

# 3

# *Light and*

# *Temperature*

## **INTRODUCTION**

Light and temperature are important abiotic variables influencing algal growth. Benthic algae are an important floral component in Biscayne Bay seagrass habitats, as well as in other bays and estuaries in subtropical and tropical regions (Zieman 1982; Fong and Harwell 1994). They are an important habitat for many estuarine animals and contribute to the overall productivity of seagrass systems (Zieman 1982), therefore it is important to understand how abiotic variables affect the growth of these algae over the range of seasonal conditions encountered in Biscayne Bay. In this chapter I describe both the seasonal variations in light and temperature, as well as the responses by the three functional groups to these two abiotic variables. In the subsequent two chapters I will cover salinity and nutrients, completing the discussion of the abiotic variables important to macroalgal growth in the model described in Chapter 7.

## **Light**

Plant growth under water is limited by the attenuation of light, penetration of which is at least 2000 times less through water than it is through air (Dring 1982). The wavelengths of light used in photosynthesis are 400-700nm and are collectively termed

photosynthetically active radiation (PAR) (Kirk 1994). This radiation is measured as photon-flux fluence rate or quantum irradiance, i.e., the rate of arrival of visible photons per unit area, in units of  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  using cosine-corrected irradiance sensors (Ramus 1985; Lobban and Harrison 1994). As light passes through water it is subject to both absorption and scattering, resulting in exponential attenuation which can be calculated as a light attenuation coefficient ( $k$ ), derived from the Beer-Lambert law (Ramus 1985).

The spectral composition of underwater light is an important determinant of the lower depth limits of algae, as different groups of algae possess pigments that absorb favorably in different portions of the PAR spectrum (Raven and Richardson 1986). In clear oceanic waters, blue light (465nm) penetrates deepest, while as one approaches the coastline, dissolved organic substances and suspended particles (turbidity) alter the spectral transmittance, such that green (525nm) or even yellow light (575nm) will penetrate furthest (Kirk 1994). The lower boundary of the photic zone is defined by convention as the depth to which 1% of surface irradiance penetrates (Steeman-Nielsen 1975); in turbid coastal waters this can be less than a few meters (Dring 1982), potentially limiting light for photosynthesis in benthic plants (Raven and Richardson 1986; Dennison *et al.* 1993).

The physiology of photosynthesis is influenced by both light and temperature (Dring 1982; Raven and Richardson 1986; Lüning 1990; Lobban and Harrison 1994). The light and dark reactions can be expressed in a photosynthesis versus irradiance (P-I) curve (Fig. 1) (Steeman-Nielsen 1975; Dring 1982; Markager and Sand-Jensen 1994). The slope ( $\alpha$ ) of the initial part of this curve shows the rate of the light reaction with increasing irradiance (Fig. 1). Steep slopes, or high values of  $\alpha$ , indicate high quantum yield, while more gradual slopes indicate lower activity (Arnold and Murray 1980; Littler *et al.* 1988). The horizontal part of the curve represents the maximum rate of the enzymatic processes ( $P_{\text{max}}$ ) involved in the dark reaction of photosynthesis at the prevailing temperature (Fig. 1). The intersection of the slope  $\alpha$  and  $P_{\text{max}}$  is defined as the saturation irradiance ( $I_k$ ) and describes the ratio between the photochemical and enzymatic parts of the photosynthetic reaction

pathway (Talling 1957; Steeman-Nielsen 1975; Markager and Sand-Jensen 1994). At higher irradiances photo-inhibition can occur, leading to a reduction in photosynthetic efficiency. This is thought to be caused by excess light energy, which can damage chlorophyll by photo-oxidation (Harris 1980), or be dissipated as heat (Chow 1994), or by temperature-mediated damage (Franklin 1994; Franklin *et al.* 1996).

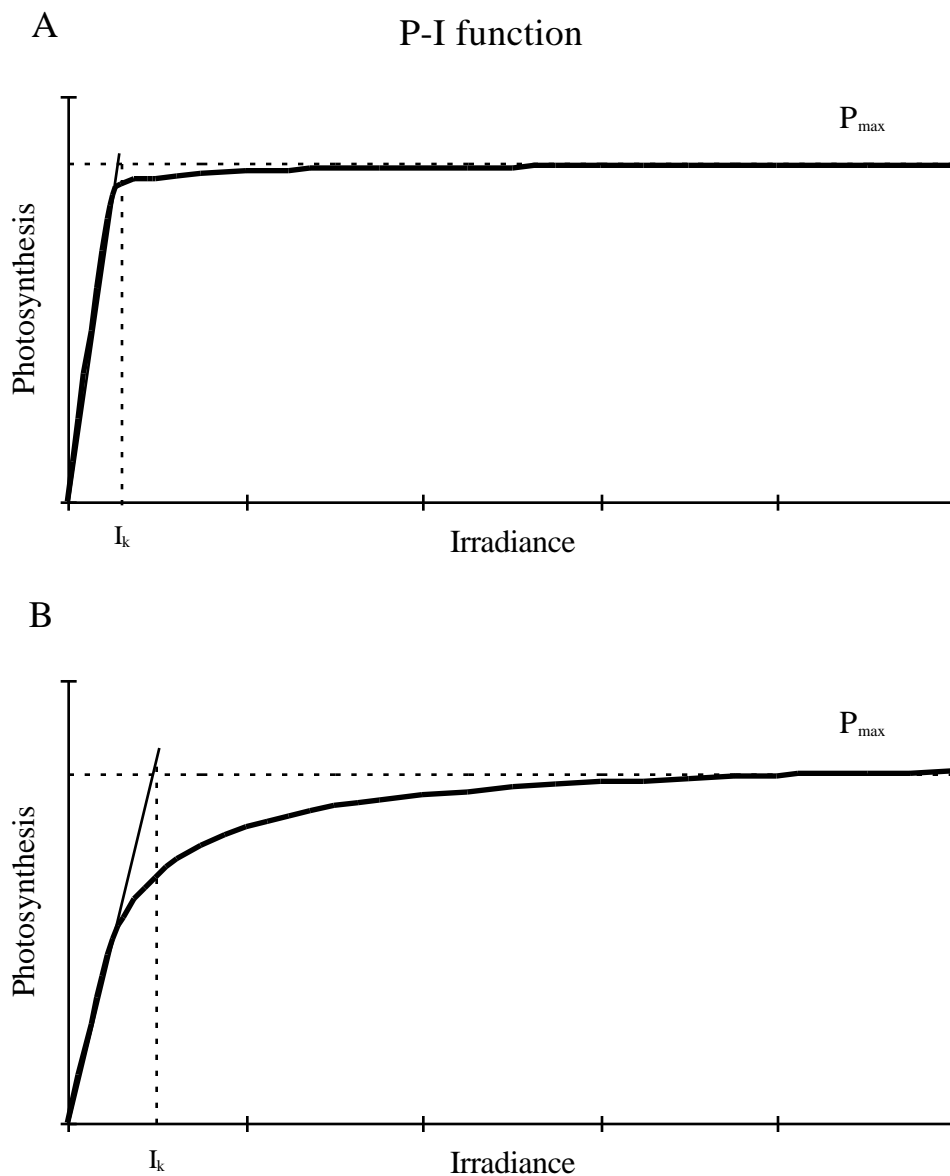


Fig. 1: Theoretical P-I curves for two different algae showing the relationship between the photochemical ( ) and enzymatic reaction ( $P_{\max}$ ) steps of photosynthesis. Fig. 1A: An alga with a high and therefore a low  $I_k$ . Fig. 1B: An alga with a lower , but the same  $P_{\max}$ , yielding a higher  $I_k$ .

Accessory pigments differ in the green (chlorophyte group), brown (chromophyte group), and red (phycobilin group) algae (Raven and Richardson 1986). The accessory pigments, in conjunction with chlorophyll a, are collectively termed the light-harvesting complex (Dring 1982; Lobban and Harrison 1994). The importance of the accessory pigments to overall photosynthetic contribution can be judged from *in vivo* absorption and action spectra (Dring 1982; Lobban and Harrison 1994). Both genotypic and phenotypic variation in pigment composition occurs among individuals and species (Dring 1982). Phenotypic changes in pigments can occur within a few days of plants being exposed to altered irradiance conditions (Dring 1982), with two possible types of responses involving the photosynthetic unit (PSU). First, pigment content can be augmented by increasing the size of the PSU; second, the number of PSUs present can increase (Harrison 1988). These changes can be differentiated by comparing the P-I curves with  $\alpha$ , the initial (light-limited) slope, increasing under the first scenario, while  $P_{max}$ , the light saturated rate of photosynthesis, increases with an increase in the number of PSUs under the second scenario (Dring 1982; Harrison 1988).

Photosynthesis is a major, easily measured metabolic process, and is routinely used to gauge the effects of environmental conditions on algae (Lobban and Harrison 1994). However, as is evident from the above review, this is a highly complex process that is further complicated by intrinsic variability within the plant, as well as complex changes in the irradiance field on time scales of seconds to years. Further complications arise from the effects of other environmental factors including temperature, salinity stress, and nutrient availability, on algal metabolic rates.

## **Temperature**

The high specific heat of water causes diel and seasonal fluctuations in temperature to be damped out in the ocean (Raven and Richardson 1986). The largest mean annual temperature range for marine habitats is recorded from coastal waters, and amounts to 10-

15°C (Dring 1982). Daily temperature fluctuations are consequently of less importance compared to light fluctuations in controlling growth of submerged seaweeds over short time periods (Raven and Richardson 1986; Sand-Jensen 1989).

Photosynthetic rates of all algae are stimulated by increases in temperature, within a certain range, depending on species and acclimation (Sand-Jensen 1989). High temperatures are deleterious to plant survival, and often occur in combination with high irradiances, which can adversely affect photosynthesis (Biebl 1970; Steeman-Nielsen 1975). The light reaction is temperature-independent over a wide range, until high temperatures cause the breakdown of the PSII unit resulting in photo-inhibition (Davison 1991). Temperature increases enhance the dark-reaction rate of photosynthesis (Steeman-Nielsen 1975; Lobban and Harrison 1994), up to an upper thermal tolerance limit (Epply 1972; Dring 1982; Lüning 1990). Temperature increases will change the rates of enzyme-mediated biological reactions, such as occur in the dark reactions of photosynthesis (Epply 1972; Steeman-Nielsen 1975). However, respiration also increases with temperature; thus, the amount of light required to reach the compensation irradiance ( $I_c$ ) also increases with temperature (Lobban and Harrison 1994). Acclimation by algae to seasonal changes in temperature allows photosynthesis to be maximized relative to ambient temperatures. The photosynthetic temperature optimum within a species may shift seasonally by up to 5°C (Steeman-Nielsen 1975; Niemeck and Mathieson 1978; Lüning 1990).

Growth rates also have a species-dependent optimal temperature according to Shelford's zone of tolerance concept (Ricklefs and Miller 2000). The temperature tolerance curve usually exhibits a rapid decline near the species-specific upper lethal limit (Lüning 1990). Deleterious effects of high water temperatures are therefore likely to occur in tropical shallow waters, where high diel and seasonal temperature extremes take place in the summer. In general, tropical species survive higher temperatures better than closely related species from cooler temperate zones (Vernberg and Vernberg 1974; Hutchinson 1976). Tropical marine organisms are thought to exist near or at their upper thermal limit,

especially during the summer (Thorhaug 1976; Miller *et al.* 1976). Studies associated with thermal plant discharges from Turkey Point nuclear power plant, into southern Biscayne Bay and Card Sound (Zieman 1970), yielded a wealth of data on inherent thermal tolerances of tropical flora and fauna, as well as their ability to withstand additional thermal stress from heated power plant effluents (Bader and Roessler 1971, 1972; Roessler 1974; Thorhaug 1974).

The possible causes of algal death at high temperatures include processes such as denaturation of proteins, and damage to heat-labile enzymes or membranes (Lüning 1990). Temperatures of 33-35°C represent the long-term upper survival-limit for tropical benthic algae, with a low temperature tolerance ranging from 5-14°C (Lüning 1990). Temperature tolerances of different species of seaweeds are at least partly responsible for patterns in their geographical distributions (Lüning 1990) and seasonal blooms (Lobban and Harrison 1994). Biomass of certain groups of algae may show pronounced seasonal blooms correlated with species-specific responses of photosynthesis, respiration, and growth, to ambient temperatures (Sand-Jensen 1989).

The major effect of light and water temperature on the growth of the three functional groups of algae studied in Biscayne Bay is a response to seasonal variation. The aims of the work presented in this chapter are to:

- collect and analyze field data on seasonal light and temperature variations in Biscayne Bay;
- determine response curves for representatives of the three functional groups of algae to light and temperature variations over the range of conditions commonly encountered in Biscayne Bay.

## METHODS

The first two forcing functions required for the model (Chapter 7) are light and temperature. The responses to these two variables by the benthic algae studied are as yet largely unknown, as is still the case for many tropical species (Littler and Littler 2000).

### Light

#### 1. Light Regime

Long-term, high-frequency light data were not available for sites within Biscayne Bay. Data from 1993-98 obtained from the NOAA Coastal Marine Automated Network (C-MAN) weather station at Fowey Reef (25°35.4'N, 80°06.0'W) were used. Hourly readings of light in the 400-700nm spectral band were averaged to obtain daily mean, and minimum and maximum surface irradiance values. A 30-day moving average was calculated to elucidate monthly trends in surface irradiance ( $I_0$ ). Attenuation coefficients ( $k$ ) measured at canal (FP) and oceanic (SK) sites were used to determine the average daily light available to benthic algae at one meter depth.

Total benthic irradiance flux were measured in the field using 4 spherical quantum sensors (LI-COR model LI-193SA, Lincoln, NE). Light attenuation was measured at FP and SK in May 1997 and again in 2000, between 10:30 and 13:00 hrs Eastern Standard Time on cloudless days. Irradiances were recorded on an LI-1000 data-logger as integrated one-minute values (mean, minimum, maximum) of five-second instantaneous measures, over periods of 5-6 minutes at 10 cm depth increments. Light attenuation coefficients ( $k$ ) of the water column for each site were calculated according to Dring (1982) using the Beer-Lambert attenuation function (Kirk 1994):

$$I_d = I_0 e^{-kd}$$

where:

$$I_d = \text{PAR at depth (m)}$$

$$I_0 = \text{PAR at surface}$$

$k$  = attenuation coefficient

Benthic light levels were recorded at midday on days with minimal cloud cover. Measurements were taken at the seagrass canopy surface at sites in each salinity regime. Tidal depth differences among sites were less than 20cm. The light flux data were analyzed by ANOVA.

## 2. Light Responses

Light responses for the three functional groups of algae were determined in the form of photosynthesis-irradiance (P-I) curves in the dry season (February) and wet season (August). Drift and rhizophytic algae for these experiments were collected from Biscayne Bay and returned to the RSMAS campus in coolers, where they were placed in flow-through holding tanks for no longer than 24 hours before each experiment. Epiphytes were cultured on artificial seagrass blades placed in the CMEA mesocosms for four months.

Approximately 1-3 g blotted wet weight of algae were placed in each of six replicate 300 ml light bottles per irradiance level. The bottles were maintained at ambient water-temperature in a flow-through water bath for the duration of the three-hour incubation, performed in the morning (9:00-12:00). Light was reduced from ambient sunlight by placing neutral-density shade cloth of pre-determined transmissivity over the light bottles to give experimental light levels (100%, 50%, 25%, 12%, 5.8%, 2%, 0.5%). Foil-wrapped dark bottles were used for the 0% light level. Dissolved O<sub>2</sub> was measured initially and at the end of the incubation period using a self-stirring BOD probe (YSI model 5010) attached to a dissolved oxygen meter (YSI model 5000, Yellow Springs International, Yellow Springs, OH). Gross photosynthesis rates were calculated and expressed per gram dry weight of tissue per hour, according to the recommendations of Littler and Arnold (1985).

The P-I model of Smith (1936) was fitted to the data points (see Fig. 1):

$$Pg = \frac{P_{\max} \alpha I}{\left[ P_{\max}^2 + (\alpha I)^2 \right]^{0.5}}$$

where:

$P_g$  = gross photosynthesis ( $\text{mg O}_2 \cdot \text{g dry wt}^{-1} \cdot \text{hr}^{-1}$ )

$P_{max}$  = light-saturated rate of gross photosynthesis

= slope of the light dependent gross photosynthetic rate

$I$  = irradiance ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )

This model was found to best describe the experimental data for marine macrophytes of the various models tested (Nelson and Siegrist 1987; Fourquaran and Zieman 1991). The initial slope ( ) of the light-dependent reactions was calculated from least squares linear regressions fitted to the data (Arnold and Murray 1980); while  $P_{max}$  was calculated as the mean of the light-saturated photosynthetic rates obtained in a particular P-I curve (Talling 1957; Littler *et al.* 1988).

## Temperature

### 1. Temperature Regime

Water temperature data for Biscayne Bay were obtained from monthly measurements taken by the Dade County Department of Environmental Resources Management (DERM), field data collected by the University of Miami's Center for Marine and Environmental Analyses (CMEA), and hourly datasets collected in Biscayne National Park (BNP). Table 1 lists locations of the sites and parameters measured. Monthly surface water temperatures from a ten-year time-series measured at DERM sites and three years of data collected at my study sites were averaged and compared. The minimum and maximum monthly values for both data sets were also plotted to show the range of possible values. The DERM data set includes both surface and bottom water temperatures. I tested for significant differences in water temperature with depth using Student's t-test to determine if a thermocline exists. BNP's hourly datasets were collected with bottom sondes from two canal sites and two oceanic sites. Mean daily temperatures were plotted for each site, as well as minimum and maximum temperatures for the two regimes.

Table 1: Locations of sites from three sampling programs; CMEA, DERM, and BNP; see text for explanation. The physical variables sampled include: T = temperature ( $^{\circ}\text{C}$ ), S = salinity (psu), and N = nutrients (including  $\text{NO}_2+\text{NO}_3$ ,  $\text{NH}_4$ ,  $\text{PO}_4$  in  $\text{mg}\cdot\text{l}^{-1}$ ).

Regime	Site	Lat. (N)	Long. (W)	Depth(m)	Parameters	Period	Intervals, depth sampled
<u>Canal</u>	<b>CMEA</b>						
	FP	25°29.643'	80°19.822'	1.0	T, S	1996-99	intermittent, surface
	BKP	25°33.548'	80°17.959'	1.0	T, S	1996-99	intermittent, surface
	<b>DERM</b>						
	BL01	25°32.060'	80°19.340'	3.4	T, S, N	1990-99	monthly, surface & bottom
	PR01	25°31.070'	80°20.060'	3.7	T, S, N	1990-99	monthly, surface & bottom
	MW01	25°28.090'	80°20.270'	4.1	T, S, N	1990-99	monthly, surface & bottom
	<b>BNP</b>						
	TG5	25°29.780'	80°19.528'	1.0	T, S	1997-99	hourly, bottom
	TG6	25°31.637'	80°18.243'	1.6	T, S	1997-99	hourly, bottom
<u>Sheet-flow</u>	<b>CMEA</b>						
	BS	25°17.949'	80°23.246'	1.1	T, S	1996-99	intermittent, surface
	LCS	25°17.814'	80°22.373'	1.1	T, S	1996-99	intermittent, surface
	<b>DERM</b>						
	BB48	25°18.480'	80°20.400'	2.5	T, S, N	1990-99	monthly, surface & bottom
<u>Oceanic</u>	<b>CMEA</b>						
	BC	25°20.939'	80°16.316'	0.8	T, S	1996-99	intermittent, surface
	SK	25°30.004'	80°11.497'	1.0	T, S	1996-99	intermittent, surface
	<b>DERM</b>						
	BB37	25°34.120'	80°11.300'	2.0	T, S, N	1990-99	monthly, surface & bottom
	BB43	25°23.430'	80°14.020'	4.9	T, S, N	1990-99	monthly, surface & bottom
	BB46	25°20.020'	80°16.140'	3.3	T, S, N	1990-99	monthly, surface & bottom
	<b>BNP</b>						
	CCK	25°23.790'	80°15.900'	2.8	T, S	1990-99	hourly, bottom
TG9	25°39.267'	80°09.580'	5.2	T, S	1997-99	hourly, bottom	

## 2. Temperature Responses

Temperature response curves for some of the species of algae being studied were available from previous studies in southern Biscayne Bay by Bader and Roessler (1971, 1972). The temperature ranges over which the drift alga, *Laurencia*, and the two rhizophytic algae, *Penicillus* and *Halimeda*, were tested for survival were replotted and their data were compared with my own data collected in the quarterly experiments described below. The number of algae that were growing after one week in the quarterly experiments was expressed as a percentage of the total number of algae in an experiment, as not all algae

grew. The percent of algae growing at the end of an experiment was plotted against ambient water temperatures, which ranged from 23 to 31°C.

## **Multi-factorial Experiments: Light x Temperature Interactions**

### *1. Experimental Facilities*

The CMEA mesocosm and microcosm facilities were used to perform the quarterly multi-factorial growth experiments. The mesocosm facility consists of nine fiberglass tanks (each 2m x 3.6m x 1.4m) with 40 cm of marine sediments on the bottom. Seagrasses and macroalgae, with associated invertebrates, were added to each mesocosm in the form of fifty 20 cm diameter cores in 1996, and again in 1998 (Irlandi *et al.* 2001). Maximum water-column depth with the sediments is set at 85 cm. The tanks are maintained as flow-through systems with a flow rate of 10 L per minute, maintaining a water turnover rate of four times a day. Unfiltered seawater is pumped from adjacent Bear Cut, allowed to settle in a large central seawater supply tank, and then gravity fed to the mesocosm and microcosm facilities. This allows natural recruitment to occur from planktonic larvae and spores.

The microcosm facility consists of thirty aquaria, each 30 gallons (113 L), housed in a 5.5 x 6 m Quonset greenhouse covered with two layers of PAR neutral Kool-lite UV Polyfilm. The aquaria can be set up for either flow-through or recirculating flow. Each aquarium has a maximum turnover of three times per hour. Aquaria are set on three tables, ten aquaria per table, with three completely separate water supply systems to ensure that water from one treatment does not mix with water from another treatment. The water in each treatment can thereby be isolated from other treatments, yet still allows for flexibility in the location of aquaria in each treatment. For static experiments of short duration, four 9.4L clear acrylic microcosm tubes can be placed inside each 30 gallon aquarium, which then acts as a water bath running flow-through seawater to maintain temperature at ambient

levels. In addition, there are four 240 gallon tanks outside the greenhouse that can be used as seawater holding tanks, or as freshwater reservoirs for salinity experiments.

## *2. Experimental Methods*

Multi-factorial growth experiments were conducted quarterly (winter = Feb., spring = May, summer = Aug., autumn = Nov.) in the CMEA microcosm facility (described above). The aim of these experiments was to determine seasonal growth responses of drift and rhizophytic algae, as well as the effects of salinity (10, 20, 35 psu) and nutrients (ambient, enriched), which will be discussed in detail in Chapters 4 and 5 respectively. For the seasonal light and temperature growth responses considered in this chapter, I looked only at growth of algae in the controls (35 psu, no nutrient additions).

Seasonal light levels during the photosynthesis and growth trials were recorded by a cosine-corrected 4 sensor (LI-COR model LI-193SA, Lincoln, NE) placed in one of the microcosm tubes, with hourly integrated mean, minimum and maximum irradiance values logged over 7-10 days on a LI-1000 datalogger. Water temperatures were measured three times daily (am, noon, pm) over the days that the experiment ran and mean temperatures were calculated for each time of day. Separate non-parametric Kruskal-Wallis tests were performed on the mean daily light levels and mean daily temperatures for each quarter (Feb., May, Aug., Nov.).

Drift algae were collected from canal sites, while rhizophytic algae came from oceanic areas of the Bay. Plants were returned to RSMAS campus in aerated coolers, where they were placed in flow-through holding tanks for no longer than 24 hours before the start of each experiment. The algae (approx. 10g blotted wet weight) were placed in 9.4 L clear acrylic microcosm tubes containing the experimental treatment (Fig. 2). An airstone placed in each tube provided circulation to reduce boundary layer effects on the nutrient uptake rates by the algae (Mann and Lazier 1996). Four tubes each were placed in a thirty gallon (113L) aquarium (Fig. 2).

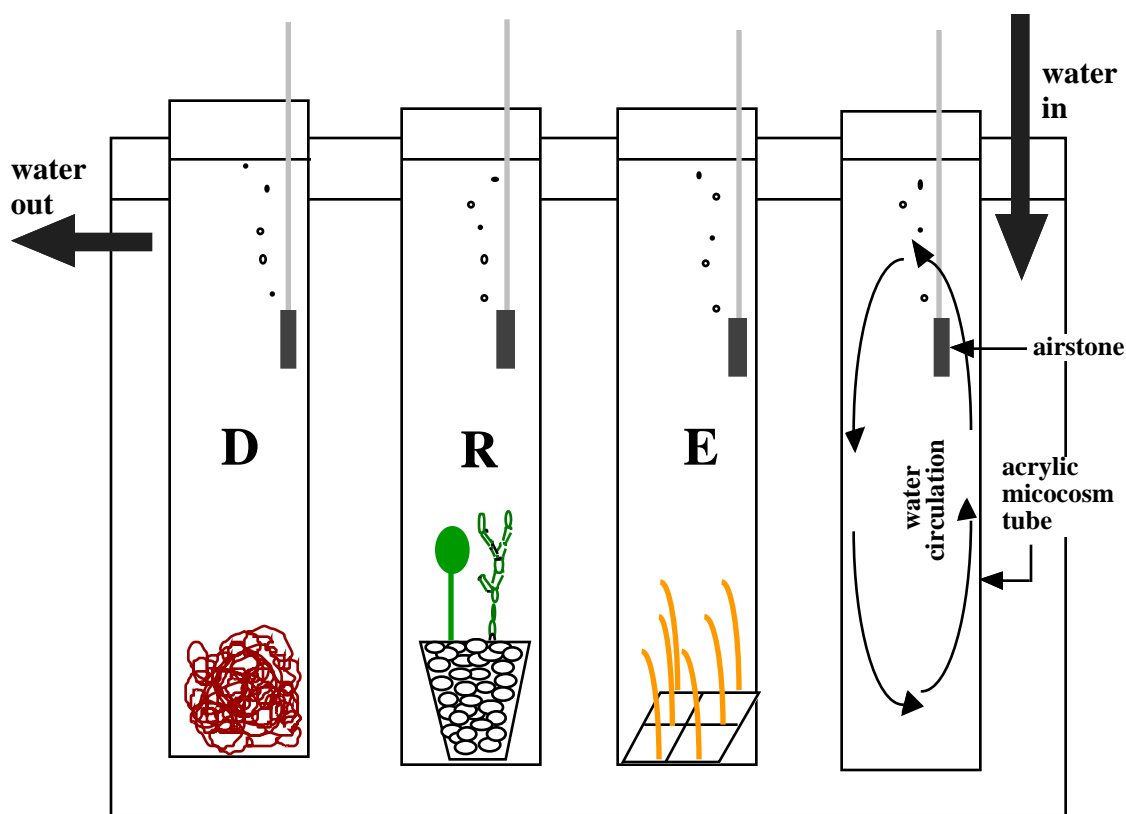


Fig. 2: Generalized diagram of four microcosms in an aquarium water bath, showing the flow of water through the aquarium and around the 9.4 L microcosm tubes ( $n=10$  per salinity x nutrient treatment). The algae were added as shown: D = drift, R = rhizophytic, E = Epiphytes. Only one species was exposed per week-long growth experiment, and all species were tested each quarter.

### 3. Growth

Drift algae: Growth of drift was recorded as change in blotted wet weight after 1 week exposure to the treatment solution, and re-expressed as percent weight change per day using the formula:

$$\% \text{ change} = \frac{(\text{final} - \text{initial})}{\text{initial}} \times 100\% \text{ } 7 \text{ days}^{-1}$$

Rhizophytic algae: *Penicillus* and *Halimeda*, were stained overnight (12-14 hr) prior to an experiment, using Alizarin Red S (Sigma Chemicals, cat. no. A3757) at a concentration

of 0.2 g·L<sup>-1</sup>. Alizarin red is used in anatomical research to stain calcium carbonate in bone (Taylor and Van Dyke 1985; Blom *et al.* 1994). It has been successfully applied to determine *in situ* growth rates of corals (Lamberts 1978; Le Tissier 1988; Swart *et al.* 1996), as well as calcified marine algae (Wefer 1980; Payri 1988; Davis and Fourqurean 2001). The algae were subsequently rinsed thoroughly in flowing seawater to purge residual stain that had not been incorporated into the thallus. One individual of each genus was “planted” into a 500 ml plastic flower pot using weathered limestone gravel to anchor the thalli in an upright position, before placing the pot and algae in a microcosm tube. After one-week exposure to the treatment solution, the thallus was bleached for 10-20 minutes in a 25% bleach solution, dried at 70°C to constant weight, and any unstained tissue was removed and weighed separately. This new growth was compared to the initial biomass (stained tissue), and daily growth rates calculated using the formula:

$$\% \text{ change} = \frac{\text{unstained}}{\text{stained}} \times 100\% \text{ } 7 \text{ days}^{-1}$$

Epiphytic algae: presented a challenge as they naturally grow on seagrass leaves, a living substrate, which is also affected by changes in abiotic conditions. To separate any responses by the seagrass, which could influence the measurements on the epiphyte community, I had to devise a method for cultivating a natural epiphyte community on an inert, non-biological substrate, so that any changes measured with respect to experimental conditions would be purely from the epiphyte community.

Epiphytes were cultured on artificial seagrass blades in the CMEA mesocosms. Artificial seagrass leaves have been successfully used to study seagrass-epiphyte interactions in the past (Virnstein and Curran 1986; Horner 1987). I used green colored ribbon (Lime Green 521-5P, American Greetings, Cleveland, OH) of 1 cm width and cut to 10 cm lengths, nearly identical with the average morphology of *Thalassia* throughout much of Biscayne Bay (Irlandi *et al.* 2002). Six pieces of ribbon were tied to a square

piece of 2.54cm<sup>2</sup> (1 inch<sup>2</sup>) Vexar mesh, weighted with a lead sinker to keep it submerged, and placed in the mesocosms for 4 months, allowing algal epiphytes to settle from natural recruitment of planktonic spores and fragments entering with the unfiltered seawater. One artificial seagrass unit (AGU) was placed in each microcosm tube for an incubation period of 2 days, and photosynthesis by the epiphyte community was measured at the end of the exposure. I could not measure epiphyte biomass at the outset of the experiment, as this requires destructive sampling. One “blade” (with its attached epiphytes) was used per bottle in the light:dark bottle incubations (see below). Biomass was determined at the end of the incubation, using the same methods described previously for epiphytes collected from the field (see Chapter 2).

#### *4. Photosynthesis*

Because growth measurements, using changes in biomass, were not possible for all functional groups (e.g., epiphytes), and in other cases were found to be negligible (e.g., rhizophytes), photosynthesis was also used to measure productivity. Photosynthesis was measured on the first and last days of the week-long exposure for drift and rhizophytic algae, and at the end of the 2 day incubation for epiphytes. I used a light-dark bottle technique (Littler 1979; Thomas 1988) to quantify changes in dissolved oxygen levels in bottles incubated over 2-3 hrs following the recommendations of Buesa (1977). Incubations were done in the morning (9:00-13:00) to maximize the photosynthetic response, based on diel patterns of photosynthesis in algae (Payri 1988; Baker and Bowyer 1994; Franklin *et al.* 1996). Approximately one gram dry weight of algal tissue per liter (Littler 1979; Buesa 1977) was placed in each of four to six replicate 300 ml light and dark bottles and maintained at ambient seasonal light levels and water temperatures in a flow-through water bath for the duration of the incubation. Dissolved O<sub>2</sub> was measured initially and at the end of the incubation period using a self-stirring BOD probe (YSI model 5010) attached to a dissolved oxygen meter (YSI model 5000, Yellow Springs International,

Yellow Springs, OH). Control bottles without algae (=blanks) were also run concurrently and used to adjust net photosynthesis (light) and respiration (dark) results. The blank-adjusted dissolved oxygen values were standardized to hourly net photosynthesis and respiration rates per gram dry weight of tissue, according to the recommendations of Littler and Arnold (1985). Gross photosynthesis was calculated from the standardized net photosynthesis values in light bottles and respiration obtained from the dark bottles.

### *5. Statistics*

All statistical analyses in this chapter were performed using JMP version 3.1.5 for Apple Macintosh from the SAS Institute Inc., Cary, N.C. Growth and photosynthesis data in the quarterly experiments were tested for normality and heteroscedasticity. I followed significant ANOVA results with Tukey's post-hoc comparison to determine groups with like means.

## **RESULTS**

### *1. Light Regime*

Light and temperature ranges were similar between eastern and western sides of the Bay (Figs. 3&6). Mean daily surface irradiance values ranged from 300 to 900  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  with highest levels during Apr.-May (Fig. 3A). Summer cloud cover reduced total light availability even though higher solar irradiance can occur in the summer. Minimum irradiance occurred in December, when mean light levels fell below saturation levels of the benthic algae studied (Fig. 5, Table 3).

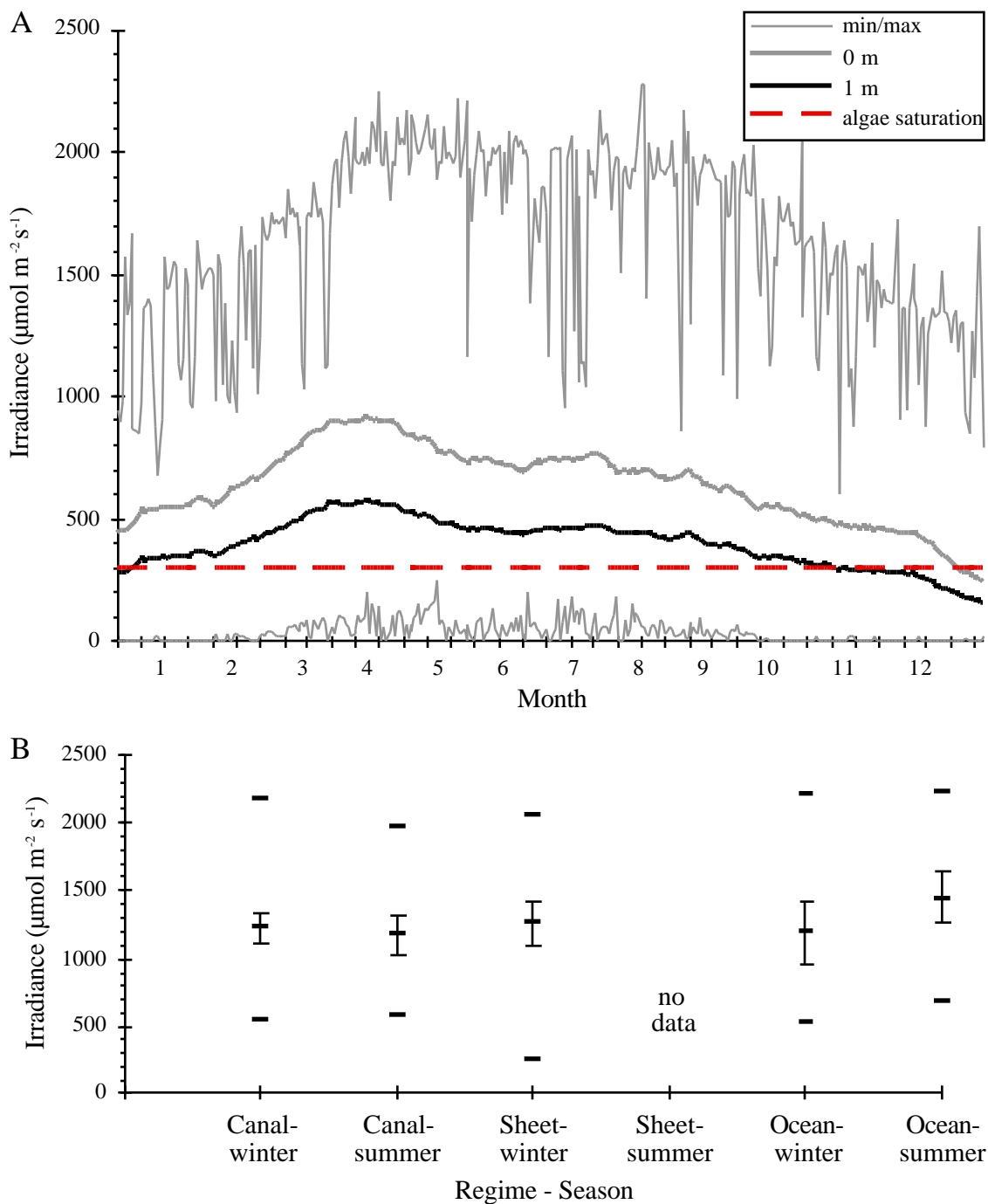


Fig. 3: Average daily irradiance for Biscayne Bay. Fig. 3A shows daily maximum and minimum irradiance values for 1993-96 measured at the water surface at the Fowey C-MAN station. Using the light-attenuation functions in Fig. 4, the mean daily irradiance at 1 m depth was calculated, and this is compared to approximate saturation intensities for the algae studied. Fig. 3B shows mean ( $\pm$ SE), minimum and maximum noon-time benthic irradiance corrected for atmospheric changes at the study sites, measured in winter (Feb.) and summer (Aug.).

Table 2: <sup>a</sup>Two-way ANOVA of noon-time light levels at canal and oceanic sites (fixed factor) and two seasons (fixed factor) presented in Fig. 3B. Because of missing data for summer sheet-flow sites a two-way ANOVA could not be conducted on the entire dataset so site effects were tested with a <sup>b</sup>one-way ANOVA of noon-time light levels at three sites (fixed factor) in winter. Significant results at  $\alpha = 0.05$  are highlighted in bold, and at  $\alpha = 0.1$  are highlighted in italics. Tukey's post-hoc comparison of significant ANOVA results indicate groups that are not significantly different by the same letter.

Source	df	SS	MS	F	P
<sup>a</sup> Site (Si)	1	83553.79	83553.79	3.0338	<b><i>0.0859</i></b>
Season (Se)	1	309981.84	309981.84	11.2552	<b>0.0013</b>
Si x Se	1	235024.27	235024.27	8.5336	<b>0.0047</b>
Error	71	1955419.70	27541.00		

Tukey's	Canal	Ocean		winter	summer
	winter	n.s.	Canal	B	n.s.
summer	B	A	Ocean		A

<sup>b</sup> Site	2	28109.2	14054.60	0.6078	0.5486
Error	49	1133005.3	23122.56		
Total	51	1161114.5	22766.95		

<sup>a</sup>Data are normal (Shapiro Wilk's  $W=0.9781$ ,  $P<0.5212$ ) and homoscedastic (Bartlett's  $F=7.4739$ ,  $P<0.1521$ ),  $n=12-24$ . <sup>b</sup>Data are normal (Shapiro Wilk's  $W=0.9815$ ,  $P<0.7741$ ) and homoscedastic (Bartlett's  $F=0.9836$ ,  $P<0.3739$ ),  $n=12-20$ .

The mean daily light flux at one-meter depth exceeded the saturation irradiance ( $I_k$ ) required for photosynthesis in all three functional groups, except during the month of December (Fig. 3A). Site differences in mid-day benthic irradiance flux were significant in the summer, with light levels higher in the ocean site ( $1447 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) than the canal site ( $1175 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), but were not significantly different in winter (Table 2, Fig. 3B). Seasonal differences were not significantly different in the canal site between the winter dry season ( $1222 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) and summer wet season ( $1175 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) light levels, whereas in the oceanic site there was a significant increase in benthic irradiance in summer (Table 2, Fig. 3B). There were no significant differences among the three regimes in the winter (Table 2, Fig. 3B).

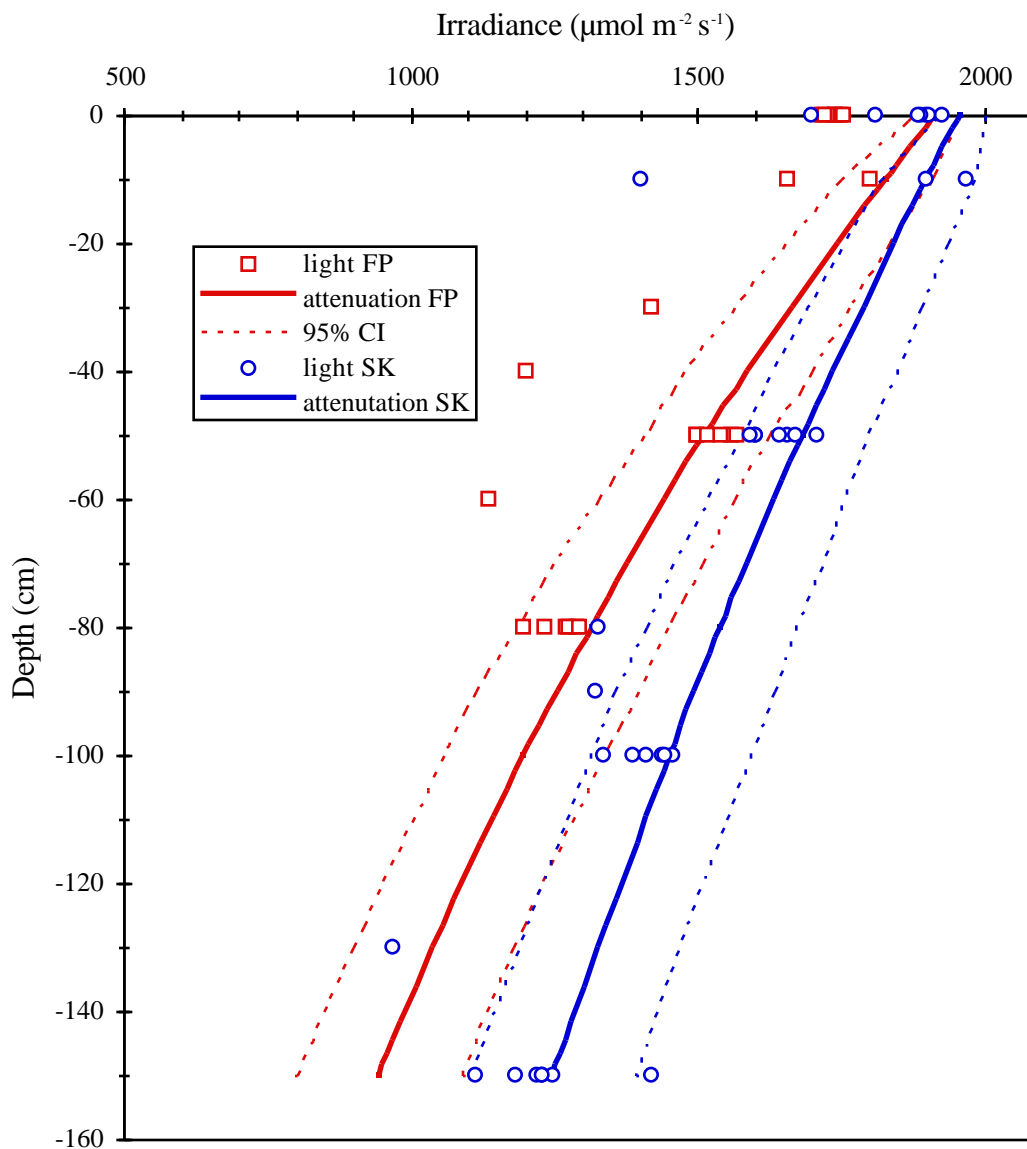


Fig. 4: Light attenuation with depth at a canal site (FP) and an oceanic site (SK) measured at 10 cm depth increments around 12:00 noon on a cloudless day.

Attenuation was less for oceanic ( $k=0.30$ ) compared to canal ( $k=0.47$ ) sites (Fig. 4). These values of  $k$  were somewhat higher than reported previously for *Thalassia* habitats in Florida (Dennison *et al.* 1993). The higher light levels present at Sands Key probably included a large back-scatter component, which can be a significant fraction of total irradiance seen by plants in shallow-water tropical sites with reflective carbonate sediments (Gallegos *et al.* 1990). Light attenuation is a function of the optical properties of the water

column (Kirk 1994), the concentration of phytoplankton and other suspended particles, and for benthic macrophytes, the additional shading effects of both epiphyte cover (Borum and Wium-Andersen 1980; Silberstein *et al.* 1986) and drift algae (Bach 1979; Virnstein and Carbonara 1985). Shading by epiphytes can attenuate the available benthic irradiance by about 30% (Silberstein *et al.* 1986).

## 2. Light Responses

The P-I curves for drift and epiphytic algae (Fig. 5) showed these two groups had productivities ( $P_{\max}$ ) in the summer that were less than half those in the winter (Table 3). In contrast, summer productivities of the two rhizophytic species were about double the winter values (Table 3). The ranges of  $P_{\max}$  measured were between 2-40 mg O<sub>2</sub>·g dry wt<sup>-1</sup>·hr<sup>-1</sup> (Table 3), which agree with previous measurements made in Biscayne Bay for these algae (Jones 1968; Josselyn 1977; Bach 1979). Epiphytes had the highest photosynthesis ( $P_{\max} = 40$  mg O<sub>2</sub>·g dry wt<sup>-1</sup>·hr<sup>-1</sup>), while rhizophytes, particularly *Halimeda*, were least productive ( $P_{\max} = 2$  mg O<sub>2</sub>·g dry wt<sup>-1</sup>·hr<sup>-1</sup>) (Table 3).

Table 3:  $P_{\max}$  and  $I_k$  values for winter and summer for P-I curves.  $P_{\max}$  was calculated as the mean of the light-saturated photosynthetic rates presented in Fig. 5. The intersection of the initial slope ( ) and  $P_{\max}$  is the saturation irradiance,  $I_k$ .

Species	$P_{\max}$ (mg O <sub>2</sub> ·g <sup>-1</sup> ·hr <sup>-1</sup> )	$I_k$ ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )
<b>Winter</b>		
Drift	25	192
Epiphytes	40	117
<i>Halimeda</i>	2	107
<i>Penicillus</i>	5	174
<b>Summer</b>		
Drift	10	298
Epiphytes	15	156
<i>Halimeda</i>	4.5	157
<i>Penicillus</i>	10	272

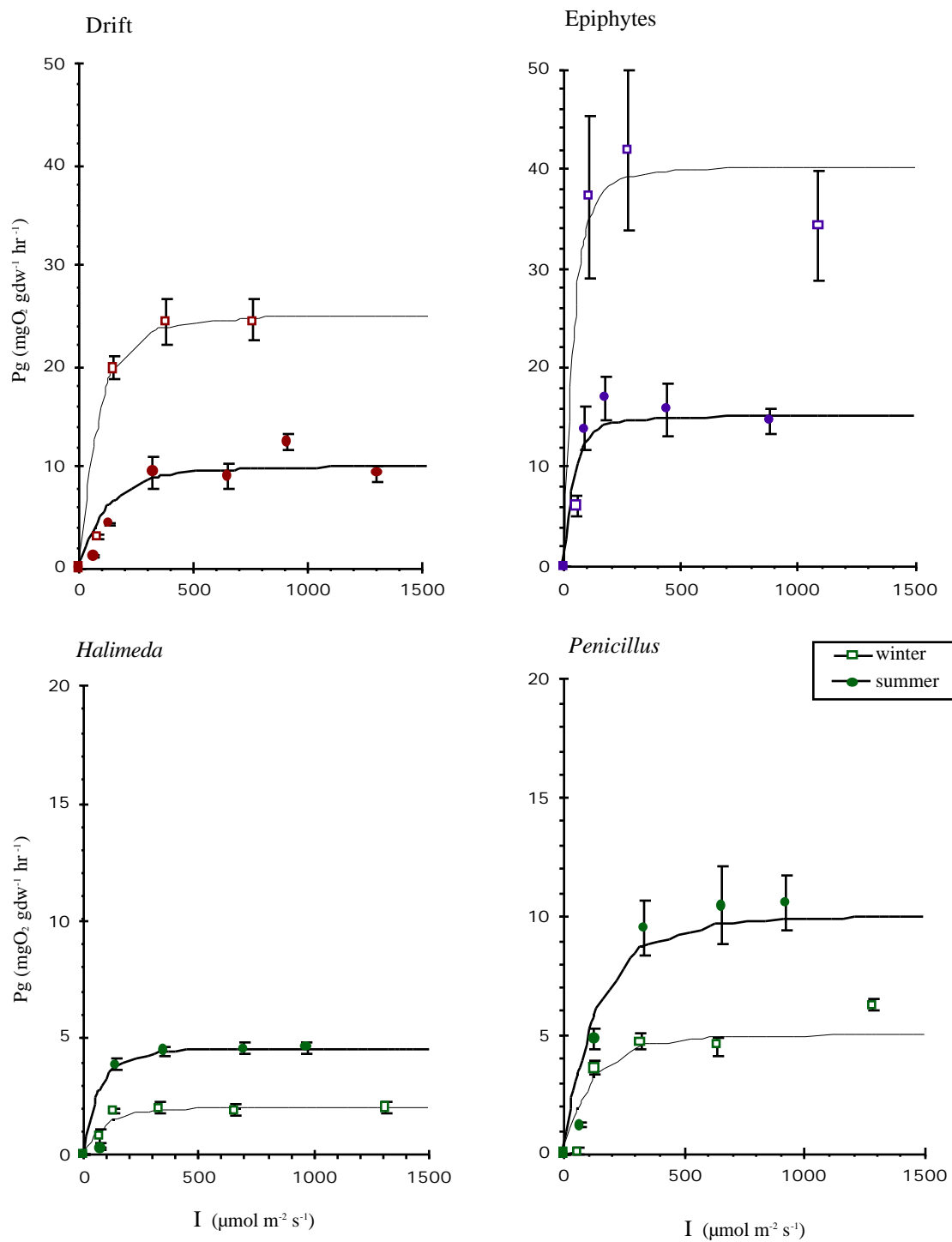


Fig. 5: P-I curves for the three functional groups of algae. Mean ( $\pm$ SD) of five replicate incubations per light level are plotted for the winter (Feb.) and summer (Aug.) experiments. Curves based on the P-I model of Smith (1936) are fitted to the data points. Note the different Y-axis scales among functional groups.

Light saturation ( $I_k$ ) values ranged from 107-298  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , which is somewhat greater than the range of 150-250  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  previously reported for upper- and mid-sublittoral species (Lobban and Harrison 1994). Light saturation intensities ( $I_k$ ) were more similar between seasons and among groups than  $P_{\text{max}}$  values. For all three functional groups, saturation levels ( $I_k$ ) were higher in the summer than the winter (Table 3). Saturation levels were less than 300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for all groups, which is less than the daily average PAR at the study sites over much of the year (Fig. 3A).

### *3. Temperature Regime*

Monthly mean temperature ranged from 18 to 32°C over a typical year (Fig. 6A). Mean monthly temperatures measured at my study sites were almost identical to monthly means measured by DERM over a ten-year period at similar sites. Further, there was little or no difference in mean monthly temperatures among the three salinity regimes: canal, sheet-flow, and oceanic (Fig. 6A). Both surface and bottom water temperatures were measured by DERM. Results of Student's t-test ( $t = -0.512$ ,  $df = 1516$ ,  $P < 0.609$ ) showed there was no significant difference in water temperature with depth, indicating no vertical thermal stratification of the water column.

Data measured hourly with bottom sondes in BNP show high-frequency variations in water temperatures (Fig. 6B). Winter and summer temperature extremes averaged from 12 to 35°C, an annual range of 23°C. Temperature fluctuations in canal sites were greater than at oceanic sites in the winter months. These low-temperature events were associated with winter cold fronts, which bring cold air temperatures and strong winds into South Florida (Chen and Gerber 1990). Rapid changes in the water temperature occurred, especially at

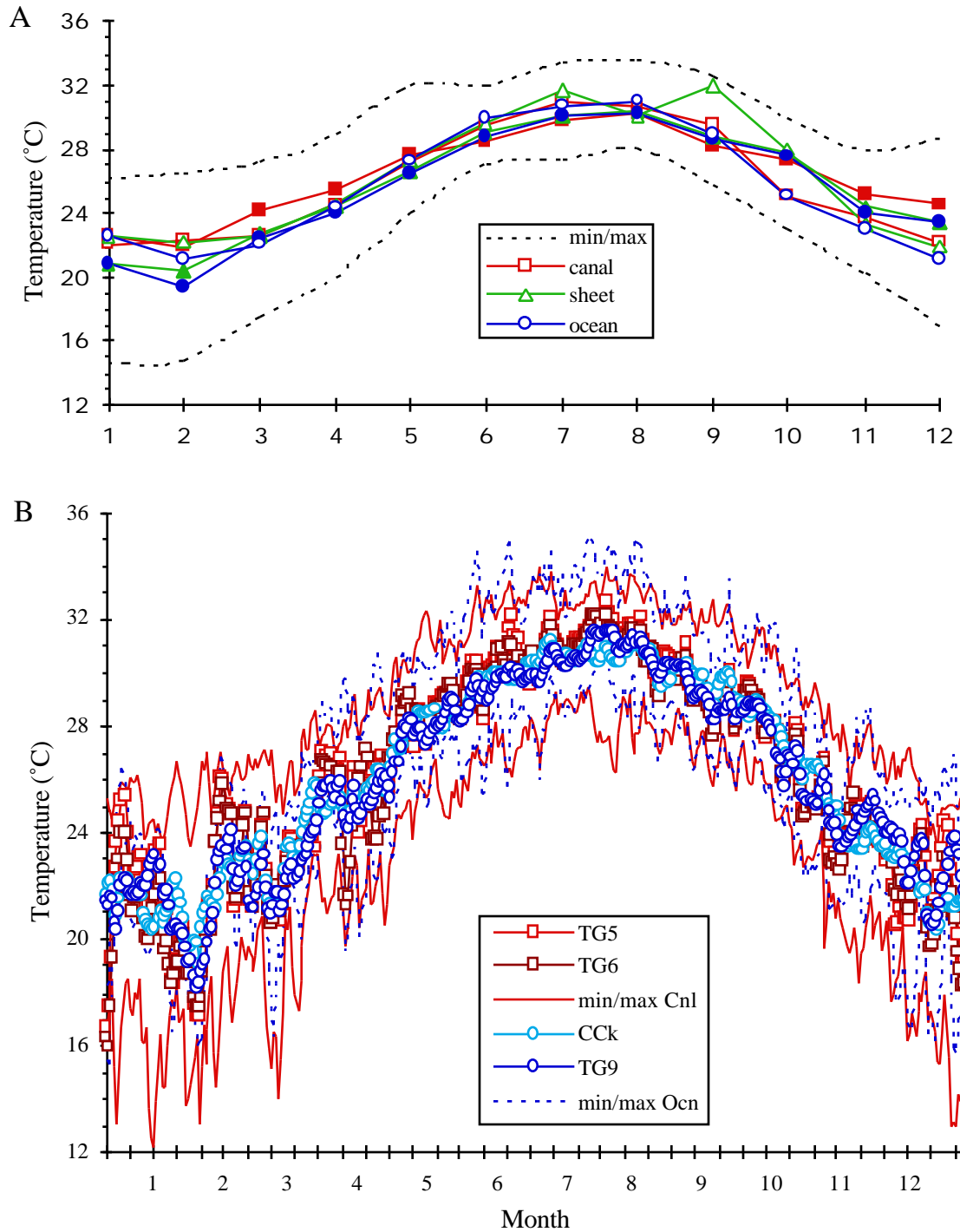


Fig. 6: Water temperatures in Biscayne Bay. Fig. 6A mean monthly values are plotted for CMEA data set 1996-99 (open symbols) and DERM data set 1990-99 (filled symbols) for each regime with minimum and maximum temperatures for the entire data set. Fig. 6B shows mean daily temperatures and minima/maxima measured at two canal (TG5, TG6) and two oceanic (CCK, TG9) sites in BNP (see Table 1 for locations).

shallow sites near canals, because of rapid wind-induced mixing of the water column during the winter months (Fig. 6B). This mixing effect can cause rapid drops in water temperature of  $>5^{\circ}\text{C}$  on the order of 12-24 hr.

#### 4. Temperature Responses

The temperature response curves for growth in all three species of algae show the upper thermal limit to lie between  $31\text{-}34^{\circ}\text{C}$ . *Laurencia*, the main component of drift algae, had a lower upper thermal tolerance ( $27^{\circ}\text{C}$ ) than the two rhizophytic species, *Penicillus* ( $29^{\circ}\text{C}$ ) or *Halimeda* ( $31^{\circ}\text{C}$ ) (Figs. 7A&B). *Halimeda* had a slightly higher upper thermal tolerance limit than *Penicillus*, which has been reported previously (Thorhaug 1976).

High summer seawater temperatures were observed to cause sub-lethal and lethal effects on the drift algae when temperatures exceeded  $27\text{-}28^{\circ}\text{C}$ , both in the field and in the microcosm experiments. The tissues became bleached, and the thallus became flaccid within a few days, followed rapidly by loss of tissue integrity and decay of the thallus. The rhizophytic algae, in contrast, had reduced tolerance to low temperatures with their lower thermal tolerance-limit coinciding with low temperature extremes measured in the Bay ( $12\text{-}14^{\circ}\text{C}$ ), whereas the drift algae were able to tolerate temperatures down to  $5^{\circ}\text{C}$  (Figs. 7A&B).

#### 5. Light x Temperature Interactions

Abiotic variables: Daily light and temperature dynamics in the mesocosm facility during the quarterly multi-factorial experiments are plotted in Figure 8. Mean daily light levels were not significantly different between the seasons (Table 4). The major change in seasonal irradiance was shortened day length in fall and winter compared to longer photoperiods in spring and summer. (Fig. 8A). Mean daily water temperatures, in contrast, were significantly different between seasons (Table 4, Fig. 8B), with cooler water temperatures in fall and winter (= dry season), compared to spring and summer (= wet

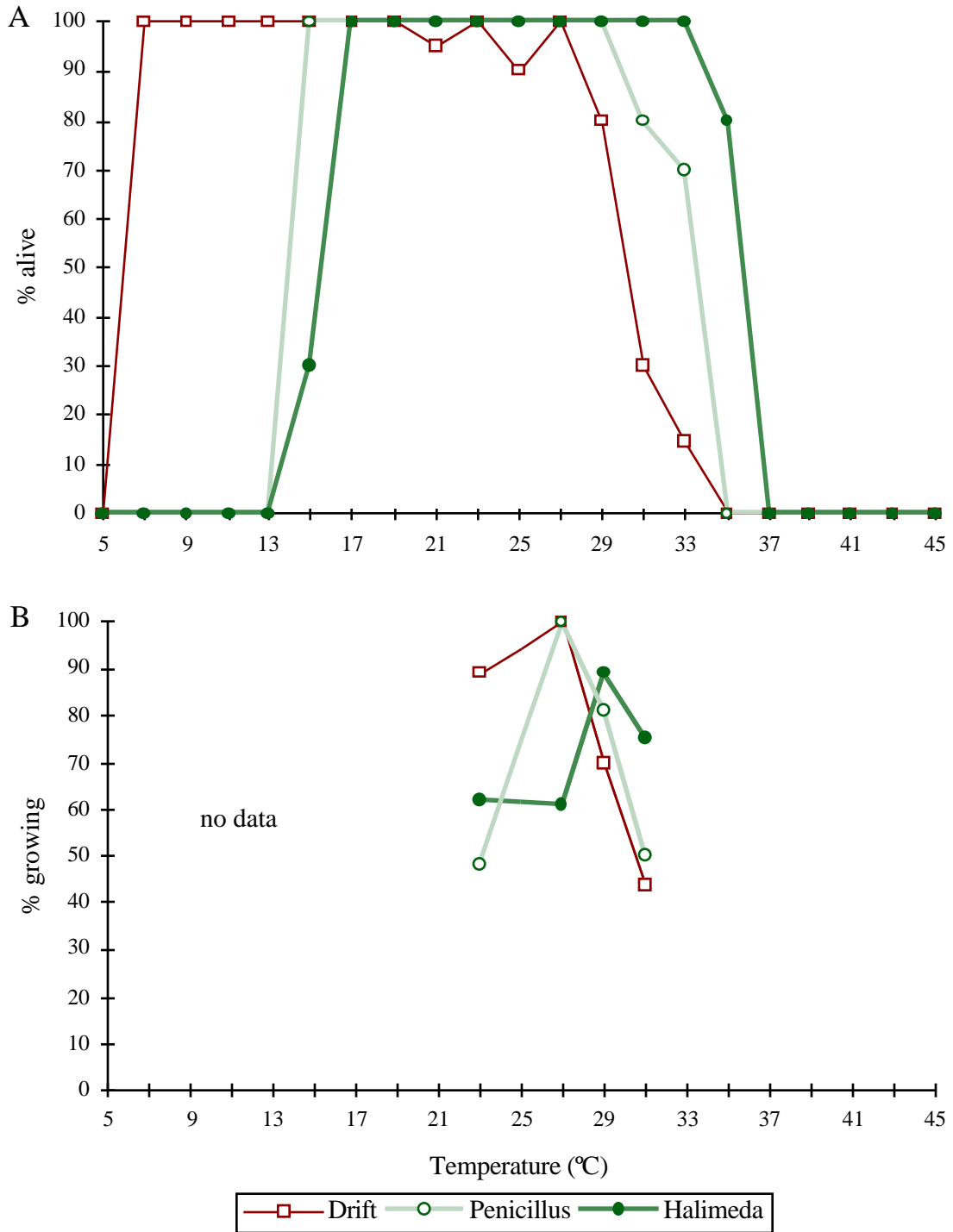


Fig. 7: Temperature response curves for three common algae in Biscayne Bay. Fig. 7A is adapted from data presented in Bader and Roessler (1971). Fig. 7B is based on quarterly growth experiments, as described in the text.

Table 4: Non-parametric Kruskal-Wallis tests on mean daily light levels (n=96-201) and mean daily temperatures (n=25-59) in the microcosms measured in four seasons. Significant results at  $\alpha = 0.05$  are highlighted in bold. Tukey's post-hoc analysis of the temperature data indicates significant differences among the four seasons.

<b>Factor</b>	<b>Source</b>	<b>df</b>	$\chi^2$	<b>P</b>
<b>Light</b>	Season	3	0.3294	0.9544
<b>Temperature</b>	Season	3	141.6130	<b>&lt;0.0001</b>
<b>Tukey's</b> Temperature	<u>spring</u> <b>B</b>	<u>summer</u> <b>A</b>	<u>fall</u> <b>C</b>	<u>winter</u> <b>D</b>

season). In the cooler dry season months, seawater temperatures decreased in the afternoon after mid-day peaks; in contrast, in wet season seawater temperatures continued to increase in the afternoon (Fig. 8B) and did not begin to decrease until after dark.

**Growth:** Mean daily growth rates for drift algae were significantly higher in winter and fall (dry season), when water temperatures were cooler (23-26°C), than spring and summer (wet season), when temperatures were higher (28-31°C) (Table 5, Fig. 9A). Growth rates of the two rhizophytic algae were not significantly different across the range of light levels and temperatures tested (Table 5, Fig. 9A). Daily growth rates of the two rhizophytic species (<0.5% day<sup>-1</sup>) were lower than those of the drift algae (2% day<sup>-1</sup>) with *Halimeda* having negligible growth in all seasons tested (Fig. 9A).

**Photosynthesis:** Photosynthetic rates agreed qualitatively with the growth rate data. Drift and epiphytes both had significantly higher photosynthetic rates in the cooler dry season months than in the warmer wet season months (Table 6, Fig. 9B). For drift algae, photosynthesis ranged from 15-20 mgO<sub>2</sub>·gdw<sup>-1</sup>·hr<sup>-1</sup> in the dry season, but only 9-13 mgO<sub>2</sub>·gdw<sup>-1</sup>·hr<sup>-1</sup> in the wet season (Fig. 9B). The epiphytes had a mean productivity of 24 mgO<sub>2</sub>·gdw<sup>-1</sup>·hr<sup>-1</sup> in the dry season, compared with 5 mgO<sub>2</sub>·gdw<sup>-1</sup>·hr<sup>-1</sup> in the wet season (Fig. 9B). Photosynthetic productivity in *Penicillus* and *Halimeda* showed different seasonal patterns for each species. In *Penicillus*, significantly higher photosynthesis was

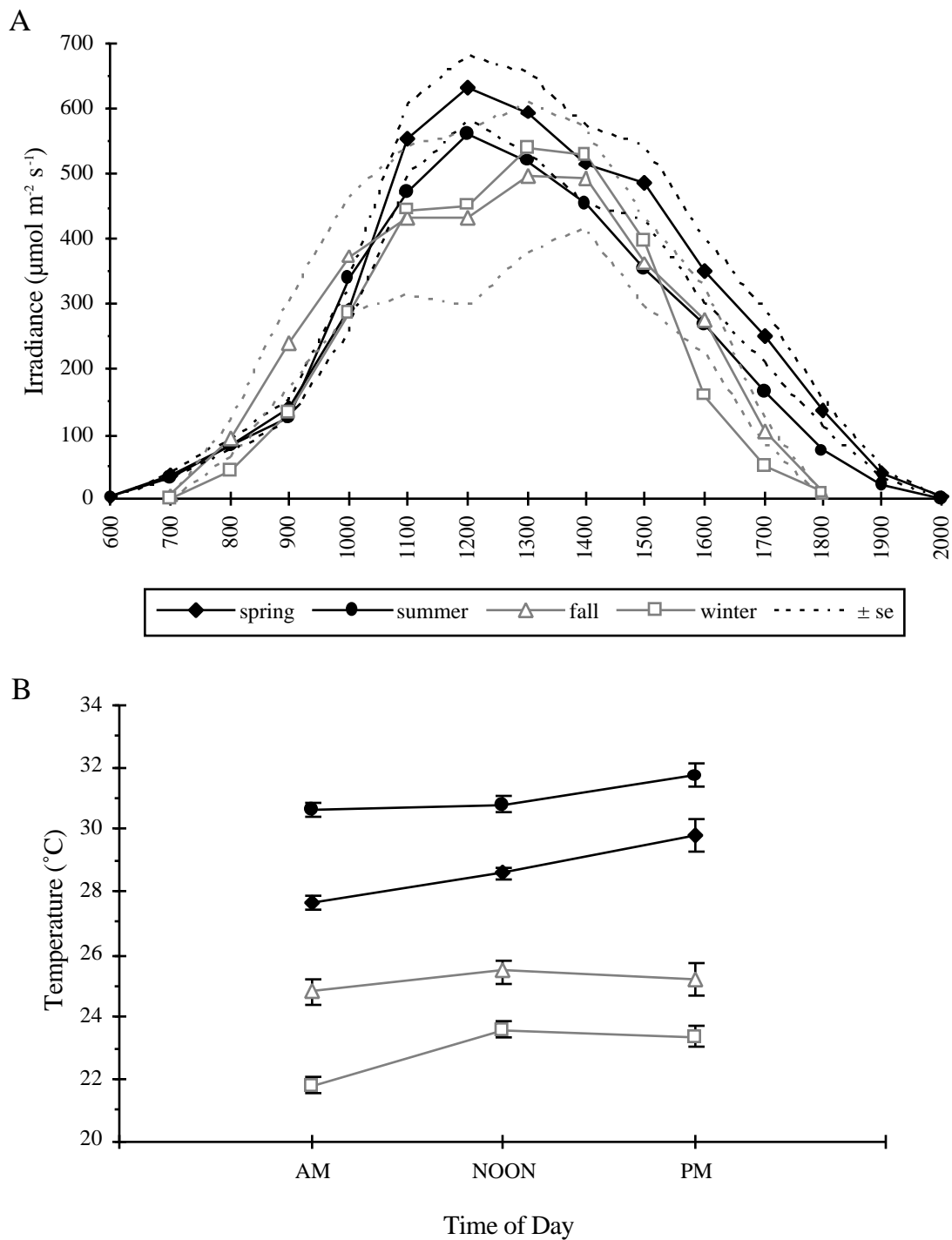


Fig. 8: Seasonal light levels and temperatures during the quarterly multi-factorial experiments. Fig. 8A shows the mean hourly irradiance values over 8-10 days plotted for each quarter, along with the SE for the dry and wet season conditions. In Fig. 8B, the mean ( $\pm$ SE) temperatures are plotted for measurements made three times a day.

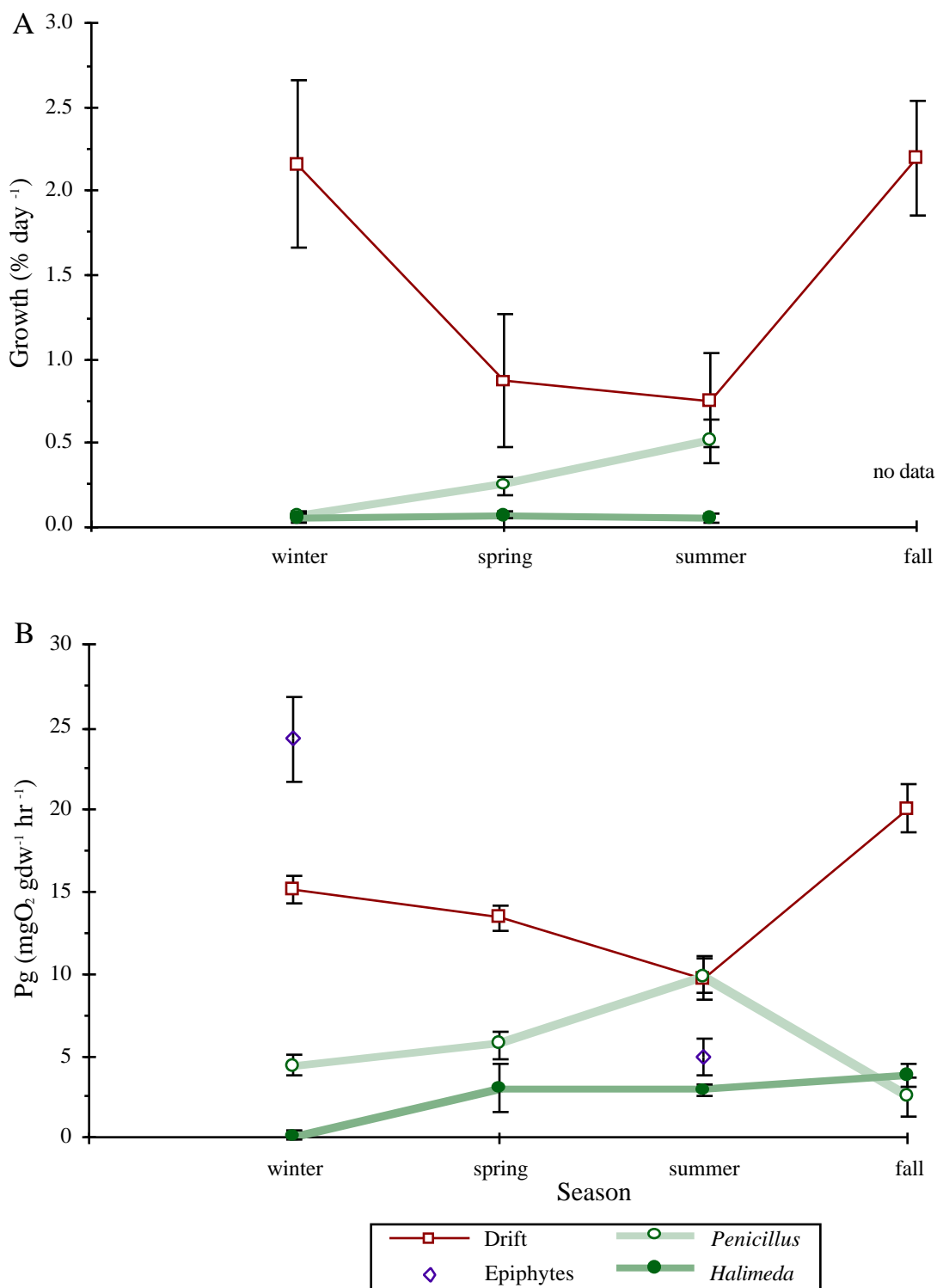


Fig. 9: Mean ( $\pm$ SD) daily growth (Fig. 9A) and photosynthesis (Fig. 9B) of three functional groups of algae.

Table 5: Non-parametric Kruskal-Wallis tests on growth rates by season (fixed factor) of the three groups of algae (n=8-9) presented in Fig. 9A. Significant results at  $\alpha = 0.05$  are highlighted in bold. Tukey's post-hoc analysis of the growth data indicates significantly higher growth in the dry season for the drift algae.

<b>Algae</b>	<b>Source</b>	<b>df</b>	$\chi^2$	<b>P</b>
Drift	Season	3	10.6963	<b>0.0135</b>
<i>Penicillus</i>	Season	2	4.0123	0.1345
<i>Halimeda</i>	Season	2	1.1113	0.5737

<b>Tukey's</b>	<u>spring</u>	<u>summer</u>	<u>fall</u>	<u>winter</u>
Drift	<b>B</b>	<b>B</b>	<b>A</b>	<b>A</b>

Table 6: Non-parametric Kruskal-Wallis tests on photosynthesis by season (fixed factor) of the three functional groups of algae presented in Fig. 9B. Drift (n=8-12), epiphytes (n=25), *Penicillus* (n=8-10), *Halimeda* (n=8-10). Significant results at  $\alpha = 0.05$  are highlighted in bold. Tukey's post-hoc analysis of the photosynthesis data indicates significantly higher means in the shaded cells.

<b>Algae</b>	<b>Source</b>	<b>df</b>	$\chi^2$	<b>P</b>
Drift	Season	3	18.0953	<b>0.0004</b>
Epiphytes	Season	1	28.5756	<b>&lt;0.0001</b>
<i>Penicillus</i>	Season	3	15.3972	<b>0.0155</b>
<i>Halimeda</i>	Season	3	10.3953	<b>0.0155</b>

<b>Tukey's</b>	<u>spring</u>	<u>summer</u>	<u>fall</u>	<u>winter</u>
Drift	<b>B</b>	<b>BC</b>	<b>A</b>	<b>B</b>
Epiphytes		<b>B</b>		<b>A</b>
<i>Penicillus</i>	<b>B</b>	<b>A</b>	<b>B</b>	<b>B</b>
<i>Halimeda</i>	<b>AB</b>	<b>AB</b>	<b>A</b>	<b>B</b>

measured in the wet season trial ( $10 \text{ mgO}_2 \cdot \text{gdw}^{-1} \cdot \text{hr}^{-1}$ ), compared to the dry season experiments ( $2.5\text{-}4.5 \text{ mgO}_2 \cdot \text{gdw}^{-1} \cdot \text{hr}^{-1}$ ), whereas for *Halimeda* photosynthesis was significantly greater in the dry season trial ( $3 \text{ mgO}_2 \cdot \text{gdw}^{-1} \cdot \text{hr}^{-1}$ ), compared to the wet season experiments (Fig. 9B).

## DISCUSSION

### Light

#### *P-I Curves*

Analysis of the P-I relationship yields estimates of the saturation irradiance ( $I_k$ ) required for maximum photosynthesis ( $P_{\max}$ ). These values vary over time because of acclimation by the plants to ambient light and temperature levels (Markager and Sand-Jensen 1994). When irradiance changes,  $I_k$  changes within 24-48 hr as the plant adapts to the altered light levels by increasing the number or size of the PSUs (Harrison 1988). Additionally, acclimation to changes in temperature can occur in a few days via changes in enzyme concentrations (Steeman-Nielsen 1975). This makes comparisons of  $I_k$  and  $P_{\max}$  values measured here, with reports in the literature difficult, as it is rare that experiments are conducted under identical conditions, even by the same investigator! Even so, the values for  $I_k$  for the three functional groups in this study lie within the range previously for tropical marine algae (Gordon *et al.* 1980; Abel and Drew 1985; Mathieson and Dawes 1986; Littler *et al.* 1988; Pollard and Kogure 1993). At saturating irradiances,  $P_{\max}$  increased about a factor of two (range = 1-4) when performance of summer and winter plants were compared under otherwise identical conditions.

Rhizophytic algae - Summer-adapted plants of *Halimeda* and *Penicillus* had higher  $P_{\max}$  than winter plants of the same species. At light-saturated levels, *Halimeda*  $P_{\max}$  decreased at temperatures above 30°C because of an increase in respiration, an indication of temperature stress (Abel and Drew 1985). Furthermore, shallow-water *Halimeda* plants

have been found to be tolerant of higher temperatures ( $>30^{\circ}\text{C}$ ) than deep-water individuals of the same species (Abel and Drew 1985).

Drift algae and Epiphytes - The P-I curves for drift and epiphytes show the opposite seasonal response in  $P_{\max}$  compared to the rhizophytes. This is probably caused by an even greater increase in respiration compared to net photosynthetic rates in the summer, because temperatures are above the optimal zone of tolerance for these two functional groups. The gross photosynthesis results may partially explain the seasonal standing stock biomass patterns presented in Chapter 2, with drift algae more abundant during cooler periods, when they are more productive.

A reduction in  $P_{\max}$  with increasing water temperatures has been reported before by Penhale (1977) for epiphytes of seagrasses in North Carolina, with higher summer seawater temperatures causing a reduction in  $P_{\max}$ . Similarly for drift algae, Mathieson and Norall (1975) studying subtidal red algae, found that at a given irradiance, gross photosynthesis of several species was found to be maximal at lower temperatures in winter specimens, with a reduction occurring at higher summer temperatures. In contrast, in the temperate-tropical red alga *Gracilaria*, Lapointe *et al.* (1984) found that  $P_{\max}$  increased with temperature but was not significantly different in the range of  $20\text{-}30^{\circ}\text{C}$ , and decreased significantly below  $20^{\circ}\text{C}$ . The small effect of temperature on gross photosynthesis between  $20\text{-}30^{\circ}\text{C}$  was interpreted to imply that light is the important factor governing growth during the summer (Lapointe *et al.* 1984). In contrast in winter, when temperatures dropped below  $20^{\circ}\text{C}$ , then temperature became limiting as it depressed enzymatic photosynthetic rates (Lapointe *et al.* 1984). Seasonal growth and photosynthesis of the algae studied in Biscayne Bay were influenced more by temperature than by light because temperature had more of an influence on the value of  $P_{\max}$ .

### *Photosynthesis and Growth*

Growth and photosynthetic production rates of all three functional groups investigated lie within the range of values previously reported for tropical marine algae in the Caribbean and elsewhere (Dawes *et al.* 1976, 1978; Buesa 1977; Arnold and Murray 1980; Lapointe and Duke 1984; Lapointe *et al.* 1984; Dhargalkar 1985; Bay *et al.* 1985). Bach (1979) reported growth rates of 0.4-0.9% day<sup>-1</sup> for *Halimeda incrassata*, somewhat higher than values found in this study (0.1-0.6% day<sup>-1</sup>), but the upper value agrees with growth data from the Great Barrier Reef (Drew and Able 1983). Growth rates for *Penicillus capitatus* in Florida Bay ranged from 1-3.5% day<sup>-1</sup> (Stockman *et al.* 1967), again results from these investigations lie in the lower end of this previously reported range. Drift algae and epiphytes had higher growth rates than the rhizophytes, ranging from 1.0-2.5% day<sup>-1</sup> compared with previously recorded values of 1.0-12% day<sup>-1</sup> in South Florida (Josselyn 1977; Thorhaug and Marcus 1981; Delgado and Lapointe 1994).

The functional-form model proposed by Littler and Littler (1980) may explain much of the difference in productivity seen among the three groups of algae. Kanwisher (1966) proposed that algae with a greater percentage of structural tissue should have lower biomass-specific photosynthetic rates. Correlations between seaweed morphology and rates of maximal photosynthesis support this idea (Littler 1979; Arnold and Murray 1980; Steneck and Dethier 1994).

In terms of the functional-form classification, productivity is higher in sheet-like forms with high surface-to-volume ratios, compared to more corticated forms (Littler 1979). Large fleshy and calcified macroalgae had biomass specific net productivity less than half that of algal turfs. The decrease in weight-specific productivity could be attributed to an increase in thallus complexity (Morrisey 1985). *Cladophora* mats studied by Gordon *et al.* (1980) exhibited the high productivity levels for filamentous, branched morphologies predicted by the functional-form model. Buesa (1977) also found that epiphytic red and

green algae had high rates of primary productivity, greater than rates in corticated and fleshy macroalgae, like the drift algae.

Among the thallus types, calcareous algae had the lowest biomass specific primary production because of the high proportion of structural  $\text{CaCO}_3$  and low thallus surface area-to-volume ratios (Borowitzka and Larkum 1976a,b; Morrisey 1985). However, Payri (1988) correctly pointed out that when productivity is expressed per gram dry weight the contribution of calcified algae to total algal productivity is underestimated because of the high level of  $\text{CaCO}_3$  inorganic matter (up to 90% dry weight) in the thallus. The estimated production of *Halimeda* expressed on an AFDW basis shows that *Halimeda* productivity is not significantly different from that calculated for non-calcified fleshy macroalgae (Payri 1987, 1988). In this dissertation *Penicillus* and *Halimeda* had similar rates of photosynthesis, as also reported previously by Goreau (1963), therefore, on a decalcified-weight basis the productivity of these two rhizophytic algae is likely to be similar to the drift algae.

Measurements of photosynthetic production in the calcified siphonaceous green algae can be further complicated by the diel migrations of the chloroplasts (Drew and Abel 1988). Chloroplasts of *Halimeda* are normally located in the surface utricles in a position to receive maximum light. However, the plant responds to injury, such as cutting branches for use in experiments, and darkness, by retracting the chloroplasts from the peripheral utricles into the central medullary filaments. This leaves the segments bleached in appearance, and reduces photosynthetic rates. Chloroplasts, which move deeper into the matrix away from the surface, may become shaded by the calcium carbonate skeleton, further reducing photosynthesis (Abel and Drew 1985; Drew and Abel 1983, 1988).

#### *Light and Temperature Interactions*

Light and temperature can have synergistic interactions on the photosynthesis and growth rates of algae. For instance the drift alga, *Laurencia poiteaui*, grown under a range

of temperatures from 20-27°C and light intensities of 40-174  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  was found to grow most rapidly at high light (134-174  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) and low temperatures (20 °C), with biomass doubling in 12 days (Thorhaug and Marcus 1981). At the same light levels but at higher temperatures (27 °C), biomass increased only 50% over the same time (Thorhaug and Marcus 1981). This response was evident in the drift algae during the warmer summer trials, with reduced growth even under increased irradiance.

The combination of irradiance and day length can significantly affect seasonal macroalgal biomass (Fong and Zedler 1993). Josselyn (1975) summed up the seasonal dynamics of *Laurencia poiteaui* in relation to light and temperature as follows:

It appears that optimal temperatures for growth (20-25°C) occur during the winter and early spring months. However, during the winter the lower solar irradiance combined with turbidity created by the passage of cold fronts, limits the light available. During spring, temperatures still remain near optimal, and with increasing solar irradiation, rapid growth takes place. The high water temperatures during the summer and fall may stress the plants, but growth may occur under certain light and nutrient conditions. Increased growth may occur again in the late fall when optimal temperatures are reached, and while subsurface light intensity remains sufficient.

Temperature influences algal growth rates by affecting chemical reaction rates that contribute to (photosynthesis) or take away from (respiration, excretion) the overall growth process. A lack of correlation between growth and photosynthesis can occur when high rates of photorespiration and excretion at high temperatures result in lower levels of carbon being allocated to growth (Lapointe *et al.* 1984; Frank and Dubinsky 1999). This “hidden” loss of carbon, normally allocated to growth, illustrates why instantaneous measures of net photosynthesis cannot always be equated to growth (Lapointe *et al.* 1984; Frank and Dubinsky 1999). The maximum temperature for growth is therefore less than for photosynthesis, and this suggests that growth at high temperatures is costly in terms of increased respiration and excretion (Lapointe *et al.* 1984).

High temperatures in combination with high irradiances often lead to photo-inhibition, which can be harmful to photosynthesis and plant survival (Biebl 1970). Tolerance of high irradiance levels by tropical subtidal algae, without photo-inhibition, have been reported for

the red algae *Laurencia* (Mathieson and Dawes 1986), *Hypnea* (Dawes *et al.* 1976), and *Gracilaria* (Dawes *et al.* 1978), and for numerous green algae (Mathieson and Dawes 1975), including *Halimeda* (Littler *et al.* 1988) and *Cladophora* (Gordon *et al.* 1980). No photo-inhibition was observed in the algae I studied.

## Temperature

Tropical flora and fauna can be thought of as “living on the edge”. Optimal growth conditions are close to their upper thermal tolerance limits, which are within a couple of degrees of the mean ambient summer temperatures (Biebl 1962; Moore 1972; Thorhaug 1976). This thermal stress effect may make tropical organisms more susceptible to additional stressors, compared to their temperate counterparts (Moore 1972).

Time-temperature relationships are important in determining the magnitude of thermal stress effects; for example, short periods at an elevated temperature may be more important than a longer time period at a slightly lower temperature (Thorhaug *et al.* 1971). However, short-term thermal tolerance can exceed seasonal tolerance limits without long-term adverse consequences; for instance, in several species of *Gracilaria*, McLachlan and Bird (1984) reported that for short periods, growth continues even above the long-term upper survival range.

The temperature response for growth was a more sensitive indicator than death as an endpoint. Temperature tolerances of the algae studied were found to be consistent with previous reports from southern Biscayne Bay (Bader and Roessler 1971, 1972; Thorhaug 1974, 1976; Thorhaug *et al.* 1979). From Thorhaug 1974:

Mean standing crops of algae in Card Sound show temperature dependence, with maximum standing stock biomass occurring between 30-31°C. The percentage of senescent or unhealthy individuals was highest at 33-34°C. The standing crop of *Penicillus capitatus* peaked at 29-31°C and declined markedly above 32°C. *Halimeda incrassata* was maximal at 31-32°C and also declined abruptly above that temperature. *Laurencia poiteaui*, the major red alga, was not found above 32°C. After 3 to 10 days exposure to temperatures between 31 and 33°C these macrophytes became far less productive and many died, especially *Laurencia*. None of the macroalgae survived above 34°C.

Field data from Card Sound indicated that upper thermal limits are a few degrees less than those reported in laboratory studies for these species (Thorhaug 1976).

Drift algae - From other studies on the seasonal abundances of tropical algae, approximate temperature responses can often be inferred. The biomass of *Laurencia* was found to be greatest when temperatures dropped below 24°C and was least in summer at higher temperatures (Josselyn 1977; Thorhaug and Marcus 1981). Optimal temperatures for growth in this genus occurred between 20-25°C (Josselyn 1975). The reduced upper thermal limits may indicate a historical temperate affinity (Lüning 1990), possibly reflected in the tropical into temperate distribution of the genus *Laurencia* (Schneider and Searles 1991; Littler and Littler 2000).

Similar trends in seasonal growth with higher biomass in cooler temperatures have been reported for other rhodophytes, including *Hypnea* (Schenkman 1989) and *Gracilaria* (Lapointe *et al.* 1984). *Laurencia* appears to follow a seasonal adaptation strategy (*sensu* Lüning 1990), whereby the temperature tolerance range is seasonally adjusted, resulting in a slight time-lag in growth with regard to the ambient temperature. Abrupt changes in temperature (e.g., winter cold fronts) outside the acclimation range of the alga can result in lag periods in growth until the plants become re-acclimated (Lapointe *et al.* 1984).

Rhizophytic algae - In contrast, growth rates of the green rhizophytic algae *Halimeda incrassata* and *Penicillus capitatus* were maximal in the late summer, as has been reported previously (Bach 1979; Payri 1988; Garrigue 1991). This is related to higher light intensities and temperatures. The optimal temperature for growth in the genus *Halimeda* has been reported as 27-29°C (Hillis-Colinvaux 1980). *Halimeda incrassata* can tolerate slightly higher temperatures than *Penicillus capitatus* (Thorhaug 1976). Photosynthesis and growth were reduced in the winter, resulting from dormancy during these colder months (Wefer 1980, Payri 1987). Winter cold fronts bring low water-temperature extremes, which are more evident in shallow-water canal sites, and this may partially explain why rhizophytic algae occurred in low abundance at canal sites (see Chapter 2).

Seagrass Epiphytes - The temperature tolerance of seagrass epiphytes is poorly studied. As many species of drift algae in Biscayne Bay initially grow as epiphytes (Humm 1964), it may be inferred that temperature responses are similar. Penhale (1977) noted that rates of photosynthesis of epiphytes increased with temperature in a temperate *Zostera* community, and were highest in the late summer and fall. Epiphyte photosynthesis in Indian River lagoon was also higher in the summer (July) than the spring (March) (Heffernan and Gibson 1983), although still lower than rates reported for Biscayne Bay (Jones 1968).

## **SUMMARY**

Light is a complex abiotic variable, which varies over a wide range of time scales. Saturation intensities (mean  $I_k$  approx.  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) for all three functional groups were similar. Drift and epiphytic algae had higher photosynthetic productivity in the winter dry season and grew better at lower water temperatures (20-25°C). The rhizophytic species grew optimally in the wet season at high summer water temperatures (28-30°C). Low temperature tolerance ranged from <10°C for *Laurencia* to 12-14°C for the rhizophytic species, while upper lethal limits were 32-34°C for all groups. Light and temperature interacted to alter the seasonal photosynthetic and growth rates of the algae studied, with temperature the more important effect.