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# *Summary* & *Conclusions*

Macroalgae in Biscayne Bay, Florida, seagrass habitats were investigated. These *Thalassia testudinum* (turtlegrass) dominated habitats occur throughout the Bay, along a gradient of stressors from point-source canal inputs, as well as diffuse terrestrial runoff. The proposed alterations in the management of these point-source discharges with regional landscape restoration of the adjacent Everglades system may have consequences for the seagrass habitats in Biscayne Bay.

Seagrass systems are ecologically important as they provide habitat, stabilize sediments, and are the dominant primary producers where they occur. In addition to seagrass plants, three functional groups of macroalgae contribute to system structure and function. These are drift algae, rhizophytic algae, and seagrass epiphytes. Drift algae as a group are comprised primarily of rhodophytes, and occur as free-floating mats that are vagile. Rhizophytic algae are exclusively chlorophytes that possess a root-like structure enabling them to anchor in soft sediments; many are calcified. Epiphytes are a heterogeneous assemblage of filamentous and encrusting algae that occur on seagrass blades. Both drift algae and epiphytes have the potential to reduce incident light and

thereby shade the seagrass. This may occur especially under conditions of elevated nutrients that favor algal growth.

The aims of this dissertation were to:

- describe the algal community along the stress gradient across Biscayne Bay;
- describe the seasonal dynamics of the three functional groups;
- determine the responses of the macroalgae to abiotic variables including light, temperature, salinity, and nutrients, as well as the importance of flow to drift algae.

The potential use of macroalgae as indicators of seagrass habitat health in relation to canal discharge stressors was the first topic investigated. Three different stress regimes related to canals were identified. Canal sites were located in close proximity to canal mouths, within the low-salinity discharge plume. These sites were characterized by low, but highly variable salinity, and high nitrogen loadings. Sheet-flow sites were also found along the mainland coastline, and were selected to be typical of terrestrial inputs prior to the advent of canal construction. Oceanic sites were located far from the mainland, and were selected as control sites to compare and contrast the effects of terrestrial inputs on algae in seagrass systems. The control sites had high, near constant salinity, and low nutrient concentrations typical of tropical waters.

The seasonal and spatial biomass-dynamics of the three functional groups of algae showed distinct changes in composition of the algal community along the stress gradient posed by canals (Fig. 1). Based on four years of sampling (1996-1999), drift algae were most commonly found at canal-influenced sites (20-100 g dry wt·m<sup>-2</sup>), while rhizophytic calcareous green algae were more abundant at sites with oceanic salinity (5-50 g dry wt m<sup>-2</sup>). Epiphytes were the most abundant group by biomass (50-120 g dry wt·m<sup>-2</sup>) and were distributed about evenly across the three types of study sites, with the highest abundance generally occurring at the oceanic sites. Composition of the epiphyte community changed from filamentous/diatom dominated in the canal sites to calcareous-crustose forms in the oceanic sites.

Multivariate analyses showed that the composition and abundance of the algal community changed significantly along the stress gradient. Drift algae common at the canal sites were dominantly the red algal genera *Laurencia*, *Chondria*, and *Polysiphonia*. In contrast in the oceanic sites the rhizophytic algae dominated, with *Halimeda* and *Penicillus* the notable genera. There was a commonality in species composition among sites and the differences between the sites were a matter of degree (abundance) rather than of kind (composition), which is exactly the kind of relationship that is to be expected of changes in community composition along a gradient.

Seasonal patterns exhibited by the three functional groups differed also. Drift algae were most abundant during the spring, with a decline in biomass during the summer. The rhizophytic algae in contrast had highest biomass during the summer and least during the winter period. Crustose-calcareous epiphytes were abundant year-round at the oceanic sites, while at the canal-sites epiphytes became more abundant in the dry season, when filamentous forms were prevalent.

These seasonal responses may be in part driven by light and temperature changes over the course of a year. In Biscayne Bay, mean daily benthic irradiance levels ( $I_z$ ) ranged from 300-900  $\mu\text{mol}\cdot\text{photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , with maximum light levels in April-May, followed by a decline as increased cloud cover in summer resulted in a reduction in light levels. Minimum irradiance levels were reported in December. Attenuation coefficients ( $k$ ) ranged from 0.3 at the oceanic sites to 0.47 at the canal sites, a result of increased color, suspended matter, and phytoplankton.

The responses of the macroalgae to light levels were determined with photosynthesis-irradiance (P-I) curves. Saturation levels ( $I_k$ ) for the drift algae were in the range 200-300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , for the rhizophytic algae 100-300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , and epiphytes had the lowest light saturation levels at 120-150  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . These results indicate that these algae may rarely be light-limited in the shallow-water sites studied.

Mean daily water temperatures in Biscayne Bay were between 18-32°C over the course of a year, with a range of 12-35°C. Winter cold fronts can rapidly reduce minimum temperature by up to 5°C in a matter of a day or less. The upper temperature tolerance limits for growth and photosynthesis were about 32-34°C in all the algae studied. Drift algae and epiphytes had a thermal tolerance range of 5-30°C, while rhizophytic algae preferred 12-34°C. This is reflected in the seasonal abundance of these algae.

Different functional groups of algae responded to these variations in seasonal light and temperature conditions with unlike strategies. Drift algae and epiphytes grew and photosynthesized at faster rates in winter (dry season), when water temperatures were cooler. In contrast, the rhizophytic genera *Halimeda* and *Penicillus* had higher photosynthetic rates in summer (wet season), with dormancy during the winter. From experimental results it appears that water temperature was the more important factor than light influencing seasonal growth and abundance.

Spatial differences in algal community structure may occur because of the salinity gradients across Biscayne Bay from canals that drain large portions of Dade County, South Florida. Salinity varies considerably on a short time-scale of hours, as a result of discrete, pulsed freshwater discharge events from point-sources, at the canal mouths. This management practice is thought to have caused major changes in the salinity regime and the resultant biota in the Bay.

During the wet season large areas of the south-western Bay experience low salinities (<20 psu). Canal discharges of freshwater occur as pulses and can reduce the salinity of the surrounding Bay-water to between 7-25 psu. Additionally, stratification of the water column can occur, with a lens of low-salinity water overlying higher salinities at the benthos. Salinity at the canal sites ranged from 0-40 psu with average values varying between 10-30 psu on a seasonal basis. This was lower than the sheet-flow sites, where seasonal average salinity ranged from 25-30 psu. Contrast this with the oceanic-influenced areas along the eastern side of the Bay, where a higher mean salinity (35 psu) occurred.

The effect of the annual mean (20 psu) and average low (10 psu) salinities in canal-influenced areas of Biscayne Bay, on the growth and photosynthesis of representatives of three functional groups of algae was studied. Salinity response curves were determined for drift, rhizophytic, and epiphytic algae exposed to static salinity regimes of 10, 20, and 35 psu. Photosynthesis was measured after 24 hrs (short-term stress response) and growth over one week (long-term stress response). Drift algae and epiphytes were euryhaline with positive net photosynthesis and growth from 5-10 to 35+ psu, while rhizophytic algae were stenohaline and preferred salinities of 15-35+ psu. In addition to growth, health of the rhizophytic algae was determined based on visual criteria after one-week exposure. These measures confirmed the stenohaline tolerance limits of the rhizophytic algae indicated by the photosynthesis and growth results.

Spatial differences were found in the low-salinity tolerance between algae of the same species collected from oceanic and canal-influenced parts of the Bay. Both *Laurencia* (drift algae) and *Penicillus* (rhizophytic algae) from the canal sites had better low-salinity tolerances than did their counterparts collected from the oceanic sites. In addition to this spatial difference on the adaptation of these species to low-salinity stress there appeared to be seasonal acclimation in the canal population, with better low-salinity tolerance occurring in drift algae during the wet season.

Dynamic salinity pulse experiments using drift algae subjected to low salinities for 4 to 24 hr showed that longer duration, low-salinity events were more stressful than shorter pulses. Drift algae exposed to salinities of 10 psu grew poorly in both long and short duration exposures. At salinities of 20 psu, however, algae in the 24 hr exposure were more stressed than algae in the 4 hr exposure, as indicated by the reduced growth rates.

The euryhaline salinity tolerance of drift and epiphytic algae allows these functional groups to persist in the canal-influenced sites, even during periods of low-salinity pulses that occur with canal discharges. In contrast, the stenohaline character of the rhizophytic algae may in large part be responsible for the exclusion of this group from canal sites.

Elevated nutrient loadings co-occur with low-salinity waters entering Biscayne Bay from canal discharges. This high-nutrient, low-salinity water mixes with low-nutrient, high-salinity oceanic water, resulting in a gradient across the Bay. Primarily nitrogenous nutrients, especially ammonium, are entering the Bay in high concentrations (20-50  $\mu\text{M}$ ) via canals discharging runoff from the South Dade Agricultural Area. Phosphates also enter from terrestrial runoff along the coastline, but are generally found at low concentrations ( $<0.1 \mu\text{M}$ ) throughout the Bay. At all sites studied, nutrient concentrations were higher during the wet season, when terrestrial runoff and canal inputs bring nutrients into the Bay, than during the dry season.

Tissue N:P ratios may reflect the integrated nutrient regime available to the algae. Algae collected from canal sites had higher N:P ratios than those from oceanic sites, indicating higher N availability. Based on an N:P ratio of 30:1, drift and rhizophytic algae appeared to be P-limited in both canal and oceanic sites. This agrees with the generally reported P-limitation arising from sequestration of P into tropical carbonate sediments.

Drift algae and epiphytes were exposed to increasing nutrients (N+P) in microcosm experiments and grew rapidly in winter but not summer, while the opposite was true for rhizophytic algae. Growth rates ranged from 1.5%  $\text{day}^{-1}$  in the rhizophytic algae, 5%  $\text{day}^{-1}$  in the drift, to 30%  $\text{day}^{-1}$  for epiphytes. Tissue-nutrient concentrations indicated that drift algae and *Halimeda* were P-limited, while *Penicillus* was N-limited.

To determine the limiting nutrient, drift and rhizophytic algae were grown under three nutrient enrichment treatments: +N, +P, and +NP; growth was compared to plants in an un-enriched control. In both functional groups, nutrient uptake rates averaged 10-15  $\mu\text{M}$  P and 15-40  $\mu\text{M}$  N over 24 hours. The addition of P did not stimulate uptake of P, whereas the addition of N enhanced the uptake of both N and P. Uptake rates were higher at salinities of 20-35 psu than at 10 psu. Photosynthesis and growth in both functional groups were stimulated primarily by the addition of N, but not P. Photosynthesis and growth increased with salinity, and were further stimulated by the addition of nutrients

(primarily N). Tissue nutrient contents ranged from 1-4% N and 0.05-0.2% P, with N:P elemental ratios between 30:1 to 600:1. Tissue N:P ratios indicated drift algae and *Halimeda* were P-limited, while *Penicillus* was N-limited, suggesting that there may be differences in nutrient requirements among genera of rhizophytic algae that are filling a similar ecological niche.

The effects of seasonal light and temperature, as well as salinity stress, were more important in determining the photosynthesis and growth responses of the three functional groups of algae than was the addition of N and/or P to the external medium. The addition of nitrogen was the primary nutrient responsible for stimulating growth in both the drift algae and the two rhizophytes, although tissue nutrient contents indicated P-limitation. Low-salinity stress did appear to be reduced by the addition of nutrients, indicating that elevated nutrients in canal waters may be important to reduce the negative effects of low-salinity stress on macroalgae in the discharge plume.

In addition to the availability of elevated nutrients near canals, the hydrodynamic flow regime within Biscayne Bay may be an important factor influencing the spatial distribution of drift algae. High-energy sites are less likely to accumulate drift biomass compared to low-energy, depositional environments (Fig. 1). Oceanic inlets are areas of high tidal-flows, 50-100  $\text{cm}\cdot\text{s}^{-1}$ , while canal sites typically had flows of  $<10 \text{ cm}\cdot\text{s}^{-1}$ . Drift algae require flow velocities of 10-20  $\text{cm}\cdot\text{s}^{-1}$  to be transported by currents. Four experiments were performed to address a series of hypotheses related to the transport of drift algae by currents.

The composition and abundance of drift algae entering through Bear Cut, one of a number of inlets allowing exchange between the Bay and the Atlantic Ocean, were determined seasonally. Approximately 0.5-1 ton wet weight of algal material is transported on tidal currents daily through these inlets into the Bay. Similarity in the composition of drift algae entering via Bear Cut compared to canal sites was 50% at the genus level, and difference in species abundance was even greater. It, therefore, appears unlikely that drift

algae originate from outside the Bay, rather, *in situ* origin in nearby hard-bottom areas and continued growth of epiphytes after seagrass senescence is the more likely provenance of the drift algae found at the canal sites.

The persistence time of drift algae in three flow regimes was recorded, with high flow regimes ( $50 \text{ cm}\cdot\text{s}^{-1}$ ) immediately entraining drift, intermediate flow speeds ( $20 \text{ cm}\cdot\text{s}^{-1}$ ) resulting in exponential removal of the drift in 5 days, and negligible flows ( $0 \text{ cm}\cdot\text{s}^{-1}$ ) allowing drift algae to persist for 30 days in summer and 45 days in winter.

The current speeds required to transport drift algae were determined both *in situ* and in an experimental flume, with transport rates between one-half to two-thirds of the current velocity. Seagrass substrate type was found to influence transport speed significantly, with more “complex” seagrass habitats retaining drift clumps, unless exposed to very high flow-speeds ( $50 \text{ cm}\cdot\text{s}^{-1}$ ). At high flow speeds ( $50 \text{ cm}\cdot\text{s}^{-1}$ ) the seagrass blades bend over and provide little resistance to the passage of drift algae. At intermediate flow speeds ( $20 \text{ cm}\cdot\text{s}^{-1}$ ) entangling of the drift algae creates significantly slower net transport speeds, with alternating periods of entrainment into the water column and transport, followed by settling out of the drift clumps.

The probability of drift algae remaining within a permanent  $1\text{m}^2$  quadrat at six field sites was determined and found to be higher in the quiescent canal sites than the high-energy oceanic cuts, where the probability of a quadrat remaining free of drift algae was higher. In canal sites where flows were typically  $<10 \text{ cm}\cdot\text{s}^{-1}$  drift algae had a probability of persistence of 0.6-0.8, whereas at the high energy oceanic inlets flows of  $50 \text{ cm}\cdot\text{s}^{-1}$  resulted in low persistence probabilities ( $<0.2$ ).

To synthesize all these data, a community model was developed to examine the dynamics of the three functional groups of macroalgae in seagrass systems in Biscayne Bay. The model was developed to augment a pre-existing primary production model (Fong and Harwell 1994) for seagrasses in the same region. Data from field and experimental studies on South Florida species, representing each functional group, were used in

conjunction with literature values to parameterize and calibrate the model to three scenarios: canal-influenced, sheet-flow runoff, and oceanic conditions. The program was encoded in Stella, and implemented under the Macintosh OS.

The biomass of the three functional groups of macroalgae were separately simulated using logistic growth equations, multiplied by 0-1 scalars representing the responses to light, temperature, salinity, and nutrients. Growth rates for the seagrass epiphytes were 2-35% day<sup>-1</sup> with a mean of 15%, drift algae were 5-60% day<sup>-1</sup> with a mean of 10%, and rhizophytic algae 2-9% day<sup>-1</sup> with a mean of 5%. Growth incorporated a lag time for turnover into standing stock biomass of 0 days for the epiphytes, 60 days for the drift algae, and 90 days for the rhizophytic algae. Death rates included mortality and herbivory and were 0.5-1.5% day<sup>-1</sup>, with a mean of 1% for all three groups.

The simulation results agreed closely with observed field data for both drift and rhizophytic algae, but were less well in agreement with the observed epiphyte data. Drift algae were simulated as most abundant at the canal site, followed by sheet-flow and least in the oceanic site; highest biomass occurred during the spring and summer. The rhizophytic algae were predicted to be most abundant at the oceanic site, followed by the canal site and least at the sheet-flow site; highest biomass occurred during the summer. The epiphytes were the most abundant of the three functional groups, with highest biomass at the oceanic site and about equal biomass at the canal and sheet-flow sites; highest biomass occurred during the spring at the canal site and in the summer at the oceanic site. Model simulation fit to observed data was good, with agreement >0.75. The poorest fit occurred for the canal site with the epiphyte functional group. Drift algae were the best simulated functional group across all three sites.

Sensitivity analyses indicated a number of parameters that had important influences on model behavior: for all three functional groups, intrinsic growth and mortality rates, and environmental carrying capacity; for the epiphytes, seagrass blade turnover rate; and for the drift algae, probability of removal or deposition by currents. Some of the environmental

response functions, primarily those related to nutrient uptake and growth were also important variables influencing model behavior. Light limitation occurred for all three functional groups in simulated turbid conditions, but there was no effect of temperature. Salinity stress was reduced in canal sites when drift algae and epiphytes were given better low-salinity tolerance, but did not change the exclusion of the rhizophytic algae as they had poor low-salinity tolerance to begin with. Nutrients were found to become N-limiting to epiphytes and P-limiting to the rhizophytic algae at the oceanic site, whereas all groups became P-limited at the canal site because of the high N-loadings observed. Overall, the model appeared to simulate the observed biomass dynamics of the three functional groups over the range of conditions encountered in Biscayne Bay, and helps to suggest abiotic factors important in determining the observed distribution and abundance of the three functional groups.

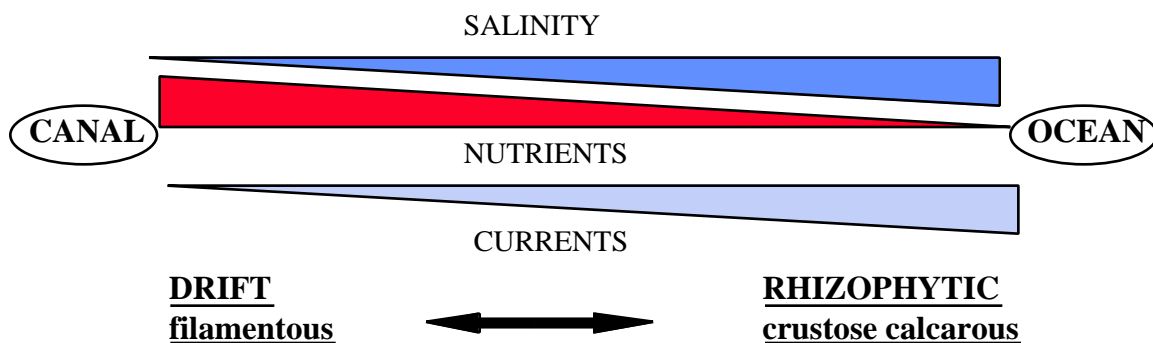


Fig. 1: Summary of important abiotic factors influencing the spatial distribution and abundance of macroalgae in Biscayne Bay seagrass habitats.

To summarize the important abiotic factors and their influence on the spatial distribution of the three functional groups of macroalgae the following key points are made (see Fig. 1):

- Rhizophytic algae have reduced biomass in canal sites because of low-salinity stress from freshwater inputs.

- Drift algae are transported west by tidal and wind-driven currents. Blooms occur under favorable conditions because of positive feedback from elevated nutrients (nitrogen).
- Epiphytes undergo a phase-shift in community composition because low-salinity, high-nutrient conditions exclude encrusting calcareous and favor filamentous forms and diatoms.

Drift algae accumulate under conditions of low current velocities, such as at canal sites. The high nutrient (N) concentrations available from canal inputs allows blooms to form under favorable spring-time conditions (maximum irradiance, lower temperatures, higher salinity). The ability of the drift to tolerate reduced salinities (euryhaline) allows persistence during the wet season. However, because of the high summer water temperatures much of the biomass built up during the spring bloom undergoes senescence and decay. This liberates much of the stored N, which, combined with new N-inputs from canal discharge, forms the nutrient pool for drift growth in the fall when water temperatures decrease and salinity increases again at the end of the wet season.

Rhizophytic algae, in contrast, are able to persist in high-flow conditions because of the anchoring rhizome. This also allows these algae to take advantage of the high porewater nutrient concentrations that are not available to drift algae and epiphytes. Rhizophytic algae have maximum growth during the summer, when water temperatures and irradiance levels are high. However, at the canal sites this corresponds to a time of low salinities from freshwater inputs. Because the rhizophytic algae have poor low-salinity tolerance (stenohaline) this likely excludes this functional group from these sites. During winter, when salinities return to higher, more favorable conditions, rhizophytic algae are not able to take advantage of this because the low water temperatures induce a state of dormancy.

Seagrass epiphytes are a heterogeneous assemblage of species that include diatoms, filamentous forms, and encrusting calcareous algae. The filamentous forms respond like the drift algae, therefore, they are favored under canal conditions, while the calcareous forms respond more like the rhizophytic algae, being favored under oceanic conditions.

This results in a phase-shift in epiphyte community composition between the eastern and western sides of Biscayne Bay, which mirrors the change in the drift and rhizophytic algal functional groups.

With anticipated changes in the management regime of water usage in South Florida, there will be changes in the timing and amount of freshwater released into Biscayne Bay via canals. It is anticipated that there will be an increase in freshwater inputs, resulting in a more estuarine salinity regime at the canal sites. The continued release of freshwater from these canals in a pulsed fashion will ensure that salinity stress effects remain high in areas adjacent to the canals. Given the responses of the three functional groups of macroalgae, it may be anticipated that blooms of drift algae will be affected by the longer periods of low-salinity conditions, possibly resulting in reduced drift biomass over a longer period during the wet season. The rhizophytic algae, which are currently excluded because of the low-salinity conditions, are likely to continue to be excluded from these areas, which may have important consequences for seagrass successional processes. The epiphyte community may also change to reflect conditions that are more favorable for the persistence of filamentous forms at the canal sites. This, combined with possible changes in drift biomass are likely to influence light limitation that the seagrass may currently be experiencing, thereby resulting in increased stress to seagrasses in the canal-influenced areas of Biscayne Bay.