no measurable *H. wrightii* in the standing crop samples (Figure 6).

There was some interannual variation in seagrass standing crop at the control stakes, but no discernible trends. For the 5 years of the study, we measured an average *T. testudinum* standing crop of 65.7 ± 9.8 g (dry weight) m^{-2} ($n = 5$). The maximum average standing crop at the controls was 100.5 g (dry weight) m^{-2} in 1987, and the minimum was 48.0 g (dry weight) m^{-2} in 1986. The coefficient of variation for the standing crop data was 33.4%.

In contrast to the control stake data, there were clear trends in the bird perch standing crop. Within 1 year of the placement of the bird roost stakes, there was a doubling of the *T.*

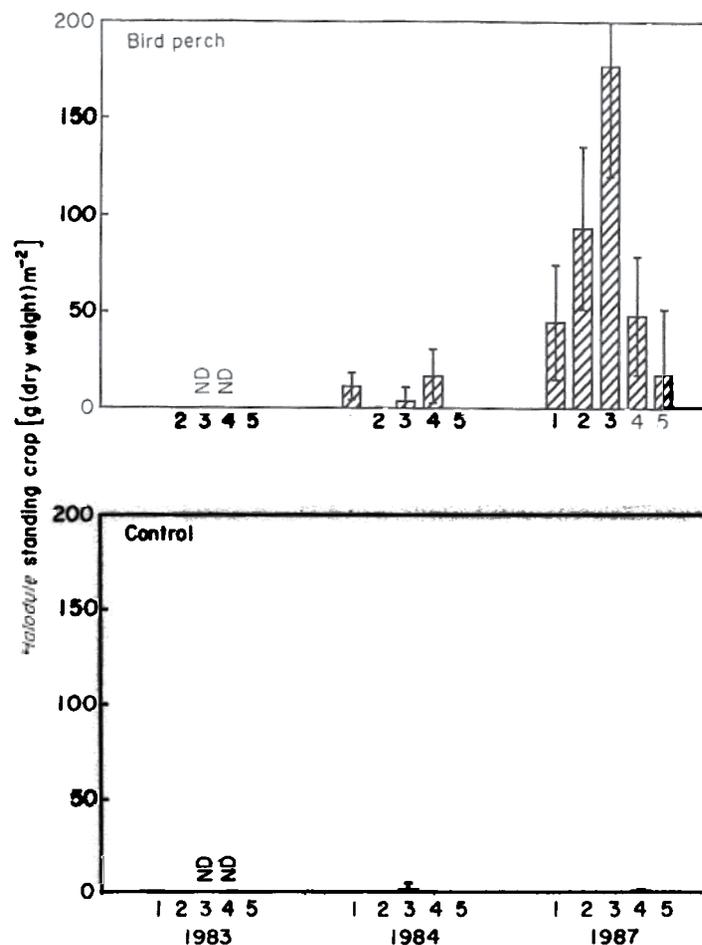


Figure 6. Standing crop of *Halodule wrightii* at the experimental bird perches and control stakes in 1983, 1984 and 1987. Data from five stations in each year. Error bars indicate 95% confidence interval.

testudinum standing crop around the stakes (Figure 5). Also within a year, low densities of *H. wrightii* were present at four of five experimental perches. By the fourth year, these four sites were dominated by *H. wrightii* (Figure 6). At this time, *T. testudinum* was completely absent from two of the four sites while it declined by an order of magnitude at two other sites. In contrast, at the fifth site where *H. wrightii* was absent, *T. testudinum* standing crop remained high (Figure 5).

Short shoot density comparisons before and after stake placement were similar to comparisons of bird colony and control islands, with relatively stable numbers of *T. testudinum* short shoots and major increases in the number of *H. wrightii* short shoots. The short shoot density of *T. testudinum* increased only slightly over the first year of the experiment when the biggest increases in standing crop were observed (short shoot density = $575 \pm 80 \text{ m}^{-2}$ in 1983, $630 \pm 60 \text{ m}^{-2}$ in 1984). In contrast, there was a 2 order of magnitude increase in *H. wrightii* short shoot density from $35 \pm 31 \text{ m}^{-2}$ in 1983 to $5050 \pm 2101 \text{ m}^{-2}$ at the four sites where the species was present 4 years later.

Discussion

The seagrass communities surrounding bird colony islands were substantially different from the communities surrounding similar nearby control islands that did not support bird colonies. The benthic vegetation around control islands was similar to that of the banks throughout north-east Florida Bay in terms of species composition (primarily *T. testudinum*) and standing crop and short shoot density (Zieman *et al.*, 1989; Powell *et al.*, 1989). Around islands colonized by birds, however, there was greater seagrass biomass and a strong zonation of species. Both *R. maritima* and *H. wrightii* exhibited lush growth and were dominant in zones near the bird islands. Further from the bird islands, *T. testudinum* biomass was enhanced over the biomass near the control islands in a zone extending up to 200 m from the shores of the islands.

The correspondence of increased seagrass standing crop and different zonation patterns with islands that support bird colonies does not prove that the presence of the bird colonies caused these differences, because birds could choose to locate colonies on islands surrounded by a particular type of seagrass meadow. However, the experimental bird perches on Cross Bank tested whether the addition of nutrients from roosting bird excrement would produce the macrophyte enrichment observed at bird colonies. Causing a bird to perch consistently at the same location rapidly led to changes in the seagrass beds surrounding that location. Not only was the biomass of seagrass around the perches increased over the surrounding seagrass bed, but at four of the five sites the dominant seagrass species surrounding the perch changed from *T. testudinum* to *H. wrightii*. The lack of any changes around the control stakes indicates that the stake in the water was not responsible for the observed changes at the experimental bird perches. After 1 year of nutrient additions from bird faeces, the average standing crop of *T. testudinum* around the bird perches [124.3 ± 67.9 g (dry weight) m^{-2}] was similar to that of the high-density band of *T. testudinum* surrounding bird colonies (Figure 5). At the end of 4 years, the standing crop of *H. wrightii* at the four stakes where it was present [90.6 ± 61.6 g (dry weight) m^{-2}] was again similar to the standing crop in the *H. wrightii* zone at the bird colonies (Figure 6).

In a previous study of the seagrass beds on Cross Bank, the nutrient input from bird faeces was quantified: the loading rates of nitrogen and phosphorus around artificial bird perches were 21.7 and 1.2 g m^{-2} year⁻¹, respectively (Powell *et al.*, 1989). That study concluded that seagrass biomass could be increased in an area by fertilization of the seagrass beds by bird faeces. The similarity between the seagrass meadows around experimental bird perches and the seagrass meadows around bird colony islands strongly suggests that it was the addition of nutrients through bird defaecation at bird colonies that was responsible for the observed differences in macrophyte communities of bird and non-bird islands.

The replacement of *T. testudinum* by *H. wrightii* at four of the five experimental bird roosts was in contrast to the usual secondary successional sequence in Caribbean seagrass meadows. Normally, *H. wrightii* is the pioneer and is ultimately replaced by the climax species *T. testudinum* (den Hartog, 1971; Patriquin, 1975; Zieman, 1982). Apparently, in the conditions produced here, high nutrient loading and relatively low energy, the pioneer species *H. wrightii* is favoured over *T. testudinum*. In the absence of high rates of nutrient loading, *T. testudinum* was the dominant species.

The zonation of seagrasses around bird colony islands may be partially explained by the predominance of *H. wrightii* over *T. testudinum* in areas of nutrient enrichment. If we

assume that the nutrients supplied by birds are deposited on the islands, then there would be a decrease in the nutrient-loading rate as the radial distance from the island increased. At some distance from the island, the nutrient supply would not be sufficient to favour *H. wrightii* over the usual climax species *T. testudinum*. The fact that the zone of *H. wrightii* dominance was closer to the islands than the zone of *T. testudinum* dominance in all cases (Figures 3 and 4) supports this hypothesis.

The presence of zones dominated by *R. maritima* at the bird colony islands A and B closer to the shores of the islands than the *H. wrightii* zones suggests that high nutrient loading favoured growth of *R. maritima*. Previous work has suggested that *R. maritima* distribution is controlled by its intolerance of high salinity (Phillips, 1960; Zieman, 1982), but around these bird colony islands all of the benthic vegetation was routinely subjected to hypersaline conditions (pers. obs.). Therefore, the inability of *R. maritima* to survive in low-nutrient environments may also be an important factor controlling the distribution of this species.

The zone devoid of seagrass next to the two islands with large bird colonies may have been a result of very high nutrient-loading rates that promoted rapid growth of phytoplankton and periphyton. Competition for light with microalgae, both planktonic and epiphytic, has been implicated in seagrass declines in polluted environments (Zieman, 1975; Orth & Moore, 1983; Cambridge & McCoomb, 1984). While the microalgal communities around these colony islands were not quantified, there was a thick coating of benthic microalgae covering the mud in the areas devoid of seagrasses near the bird islands.

The extent of influence exerted by historic bird colonies on seagrass meadows in Florida Bay, and thus on the Florida Bay ecosystem in general, is potentially very large. The results of the bird perch experiments demonstrated that the presence of a single bird roosting consistently at the same location can alter the species composition and increase the biomass of a small patch of the surrounding seagrass bed. The impact of thousands of birds that nest or roost at night in Florida Bay in scattered locations (Table 1) is large. These birds once numbered in the hundred of thousands, so that this bird effect was historically orders of magnitude greater than at present. The implications of the declines in the bird populations throughout coastal southern Florida on the inshore ecosystems is undoubtedly significant. Because the majority of these birds forage in habitats generally outside of the roosting area, their effect is a net transport of nutrients into the mangrove-seagrass interface, areas that are nursery and recruitment areas for fish and invertebrates in Florida Bay (M. B. Robblee, unpubl. data; Thayer *et al.*, 1987). Furthermore, the strong response of *H. wrightii* to bird enrichment is of particular ecological importance because areas dominated by this seagrass are the primary habitat for recruitment of larval pink shrimp *Penaeus duorarum* (Costello *et al.*, 1987). In addition to the large economic importance of pink shrimp, they are a major food item for the fish (Rutherford *et al.*, 1982, 1983) and wading birds (G. V. N. Powell, unpubl. data) of Florida Bay.

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