

1 Introduction

Coastal ecosystems are characterized by high biotic diversity and high levels of primary production. These regions yield important food resources, as well as transportation and recreational opportunities for human populations worldwide. However, at the same time they are under increasing threat from non-sustainable land-use practices. The ongoing rise in global human population (Brown *et al.* 1998) and the concomitant changes in land-use to support this growing population, are inevitably affecting the quantity and quality of terrestrial inputs into the world's coastal ecosystems (GESAMP 1994; Hobbie 2000). This is especially true for southern Florida, with human population doubling in the last 20 years and a projected increase of another 20-30% by 2020 (BEBR 1999; Solecki *et al.* 1999).

Tropical regions harbor a high diversity of marine flora and fauna in coral reefs, mangroves, and seagrass habitats (Wood and Johannes 1975; Ogden and Gladfelter 1983). The habitats are at risk from anthropogenic stressors as coastal systems are experiencing the main brunt of human population pressures in the form of over-exploitation of fishery resources, chemical pollution from inadequately regulated industrial sources in developing nations (often located in tropical regions), and possibly most damaging of all: the loss of habitat from alterations made to landscape structure and function to support the burgeoning human population (Viles and Spencer 1995; Cicin-Sain and Knecht 1998; Brown *et al.* 1998).

Effective management and conservation of aquatic ecosystems and their biological diversity require a system-wide perspective because watersheds and estuaries are

interconnected by flows of water and nutrients, and migration of organisms (Fraenkel 1995; Knox 1986; Hobbie 2000). These connections must be considered when managing aquatic ecosystems and require coordination of agencies at the regional or landscape scale (Turner *et al.* 1998; Turner and Gardner 1991). The successful management required for the sustainable use of coastal ecosystems now and into the future requires that the scientific and management communities bring all applicable knowledge to bear on the development of practical models to investigate the results of various management scenarios (Costanza and Voinov 2000).

Despite the extent of scientific research on coastal systems, we are, as yet, limited in our ability to predict the consequences of change (Boesch *et al.* 2000). One reason for this is the inherent complexity and variability of ecological systems (Patten and Jørgensen 1995; Pahl-Wostl 1995) such as coastal ecosystems, where tremendous temporal and spatial variations in physical, chemical, and biological characteristics exist (Mann 1982; Alongi 1997; Kennish 1986; Day *et al.* 1989). Because of this complexity, ecosystem management solutions to the problems plaguing coastal systems require multi-factor risk-assessment and regulatory strategies that take into account indirect, cascading and scale-related effects, all of which require an ecosystem-wide perspective (N.R.C. 1994; Harwell *et al.* 1996).

This dissertation was developed in large part under the aegis of the NOAA Coastal Ocean Program research project entitled: “Human Environmental Linkages in the South Florida Coastal Ecosystem: Effects of Natural and Anthropogenic Stressors” (Harwell *et al.* 1994). The focus of said project was to understand the regional ecosystem and to define ecosystem management recommendations for sustainability of the coupled human-ecological system of South Florida. This required the development of predictive ecosystem- and seascape-level models and their implementation to evaluate the efficacy of management alternatives through rigorous scientific assessment of defined ecological and economic endpoints.

Using ecosystem management approaches in conjunction with the EPA's Ecological Risk Assessment Paradigm (Harwell and Gentile 1992; US EPA 1992) conceptual frameworks for model development and implementation were realized (Gentile *et al.* 2001). A scientific research program addressed physical, chemical, and biological characteristics of the South Florida ecosystem identified by this conceptual framework. Three research approaches were used to determine the relationships between physical and ecological conditions: 1) field studies along gradients of stress, 2) experimental manipulations in microcosms, and 3) development of process-oriented ecological models. In developing the macroalgal models presented in this dissertation, I used aspects of all three of these research approaches.

Evaluation of various scenarios was facilitated by the SEASCAPE model. This is a spatially explicit computer simulation model of the South Florida coastal habitats that includes mangrove, seagrass bed, hard-bottom, and offshore reef community models (W. Cropper Jr., pers. comm.). The SEASCAPE model provides an integrated management tool providing information describing the effects of changes in the physical environment on the habitats in Biscayne Bay. It is important for the reader to realize at this stage that the macroalgal models presented in this thesis were developed to complement the existing seagrass ecosystem model component of SEASCAPE. As part of the scenario-based SEASCAPE approach to evaluating management options for Biscayne Bay, an understanding of the broader regional scale context is a prerequisite.

A Regional Context: South Florida, the Everglades, and Biscayne Bay

The southern portion of the Florida peninsula is a complex mosaic of land, freshwater, and shallow marine ecosystems strongly inter-linked by the flow of water (Stoneman-Douglas 1978; Lodge 1994). South Florida has the only subtropical marine seascape in the continental U.S., an interconnected ecosystem of mangroves, seagrass beds, and coral reefs (USFWS 1999). The large shallow estuaries of Florida Bay and Biscayne Bay link

both wetland and marine habitats. These coastal bays remain relatively robust compared to other eastern U.S. estuaries (Mac *et al.* 1998). Nevertheless this system is affected by natural stresses (such as hurricanes) inherent to the area's subtropical location, and anthropogenic stresses from intense urban and agricultural development impacting the region since the early 20th century (Lodge 1994; USFWS 1999).

Canals and flood-control structures in the Central and South Florida (C&SF) Project (U.S. ACOE 1999) drain land and regulate water levels for agriculture and urban usage, and to some degree, natural habitat requirements. These canals allow rapid removal of rain water, which reduces flooding in developed areas (Light and Dineen 1994). A history of use and abuse has ensured sufficient freshwater for urban needs and lowered standing water levels to allow for successful agricultural development (DeGrove 1984; Perry and Perry 1994; Solecki *et al.* 1999). But the ecological cost has been enormous, and the changes to the South Florida/Everglades system are likely to be long-term (Davis and Ogden 1994).

Historically, the South Florida/Everglades ecosystem extended from the Kissimmee watershed and Lake Okeechobee in the north (Fig. 1) down to Florida Bay in the south (Parker 1984; Davis *et al.* 1994; Lodge 1994). The Everglades today are bordered by the Everglades Agricultural Area to the north and by urbanization on Florida's west and east coasts (Davis and Ogden 1994; USFWS 1999).

The amount, seasonal variation, and quality of the water supply are critical to the ecosystems of South Florida (Davis and Ogden 1994; Browder and Ogden 1999). The flow of water is currently strongly regulated by a series of impoundments to control flooding and provide water for agriculture and human populations (SFWMD 1990). Since 1900 water flow has followed numerous different hydrological regimes under human influence (DeGrove 1984; Schomer and Drew 1982), resulting in a reduction in the extent and duration of inundation within Everglades National Park and a reduction of freshwater flows to Florida Bay (Fennema *et al.* 1994; Light and Dineen 1994; Solecki *et al.* 1999).

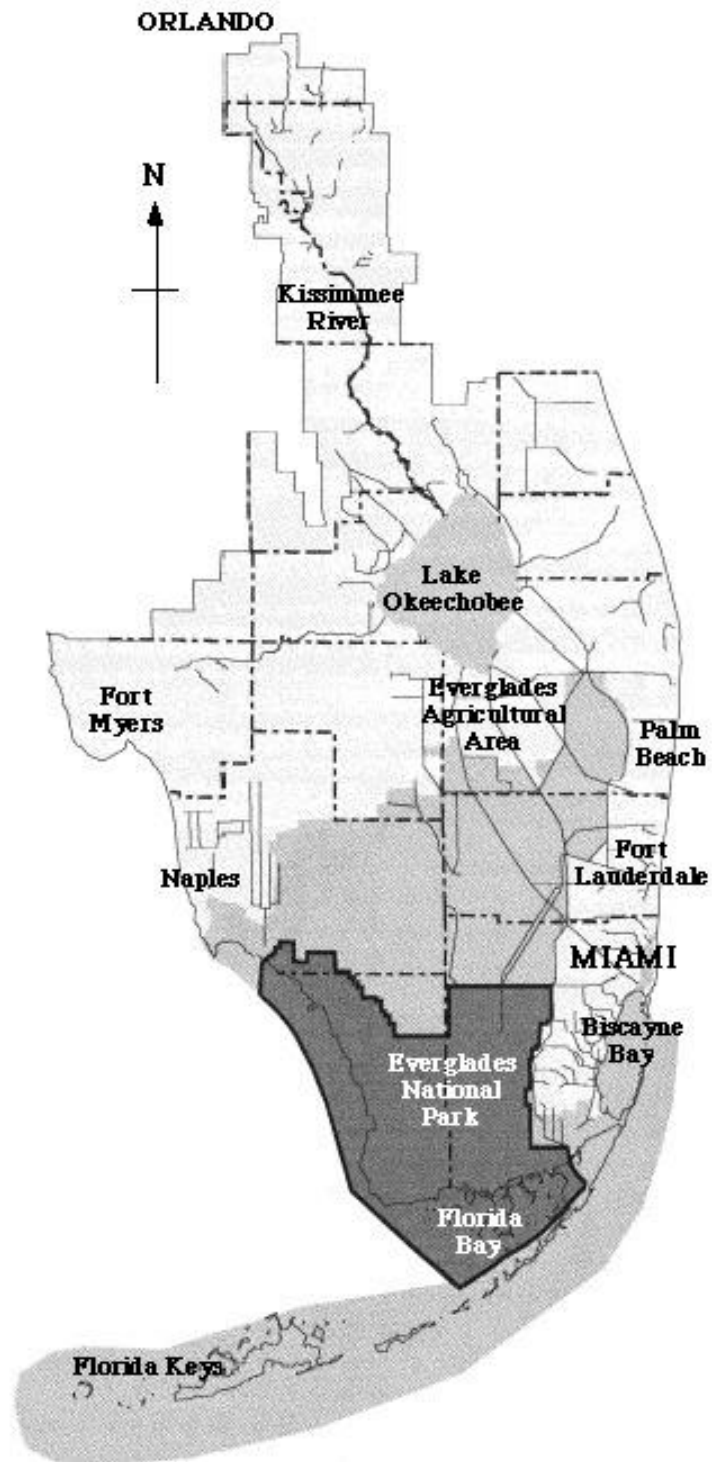


Fig. 1: South Florida region showing interconnectivity of the Everglades with the surrounding watershed. Biscayne Bay is one of two major coastal bays that receive surface waters, which have been altered or reduced since instigation of the C&SF Project that drains major portions of the South Florida/Everglades system. Modified from Harwell *et al.* (1996).

The control of water in South Florida/Everglades is an example of a change in water quantity, quality, and timing that no longer reflects natural variation, to the detriment of native species (Light and Dineen 1994; Mac *et al.* 1998). Most of the ecosystem is denied sufficient water at the proper time, resulting in major shifts in habitat function, and to some degree, structure as well. Today the remnants of this disrupted ecosystem are no longer self-sustaining (Davis *et al.* 1994; Harwell *et al.* 1996; Browder and Ogden 1999; USFWS 1999).

The absence of baseline research prior to the major anthropogenic alterations in the South Florida/Everglades system makes understanding the extent of ecosystem decline difficult. Notwithstanding the lack of availability of baseline information, recent studies (Tilmant 1989; Davis and Ogden 1994; Walt Dineen Society 1997; Browder and Ogden 1999) provide a good understanding of how the ecosystem functions in the present. By using this research as the basis for modeling the future Everglades/South Florida ecosystem, the efficacy of various potential management scenarios can be evaluated (USFWS 1999; Mac *et al.* 1998; Gentile *et al.* 2001).

The hydrologic cycle links the Everglades to the adjacent Florida Bay and Biscayne Bay systems (Schomer and Drew 1982; Livingston 1990). Altered amounts and timing of freshwater flows to and through the Everglades have altered the natural cycles of freshwater influx to these two major estuaries (Schomer and Drew 1982; Light and Dineen 1994; USFWS 1999). The resultant abnormal salinity distribution in time and space have had important repercussions for estuarine function (Livingston 1990; Montague and Ley 1993).

Biscayne Bay is a shallow subtropical estuary located southeast of Miami, Florida. The Bay is approximately 55 km long, with a maximum width of 13 km, and is enclosed to the east by a series of barrier islands. Mean water depth is 2 m, with a maximum depth of about 4 m in the south central portion of the Bay (Thorhaug and Roessler 1977; Alleman 1995). Hoffmeister (1974) reviews the geological processes that gave rise to Biscayne Bay

during the Quaternary period. The Bay incorporates a number of different disturbance regimes, with much of the northern portion heavily influenced by urbanization, whereas most of the central and southern portions of the Bay are affected by drainage canals that control flooding of urban and agricultural areas (Alleman 1995; Gentile *et al.* 2001).

These drainage canals have altered the natural diffuse sheet flow and ground-water delivery to the Bay, resulting in the discharge of large volumes of freshwater (often contaminated and/or with elevated nutrients) from point sources (Alleman 1995; Meeder *et al.* 1999). Canal discharges into Biscayne Bay represent a stress to the natural benthic community dominated by seagrass habitats (Brook 1981). Two potentially important stressors to the primary producers are salinity fluctuations (Nnaji 1988; Fatt 1989; Montague and Ley 1993), and increased nutrients derived from upstream agricultural production (Alleman 1995). Even so, seagrass beds in Biscayne Bay occur both in areas of fluctuating salinities and potential nutrient input near canal discharge sites (western portion of the Bay), as well as in areas where salinities are relatively high and are typically more stable (eastern portion of the Bay).

Algae in Seagrass Habitats

1. Structural aspects

Seagrass meadows are highly productive and ecologically important habitats within South Florida's estuaries and coastal lagoons, as well as throughout the world (Zieman 1982; Larkum *et al.* 1989; Bortone 2000). The seagrass community of the South Florida region is structurally and functionally complex. The dominant species of seagrass is generally *Thalassia testudinum* König, while *Halodule wrightii* Ascherson and *Syringodium filiforme* Kutz may co-occur or dominate in some areas. *Halodule* is important as an early colonizer of disturbed areas and is also found where *Thalassia* or *Syringodium* are excluded because of the prevailing environmental conditions (Zieman 1982). The structural complexity of the seagrass community further includes many species

of algae (Zieman 1982) that can be coarsely grouped into drift algae (e.g., *Chondria* spp., *Laurencia* spp.), rhizophytic algae (e.g., *Caulerpa* spp., *Halimeda* spp., and *Penicillus* spp.), psammophytic algae (e.g., *Acetabularia* spp. and *Batophora* spp.), and epiphytes (e.g., *Ceramium* spp., *Fosliella* spp., and *Melobesia* spp.)

Macroalgae may be present in seagrass beds as large clumps of detached drift algae (Josselyn 1977; Williams-Cowper 1978; Benz *et al.* 1979; Virnstein and Carbonara 1985; Bell and Hall 1997). Species of drift algae commonly found in South Florida include members of the genera *Chondria*, *Hypnea*, *Laurencia*, *Polysiphonia*, *Spyridia*, and *Dictyota*. *Laurencia poiteaui* is abundant in some locations, with high biomass reported during the winter, and low biomass during the summer (Josselyn 1977). This seasonal trend in biomass is evident for many species of drift algae in the region and is probably caused by seasonal changes in light and water temperature, although salinity may be important (Josselyn 1977), especially in areas influenced by freshwater canal discharges (Brook 1981). However, the factors that control drift algal distribution and abundance are not fully known and need to be studied further. Drift algae have been found to be important contributors to primary production and have also been recognized as important habitat for numerous invertebrate species (Virnstein and Carbonara 1985; Holmquist 1994).

Benthic macroalgae, such as rhizophytic algae in the genera *Caulerpa*, *Halimeda*, and *Penicillus*, are important in stabilizing sediments and adding organic matter, thereby facilitating seagrass succession (Williams 1990; Thayer *et al.* 1994). Rhizophytic algae have been intensively studied in South Florida and elsewhere as producers of carbonate sediments (Stockman *et al.* 1967; Bach 1979; Wefer 1980; Drew 1983; Hudson 1985; Bosence 1989; Garrigue 1991). They have been found to be highly productive (Bach 1979; Wefer 1980), even though standing stock biomass is low on average. Productivity is seasonal, with higher productivity in the summer months and reduced productivity, or even dormancy, during the colder winter months (Bach 1979; Hudson 1985).

Epiphytic micro- and macro-algae, especially filamentous and sheet-like reds and greens, grow attached to the seagrass blades (Humm 1964). Epiphytes shade light to the seagrass blades and thereby reduce productivity of the seagrasses (Jones 1968; Zieman 1975; Bulthuis and Woelkerling 1983; Jensen and Gibson 1986). Nutrient enrichment, as occurs around sewage outfall areas, greatly stimulates epiphyte production (Jones 1968; Lapointe *et al.* 1994). Epiphytes have been identified as important contributors to primary production in seagrass systems and may dominate total primary production in some systems (Jensen and Gibson 1986; Moncreiff *et al.* 1992). This is in part caused by the ephemerality of seagrass blades, causing the epiphytes to have a rapid turnover rate (Zieman 1982). Numerous species of drift algae may originate as epiphytes that grow sufficiently large to break away from the seagrass blade as it senesces (Benz *et al.* 1979). Calcareous epiphytes can be important contributors to biogenic carbonate production along with the rhizophytic algae (Frankovich and Zieman 1994)

2. *Functional aspects*

The functional roles of algae in seagrass system are numerous. They include increased habitat complexity, primary production and trophic cycling, as well as sediment stabilization and potential successional facilitation in the case of rhizophytic algae (Zieman 1982, Larkum *et al.* 1983).

Habitat complexity is increased by the presence of all three groups of algae, but especially in the case where aggregations of drift algae occur. This increases the potential number of niches available, leading to greater species richness and abundance (Stoner and Graham-Lewis 1985). Drift algae have been found to support an abundance of benthic fishes and invertebrates (Kulczycki *et al.* 1981; Virnstein and Howard 1987). Drift algae are both a predation refuge and a habitat that is often preferentially selected by benthic fauna (Stoner 1980; Coen *et al.* 1981; Heck and Thoman 1981; Smith and Herrnkind 1992). Juveniles of numerous benthic species, including the commercially important spiny lobster,

preferentially settle and then spend a large portion of the juvenile stage amongst drift algae (Herrnkind and Butler 1986). Holmquist (1994) further demonstrated the ability of benthic fauna to disperse using clumps of drifting algae, which may be especially beneficial to species without extended planktonic larval stages.

Seagrass community primary production is enhanced in the presence of algae, especially epiphytes. Up to 50% of the primary production in seagrass beds can be attributed to epiphytes (Jones 1968; Borum *et al.* 1984; Heijs 1984; Morgan and Kitting 1984; Moncreiff *et al.* 1992). Up to 90% of the material assimilated by grazers is algae rather than seagrass (Dimberger and Kitting 1988). This has been shown by feeding preference studies (van Montfrans *et al.* 1984; Gleason 1986), as well as research using stable isotopes, which have been used to follow trophic utilization of algal vs. seagrass detritus (Fry and Parker 1979; Fry *et al.* 1982; Kitting *et al.* 1984; Sullivan and Moncreiff 1993). This may be in large part because algae can be assimilated by herbivores with greater efficiency than seagrass (Moore *et al.* 1963; Zimmerman *et al.* 1979). Algae contain less refractory matter and have been found to break down quicker under microbial action, with subsequent nitrogen enrichment of the breakdown particles (Tenore 1977; Thayer *et al.* 1977; Odum and Heald 1972).

Rhizophytic algae play a role in sediment stabilization and are important in succession of seagrass beds (Williams 1984; Zieman 1982). Williams (1990) found rhizophytic algae in the genera *Halimeda*, *Penicillus*, and *Caulerpa* to be primary colonizers invading empty plots within a few months. These algae stabilized the unconsolidated sediments and were found to increase nutrients in the sediment upon their demise, thereby facilitating the ability of seagrass to recolonize the bare patches.

3. Identification of Functional Groups

There are over 200 species of algae in Biscayne Bay (Humm 1963, 1964; Herbarium collection at Fairchild Tropical Gardens). I have recorded approximately 70 species of drift and rhizophytic algae from seagrass sites around the Bay. With this large number of species, it is impossible to collect data to model separately the dynamics of each species. Furthermore, many of the species appear to have similar ecological roles in the seagrass ecosystem and can thus be placed into the following functional groups: drift algae, rhizophytic algae, and epiphytes. This approach can be used to assess the importance of the functional group in community processes by using one or two species as representative of the entire functional group. The functional groups and typical genera used in this study are: drift algae (*Chondria*, *Laurencia*); rhizophytic algae (*Halimeda*, *Penicillus*); and epiphytes (*Ceramium*, *Melobesia*).

Littler and Littler (1980) proposed a functional form characterization to relate thallus form to ecological strategies (*sensu* Grime 1979) for algae. This model has been used successfully to understand and predict ecological patterns in a wide range of algal flora (Gaines and Lubchenco 1982; Littler and Arnold 1982; Steneck and Watling 1982; Hanisak *et al.* 1988; Borden 1995). The basic assumption of this approach is that form-function relationships can be used as indicators to interpret and/or predict community patterns, and to identify important environmental factors without the need for detailed species by species studies.

The three functional groups used in this study correlate with functional form groupings identified by Littler *et al.* (1983). Drift algae are comprised of algae with a predominantly coarsely branched morphology and a fleshy-wiry texture. Epiphytes are either filamentous or encrusting calcareous forms. Rhizophytic algae have a jointed calcareous or coarsely branched morphology, are usually calcified, and are further differentiated from the other two functional groups by the rhizome, with which the thallus can be anchored in soft sediments. Based on the Littler and Litter functional form characterization, a number of

ecological differences can be predicted for these three groups. Epiphytes have the highest net primary productivity, especially in nutrient rich waters, but are subject to high potential grazing losses. Rhizophytic algae are slow-growing, with low net photosynthesis, but are structurally and chemically well defended against grazers. Drift algae fall in between these two ends of the spectrum.

From this broad brush ecological characterization, it is apparent that the potential for changes in the community structure of algae present in seagrass habitats can be correlated with changes in environmental regime. As Biscayne Bay presents an environment in which gradients in a number of ecologically important variables occur, this provides a suitable location to test whether the abundance of the three functional groups does indeed change in response to these gradients, and subsequently to determine which of the factors present may be driving this community shift. Ecological modeling provides an integrated approach for exploring the dynamics of this system. For each of these functional groups, a number of model parameters needs to be quantified to determine maximum growth rates, along with growth rate modifiers, as well as loss rates resulting from predation and disturbance.

Overview of Ecological Modeling and Development of Algal Models

1. Modeling methodology

At this stage in the dissertation it is useful to discuss the process of ecological modeling and why models are helpful tools in dealing with complex systems where uncertainty is present, as is often the case for ecological systems (Patten and Jørgensen 1995).

A model is a representation of the real system (*sensu* von Bertalanffy 1968). It is isomorphic, meaning it is collapsed into the crucial states and processes of the system (Hannon and Ruth 1997; Jørgensen 1994). Because of this property, the model can only be as good as the elements that are included. Omission or poor parameterization of an important variable or process can result in the model not being able to simulate the full richness of behaviors exhibited by the real system. In part, the art of modeling lies with the

ability of the modeler to determine which variables must be included to answer the question posed (Kitching 1983; Jørgensen 1994). Models, when correctly developed, have useful predictive properties; they can help answer “what if?” questions, generate testable hypotheses, and increase our understanding of how real systems function (Jørgensen 1994).

Models are a crucial component of research on landscape use, ecological function, and biological diversity (Costanza and Voinov 2000). Models permit us to project the effects of the land-use experiment that society is unwittingly conducting on biota, and to explore alternative future scenarios. Critical scientific tasks are to formulate, build, and verify these models to produce ecologically useful forecasts (NRC 1994). Models cannot be perfect replicas of the actual natural system; therefore, we must expend considerable effort to test models against the expanding base of field and laboratory data available. This not only allows us to assess the credibility of current simulations, but it also reveals improvements for the next generation of models (Costanza et al. 1993; Hobbie 2000).

Modeling is a process of simplifying a real world system, in an attempt to understand some aspect of the system, which is important to the question or problem posed. A flowchart of modeling would include at least the following steps (Jørgensen 1994): Conceptual model Parameterization Calibration and Sensitivity Analysis Validation.

Conceptual model - A conceptual model can be considered a list of state variables and forcing functions of importance to the system and the problem being studied. The conceptual model diagram shows how these variables are connected by flows of material and information (Jørgensen 1994; Gentile *et al.* 2001). It is a tool employed to create abstractions of the ecosystem and to delineate the hierarchical level of organization (O'Neill *et al.* 1986) that best meets the objectives of the model.

Good knowledge about the system and the problem facilitate the conceptualization step and increase the ability of the modeler to select the appropriate degree of complexity

(Costanza and Sklar 1985; Kitching 1983; Jørgensen 1994). The next phase of the conceptual stage is to choose and/or develop the mathematical equations describing the functional relationships between state variables. This will determine the dynamic behavior of the simulated system. Once the conceptual model is completed and encoded, the model can be parameterized based on the available data.

Parameterization - Model parameterization is the process of inserting values to the coefficients in the functions (= flows) between state variables (= compartments). As stated previously, the art of modeling lies in appropriately defining a conceptual model, to balance the conflict of answering the problem as well as possible, given a limited amount of data. The available data will often restrict or determine the types of functions that can be used in the model.

Parameters are initially determined from a range of values reported in the literature. However, the appropriate mean and range used to parameterize the model often needs to be determined more precisely from experimental work on the process(es) under investigation. Parameterization can be by interpolation, based on a statistical relationship (often a regression) over the range of interest, or it can be by extrapolation, based on a mechanistic understanding of the process being modeled (Kitching 1983; Swartzman and Kaluzny 1987).

Deterministic models use only a fixed value of the parameter in a run, and ignore the natural variation inherent about this mean, resulting in a model that always gives the same output for a given set of inputs (Jeffers 1988). A stochastic model includes the variance about the mean, and as such is thought to better reflect the range of behavior of ecological systems (Swartzman and Kaluzny 1987). The drawback of including this variance is that many, often hundreds, of model runs are required with the same forcing functions to describe the range of behavior of the model. Parameterization is completed when model

output is within some acceptable deviation of the real world data (Jørgensen 1994). This is accomplished by calibrating the model.

Calibration and Sensitivity Analysis - Model calibration is the process of fine-tuning the parameter values to fit simulated (model output) and real data better. This process can be accomplished by trial-and-error, often based on the modeler's intuition of which processes are most important in affecting the output, as well as a knowledge of the inherent uncertainty in the parameter values being used (Jørgensen 1994). Another approach is to develop an optimization program to search automatically for the optimal parameter value(s) based on some acceptable maximum error between simulated and real data (Swartzman and Kaluzny 1987). Calibration is often closely tied with sensitivity analysis, and the two processes are often used concurrently to understand and improve model output (Swartzman and Kaluzny 1987).

Model output can be evaluated a number of ways; the most common is comparing time series of simulated and real data graphically. Tabulated values are also useful, especially when dealing with "noisy" time series, where the rate of change is rapid over time and numerous inflection points occur, making it difficult to evaluate the graph easily. Finally, goodness-of-fit tests can be used to determine the fit of observed (real) vs. predicted (simulated) data (Smith and Rose 1995). A good initial method of looking at these data is a scatter plot of observed vs. predicted values (Swartzman and Kaluzny 1987). Calibration is accomplished when the model attains some predetermined acceptable maximal deviation from the real system, *i.e.*, minimal error. It must be noted at this stage that the modeling process is highly iterative, with changes in parameters, as well as model formulation where necessary, to improve the output while maintaining a realistic construct (Jørgensen 1994).

Validation - The final, important, but often neglected step for modeling is validation. This is a test of the model under a different set of forcing functions or initial conditions

(Jørgensen 1994), which can be accomplished by using a data set with a different time series or a different range of possible environmental conditions, e.g., eutrophic vs. oligotrophic conditions for a lake model. This step is probably the most important for creating confidence in the model. Almost always there will be a trade-off in the ability of a model to simulate a specific time series, and yet still be generalized enough to simulate accurately the system under different circumstances from which it was developed (Caswell 1979). For a model to be realistic there is an inherent trade-off between precision and generality (Levins 1966). User confidence in the model should only be extended to the range of conditions for which it was parameterized. Extrapolation beyond this range of values is fraught with inherent hazard because of the dynamic nature of ecological systems, which are extremely adaptable, far from equilibrium systems. They possess a high level of organized complexity, maintaining them in a dynamic steady-state to minimize entropy and maximize optimality criteria (Patten and Jørgensen 1995).

2. *Development of Algal Models*

Seagrass habitats exhibit exactly the kind of dynamic complexity that makes ecological models difficult to validate across the entire range of real system behaviors. An initial seagrass systems model was developed by Fong and Harwell (1994) that predicts dynamic changes in biomass of the three potentially dominant seagrass species in South Florida, as well as two algal groups. Biomass of a “population” of plants in a meter square area is simulated. Modeled changes in biomass are based only on literature-derived relationships among autotrophs and environmental factors.

The model attempts to explain the influence of environmental factors on competitive dominance by one of three species common in South Florida: *Thalassia*, *Halodule*, and *Syringodium*. Light is important, and shading can come from phytoplankton, drift algae, and epiphytes. The response of the three species of seagrass to shading is fairly similar, however, so the major changes in community composition actually come about as a result

of responses to salinity and disturbance stressors. *Halodule* has greater tolerance and higher growth rates under marginal conditions and so is often a primary colonizer in disturbed or suboptimal environs, whereas *Syringodium* and *Thalassia* are competitive dominants under slightly different regimes (Fong and Harwell 1994). *Syringodium* prefers lower nutrient, more oceanic conditions than *Thalassia*. *Syringodium* is more frequently found offshore, while *Thalassia* is more common in bays and estuaries (Zieman 1982; Fong *et al.* 1997).

The Fong and Harwell (1994) seagrass community model was used as a starting point for my modeling efforts. I use a similar approach, but separated the three functional groups (drift, rhizophytic, and epiphytic algae) into discrete, independent models. The three algal models require quantitative parameterization for temperature, light, salinity, and nutrient responses of growth. A comprehensive literature survey found only a few useful studies pertaining to Biscayne Bay (Jones 1968; Josselyn 1977; Bach 1979; Morrison 1984) that would allow these functions to be parameterized on the basis of literature values alone.

From the generalized conceptual model (Fig. 2) upon which the three separate algal models are based, it can be seen that the following data can be used to parameterize each model:

- 1) initial standing stock expressed as biomass ($\text{g dry wt}\cdot\text{m}^{-2}$);
- 2) a maximum daily growth rate expressed in percent standing stock;
- 3) growth rate modifiers if the environment becomes sub-optimal with respect to light, temperature, salinity, nutrient levels;
- 4) a natural daily senescence rate expressed in percent standing stock;
- 5) a daily grazing rate expressed in percent standing stock;
- 6) for drift algae, a hydrodynamic transport function.

In addition to the experimental data gathered to parameterize these models, data for similar seagrass systems (e.g., Caribbean) available from the literature are used where appropriate.

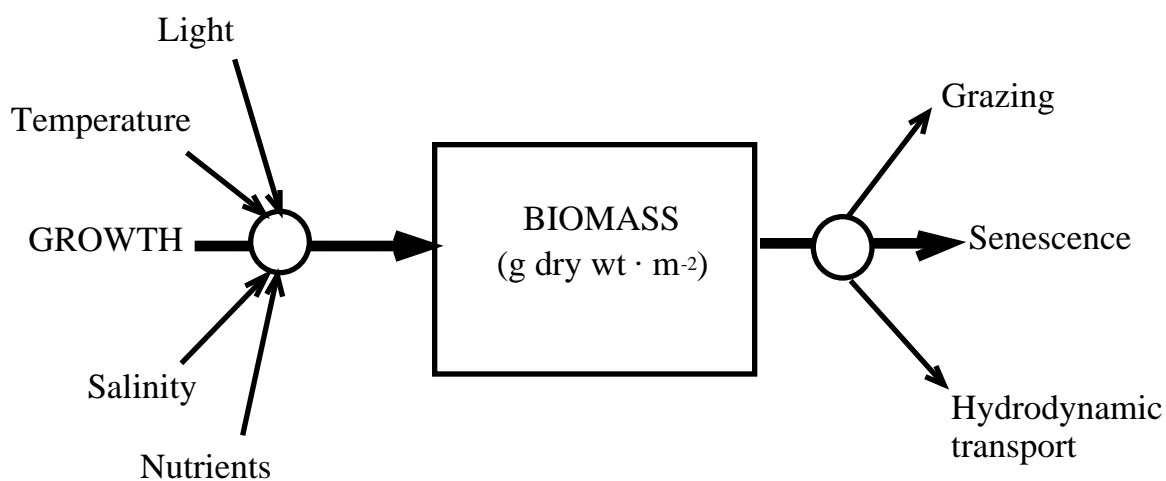


Fig 2: Generic conceptual model of processes influencing algal biomass. Growth is expressed in percent biomass increase per day. Modifiers of growth include: light, temperature, salinity, and nutrients. Losses occur from natural senescence, grazing, and for drift algae, transport by currents.

The three functional groups of algae each interact with the seagrass; for instance, drift and epiphytic algae are implicated in reducing light available to the seagrass blades. These interactions were modeled as part of the output data from the separate algal models. A hierarchical approach, from autecology through ecosystem levels, was adopted in studying the three functional groups of algae (drift, rhizophytic algae, and epiphytes) in seagrass communities in Biscayne Bay. These ecological data were then used to parameterize and calibrate the ecological models presented at the end of this dissertation.

Aims and Hypotheses

To fulfill the goals of this dissertation, there were a number of specific aims that needed to be satisfied. Firstly, the algal communities from the eastern vs. western side of Biscayne Bay needed to be described to determine if there were differences in community composition along the gradient of canal discharge stresses. Secondly, the seasonal dynamics of standing stock biomass and productivity of the three functional groups needed to be monitored in relevant portions of the stress gradient. Thirdly, the response of

representative species of each functional group to a realistic range of the relevant environmental variables needed to be determined under controlled conditions to develop realistic functions in the models. This was a major portion of the dissertation work presented herein. Finally, my ultimate goal was to develop a community model for algal production in seagrass habitats over the range of environmental conditions present in the Bay.

In consideration of these aims, and the requirements for parameterizing and validating the three algal models, there were specific hypotheses I tested:

- Hypothesis 1: Anthropogenic stressors from canal discharges have an effect on abundance, community composition, and distribution of algae across Biscayne Bay.
- Hypothesis 2: Seasonal variations in light and temperature affect the growth of drift, rhiziphytic, and epiphytic algae.
- Hypothesis 3: Spatial variations in salinity and nutrient stressors affect the growth and distribution of drift, rhiziphytic, and epiphytic algae.
- Hypothesis 4: The hydrodynamic regime affects the abundance, composition, and distribution of drift algae across Biscayne Bay.

Chapters presented in this dissertation will deal with each of these hypotheses in turn. Towards the end of the dissertation, I will use all the data in mathematical simulation models of biomass dynamics in the three functional groups of algae studied. These models are evaluated for a range of environmental scenarios present in Biscayne Bay, followed by the final conclusions of the work presented herein.