THE LIGHT REQUIREMENTS FOR GROWTH AND PHOTOSYNTHESIS IN SEAGRASSES WITH EMPHASIS ON TEXAS ESTUARIES: A LITERATURE SURVEY

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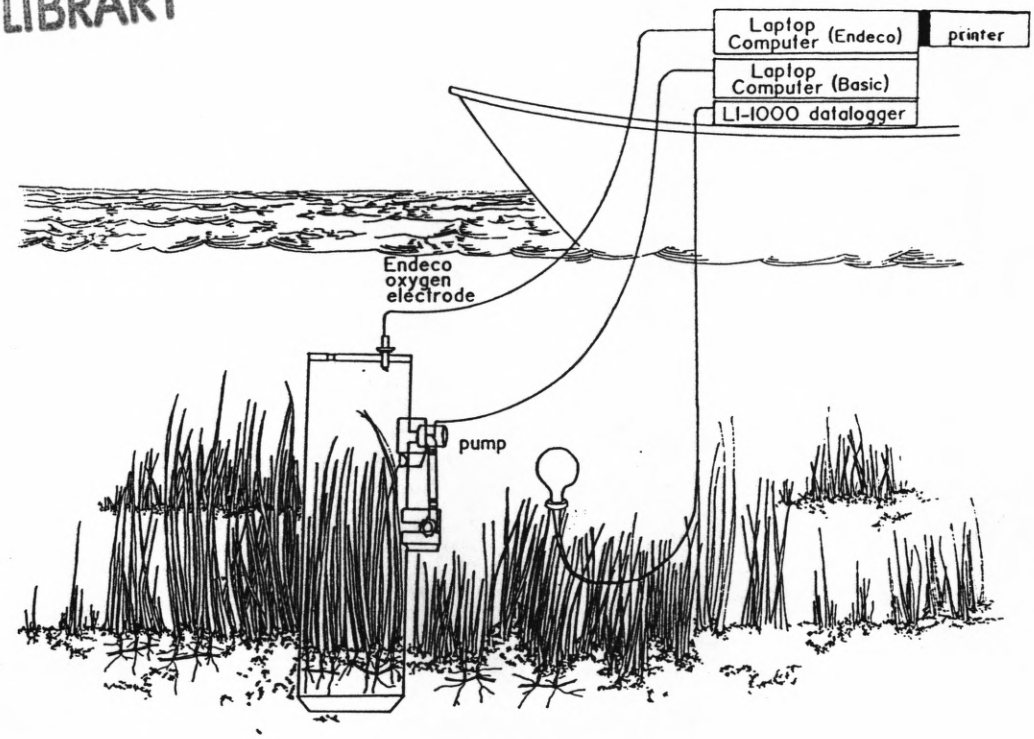

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Executive Summary

Seagrasses have been repeatedly demonstrated to be highly valuable components of coastal systems. They have high rates of primary productivity and support a diverse assemblage of consumers as well as rapidly cycling ecologically important elements such as carbon, nitrogen, phosphorus and sulphur. The high primary productivity of seagrass systems supports many commercially and recreationally important species. In addition, they also act to modify the deposition of sediments, remove nutrients, attenuate wave energy and reduce currents. In general, seagrass ecosystems are a cornerstone of healthy, productive bays and estuaries.

During the last 20 years, seagrass communities throughout the world have experienced decreased productivity and distribution. These declines have often been attributed to decreased water transparency as a result of turbidity or shading by epiphytic algae. Epiphytic shading is often an indication of nutrient enrichment caused by anthropogenic inputs. Although both epiphytes and turbidity occur as natural phenomena, human activities can exacerbate existing natural conditions with adverse effects on seagrass communities.

The objectives of this study were (a) to review the existing literature and data available on the effect of natural and anthropogenic factors on the underwater light environment; (b) to examine the relationship between light and seagrass distribution and productivity; and (c) to make recommendations on how to protect seagrass habitats in Texas bays and estuaries. To meet these goals, we have examined the available literature,

Table 1. List of all submerged aquatic plant species (in italics) cited in the text. Species are listed by family and include the author who first described each species (not shown in italics).

Seagrasses
Cymodoceaceae
Amphibolis antarctica (Labill.) Sonder ex Aschers.
Cymodocea nodosa (Ucria) Aschers.
Halodule wrightii Aschers.
Syringodium filiforme Kützing
Hydrocharitaceae
Enhalus acoroides (Linnaeus f.) Royle
Halophila decipiens Ostenfeld
Halophila engelmannii Aschers.
Halophila johnsonii Eisman
Halophila stipulaceae (Forsk.) Aschers.
Thalassia testudinum Banks ex König
Posidoniaceae
Posidonia angustifolia Cambridge et Kuo
Posidonia australis Hook. F.
Posidonia oceanica (L.) Delile
Posidonia sinuosa Cambridge et Kuo
Zosteraceae
Heterozostera tasmanica (Martens ex Aschers.) den Hartog
Phyllospadix scouleri Hooker
Phyllospadix torreyi S. Watson
Zostera angustifolia (Hornem.) Reichb.
Zostera marina L.
Zostera muelleri Irmisch ex Aschers.
Freshwater and Estuarine Plants
Hydrocharitaceae
Elodea canadensis Michx.
Vallisneria americana Michx.
Potamogetonaceae
Potamogeton pectinatus L.
Potamogeton perfoliatus L.
Ruppia maritima L.

emphasizing the physiological response of seagrasses to light and temperature. By using data and observations collected on a variety of species (Table 1) from around the world we may be better able to define the light requirements of Texas seagrasses. A knowledge of the minimum annual light requirements for seagrass growth is necessary to maintain the current distribution of Texas species. This information will also be required in the development of a management plan that permits the expansion and establishment of new seagrass habitat.

Five species of seagrasses from three families comprise the submerged vascular flora of the Texas bays and estuaries, encompassing some 209,738 acres (Onuf 1993). Most of these species have tropical or sub-tropical affinities and are near the northern end of their distribution in Texas. One species, *Ruppia maritima*, is considered cosmopolitan and occurs as far north as New Hampshire, while *Halodule wrightii* occurs as far north as North Carolina. Most seagrasses are perennial; however, *Ruppia* has been reported as both an annual and a perennial in some Texas estuaries. Although flowering in *Thalassia testidinum* has been documented only once in Texas (Phillips *et al.,* 1981), all five seagrass species are known to flower and set seed.

Lunar tides seldom exceed 15 cm in Texas bays and estuaries, and therefore are heavily influenced by local meteorology. Meterological events (particularly winds and storms) also control the turbidity of the bays along the Texas coast. However, anthropogenic factors can also influence turbidity. Dredging activities can increase light attenuation and prevent the plants from receiving their daily minimum light requirements for growth and survival. In Texas, increased turbidity as a result of dredging and

construction appears to be the largest threat to seagrasses. Presently, other anthropogenic influences such as eutrophication, which results from increased nutrient loading, occurs only in a few localized areas (i.e. portions of the Galveston Bay System and Copano Bay). However, as the human population of Texas coastal zone increases, so does the threat of eutrophication.

Several recent publications have proposed a novel method for assessing water quality in estuarine systems (Batuik *et al.,* 1992; Dennison *et al.,* 1993). The basic premise of the technique is that plants will not grow in areas where their habitat requirements (i.e. light, nutrients etc.) are not adequatly met. Thus, if the minimum habitat requirements are known, the parts of the system that are not meeting the minimum requirements can be inferred using mapping techniques. Some aspects of this technique may be appropriate for use in Texas systems, but many are not. This is a result of the management history of each estuarine system; Chesapeake Bay is highly impacted, and the goals are to restore and conserve the remaining resources. Texas systems, with some exceptions, are relatively pristine and preservation of the existing seagrass habitats is the major goal.

In general, lower irradiance results in reduced density and biomass of seagrasses. Laboratory and field studies show that seagrasses may also respond to a drop in irradiance by altering their morphology. The minimum light requirements of seagrasses can be quantified through measurement of the daily minimum number of hours of saturating irradiance (H_{sat}) needed to meet their respiratory demands. The H_{sat} value for some seagrasses (i.e. *Zostera marina*) may approach 6 h to maintain a positive carbon balance; however, the H_{sat} requirements for most Texas species have not been determined. In Texas,

Halodule wrightii has recently been shown to have an H_{sat} of 3 to 5 h (Dunton, submitted). A review of the literature suggests that most seagrass species, including those along the Texas coast, require 10 to 20% of surface irradiance as an absolute minimum during most of the year.

Although light is a critical factor controlling seagrass growth and distribution, temperature is also important. A light level that is photosynthetically saturating (I_k) at low temperatures may be the compensating irradiance (I_c) at a higher temperatures. As a result of seasonal variation in temperature, most seagrasses exhibit seasonal patterns with respect to productivity, P vs. I parameters and organic composition. The temporal dynamics of seagrasses are such that the winter appears to be a period of low physiological activity, while the extent of photosynthetic activity in spring, summer and fall determine the long-term success of a species. We recommend that human disturbance be kept to a minimum during critical periods of seagrass growth, which is greatest during spring and early summer.

CHAPTER 1: INTRODUCTION

The Texas seagrass flora

Seagrasses are flowering plants which re-invaded the marine environment. The earliest fossils of seagrasses date from the Cretaceous -- about 140 million years ago (den Hartog, 1970). Unlike the algae, which are in the Kingdom Protista, seagrasses are vascular plants that have xylem and phloem elements for the transport of water and photosynthate (Pedersen and Sand-Jensen 1993, Barnabas and Arnott 1987, Barnabas 1989, 1991). These plants also differ from algae in the degree of cellular differentiation and organization; seagrasses have true roots, stems, and leaves. Algae do not possess these organs.

As marine angiosperms (flowering plants), seagrasses complete their life-history underwater. They reproduce sexually by flowering and vegetatively by rhizome branching. Rhizome branches, formed by the initiation of axillary meristems, may become physiologically independent and create new plants. In plants, sexual reproduction occurs via flowering and pollen exchange. To exchange pollen in the aquatic environment, plants have evolved three strategies (Fig. 1). These include (Cox, 1988) the transport of pollen above the water surface (category I), pollen transported on the water surface (category II), and pollen transported beneath the water surface (category III). Category I pollen transport has been reported for only one species of seagrass (*Enhalus acoroides*); however, it is common in freshwater submerged aquatics. Most seagrasses exhibit either category II or III pollen transfer.

Seed germination occurs underwater and is influenced by both temperature and

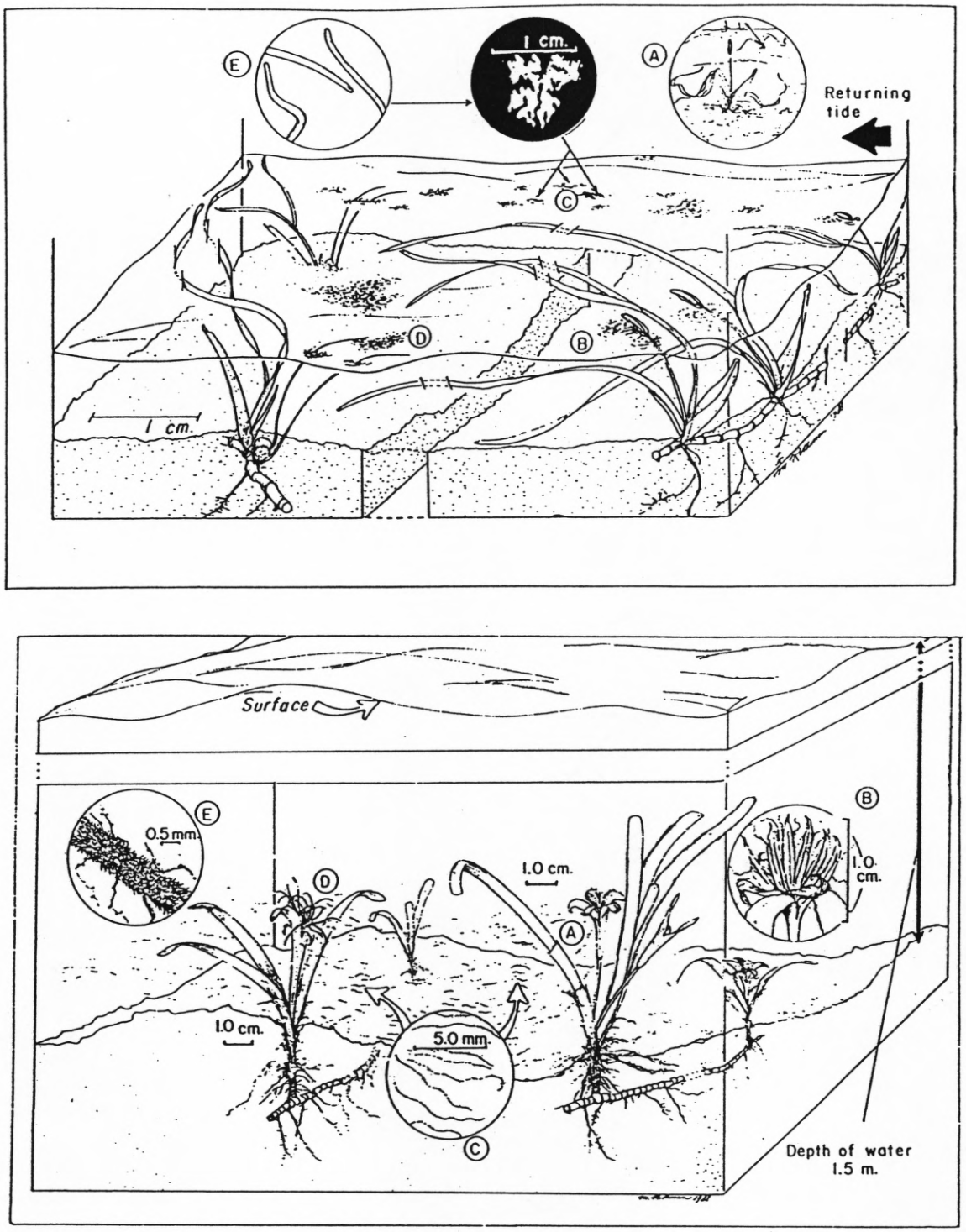

Figure 1. Schematic diagrams of category 2 (top panel) and 3 (bottom panel) hydrophilly. Category 2 hydrophilly exemplified by *Halodule pinifolia* (top panel). A. Erection of another at low tide; B. Another dehiscence and assembly of search vehicles; C. Search vehicles floating on water surface with insert showing dark field silhouette; D. Pollination by collision of search vehicles with filamentous stigmas; E. Close-up of filiforme pollen. Category 3 hydrophilly exemplified by *Thalassia testudinum* (bottom panel). A. Male flowers; B. Mucilage string containing pollen; C. Underwater dispersal of mucilage strand; D. Female flowers with rigid stigmas; E. Pollination by collision. From Cox 1988.

salinity. The details of seed and germling anatomy have been described for *Zostera marina* (Taylor 1957a,b) and *Thalassia testudinum* (Orpurt and Boral 1964). In the early development of the seedling, seagrasses exhibit a single cotyledon ("seed leaf"). Thus seagrasses are monocots which have been placed in the class Liliopsida, subclass Alismatidae (Cronquist 1981).

C.J.G. Petersen and colleagues were the first researchers to realize the importance of seagrass communities to coastal ecosystems (Petersen 1891, 1918; as cited in den Hartog 1980). They suggested that seagrass production (8 million dry tons/year) was the basis of the food web for all marine fauna (Petersen and Boysen-Jensen 1911, Petersen 1913, 1915, 1918, Boysen-Jensen 1914; as cited in Rasmussen 1977). However, they underestimated the importance of phytoplankton, as reflected in the absence of finfishery failure with the onset of the wasting disease of the 1930's (Rasmussen 1977). Much of the other early work on seagrasses was related to taxonomy (Ascherson 1907, Hutchinson 1934, Markgraf 1936; as cited in den Hartog 1970), while much of the physiological and ecological research has been conducted since the late 1960's.

There are about 48 species of seagrasses that occur between the Arctic and Antarctic Circles (Phillips and Meñez 1988). Many of these species have a circumglobal distribution (e.g. *Zostera marina*, which occurs on both sides of the Atlantic and the Pacific; den Hartog 1970). Almost all seagrass species display continuous areas of distribution (Phillips and Meñez 1988). However, some species have disjunct distributions, which may be due to the movement of the continents during the geological epochs (den Hartog 1970). Because of the time scales involved, inferential data (i.e. geological data and fossil foramanifera

associated with seagrasses) have been used to account for the present day distribution of seagrasses (Phillips and Meñez, 1988). Like many other organisms, the areas of highest species diversity are tropical and subtropical environments (den Hartog 1970). There are seven genera that are considered characteristic of tropical areas and five genera that are considered temperate in character (Table 2). Although the Pacific coast of South America and the Caribbean have relatively high species diversity, they are not as diverse at the Indo-West Pacific. The seagrass flora of most areas of the world is well documented, except for the Atlantic Coast of South America, which remains relatively unexplored (den Hartog 1970, Phillips and Meñez 1988).

Strictly speaking, there are four seagrasses (*Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii* and *Halophila engelmanni*) and one euryhaline aquatic plant, *Ruppia maritima*, that occur along the Texas coast. Because *R. maritima* is found in freshwater, neither den Hartog (1970) nor Phillips and Menez (1988) consider *R. maritima* a seagrass. However, *Ruppia* does grow and complete its life history in many of the hypersaline bays and estuaries of Texas (Dunton 1990) and for the purpose of this review we will include *Ruppia* with the seagrasses (Table 3; Figure 2). With the exception of *Ruppia*, the Texas seagrasses have tropical or subtropical affinities. *Ruppia* is cosmopolitan and occurs as far North as New Hampshire (J. Kaldy, pers. obs.), while *Halodule wrightii* occurs as far north as North Carolina. The seagrasses also tend to be perennial (Table 4); although, *Ruppia* in Texas has been reported as a perennial (Pulich 1985) and as a annual (Dunton 1990). Texas seagrasses, except *Thalassia*, exhibit category II pollenation; it is unclear whether *Ruppia* exhibits category II or III pollen transfer.

Table 2. The affinities of the major seagrass species. Some of the species with tropical affinities overlap into subtropical or warm areas. From den Hartog 1970.

Tropical Genera	Temperate Genera
Enhalus	*Halodule*
Thalassia	*Heterozostera*
Halophila	*Phyllospadix*
Cymodocea	*Posidonia*
Syringodium	*Zostera*
Thalassodendron	

Table 3. A listing of Texas seagrass species.

Family and Species	Common Name
Cymodoceaceae	
Halodule wrightii Aschers.	Shoal grass
Syringodium filiforme Kützing	Manatee grass
Hydrocharitaceae	
Halophila engelmanni Aschers.	Clover grass
Thalassia testudinum Banks ex König	Turtle grass
Potamogetonaceae	
Ruppia maritima L.	Widgeon grass

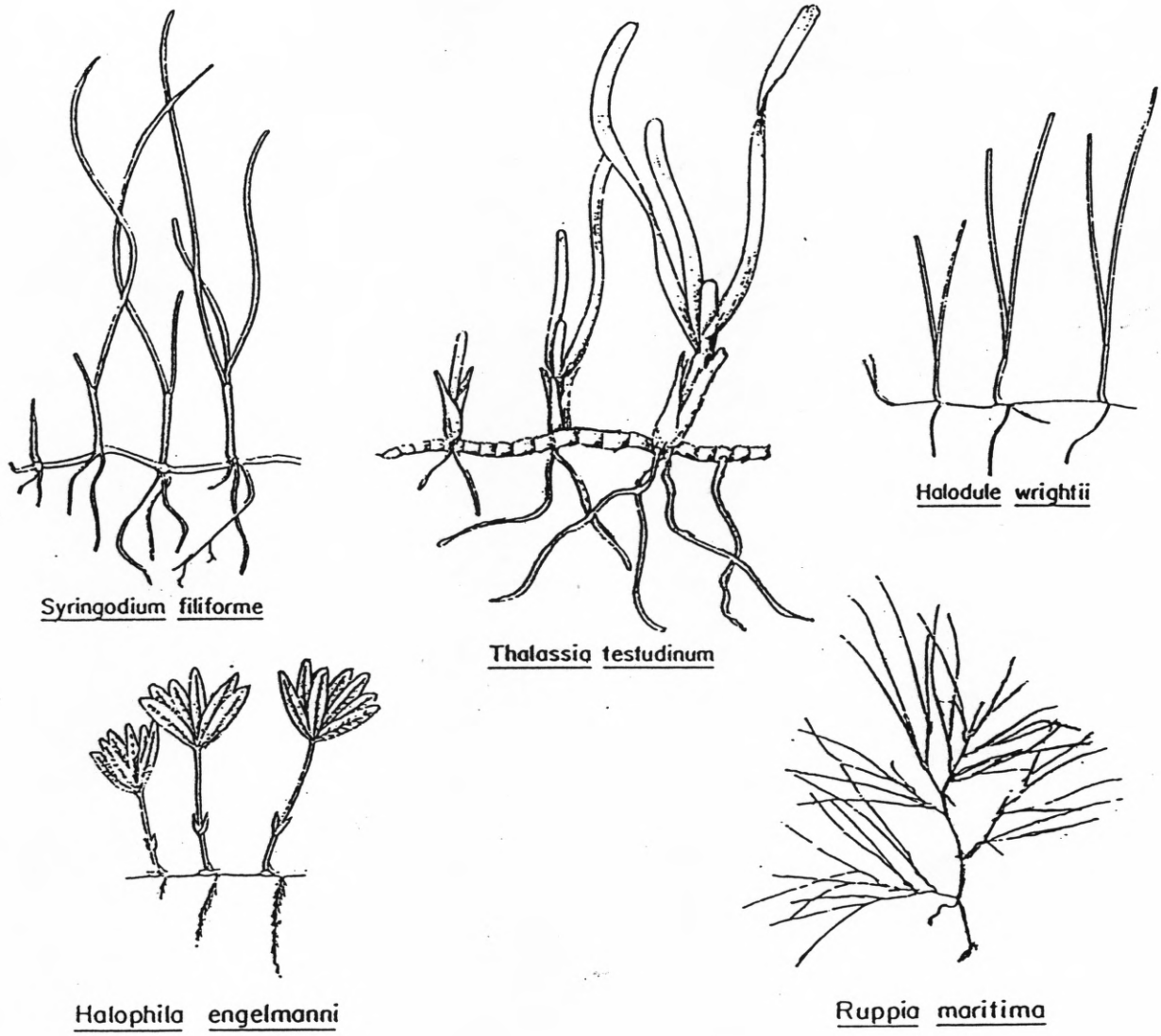

Figure 2. Schematic drawings of the seagrass flora of the Texas coast. Modified from Zieman 1989.

Table 4. Some of the characteristics of Texas seagrasses.

Common name	Pollen category	Biogeographic affinity	Longevity
Clover grass	II	tropical	perennial
Manatee grass	II	tropical	perennial
Shoal grass	II	subtrop-trop.	perennial
Turtle grass	III	tropical	perennial
Widgeon grass	II, III	cosmopolitan	annual/perennial

Most seagrasses, including Texas species, grow in protected bays and estuaries, where the root and rhizome structure of the plants permits the penetration and colonization of soft bottom substrate (i.e. sand and mud). However, there is at least one genus that inhabits the rocky intertidal along the high energy coasts of the Pacific (i.e. *Phyllospadix*). The species of *Phyllospadix* have special adaptations, such as extensive hypodermal fibers and root hair development, thickened rhizomes and small lacunae to colonize the crevices of rocks (Cooper and McRoy, 1988). With the exception of *Phyllospadix*, most seagrasses require sediment depths between 5 and 25 cm for adequate anchoring (Zieman 1972). Sediments are classified as either terrigenous (i.e., derived from terrestrial sources) or carbonate. Carbonate sediments are usually biogenic in origin (Scoffin 1970). Seagrasses also obtain at least part of their inorganic nutrients from the sediments (Thursby and Harlin 1982; Short and McRoy 1984).

Seagrasses colonize a relatively broad range of depths (Figure 3), depending upon available light and substrate type as well as the physiological requirements of the species. In the relatively clear waters of the Mediterranean Sea, *Posidonia* has been reported to grow at depths of 50 m (Gessner 1961). However, *Zostera marine* does not grow below about 1.5 m in the turbid waters of San Francisco Bay, (Zimmerman *et al.*, 1991). Meanwhile, *Ruppia maritima* along the Texas Coast has been reported growing at 0.3 m above mean low water (C. Belaire, 1993, pers. comm). Thus, the depth distribution of a species is variable and depends upon several factors.

Although neither *Posidonia* nor *Zostera* occur along the Texas coast, they serve as examples to show the extreme range of depths that these plants are able to colonize.

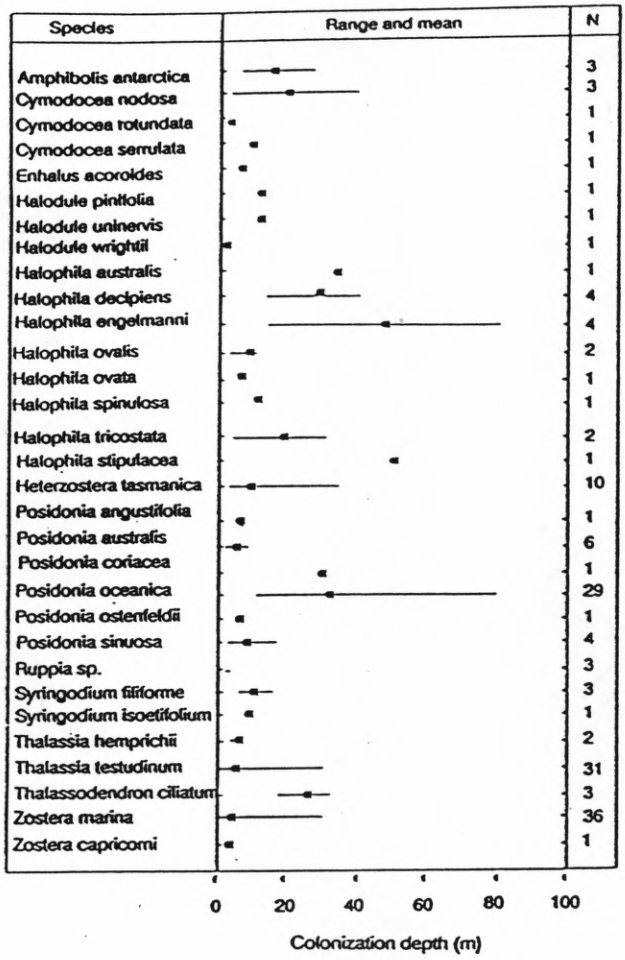

Figure 3. The reported depth limits of 31 marine angiosperm species. Bars represent the range of values encountered, while the solid square represents the average value for each species. Number in right column indiciates the number of estimates. From Duarte 1991.

Several authors have examined the depth distribution of *Thalassia testudinum* within the Gulf of Mexico. Buesa (1974) examined the population and biological parameters of *Thalassia testudinum* on the Cuban shelf. He found that *Thalassia* had a biomass of approximately 200 g m^{-2} to a depth of 1 m, while the lowest biomass, less than 50 g m^{-2}, occurred at 14 m depth (Figure 4). The depth distribution of other species varies considerably. For example, *Halophila decipiens* is found to a depth of 25 m (Figure 4). Buesa (1974) also suggested that *Thalassia* would not grow in areas where irradiance at the seabed was less than 25% of surface irradiance. Vicente and Rivera (1982) examined the depth limits of *Thalassia* growing in Puerto Rico and found a statistically significant positive correlation between mean Secchi depth and the lower limits of *Thalassia* (see chapter 2). Thus, they suggest that where the water is clearer (deeper secchi depth) the plants will colonize at lower depths. However, they also suggest that herbivory may limit the depth distribution of *Thalassia*. Dawes and Tomasko (1988) investigated the depth distribution of *Thalassia* in Florida. They found that plants collected from the deep edge of the bed had lower shoot density, greater leaf area, and greater above:below ground biomass than plants collected from the shallow areas, suggesting that deep plants were more light stressed than shallow plants.

It is generally accepted that light availability is the factor that controls the depth distribution of seagrasses. For example, Buesa (1974) concluded that light energy and temperature were the factors that control the depth distribution of *Thalassia*. Vincente and Rivera (1982) also suggested that *Thalassia* was limited to areas where irradiance at the plant depth was adequate. Iverson and Bittaker (1986) proposed that the depth

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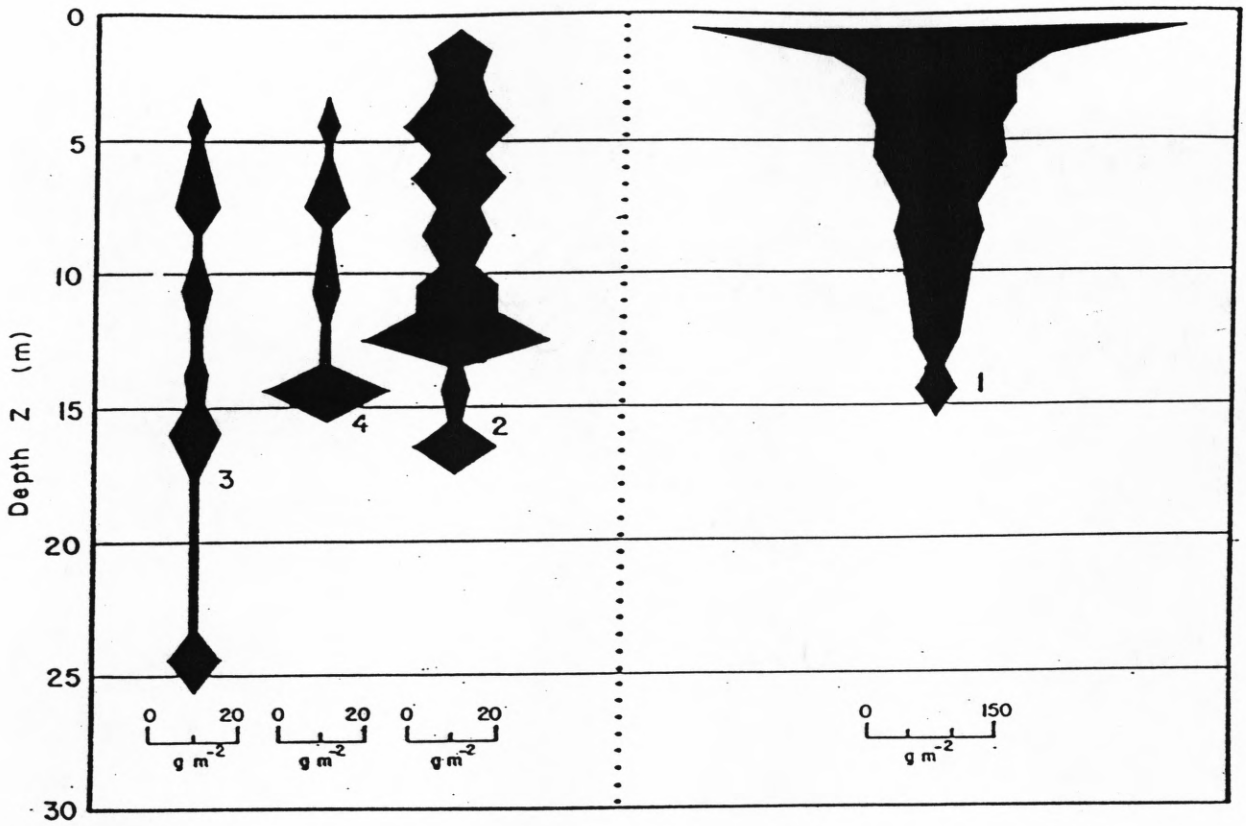

Figure 4. The depth distribution of four seagrass species on the northwest coast of Cuba. 1 = *Thalassia testudinum*, 2 = *Syringodium filiforme*, 3 = *Halophila decipiens*, 4 = *H. engelmanni*. From Buesa 1974.

distribution of *Thalassia* was light limited. Orth and Moore (1988) suggested that species zonation was a physiological response to the interaction of light and temperature.

Importance of seagrasses

We are interested in defining the light requirements of seagrasses because they are an important component of estuarine and coastal ecosystems (Zieman 1982; Phillips 1984; Thayer *et al.*, 1984; Zieman and Zieman 1989). There is a large body of literature documenting the beneficial qualities of seagrass beds. The three-dimensional habitat that seagrass beds create is important to many species of fish and shellfish including commercially important species (Figure 5). There were two studies during the 1970's that documented the importance of seagrass beds. Thayer *et al.* (1975) found that eelgrass beds support numerous types of macrofauna and epifauna, which may consume more than half of the net production of the eelgrass-plankton-algal system. Rassmussen (1977) showed that the species composition and abundance of invertebrate organisms changed with the loss of eelgrass (*Zostera marina*) due to the 1930's outbreak of the wasting disease.

During the 1980's several other investigators documented the importance of seagrass habitat. Orth *et al.* (1984) compared unvegetated areas with seagrass meadows and found that seagrass beds contained a dense and rich assemblage of vertebrates and invertebrates. Species abundance was positively correlated with two aspects of plant morphology: 1) the root-rhizome mat, and 2) the plant canopy. The increased species diversity and abundance suggests that the three-dimensional habitat was beneficial to the

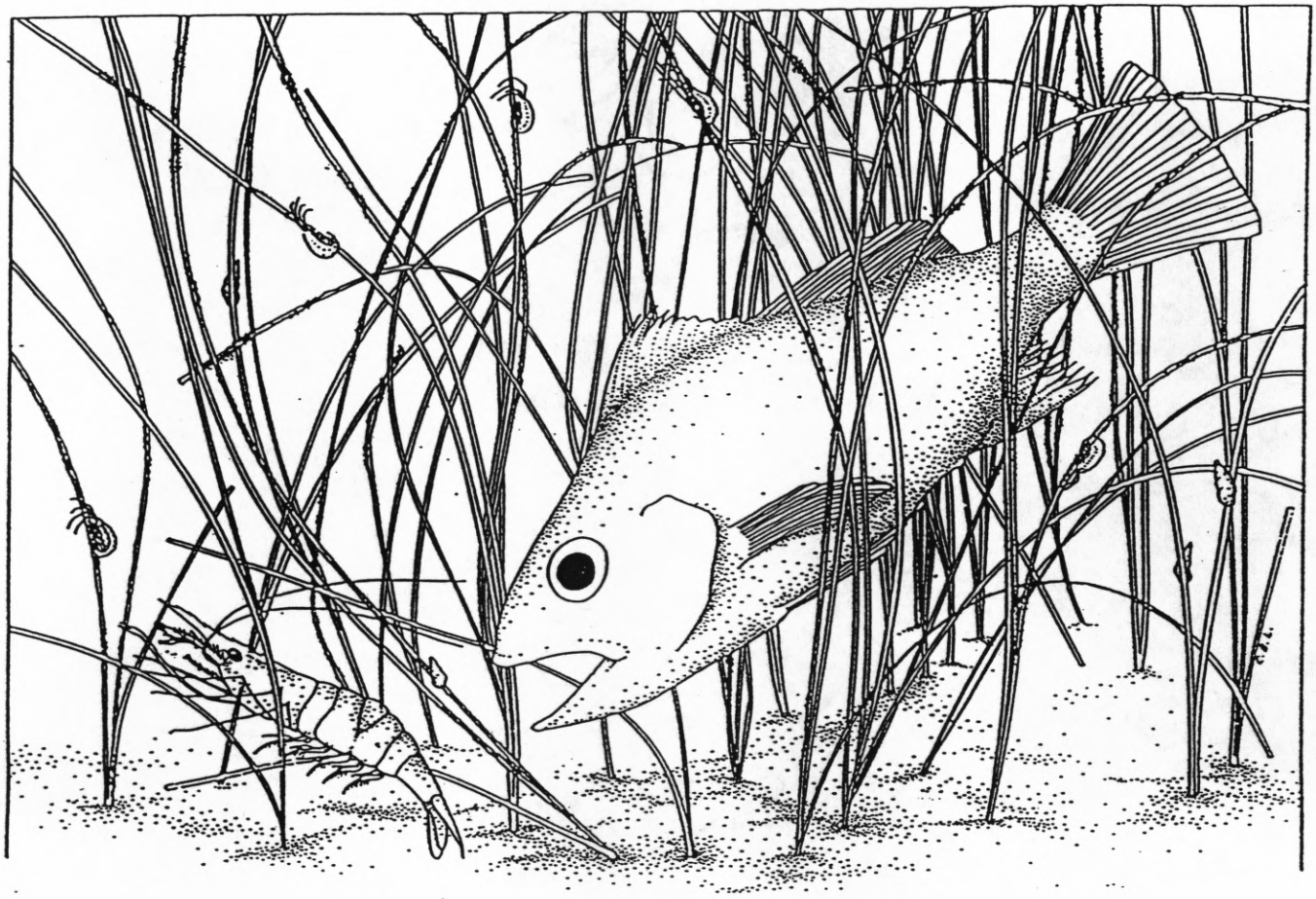

Figure 5. Proposed food web for a seagrass bed, based on dominant organisms of Indian River Lagoon, Fla. The grazing amphipod (*Cymadusa compta*) is about to be preyed upon by the shrimp (*Palamonetes intermedius*) which is to be preyed upon by the fish (*Bairdiella chrysoura*). From Virnstein 1987.

secondary productivity of the system. Virnstein and Curran (1986) studied the colonization of artificial seagrass habitat. They found rapid colonization of new substrate with maximum diversity and abundance within 4-8 days, suggesting that new seagrass substrate may enhance secondary productivity within an estuary. Eckman (1987) found that eelgrass (*Zostera marina*) changed the hydrodynamics of water currents, facilitating the recruitment of scallops (*Argopecten irradians*) and the common jingle (*Anomia simplex*). Eckman also suggested that the hydrodynamic influence of seagrass was more important than predation in determining the abundance of recruits to the system. Short (1988) found that scallops actively migrated into transplanted seagrass beds.

During the 1990's there have been several more investigations of the importance of seagrass habitat. Pohle *et al.* (1991) found that juvenile scallops actively attached themselves to eelgrass blades above the substrate as a refuge from predation. Sogard and Able (1991) demonstrated that vegetated substrate (*Zostera* or *Ulva*) was superior in quality (based on fish and decapod densities) to adjacent unvegetated substrate. Sites with *Zostera* as the dominant plant had higher densities of most fish species than areas dominated by *Ulva*; however, they concluded that *Ulva* was important in areas lacking seagrass cover. Hoven (1992) suggested that eelgrass (*Zostera marina*) meadows are of considerable importance as sites for the settlement of blue mussel (*Mytilus edulis*) larvae. Although many of these studies were concerned with commercially important species, other species also benefit from seagrass habitat. In general, healthy seagrass systems help to create and foster secondary production.

Seagrasses act as a substrate for the growth of algal epiphytes which contribute large

amounts of fixed organic carbon to both the grazer and detrital food webs. Using $\delta^{13}C$ values, Fry (1984) suggested that algal epiphytes are a more important carbon source to Florida estuarine communities than *Syringodium filiforme*. Kitting *et al.* (1984) also found that epiphytic algae may have an important trophic role. Stable carbon isotope evidence showed that many invertebrates were assimilating algal epiphyte carbon rather than seagrass carbon (Figure 6; Fry 1984), reflecting the high refractory nature of vascular plant material (Fenchel 1977; Opsahl and Benner 1993).

Carbon derived from both seagrasses and their epiphytes is important to coastal ecosystems. Rapid export of seagrass leaf material was suggested as a reason for the relatively low importance of *Syringodium* to estuarine food webs in Florida (Fry 1984). Recent work from Australia (Thresher *et al.,* 1992) using a variety of techniques including stable isotopes and gut analyses suggests that seagrass detritus advected offshore during storms may be an important resource for larval fish.

Only a few marine animals (turtles and sea urchins) directly consume seagrasses; however, water fowl rely heavily upon seagrasses as a food resource. Along the Atlantic Coast the dramatic loss of waterfowl during the 1930's was attributed to the decline of eelgrass (*Zostera marina*), the bird's food source, caused by the wasting disease and pollution (Milne and Milne 1951). Widgeons (*Anas americana*) have also been observed to consume *Zostera marina* and *Ruppia maritima* as well as some freshwater macrophytes (Bellrose, 1976). McMahan (1970) found that rhizomes of *Halodule wrightii* comprised 84 and 88% by volume of the diets of redhead (*Aythya americana*) and pintail ducks (*Anas acuta*) respectively. Up to 78% of the redhead duck population winters on the

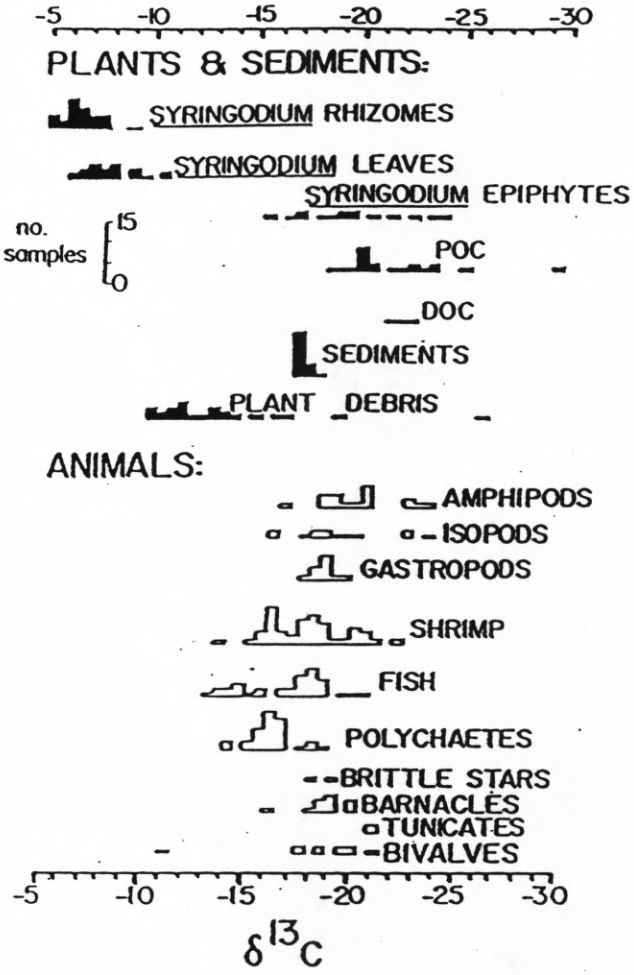

Figure 6. A $\delta^{13}C$ histogram of the plants, sediments and fauna collected in *Syringodium filiforme* seagrass meadows in the Indian River Lagoon (Florida). From Fry 1984.

Texas coast, while 80% of pintail ducks that winter in the central flyway occur along the Texas coast. McMahan (1970) found that the rhizomes of *Halodule wrightii* were the preferred food, making up the bulk of the diet for these birds. In another study, Cornelius (1977) found that 71% of the diet of redhead ducks (*Aythya americana*) consisted of *Halodule wrightii* rhizomes. Using stable isotope techniques ($\delta^{13}C$), the carbon signature of redhead ducks was shown to vary with their use of habitat. Parker *et al.* (1992) found that the $\delta^{13}C$ values of muscle tissue collected from ducks in South Dakota were closer to that of C-3 plants (-22 to -28 ‰) on which the ducks were feeding (Figure 7); in south Texas the $\delta^{13}C$ values of the tissues changed to reflect a seagrass diet (-8 to -14 ‰). Thus, seagrass beds are an important food source for a variety of water fowl species, especially along the Texas coast.

In addition to providing habitat and food to other organisms, seagrasses can dramatically alter their immediate environment. Numerous authors have shown that seagrasses act as a three-dimensional baffle, reducing currents and attenuating waves. Some of the earliest work examining seagrass-sediment interactions was done by Ginsburg and Lowenstam (1958) in Florida Bay. They found that seagrasses can modify sedimentation in two ways: (1) by stabilizing the sediments and (2) by producing a layer of semi-motionless water that allows fine particles to settle out. Ginsburg and Lowenstam (1958) suggest that as a result of binding and trapping, seagrasses alter the pattern of sediment deposition from what would be expected based on physical processes only. Similarly, it is reported that kelp beds act as traps for sand and mud particles in southern California (Ginsburg and Lowenstam 1958). Working in Bimini Lagoon in the

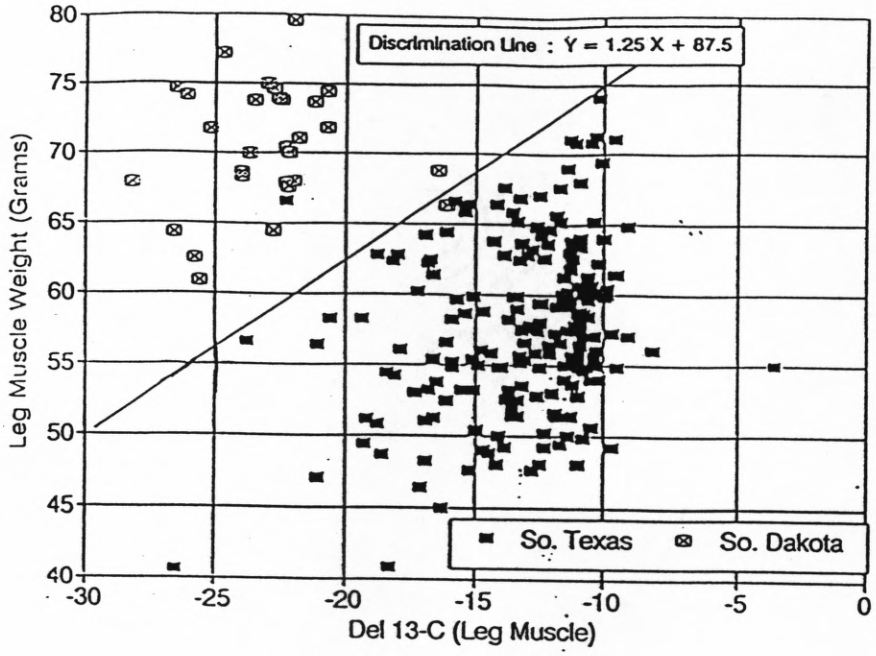

Figure 7. Scatter plot of the $\delta^{13}C$ values of leg muscle of redhead ducks. South Texas ducks are isotopically heavier (closer to seagrass carbon) than ducks from South Dakota. From Parker *et al.*, 1992.

Bahamas, Scoffin (1970) found that *Rhizophora* (mangroves) and *Thalassia* were the strongest binders of sediments. As a result these areas formed deeper sediments (relative to bedrock) than areas without plants. Scoffin (1970) also found that the distribution of plants throughout the lagoon was related to the depth of sediment overlying the bedrock.

Other research has suggested that seagrass meadows preferentially concentrate small sized particles (Burrell and Schubel 1977). Rasmussen (1977) documented the changes in beach sediment texture from a fine sand-silt complex to a very coarse cobble and associated these changes with the loss of *Zostera* to the wasting disease. Christiansen *et al.* (1981) suggested that changes in the coastline at Kyhom, Denmark were related to the dieback of eelgrass (*Zostera marina*) presumably due to the wasting disease. The loss of seagrasses in the area allowed the mobilization and redistribution of sediments in the harbor.

Scoffin (1970) presented a hierarchy of plants which attenuate current strength, where *Rhizophora* prop roots > *Thalassia* > *Thalassia* with heavy epiphytes > *Laurencia* > *Polysiphonia*. Mangroves (*Rhizophora*) and seagrass (*Thalassia*) were most efficient at reducing current flow. The ability of *Thalassia* to reduce current velocity was directly proportional to the density of seagrass blades; current velocities ≥ 150 cm s^{-1} were required to erode sediments from dense *Thalassia* beds (Scoffin 1970). To experimentally assess the impact of seagrass beds on currents, Fonseca *et al.* (1982) used a salt water flume. They found a predictable reduction in the apparent current velocity by seagrass and suggested that current reduction properties may vary between species and sites, due to morphological and hydrographical variation (Fonseca *et al.,* 1982). Ward *et al.* (1984), working in Chesapeake Bay found that seagrasses attenuated wave energy and inhibited sediment resuspension. As

a result, sedimentation rates were substantially higher in seagrass communities than in unvegetated areas. Fonseca and Cahalan (1992) evaluated wave attenuation by four seagrass species and found that broad, shallow seagrass meadows substantially attenuate up to 40% of wave energy per meter of seagrass bed.

Recent research has also shown that seagrass communities act as a "biological scrubber." Short and Short (1984) found that seagrasses, growing in mesocosms, rapidly filtered out sediments that were added to the water column, resulting in increased light penetration. Additionally, they found that seagrasses rapidly removed nutrients added to the water column (Figure 8). Thus, the seagrasses filtered out both sediments and nutrients.

In general, research has shown that seagrasses are a cornerstone to the health and productivity of estuarine communities (Zieman 1982; Phillips 1984; Thayer *et al.,* 1984; Zieman and Zieman 1989). They provide habitat and food to a wide variety of organisms. Seagrasses also physically alter the environment they inhabit, by influencing water currents and sedimentation processes. However, the long-term future of these communities is in jeopardy.

Recently, there has been a world wide decline in seagrass habitat (Figure 9). For example, Orth and Moore (1984) show that before the 1960's, submerged aquatic vegetation (SAV) was a widespread feature of the Chesapeake Bay System. However,

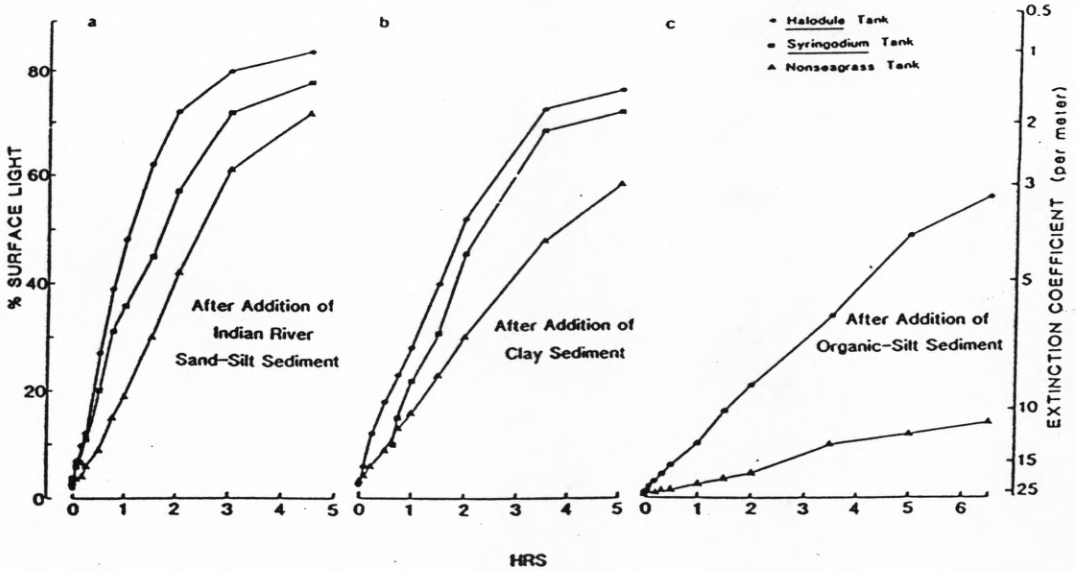

Figure 8a. Percent of surface light extinction and coefficients in a *Halodule wrightii* tank, a *Syringodium filiforme* tank and an unvegetated tank following addition of Indian River sand-silt sediment (a), clay sediment (b), and organic-silt sediment (c). From Short and Short 1984.

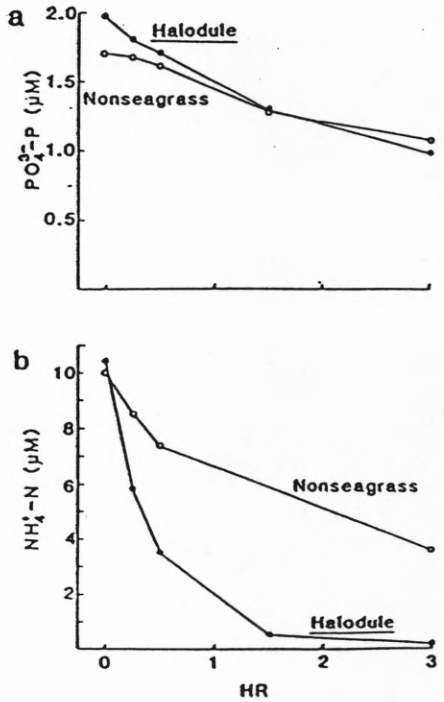

Figure 8b. Nutrient removal from the water column by the seagrass community. Changes in phosphate (a) and ammonium (b) concentration for *Halodule* and a nonseagrass control tank over time. From Short and Short 1984.

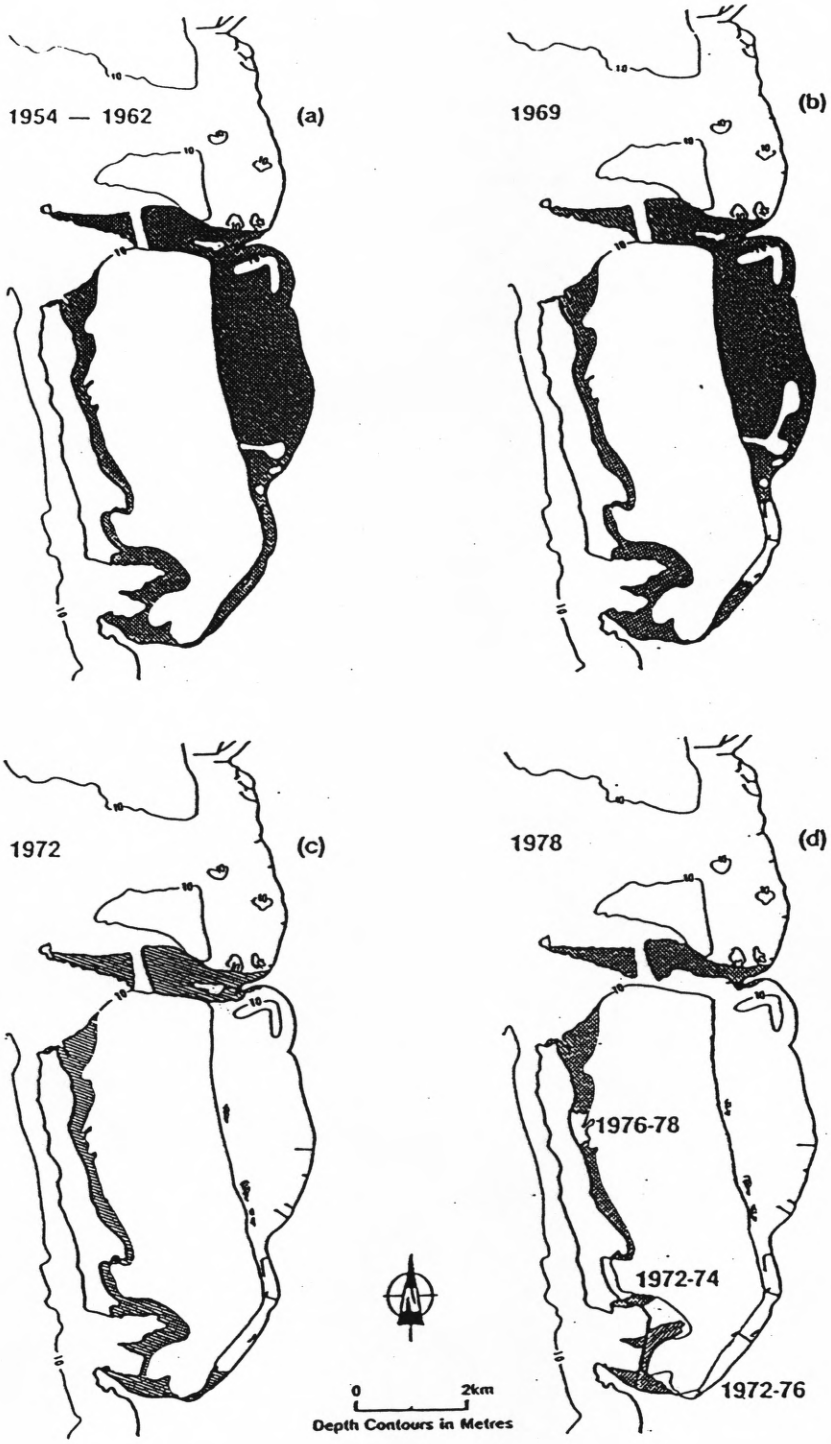

Figure 9. Changes in seagrass cover over time in Australia. From Cambridge and McComb 1984.

since the 1960's there has been a dramatic loss of SAV communities. Livingston (1987) reported that seagrasses have been virtually eliminated from Pensacola and Tampa Bays. Eleuterius (1989) has documented the loss of about 70% of the seagrass habitat from Mississippi Sound between 1969 and 1989. During the 1930's up to 90% of the eelgrass populations occurring along the Atlantic Coast were lost (Costa 1988). The decline of eelgrass was due to infection by the "wasting disease" caused by a marine slime-mold *Labyrinthula zosterae* (Muehlstein *et al.,* 1991). The wasting disease was a natural catastrophe, caused by the parasitic organism. Disease still plays a role in controlling seagrass distribution (Short *et al.*, 1991); however, the more recent declines in seagrass habitat are due primarily to anthropogenic influences.

Aerial photography and ground truthing have been used to document changes in the distribution and biomass of seagrasses. Merkord (1978) documented changes in seagrass distribution of the Laguna Madre system between 1965 and 1976. In the Upper Laguna Madre, *Halophila* and *Halodule* cover increased, while *Ruppia* cover decreased. In Lower Laguna Madre, *Syringodium* cover increased, displacing *Halodule* in some areas while *Thalassia* expanded its range northward. Additionally, significant portions of Port Isabel Bay have become bare areas, devoid of seagrass cover. Merkord (1978) suggested that the changes were a result of decreased salinity (over the long term) and increased turbidity. Costa (1988) documented changes in the abundance of eelgrass related to anthropogenic and natural disturbance using aerial photographs, charts, written reports, local residents and sediment cores. He suggests that the wasting disease took a massive toll on eelgrass populations, eliminating about 99% of the eelgrass in Buzzards Bay.

Pulich and White (1991) have documented the decline of seagrass habitat in the Galveston Bay System. They attribute various processes to the loss of specific seagrass habitat. For example, the loss of *Ruppia maritima* was related to Hurricane Carla and a rise in relative sea level due to subsidence. However, in the lower bay both *Halodule wrightii* and *Ruppia maritima* disappeared between the 1950's and the 1980's. These declines may be due to increased human activities such as urban development, wastewater discharges, chemical spills and dredging activities. Quammen and Onuf (1993) documented an increase of 140 km^2 of bare bottom in Laguna Madre, Texas. They suspect that light reduction from maintenance dredging has caused the loss of seagrass cover. Thus, historical data bases, nautical charts, and aerial photography have proven useful in documenting changes in the distribution of seagrasses.

Presently, declining water quality (both transparency and nutrients) is adversely affecting seagrasses. In general, reduced light availability as a result of anthropogenic influence is the greatest threat to seagrasses worldwide (Merkord 1978; Cambridge and McComb, 1984; Costa 1988; Giesen *et al.,* 1990; Pulich and White 1991; Short *et al.,* 1991; Quammen and Onuf 1993). Thus, before seagrass can be expected to recolonize (either with or without human intervention), water quality problems must be addressed.

CHAPTER 2: LIGHT AND WATER TRANSPARENCY

Environmental influences on water clarity

Estuarine biologists and managers often refer to the concepts of "water quality" and "water clarity" somewhat interchangeably. This is unfortunate, because there is a fundamental difference between the two expressions. Water quality refers to the chemical and physical parameters (i.e. nutrient concentrations, dissolved oxygen, salinity, temperature, etc.) that characterize a parcel of water with respect to the effect of these parameters on the health of aquatic organisms, in this case plants. Water clarity or transparency, on the other hand, is a specific character of water quality. It is defined by the amount of light transmitted through a body of water. Decreased water quality (e.g. increased nutrient concentration) can stimulate phytoplankton blooms which reduce light transmittance (e.g. water clarity). Thus, water clarity is related to and influenced by water quality, but these terms are not the same. Throughout this document we will use the terms water quality and water clarity in a manner consistent with the above definitions.

Light in the aquatic environment

Photosynthetically active radiation (PAR) is that portion of the electromagnetic spectrum utilized by plants for photosynthesis. PAR extends from about 350 nm to about 700 nm wavelength and is roughly equivalent to the range of wavelengths to which the human eye is sensitive (i.e. visible light). Seagrasses require light energy for the process of photosynthesis. However, there are several factors that influence the amount of light they

receive; three of these major factors are: (1) albedo; (2) scattering and (3) absorption. The portion of light reflected back into space is referred to as the albedo of that surface (Figure 10). The albedo of the Atlantic Ocean at 30° North latitude is approximately 0.068 (Payne, 1972). Thus, approximately 6.8% of the light energy impinging on the ocean surface at this latitude is reflected back to space and is unavailable to marine plants. Light is also scattered within the water column by suspended particles (Figure 11). In addition to albedo and scattering, light is selectively absorbed as it passes through the water column (Figure 12).

Spherical quantum sensors are used to measure the light field underwater because they measure both downwelling and scattered light. Flat cosine sensors underestimate light availability because they account only for downwelling irradiance. Because of scattering and selective wavelength attenuation, light penetration through water is modelled with an exponential decay function (Kirk 1983):

$$I_z = I_o e^{(-kz)}$$

where I_z is the irradiance at depth z, I_o is the incident irradiance at the water-atmosphere interface, and k is the light attenuation coeffecient.

Simulation models and field data have been used in the investigation of light penetration through the water column of estuaries. Hogan (1983) used a simulation model of light attenuation and found that maximum transmissivity occurred at about 465 nm in clear water and at 550 nm in turbid water (Figure 12b). He concluded that the shift was

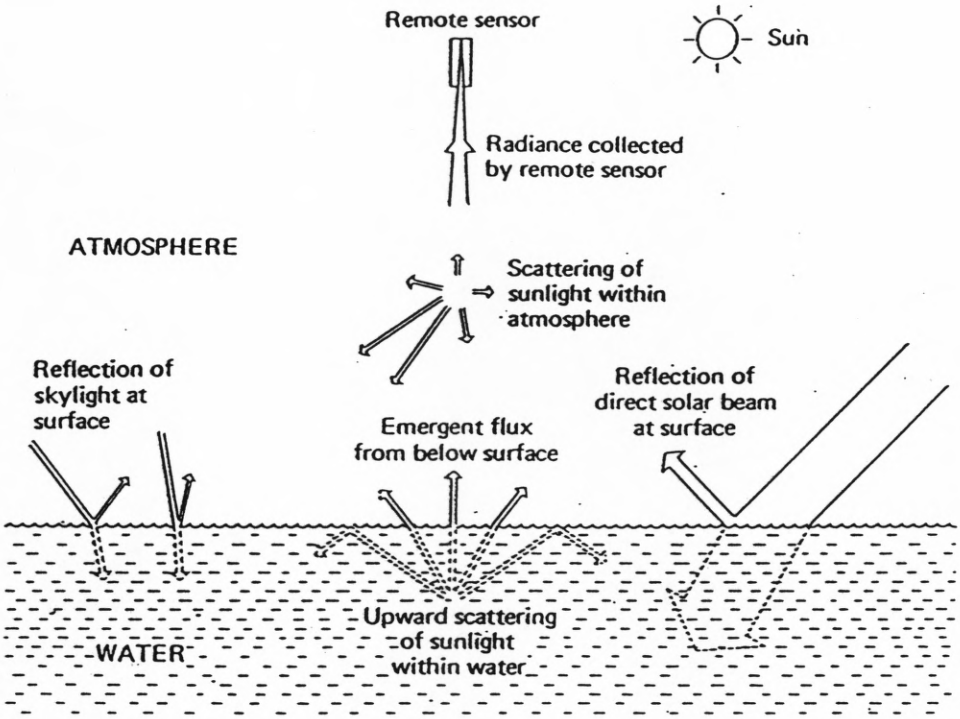

Figure 10. Schematic diagram showing the different origins of light received from a remote sensor above the water. The reflection of the direct solar beam at the surface is termed albedo. From Kirk 1983.

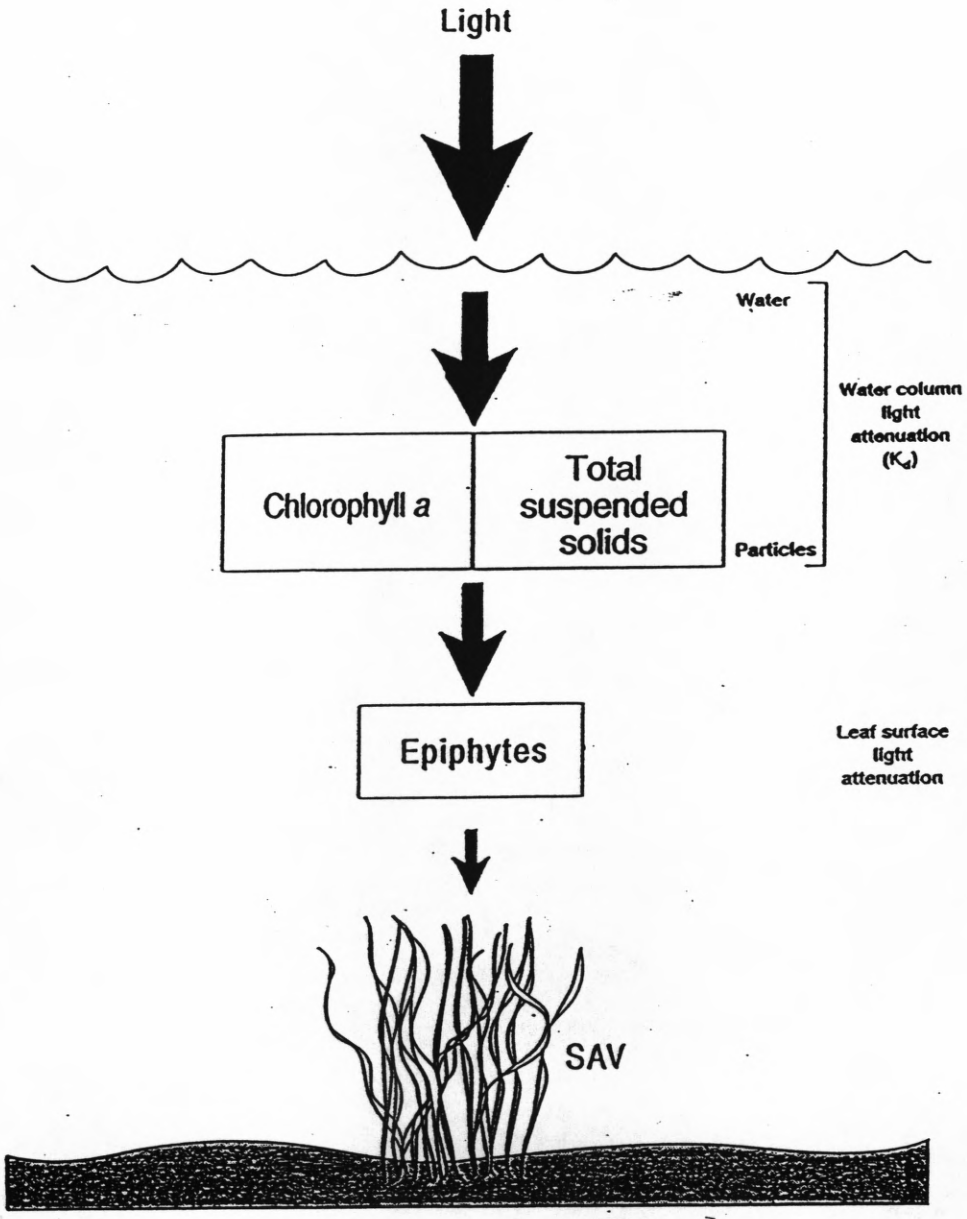

Figure 11. Light availability underwater is determined by attenuating processes. Light attenuation results from the absorption and scattering of light by particles in the water (i.e., suspended solids, phytoplankton, etc.) as well as the absorption of light by the water itself. From Dennison *et al.*, 1993.

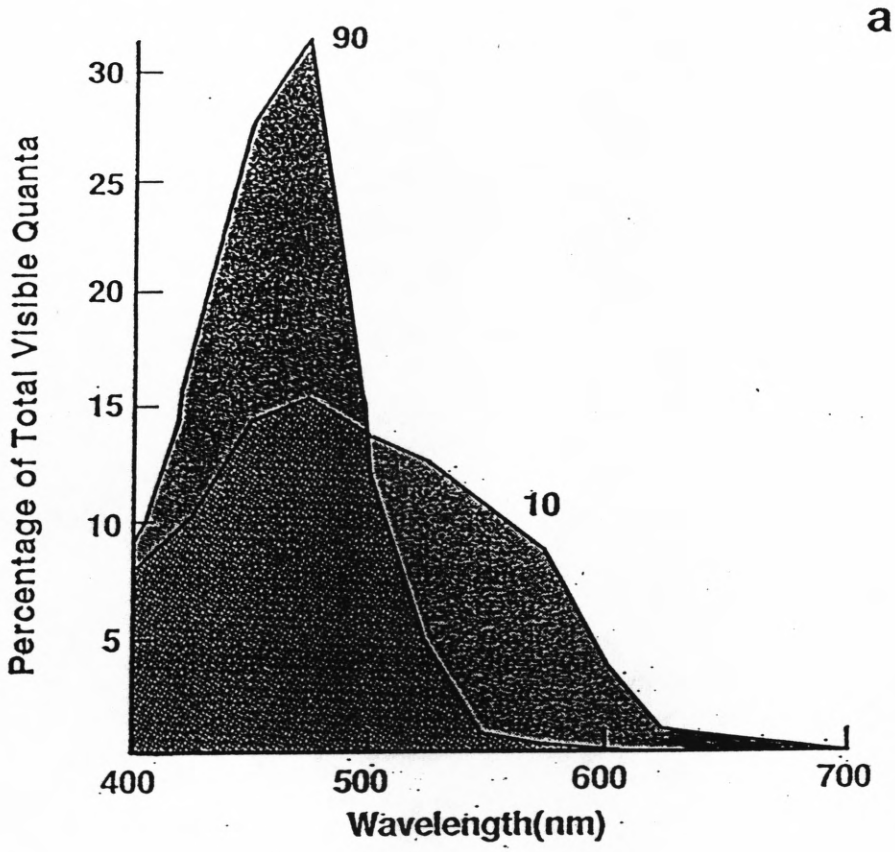

Figure 12a. The spectral range of underwater irradiance decreases with increasing depth in clear oceanic water. At 10 m the spectrum is fairly broad while at 90 m about 70% of the quanta is in the 450-500 nm band. From Saffo 1987.

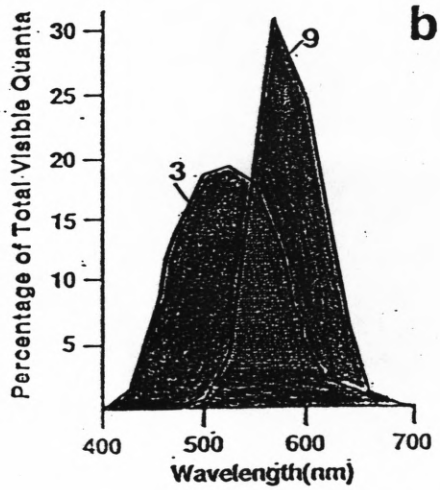

Figure 12b. Sectral changes of underwater irradiance with increasing water turbidity at 10 m depth. Moderate turbidity (3) results in maximal transmittance in green portion of spectrum while under conditions of maximal turbidity (type 9) transmitted light is mostly yellow. From Saffo 1987.

due to suspended matter in the water, which absorbed and scattered shorter wavelengths more than longer wavelengths. The ultimate result was that the maximum transmittance of light occurred in the longer wavelengths in turbid coastal environments, while total transmittance decreased. Pierce *et al.* (1986) investigated how light transmittance responded to changes in the turbidity of the Rhode River Estuary. Light transmittance, both spectral quality and intensity, varied with changes in the amount of dissolved and suspended matter. High concentrations of suspended solids and dissolved materials were correlated with increased attenuation in the upper water column; attenuation varied with wavelength depending on the materials present. Regression analysis indicated that the concentration of chlorophyll *a* and *c*, as well as mineral matter, accounted for most of the variation. These investigations suggest that light transmittance in turbid estuarine waters is more complex than clear oceanic water.

Recently, many authors have estimated attenuation coefficients from Secchi depths as a means of calculating light availability (Chambers and Kalff 1985; Duarte 1991; Batuik *et al.,* 1992; Dennison *et al.,* 1993 and others). Preisendorfer (1986) examined the theory and mathematics behind the use of the Secchi disk. He suggested that use of the Secchi disk to evaluate the attenuation coefficient, k, obliterates and abuses the primary function of the Secchi disk. He concluded that transparency measurements made with a Secchi disk do not yield valid information on the availability of light at depth. Therefore, long term *in situ* electronic light measurements are required to estimate underwater light availability. However, other investigators (Megard and Berman 1989) suggest that Secchi depth (transparency measurements) is proportional to the attenuation coeffecient for the most

penetrating waveband. However, the work of Megard and Berman (1989) was conducted in oceanic waters and was not subject to the same scattering problems endemic to nearshore and estuarine systems. Historically the Secchi depth has been taken as the 18% light level; however, new calculations suggest that Secchi depth is the 22% light level (Megard and Berman 1989). Due to the ongoing literature debate, the applicability of Secchi depth measurements to estuarine environments is questionable. As a result, researchers are starting to measure *in situ* light availability directly using photoelectric cells, such as spherical quantum sensors (Tomasko and Dunton, 1991). A long term (four-year) data set now exists for Upper Laguna Madre, Texas (Dunton, submitted).

Natural influences on water clarity

As mentioned previously, three factors control how much light reaches submerged vegetation: albedo, scattering and absorption. Albedo varies with latitude and season due to the declination of the earth with respect to the sun. However, scattering and absorption of light within the water column are affected by a number of natural and anthropogenic influences. Currents, tides and floods may increase the suspended solids, reducing the amount of light reaching the plants. In a rather extreme case, the onshore movement of coastal sand smothered a seagrass bed in Australia (Kirkman, 1978). Wind events have also been cited as influencing light; wind waves can cause the resuspension of sediments resulting in high light attenuation (Ward *et al.,* 1984). Severe wind events, in the form of hurricanes, have been cited as having adverse effects on seagrasses and light in Florida (Zieman 1975a) and in Mississippi Sound (Eleuterius 1989). In a recent manuscript Onuf (1993 in review),

had to incorporate wind speed and direction into his statistical analysis to accurately model the propagation of dredging effects in Laguna Madre, Texas.

Meteorological forcing in the form of wind waves, large-scale wind-driven gyres and flushing due to frontal passage have been shown to strongly influence the hydrography of Gulf estuaries (Ward and Armstrong 1980). The influence of meteorological forcing is a consequence of large surface area to volume ratios as well as the intensity and variability of meteorological events (Ward 1979). Wind driven waves are a result of meteorological forcing; light to moderate winds over long fetches allow the development of intense surface waves. The mixing action of these wind waves results in waters that are usually vertically homogenous, except in the deeper dredged channels (Ward 1979; Ward and Armstrong 1980). The seasonality of winds may also play a role in controlling light attenuation; for example, Rice *et al.* (1983) found that sediment resuspension occurs year-round but that it may be most active during winter storms. The seasonality of winds along the Texas coast is governed by the intensity of the Bermuda High (Ward and Armstrong 1980). As a result, light transmittance during certain times of the year may be affected more by sediment suspension than during other parts of the year (Rice *et al.,* 1983; Ward *et al.,* 1984).

Water clarity in bays and estuaries along the Texas coast is mostly meteorologically driven, but may also be influenced by biological substances dissolved in the water, such as tannins, humic acids and chlorophylls, which increase light attenuation through the water column. Gelbstoff (gilvin or 'yellow substance') is a result of decomposition of organic matter into a complex group of compounds called "humic substances". In general, humic substances are large molecular weight compounds; for example, the average atomic

composition of humic substance from the Okefenokee Swamp in Georgia was $C_{74}H_{72}O_{46}N_{0.7}$. These substances vary from a molecular weight of a few hundred to insoluble macromolecular aggregates. Humic substances absorb light, especially at the blue end of the spectrum, resulting in a shift in the maximum penetration of specific wavelengths of light (Figure 12b; Kirk 1983). Pierce *et al.* (1986) found that chlorophyll *a,c* and mineral suspensate accounted for most of the attenuation of light through the water column in the Rhode River Estuary. They suggested that the high attenuation of selected wavelengths in the upper part of the water column may reduce the availability of PAR below that necessary for benthic plants or shift community structure to favor species capable of using wavelengths greater than 525 nm. Carter and Rybicki (1990) document a dramatic shift in the quality of light reaching 1 m depth as a result of suspended solids.

Natural plankton blooms may also reduce the amount of light transmitted through the water column. Cosper *et al.* (1987) documented blooms of the chrysophyte *Aureococcus anophagefferens* with cell counts greater than 10^9 cells L^{-1}. The bloom of this alga reduced light penetration through the water column and resulted in the loss of 55% of the eelgrass habitat in Long Island bays (Cosper *et al.,* 1987; Dennison *et al.,* 1989). Texas has recently been experiencing a similar "brown tide" that has been persistent in some portion of Laguna Madre since July 1990. The brown tide organism (BTO) appears to be an undescribed type III aberrant chrysophyte related to *Aureococcus anophagefferens* and *Pelagococcus subviridis*. The BTO is a 4-5 μm in diameter; maximum chlorophyll concentrations of 70 $\mu g\ L^{-1}$ and densities up to 10^9 cells L^{-1} have been reported (Stockwell *et al.,* 1993). The BTO has also had dramatic effects on both the micro and mesozooplankton populations (Buskey and

Stockwell 1993). As a result of the high cell densities, light has been dramatically reduced (by up to 60%) in Laguna Madre (Dunton submitted) and could contribute to the loss of seagrass habitat.

Banks of drift algae may also influence seagrass communities (Cowper 1978; Benz *et al.,* 1979; Gilbert and Clark 1981; Kulczycki *et al.,* 1981; Zimmerman and Montgomery 1984; Virnstein and Carbonara 1985). The development of the drift algal communities reduce light availability to the seagrasses (Cowper 1978). Additionally, the decomposition of drift algal banks may influence nutrient dynamics (Zimmerman and Montgomery 1984; Virnstein and Carbonara 1985).

Although microalgal epiphytes do not decrease water clarity *per se*, they can influence the amount of light that a macrophyte receives. Numerous studies have documented decreased light availability to macrophytes as a result of epiphyte growth. Some of the earliest work (Sand-Jensen 1977) suggested that diatomaceous epiphytes act as a barrier to carbon uptake and reduce light availability. Bothwell (1989) found that the nutrient supply to the inner periphyton layers was diffusion limited. Additionally, Meulemans (1987) found that light is strongly and selectively absorbed in the upper layers of periphyton communities. Thus, recent studies have confirmed the findings of Sand-Jensen. Other studies have shown that microalgal epiphytes can attenuate 58-94% of light incident on the leaf surface (Batuik *et al.*, 1992; Staver 1985; Twilley *et al.,* 1985).

Anthropogenic influences on water quality and clarity

Human activities tend to cause a decrease in overall water quality. For example,

nutrient enrichment (decreased water quality) in bays and estuaries often results in eutrophication. Eutrophication is another term that has been used and abused by estuarine biologists and managers. Eutrophication is a process of environmental and community change caused by the interaction of three components: (1) excessive nutrient availability; (2) reduced illumination and (3) a shift in the species composition as a result of altered light and nutrient regimes (Kaldy, 1992). There are numerous investigations from around the world that have shown or suggested that increased nutrient loading stimulate the growth of algal competitors (epiphytes or phytoplankton) which shade out seagrasses (Zieman 1975a; Sand-Jensen 1977; Zieman 1982; Cambridge and McComb 1984; Cambridge *et al.,* 1986; Zieman and Zieman 1989; Giesen *et al.,* 1990; Short *et al.,* 1991; Kaldy 1992; Short *et al.,* in review). This sequence of events has also been shown to affect perennial macroalgae like *Fucus* (Kautsky 1991) and freshwater submerged macrophytes like *Elodea canadensis* and *Potamogeton pectinatus* (Ozimek *et al.,* 1991). Several conceptual models (Phillips *et al.,* 1978, Short *et al.,* 1991, Vogt and Schramm 1991) have been developed to examine the process of eutrophication (Figure 13; Kaldy 1992, Short *et al.,* submitted, Kaldy *et al.,* in prep.).

Presently, eutrophication problems appear to be confined to a few localized areas in Texas, including portions of the Galveston Bay System (Pulich and White 1991). However, other areas are not immune to eutrophication. Most of the watershed that drains into Copano Bay is subjected to agricultural fertilizer application that influences the nutrient regime of the bay (Shormann 1992). Additionally, a significant amount of the nutrient input to Copano Bay is from point source sewage outfalls from urban areas within the watershed.

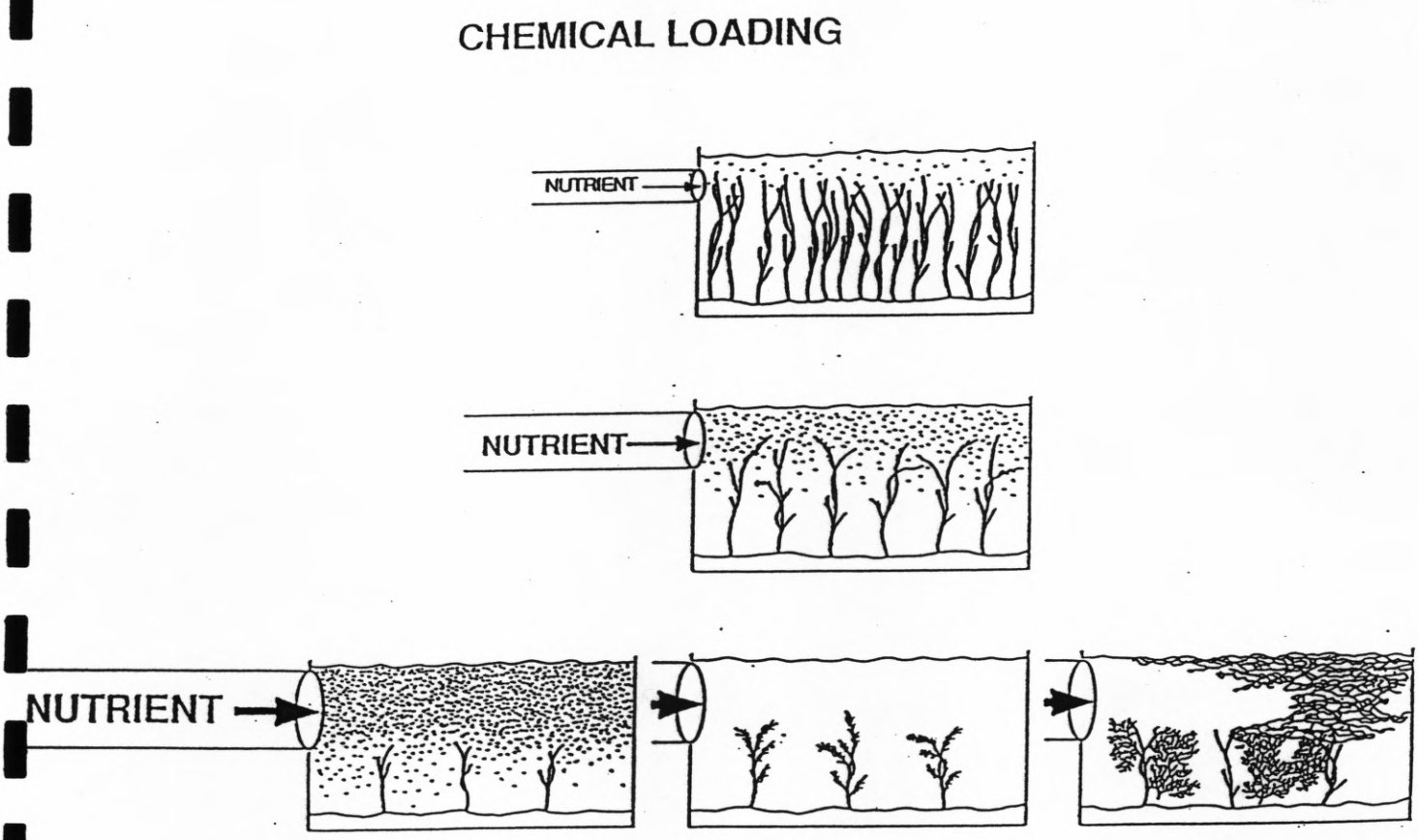

Figure 13. Chemical loading hypothesis suggests that under low nutrient levels seagrasses are dominant with some algae present. As nutrient loading increases seagrass density decreases and phytoplankton and epiphytes become more prevalent. Under conditions of excessive nutrient loading seagrass density and biomass becomes low, and one of three algal forms (phytoplankton, microalgal epiphytes or macroalgal epiphytes) becomes dominant. From Short *et al.*, 1991.

Thus, Shormann (1992) suggests that Copano Bay can be considered eutrophic. In addition, recent research suggests that a considerable amount of the nitrogen input to Texas bays and estuaries comes from rain falling directly into the bays (Shormann 1992, T. Whitledge pers. comm.). The potential for eutrophication problems along the Texas coast cannot be ignored. Reports on population growth rates indicate that the Texas Gulf coast is one of the most rapidly developing areas of the country (NOAA 1988, 1990a,b). As a result, most of the bays and estuaries along the coast are highly susceptible to pollution, including excessive nutrient loading (NOAA 1990b).

Decreased water clarity, due to increased suspended solids, also occurs as a result of dredging, construction, erosion, runoff and disturbance (Zieman and Zieman 1989). Odum (1963) showed that silt from dredging activities in the Gulf Intracoastal Waterway may have caused an imbalance in respiration and photosynthesis resulting in decreased productivity. Zieman (1975a) suggested that dredging was responsible for the destruction of seagrass as a result of direct physical damage, reduced light and hypoxia associated with the high oxygen demand of decomposing material. He also suggested that clam dredges were just as damaging as dredging navigational channels. Pulich and White (1991) suggested that construction, dredging and suspended solids all contributed to the decline of seagrasses in the Galveston Bay system. Giesen *et al.* (1990) suggested that recent large losses of eelgrass from the Dutch Wadden Sea are the result of increased turbidity from both progressive eutrophication and dredging activities. Onuf (1993, in review) found that light attenuation near the dredge spoil site remained elevated 15 months after dredging had occurred. Increased light attenuation near the edge of a seagrass beds was evident for 10

months after dredging. Thus, human construction activities often have a destructive influence on seagrass habitat.

Anthropogenic physical disruption of the environment may also exacerbate water quality problems. Bulthuis *et al.* (1984) found that the concentrations of suspended solids, phosphorus and silicate were higher in water ebbing from denuded mudflats than from seagrass covered mudflats. The efflux of nitrogen from the sediments was light mediated as a result of demand by photosynthetic organisms, and was not different between denuded and covered areas. Bulthuis *et al.* (1984) suggested that denudation of seagrass-covered tidal mudflats would lead to increased efflux of suspended solids and nutrients from the sediments to the overlying water.

While not generally decreasing water quality, boating activities have deleterious effects on seagrasses. There are several reports of motorboat propeller scars in *Thalassia* beds (Zieman 1975a, 1976; Dunton pers. comm. 1993). These scars do not recover rapidly after disturbance, and persist for 2-5 years even in healthy, thriving beds (Zieman 1976). In addition to physical damage to the plants the sediment microhabitat is impacted. For example, changes in the grain size, pH and eH of the disturbed sediments have been observed (Zieman 1976). Walker *et al.* (1989) used aerial and underwater photography to assess the adverse effects of boat moorings on seagrass beds. Moorings scoured circular patches ranging in size from 3 to 300 m^2. Although less than 2% of the seagrass area was lost to moorings the increased edge effect makes more of the beds susceptible to erosion and "blowouts". In general, the mechanical disturbance of seagrass beds is a worldwide problem typified by localized impacts associated with construction activity (Short *et al.*,

1991).

Thermal and toxic pollution also have adverse effects on water quality. Zieman and Wood (1975) have shown that thermal pollution reduces the diversity and abundance of algae and animals near effluent canals. They also suggested that several estuarine plant groups were likely to respond to pollution; seagrasses, macroalgae, phytoplankton, epiphytic microalgae and benthic microalgae (Wood and Zieman 1969). However, seagrasses were relatively more resistant to thermal stress than algae (Zieman 1975a). Tropical seagrasses live close to their thermal tolerance, (e.g. *Thalassia testudinum* has an optimal temperature range of 28-30 °C); therefore, raising the temperature regime can be deleterious to tropical and subtropical estuaries (Zieman 1975a).

Toxic pollution has also been implicated in the loss of seagrass habitat. Pulich and White (1991) suggest that pollution, including chemical spills, may have contributed to the decline of seagrasses in the Galveston Bay System. Livingston (1987) suggested that seagrass losses in Florida estuaries were mainly the result of decreased water quality from a variety of urban and industrial sources. Eleuterius (1989) also suggested that spills of toxic substances have contributed to the decline of seagrasses in Mississippi Sound.

The consensus among researchers is that light is the environmental factor that has the greatest influence on the depth distribution of seagrasses. Albedo affects the amount of light that actually enters the water and is influenced by latitude and declination of the Earth with respect to the sun. Natural and anthropogenic factors can dramatically alter the amount of light reaching seagrasses by increasing scattering and absorption. Humans have very little, if any, control over natural weather phenomena; however, we have the capability to minimize the adverse effects of human activity (Table 5).

Table 5. List of data concerning historic anthropogenic impacts on seagrass meadows in Florida. From Livingston 1987.

Study Area	Location	Status of Seagrass Meadows	Information Source
Indian River	Southeast Florida Atlantic Ocean	Historic declines in number and coverage of seagrass meadows. Declines in Vero Beach area, Fort Pierce Inlet (25%) and Sebastian Inlet (38%) from 1951 through 1984.	Goodwin and Goodwin, 1976; Florida Department of Natural Resources, unpublished data.
Biscayne Bay	Southeast Florida Atlantic Ocean	Undetermined deterioration in northern Biscayne Bay. Some damage to *Thalassia-Halodule* beds near power plant (heated effluents) in south Biscayne Bay. Card Sound unaffected by power plant discharge.	McNulty, 1961; Roessler and Zieman, 1969; Thorhaug et al., 1973; Zieman, 1970, 1982.
Florida Keys	South Florida Atlantic Ocean	Few data found. Little effect of Key West desalination plant.	Chesher, 1971
Florida Bay	South Florida	Postulated altered species relationships due to increased salinity caused by redirection of freshwater runoff.	Zieman, 1982
Tampa Bay system	Southwest Florida Gulf of Mexico	Almost forty percent reduction in Boca Ciega Bay due to dredging, filling, and associated activity from 1950 through 1968. Multiple sources (urbanization, storm water runoff, sewage discharge, industrialization, toxic substances). Reduction of seagrass meadows in Tampa Bay system from 30,970 ha to 5,750 ha.	Lewis and Phillips, 1980; Simon, 1974; Lewis et al., 1985; Taylor and Saloman, 1968
Charlotte Harbor	Southwest Florida Gulf of Mexico	Decline of 29 percent of seagrass beds from 1943 through 1984.	Harris et al., 1983
Pensacola Bay system	Northwest Florida Gulf of Mexico	Complete loss of seagrass beds in Escambia Bay, East Bay, and Pensacola Bay from 1949-1979. Some fresh-brackish water species extant in delta areas. Some *Thalassia-Halodule* beds still alive in Santa Rosa Sound. Losses due to urbanization, industrial waste discharge, dredging and filling, cultural eutrophication.	Livingston, 1979; Livingston et al., 1972; Olinger et al., 1975
Choctawhatchee Bay	Northwest Florida Gulf of Mexico	Historical deterioration of seagrass beds from 1949 through 1983. Causes unknown.	Burch, 1983
St. Andrews Bay	Northwest Florida Gulf of Mexico	No data found: Presumed impact cue to urbanization, industrialization	
St. Joseph Bay	Northwest Florida Gulf of Mexico	Extensive coverage unchanged from 1972 through 1983. Relatively unpopulated area.	McNulty et al., 1972; Savastano et al., 1984.
Apalachicola Bay system	North Florida Gulf of Mexico	Generally healthy assemblages of seagrasses. Local impact due to dredged opening in associated barrier island. Introduced species spreading in delta areas with as yet undetermined impact. Area under increased pressure from urganization.	Livingston, 1980c, 1983
Apalachee Bay	North Florida Gulf of Mexico	Impacts due to disposal of pulp mill wastes (Fenholloway estuary) from 1954 to the present. Slow recovery noted in outer portions of impact area (associated with pollution abatement program). Area now threatened by proposed inshore navigation channel and possible offshore oil drilling operations.	Heck, 1976; Hooks et al., 1976; Livingston, 1975, 1982a, 1984a; Zimmerman and Livingston, 1976a,b.

CHAPTER 3: THE CHESAPEAKE BAY APPROACH

Approaches to assessing habitat requirements of seagrasses

Recently, several documents have been published which present a novel approach to the management of seagrass habitat (Batuik *et al.,* 1992; Dennison *et al.,* 1993). Dennison *et al.* (1993) presents the major findings of a comprehensive technical synthesis conducted by Batuik *et al.* (1992). Both Batuik *et al.* (1992) and Dennison *et al.* (1993) advocate the measurement of physical and chemical water column parameters in existing seagrass beds as a means of identifying impacted systems. The premise is that by knowing the conditions required for plant growth, we can determine the water quality of a specific area through examination of seagrass presence or absence. Thus, areas where plants do not grow indicate that some water quality parameter(s) do not meet the minimum requirements of the plant. Water quality parameter requirements would be specific for each plant species and estuarine habitat. Chesapeake Bay parameter requirements were developed by monitoring water quality gradients within the system over time (Batuik *et al.,* 1992). The habitat requirements developed in this manner represent the absolute minimal water quality characteristics necessary to sustain plants in shallow water (Dennison 1993).

The growth, survival and depth distribution of submerged aquatic vegetation (SAV), including seagrasses, is related to underwater light availabilty (Chapter 4). The parameters examined to determine habitat requirements were total suspended solids, chlorophyll *a* levels, dissolved inorganic nitrogen and phosphorus and the light attenuation coefficient (Batuik *et al.,* 1992; Dennison *et al.,* 1993). These parameters affect light availability in a

variety of ways, either by directly absorbing and scattering light or by stimulating the growth of phytoplankton (see Chapter 2 for further discussion). The habitat requirement approach does not rely on understanding the interactions of water quality and light but relies on empirical water quality data and SAV survival (Dennison *et al.,* 1993).

Measurements of the water quality parameters were made monthly through the growing season, although longer databases (up to 10 years) do exist for some portions of the Chesapeake Bay System. Minimum habitat requirements for SAV in polyhaline areas (salinity greater than 18‰) was a light attenuation coefficient of 1.5 (m^{-1}), total suspended solids of 15 mg L^{-1}, chlorophyll *a* of 15 μg L^{-1} and dissolved inorganic nitrogen and phosphorous of 10 and 0.67 μM, respectively. Other minimum requirements were developed for other salinity regimes (Table 6). In areas where the water quality parameters do not exceed these values one would expect to find SAV.

Although the habitat requirement approach is unique and potentially very useful, there are some drawbacks. Measurements were carried out monthly during the growing season. Due to the immense spatial and temporal variability of marine systems, monthly sampling of water quality parameters is not adequate to characterize a system. Monthly sampling is also likely to underestimate parameter levels experienced by SAV due to the fact that most field programs avoid sampling during inclement weather. Also, while sampling during the growing season may be appropriate for plant species that overwinter as a tuber or seed, it may not be appropriate for species that grow throughout the year (i.e. *Zostera marina*). In addition, estimates of the light attenuation coefficient are derived from Secchi depths (Batuik *et al.,* 1992; Dennison *et al.,* 1993). In view of the problems related

Table 6. Chesapeake Bay submersed aquatic vegetation habitat requirements. For each parameter, the maximal growing season median value that correlated with plant survival is given for each salinity regime. Growing season defined as April-October, except for polyhaline (March-November). Salinity regime defined as tidal fresh = 0.05‰, oligohaline = 0.0-5‰, mesohaline = 5-18‰, polyhaline more than 18‰. From Dennison *et al.*, 1993.

Salinity regime	Light attenuation coefficient (K_d;m^{-1})	Total suspended solids (mg/l)	Chlorophyll *a* (μg/l)	Dissolved inorganic nitrogen (μM)	Dissolved inorganic phosphorus (μM)
Tidal freshwater	2.0	15	15	—	0.67
Oligohaline	2.0	15	15	—	0.67
Mesohaline	1.5	15	15	10	0.33
Polyhaline	1.5	15	15	10	0.67

to the use of Secchi depth to measure attenuation (see Chapter 2) it seems that direct measurement of light availability is more appropriate.

The habitat requirement approach may be a useful tool to estuarine managers in developing water quality standards to prevent the loss of SAV, including seagrasses. It should be pointed out that there is a fundamental difference between the Chesapeake Bay and the bays and estuaries in Texas. The Chesapeake Bay program is using water quality criteria for the reestablishment and restoration of a highly perturbed system. In Texas, the goal is to establish water quality criteria to prevent the destruction of seagrass habitats. Consequently, a different approach and strategy may be appropriate for preserving seagrass habitats in Texas.

CHAPTER 4: SEAGRASS PHOTOSYNTHETIC PHYSIOLOGY

Historically, much of the work on the photosynthetic physiology of marine plants has been done with phytoplankton, as they are at the base of the oceanic food web. Based on these studies, the euphotic zone was defined as the depth to which 1% of surface PAR penetrates (Bougis 1976; Raymont 1980). The 1% light level is not appropriate for defining the depth limits of seagrasses due to the higher respiratory demands of the below ground tissues (Kenworthy and Haunert 1991). Until recently, it was generally accepted that 10% of surface PAR was required to sustain seagrass populations. More recent studies suggest that most seagrass species require 15-25% of surface irradiance (Table 7; Kenworthy and Haunert 1991; Dennison *et al.,* 1993). Numerical models of seagrass depth limits have been developed and used to predict the depth distribution of submerged macrophytes. Many of the models are regression models of field data using least squares methodology. Chambers and Kalff (1985) developed regression models for a variety of fresh water macrophytes from Canada (Table 8). They used attenuation coefficients developed from mean summer Secchi depth to estimate light availability. In general, approximately 20% of surface PAR was required to sustain freshwater macrophyte species. Duarte (1991) developed a regression model (Table 8) that predicts depth distribution for a variety of seagrass species. According to his model, most seagrasses require about 11% of surface PAR (Duarte 1991).

Many of the species used in Duarte's (1991) model occur in very clear waters and thus may underestimate the minimum light requirement for seagrasses. In addition to this problem, both Chambers and Kalff (1985) and Duarte (1991) rely on attenuation coefficients

Table 7. Maximal depth limits and minimal light requirements of various seagrass species. Minimal light requirements were calculated as percent light at maximal depth. Rante of maximal depth limit and mean ± SE of minimal light requirements given for locations with multiple data points. From Dennison *et al.*, 1993.

Genus and species	Location	Maximal depth limit (m)	Minimal light requirement (%)
Amphibolis antarctica[*]	Waterloo Bay (Australia	7.0	24.7
Cymodocea nodosa[*]	Ebro Delta (Spain)	4.0	10.2
C. nodosa[*]	Malta	38.5	7.3
Halodule wrightii[+]	Florida (US)	1.9	17.2
Halophila decipiens[‡]	St. Croix (US)	40.0	4.4
H. decipiens[*]	Northwest Cuba	24.3	8.8
Halophila engelmanni[*]	Northwest Duba	14.4	23.7
Heterozostera tasmanica[*]	Victoria (Australia)	3.8-9.8	5.0±0.6
H. tasmanica[*]	Chile	7.0	17.4
H. tasmanica[*]	Spencer Gulf (Australia)	39.0	4.4
H. tasmanica[*]	Waterloo Bay (Australia)	8.0	20.2
Poisdonia angustifolia[*]	Waterloo Bay (Australia)	7.0	24.7
Poisdonia oceanica[*]	Medas Island (Spain)	15.0	7.8
P. oceanica[*]	Malta	35.0	9.2
Poisdonia ostenfeldii[*]	Waterloo Bay (Australia)	7.0	24.7
Poisdonia sinuosa[*]	Waterloo Bay (Australia)	7.0	24.7
Ruppia maritima[*]	Brazil	0.7	8.2
Syringodium filiforme[*]	Northwest Cuba	16.5	19.2
S. filiforme[*]	Florida (US)	6.8	18.3
S. filiforme[+]	Florida (US)	1.9	17.2
Thalassia testudinum[*]	Northwest Cuba	14.5	23.5
T. testudinum[*]	Puerto Rico	1.0-5.0	24.4±4.2
T. testudinum[*]	Florida (US)	7.5	15.3
Zostera marina[S]	Kattegat (Denmark)	3.7-10.1	20.1±2.1
Z. marina[#]	Roskilde (Denmark)	2.0-5.0	19.4±1.3
Z. marina[*]	Denmark	1.5-9.0	20.6±13.0
Z. marina[*]	Woods Hole (US)	6.0	18.6
Z. marina[*]	Netherlands	2.5	29.4
Z. marina[*]	Japan	2.0-5.0	18.2±4.5

[*]Duarte 1991
[+]W.J. Kenworthy, personal communication, 1990
[‡]Williams and Dennison 1990
[S]Ostenfeld 1908
[#]Borum 1983

Table 8. Regression equations used to predict the depth distribution of different aquatic plants.

Group	Equation
Freshwater	
Angiosperms	$(Z_c)^{.5} = 1.33 \log(D) + 1.40$
Bryophytes	$(Z_c)^{-.5} = -0.48 \log(D) + 0.81$
Charophytes	$\log(Z_c) = 0.87 \log(D) + 0.31$
Marine Seagrasses	
general	$\log(Z_c) = 0.26 - 1.07 \log(k)$
Thalassia	$Z_c = 0.27 - 0.93 \log(k)$
Zostera	$Z_c = 0.27 - 0.84 \log(k)$

[1]From Chambers and Kalff 1985
[2]From Duarte 1991
Z_c = colonization depth
D = mean summer Secchi depth
k = diffuse light attenuation coefficient

developed from Secchi depth measurements. Priesendorfer (1986) suggests that it is notappropriate to derive attenuation coefficients from Secchi depth (see Chapter 2).

Computer modelling

Computer simulation models of seagrass growth and productivity in relation to light and nutrients have been developed. The development of mathematical models provide a mechanism for synthesizing the information available in the literature (Short 1980). Models have become predictive tools for management, but can also provide insight to the dynamic response of seagrass ecosystems (Short 1980). One of the first mathematical models of seagrass ecosystems investigated how nutrients affected eelgrass growth; however, to realistically model the system it was necessary to incorporate light limitation (Short 1980). Short utilized Steele's equation for phytoplankton photosynthesis, which describes production as increasing with increased light up to an optimum light intensity. Beyond the optimum, production decreases as a result of photoinhibition (Short 1980). The model was run using data from Charlestown Pond, R.I. The simulation yielded a good representation of the seasonal trends and a reasonable fit to the observed data (Short 1980). Wetzel and Neckles (1986) developed a model of photosynthesis and growth for *Zostera marina* in relation to selected physical-chemical variables. They found that physical parameters such as light and temperature controlled growth and photosynthesis. Small changes in submarine irradiance or temperature resulted in decreased plant productivity and the eventual loss of the seagrass community. These simulations suggest small changes in light (or temperature) may cause the complete loss of seagrass communities on the edge of their physiological tolerance (e.g.,

the deep edge of the seagrass bed). Wetzel and Neckles (1986) concluded that ambient light was a principle factor controlling the longevity and survival of seagrass beds. Zimmerman *et al.* (1987) modelled nitrogen budgets and light availability using field and experimental data from numerous investigations, and the model predictions were tested against other field data. They found that light had a significant effect on the rate and site of nitrogen uptake in *Z. marina*. The model predicts that for eelgrass exposed to H_{sat} greater than 6 h (i.e., "normal" conditions) most of the nitrogen uptake will occur through the roots. However, in low light environments (short H_{sat}) there is an increase in the importance of nitrogen uptake and assimilation by the leaves. Thus, the site of nutrient uptake appears to be partially dependent on the light environment the plant experiences.

As a general approach to seagrass ecology, simulation models are invaluable. They can be used to synthesize the available data and point out new directions for research. Short (1980) showed that mathematical simulations could be used to adequately predict seagrass productivity as a function of several parameters including nutrients, light and temperature. Wetzel and Neckles (1986) suggested that small changes in the diffuse attenuation coefficient could result in the elimination of seagrass habitat. Zimmerman *et al.* (1987) suggest that the site of nutrient acquisition is dependent, at least in part, on the light environment the plant experiences. In general, simulation models can be very interesting and provide useful information to seagrass biologists and estuarine managers.

Effects of *in situ* light reduction

Although computer simulations are informative, researchers also need to

quantitatively evaluate the effect of model parameters on *in situ* populations. During the late 1960's and 1970's numerous studies were conducted to examine the effects of reduced light on seagrass growth, production and morphology. Some of the earliest work involving seagrass shading was done by Burkholder and Doheny (1968), who used cages to reduce available light to 100, 60, 20, 10 and 1.6 % of surface irradiance (SI). Eelgrass (*Zostera marina*) growing in these cages became noticeably stunted and did not survive at light levels less than 20% SI. In an attempt to validate a model, Short *et al.* (1974) investigated how the hydrodynamics of the Charlestown Pond R.I. were influenced by eelgrass. They examined the influence of light on seagrasses (and in turn the hydrodynamic model) by shading eelgrass with cages, which resulted in shorter plants as well as reduced biomass and density. Backman and Barlotti (1976) reduced 63% of the light reaching *Z. marina* in a coastal lagoon in California for a period of nine months. They found reduced biomass, shoot density and incidence of flowering. Congdon and McComb (1979) examined the productivity of *Ruppia maritima* in response to reduced light in an Australian estuary. They used seven light levels in the study: 100, 60, 41, 28, 19, 15, and 7.5% SI. However, they made no *in situ* measurements of irradiance. They reported a general seasonal pattern of low standing crop during winter with a rapid increase in the spring. As the duration of shading increased, the plants required higher light levels to persist. At least 20% SI was required to maintain 50% of initial standing crop for up to 100 days, while greater than 60% SI was required to maintain 50% of initial biomass for more than 200 days. They concluded that a reduction in light intensity may result in the loss of considerable quantities of *Ruppia*.

During the 1980's several other investigations examined the influence of reduced light

on various seagrass species. For example, Bulthuis (1983a) examined the response of *Heterozostera tasmanica* to *in situ* light reduction in Victoria, Australia. The light levels below the screens were approximately 18, 13, 4.7 and 1% SI. Light levels less than 4.7% SI resulted in the death of all shoots within 2 to 10 months. Light levels of 18 and 13% SI caused reduced shoot density relative to the controls, suggesting the plants were unable to survive indefinitely at these light levels. Some changes in shoot morphology were also noted; however, leaf growth rate and leaf width remained the same. Bulthuis (1983a) data indicate that *H. tasmanica* may have a higher light requirement at summer temperatures than at winter temperatures and thus may be more sensitive to reduced irradiance during summer than in winter (Bulthuis 1983a). Carter and Rybicki (1985), found that both light penetration and grazing pressure effected the survival of transplanted *Vallisneria americana* in the tidal Potomac River, Maryland. Odum (1985) examined the response of *Thalassia testudinum* to shading by epiphytes. She did an *in situ* shading experiment during the winter where light intensity was reduced to 2-10% SI. Shoot density decreased under the reduced light treatments and after eight months all the plants were dead. It was suggested that during summer the demise of the seagrasses would have occurred more quickly. Neverauskus (1988) examined the response of *Posidonia sinuosa* and *P. angustifolia* in Australia to chronic long-term light reduction (Figure 14). He constructed a canopy of 50% shade cloth, which was placed over the community. During the first six months of treatment, shoot density was unchanged but leaf density and standing crop had declined; during the second six months shoot density decreased dramatically. However, although Neverauskus (1988) documented changes in plant canopy structure, the study itself was very poorly

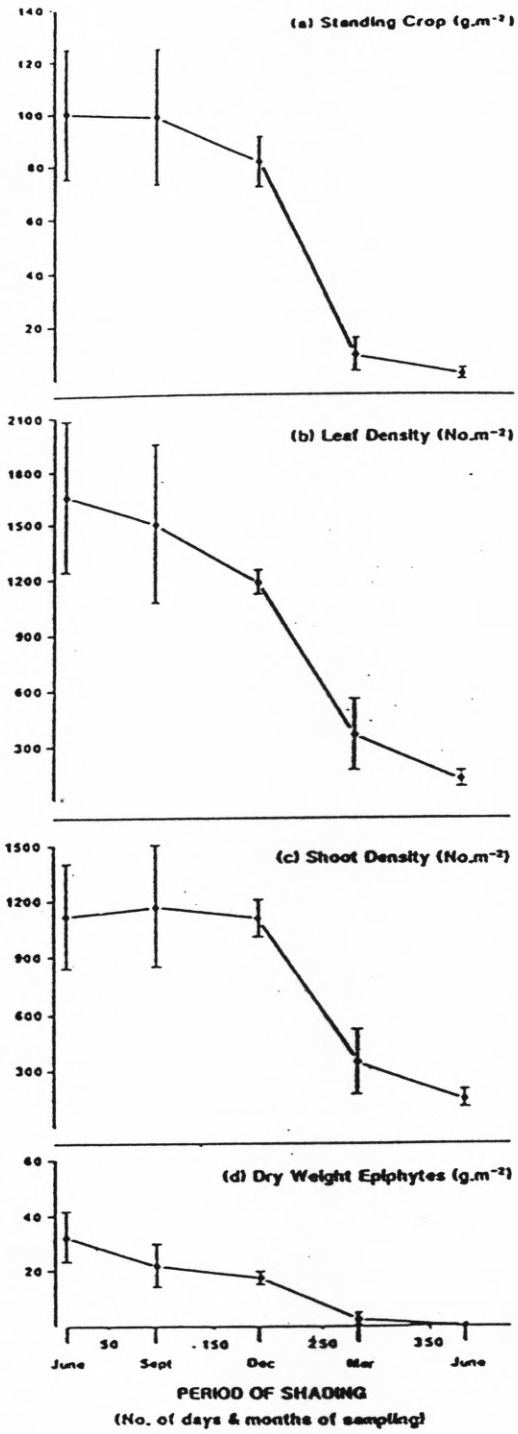

Figure 14. Changes in standing crop, leaf density and dry weight of epiphytes of *Posidonia* in response to 50% reduction in ambient light. Error bars represent standard deviation, n = 4. From Neverauskas 1988.

designed. There was no control plot, no statistical analysis nor was there any estimate of the actual amount of light received by the plants.

Stable carbon isotope ratios have been used recently to examine the effects of reduced light on seagrasses (Durako and Hall 1992). The $\delta^{13}C$ values of shaded *Thalassia* leaves were significantly lower than those of unshaded plants. Changes in the $\delta^{13}C$ values were correlated with the relative amount of light reaching the plants. The increasing isotopic fractionation with light reduction may reflect decreasing carbon demand associated with lower photosynthetic rates. Thus, at low irradiances there may be greater relative carbon availability. As light is reduced to levels that limit photosynthetic rates, carbon appears to become non-limiting.

There have been many studies describing the effects of reduced irradiance on seagrasses. Although the experiments have been carried out in many different parts of the world on a variety of seagrass species, there are some common observations that can be made. First, the standing crop and density of shoots decreases with decreasing light. Second, there are often changes in the morphology of seagrass shoots (i.e., longer and thinner blades) with reduced irradiance. Third, several studies suggest there are seasonal differences in the light requirements of seagrasses. Fourth, it appears that light availability may influence the $\delta^{13}C$ signature of seagrasses. Fifth, there is a lack of consistency in the experimental design of these studies with respect to light reduction techniques or measurements of light availability.

Experimental changes in daily light period

Several field studies have examined the effects of changes in daily light period length on seagrasses. However, before examining the findings of these studies it is necessary to define H_{comp} and H_{sat} (Figure 15). H_{comp} refers to the daily number of hours at which PAR is at or above a plant's compensation irradiance. H_{sat} refers to the daily number of hours at which PAR equals or exceeds a plant's saturation irradiance. Dennison and Alberte (1982) found that both H_{sat} and H_{comp} may be manipulated *in situ* by using light reflectors and shading screens to study the effects of changing the daily light period (Table 9). They concluded that during short-term experiments, eelgrass responded to changes in the light environment by changing leaf production rates. Dennison and Alberte (1985) examined the role of the daily light period on the depth distribution of *Zostera marina*. The length of the photoperiod was increased by suspending underwater lights over an eelgrass bed and shortened using shade screens (Table 10). Based on these manipulations, Dennison and Albert (1985) determined that eelgrass required a minimum H_{sat} of about 6 hrs to maintain a positive carbon balance. They concluded that H_{sat} was a better predictor of plant productivity than absolute PPFD (photosynthetic photon flux density). Dennison and Alberte (1986) examined photoadaptation and growth along a depth gradient for *Z. marina*. *Zostera* transplanted from deep water to shallow water survived well, while transplants from shallow water to deep water did not survive. Daily quantum flux varied with depth from 38.8 to 4.4 E m^{-2} day^{-1} at 0.8 and 7 m water depths, respectively. In addition H_{sat} varied from 12.7 to 5.8 h for 0.8 and 7 m depths, respectively. These studies suggest that in addition to the actual PFFD that plants experience, the photoperiod and particularly H_{sat}

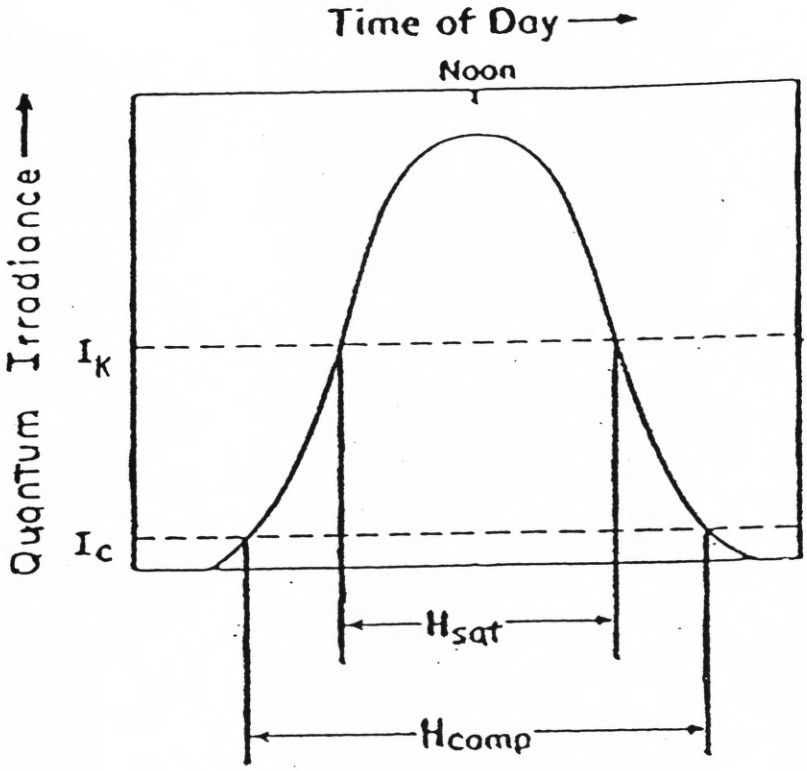

Figure 15. Generalized diurnal light curve in which the light saturation point (I_k) and light compensation point (I_c) for photosynthesis are used to determine periods of saturating (H_{sat}) and compensating (H_{comp}) quantum irradiance. From Dennison 1987.

Table 9. Changes in the H_{comp} and H_{sat} parameters for eelgrass as a result of reflectors and shading. From Dennison and Alberte 1982.

Station	percent change
Shallow (1.3 m)	
Reflectors	35% increase of light H_{comp}+2% H_{sat}+7%
Shades	55% decrease of light H_{comp}-4% H_{sat}-7%
Deep (5.5 m)	
Reflectors	40% increase of light H_{comp}+4% H_{sat}+14%
Shades	55% decrease of light H_{comp}-11% H_{sat}-52%

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Table 10. Changes in H_{sat} as a result of lights and shading. From Dennison and Alberte, 1985.

Station	Change in H_{sat}
Shallow	
Lights	+4 hours
Shades	- 4 hours
Deep	
Lights	+5 hours
Shades	- 3 hours

also influence the depth distribution of seagrasses. Dennison (1987) examined the effects of light on seagrass photosynthesis, growth and depth distribution. The longest periods of light centered around the summer solstice; increased respiration due to higher temperatures effectively decreased both H_{comp} and H_{sat}. There was an exponential relationship between light extinction coeffecients and maximum depth limits; thus, Dennison (1987) suggests that Secchi disc depths averaged throughout the year can be used to predict the maximum depth of *Z. marina* (see chapter 2 and Zimmerman *et al.,* 1991). He concluded that the perennial nature of most seagrasses represents a year-round integration of environmental factors that influence the compensation depth.

Although they did not manipulate H_{sat}, Zimmerman *et al.* (1991) found the length of H_{sat} had a pronounced impact on the survival and depth distribution of *Zostera marina* in San Francisco Bay. They estimated that an H_{sat} of between 3 and 5 h was required to meet the respiratory demands of the plants. H_{sat} requirements at the more turbid sites were longer, limiting plants to shallower depths than those predicted from estimates of carbon budgets and mean H_{sat} availability. Zimmerman *et al.* (1991) suggested that the mean diffuse attenuation of the water column is not a good predictor of the depth limit of eelgrass particularly in locations where transient and/or seasonal periods of high turbidity may be common. These findings may be applicable to the meteorologically driven systems of Texas.

Recent work in Texas (Dunton and Tomasko, submitted; Dunton submitted) have examined the light requirements of *Halodule wrightii* in Laguna Madre. They have determined that *H. wrightii* growing near the lower limit of depth penetration had an H_{sat} requirement of 3 to 5 h and an H_{comp} of 8 to 9 h. These H_{sat} and H_{comp} values represent an

annual quantum budget of 5100-5700 mol $m^{-2}yr^{-1}$ (Dunton, submitted).

The relationship between mean light availability and depth distribution of eelgrass in San Francisco Bay appears to be more complicated than simple models based on mean diffuse attenuation coefficients would suggest (Zimmerman *et al.,* 1991). Carbohydrate reserves may act as a buffer during periods when H_{sat} is less than that required by the plants; however, the reserves are limited in nature. Plants at the lower edge of the beds may not be able to build up adequate reserves to sustain them through periods of low light. Thus, brief periods of extreme turbidity may be more critical than the mean turbidity in controlling the depth distribution of existing populations and the establishment of seedlings or propagules. The average length of the daily H_{sat} period is important, as well as the number of "critical days" per month or season when H_{sat} requirements are not met. The number of extreme attenuation days (EAD) when diffuse attenuation values prevent net carbon gain or adequate root oxygenation may provide a quantitative measure of habitat suitability that may prove to be a sensitive predictor of eelgrass growth and survival in different habitats (Zimmerman *et al.,* 1991).

Laboratory studies of reduced light on seagrasses

In addition to *in situ* studies of reduced irradiance and photoperiod there have been two *in vivo* studies examining the response of submerged aquatics to reduced light. Goldsborough and Kemp (1988) examined the response of *Potamogeton perfoliatus* to changes in total irradiance. Plant populations were grown in aquaria and the light environment was manipulated using neutral density screens which alter light intensity but

not spectral quality. The treatment levels were 11, 32 and 100% SI. After three days, shaded plants showed an increase in photosynthetic efficiency and chlorophyll *a* concentrations. Following ten days of treatment there were significant changes in the morphological characteristics of the plants including elongation of stems, thinning of lower leaves, and canopy formation at the water surface. Golsborough and Kemp (1988) concluded that the physiological and morphological responses of the plants conferred improvements in plant fitness under the treatment conditions. Tomasko (1992) examined changes in the morphology of *Halodule wrightii* due to changes in the spectral composition of light. *Halodule* was grown under a canopy of *Thalassia testudinum* that changed the ratio of red:far red light. Other plants were grown under neutral density screens of equivalent light reduction that did not alter the red:far red ratio. Plants grown under *Thalassia testudinum* had longer internode lengths, while plants under neutral density screens showed reduced growth rates compared to controls. Tomasko (1992) suggested that *Halodule* minimizes competitive interaction with *Thalassia* by varying its morphology.

Studies of reduced irradiance and daily light period suggest that when seagrasses are light stressed they change their morphology (within limits) to optimize photon capture. Thus, it appears that morphological plasticity may confer some advantage to submerged macrophytes, allowing them to survive periods of reduced irradiance. The work examining H_{sat} of eelgrass and the laboratory studies of *Potamogeton* also suggest these plants may physiologically adapt to reduced light.

Photosynthesis irradiance curves

Photosynthesis irradiance (P vs. I) curves are a means of quantifying the photosynthetic rate on an area, weight or chlorophyll basis (Kirk 1983). Blade tissue is placed in a chamber with an oxygen electrode and a light sensor. Oxygen evolution or consumption is measured as a function of light intensity striking the plant (Figure 16). In the dark there is no photosynthesis and plants exhibit net consumption of O_2 as a result of respiration. As light intensity is increased, some O_2 production occurs; however, this shows up as a diminution of the O_2 consumed by the blade tissue (respiration exceeds photosynthesis). The irradiance at which photosynthetic O_2 production equals the O_2 consumed in respiration is the compensation irradiance (I_c). At light intensities greater than I_c the plants exhibit net photosynthetic production. Maximum photosynthetic production (P_{max}) is achieved when increases in PAR no longer result in an increase in oxygen evolution; the light saturation point (I_k) can be estimated from the intersection of the initial slope with P_{max} or is more accurately calculated as P_{max}/α. Alpha (α) is represented by the initial slope of the P vs. I curve and is a measure of the efficiency with which the plant biomass utilized light (Kirk 1983). It represents the efficiency with which light quanta are absorbed and used to transfer electrons through photosystems I and II. P_{max} reflects the dark reactions of photosynthesis and is regulated by recycling of the various metabolic intermediates (ATP and NADPH).

Although there have been numerous studies of the P vs. I parameters of seagrasses, few have been carried out *in situ*. Wetzel and Penhale, (1983) examined *in situ* the P vs. I characters that allow populations of SAV in Chesapeake Bay to survive in a very stochastic

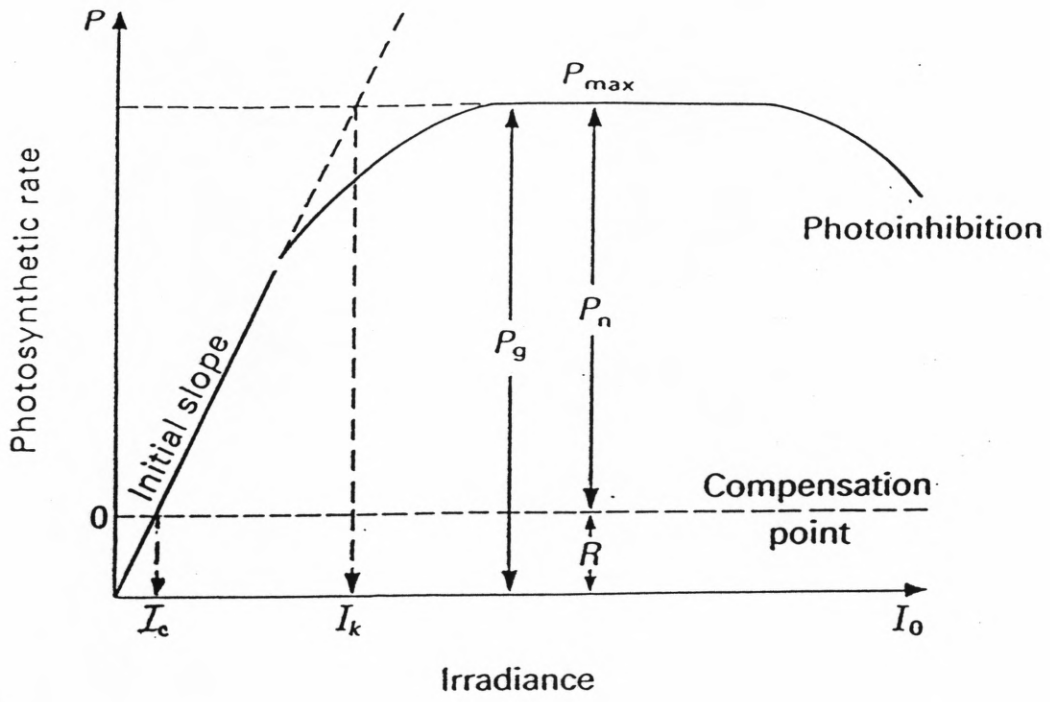

Figure 16. Light saturation curve for photosynthesis. P, photosynthesis; P_{max}, maximum photosynthesis; P_g, gross photosynthesis; P_n, net photosynthesis; R, respiration; I_o, incident PAR; I_k, saturating PAR; I_c, compensation PAR. From South and Whittick 1987.

environment. They found that submarine PAR and temperature act both singularly and interactively to control the biomass and distribution of seagrasses in Chesapeake Bay. For *Ruppia maritima*, P_{max} was correlated with temperature and there was no sign of photoinhibition. P_{max} for *Zostera marina* was not correlated with temperature, although *Zostera* appears to have a temperature optima below 28°C. Wetzel and Penhale (1983) found that the two species were therefore physiologically distinct, allowing them to coexist in the same niche. The authors suggested that changes in the distribution of seagrasses in Chesapeake Bay may be related to changes in light availability. Libes (1986) examined the P vs. I relationship of *Posidonia oceanica in situ* using C^{14} techniques. Photosynthetic efficiency was greatest in winter and least in summer. Additionally, productivity was greatest in the morning and least in the evening. Libes also found evidence of seasonal photoinhibition and suggested that *Posidonia* may have a seasonal endogenous rhythm with regard to photosynthetic capacity. I_c and I_k were similar for both the seagrass and its epiphytes. Dunton and Tomasko (submitted) made *in situ* measurements of the photosynthetic performance of *Halodule wrightii* in Texas. They documented seasonal variation in all of the parameters that describe the P vs. I curve.

Laboratory studies of P vs. I characters are easier to perform than field studies, and as a result, numerous laboratory studies of seagrass P vs. I characteristics have been completed. Drew (1978) investigated the factors affecting photosynthesis and its seasonal variation in *Cymodocea nodosa* and *Posidonia oceanica*. He measured photosynthesis, dark respiration and leaf chlorophyll content on plants from shallow (1-5 m) and deep (25-33 m) sites. *Cymodocea* had similar spring and summer light saturated photosynthetic rates, while

Posidonia had higher photosynthetic rates in spring than in summer (Figure 17). The temperature optima for photosynthesis was about 30°C for both species and dark respirationwas similar during both the spring and summer. Drew (1979) examined the physiological aspects of primary production in *Cymodocea nodosa, Posidonia oceanica, Halophila stipulacea, Phyllospadix torreyi, Zostera angustifolia* and *Zostera marina*. P vs. I curves were developed for each species (Figure 18) as were plots of photosynthesis versus temperature. All species showed similar P vs. I curves that usually shows light saturation around 2-3 mW/cm^2 (≈138 $\mu mol\ m^{-2}\ s^{-1}$). *Halophila* was the only species that showed evidence of photoinhibition. Despite a wide range of P_{max} (8.1 to 26.0 $\mu g\ C\ cm^{-2}\ h^{-1}$) all of the I_k values were about 10% of full sunlight and all of the I_c values were about 1% SI (Table 11).

Williams and McRoy (1982) examined the effects of light on carbon uptake in six seagrass species: *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii*, *Halophila engelmanni*, *Phyllospadix scouleri* and *Ruppia maritima*. Seagrasses from Texas became light saturated at high irradiances, between 64-85% SI. The five species had similar half-saturation constants ranging from 49-56% SI. Williams and McRoy (1982) suggested that *Thalassia* and *Syringodium* are "climax species" and that the other species are "colonizers". Kerr and Strother (1985) examined how photosynthesis in *Zostera muelleri* responded to irradiance, temperature and salinity (Figure 19). Photosynthesis increased with increasing light (from 17 to 185 $\mu mol\ m^{-2}\ s^{-1}$) at 16°C, with no indication of photoinhibition at the highest light levels used in the experiment.

Because the dark reactions of the photosynthetic process are enzymatically mediated,

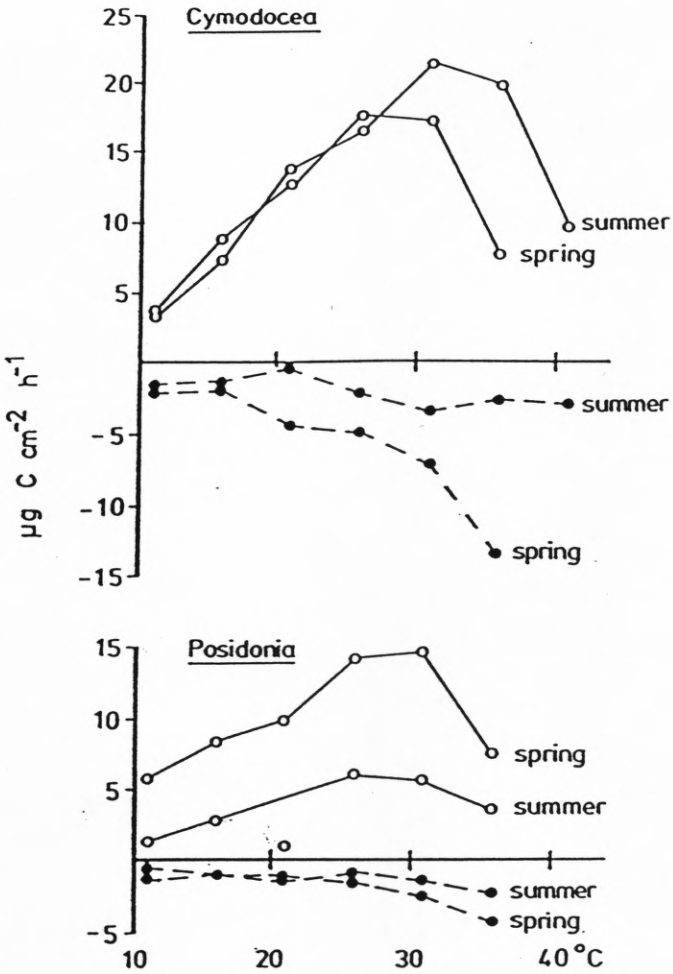

Figure 17. Effect of temperature on net photosynthesis and dark respiration in shallow-growing leaves of *Cymodocea* and *Posidonia* in spring and summer; photosynthesis measured at 20 mW cm^{-2}. From Drew 1978.

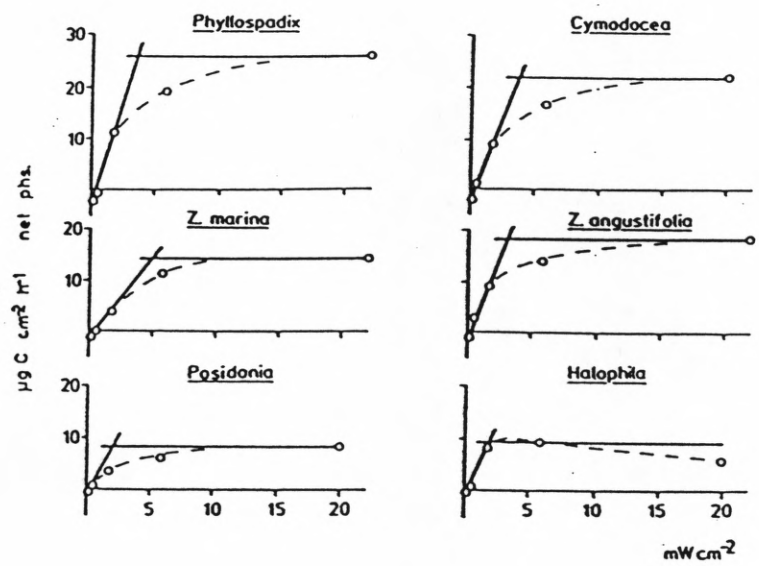

Figure 18. P vs. I curves for six seagrass species at ambient environmental temperatures. From Drew 1979.

Table 11. Photosynthetic rates, respiration rates, saturation and compensation irradiance at ambient environmental temperatures in six seagrass species. From Drew 1979.

	y_{max}	I_k	I_c	R_1	R_d	Temp. (°C)
Phyllospadix torreyi	26.0	3.6	0.5	–3.8	–5.3	15
Cymodocea nodosa	21.8	3.8	0.4	–2.5	–3.5	25
Zostera angustifolia	18.1	3.2	0.3	–1.8	–2.1	10
Zostera marina	14.2	5.0	0.6	–1.7	–1.4	15
Halophila stipulacea	9.0	2.0	0.2	–1.2	–1.1	25
Posidonia oceanica	8.1	2.6	0.4	–1.3	–1.5	17

*y_{max}, μg C cm^{-2} h^{-1}; I_k and I_c, mW cm^{-2} PAR; R_1 and R_d, μg C cm^{-2} h^{-1}.

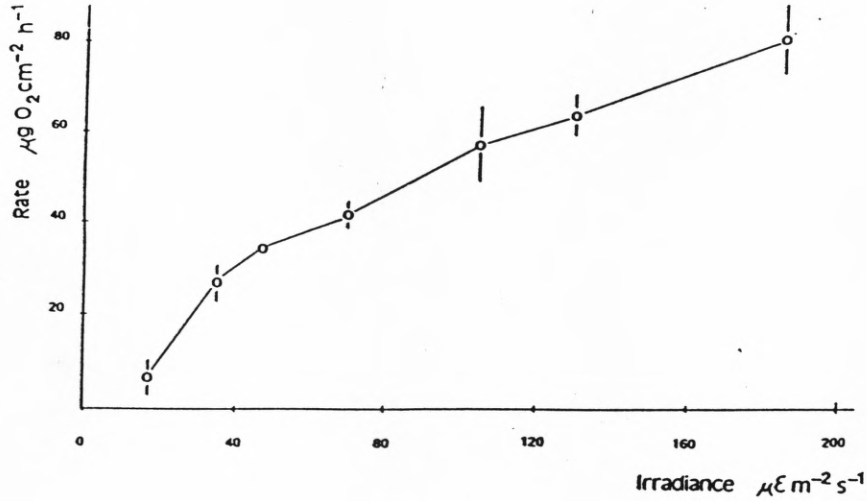

Figure 19a. Relationship between apparent photosynthesis and irradiance (PAR) in *Zostera muelleri* at 16°C. From Kerr and Strother 1985.

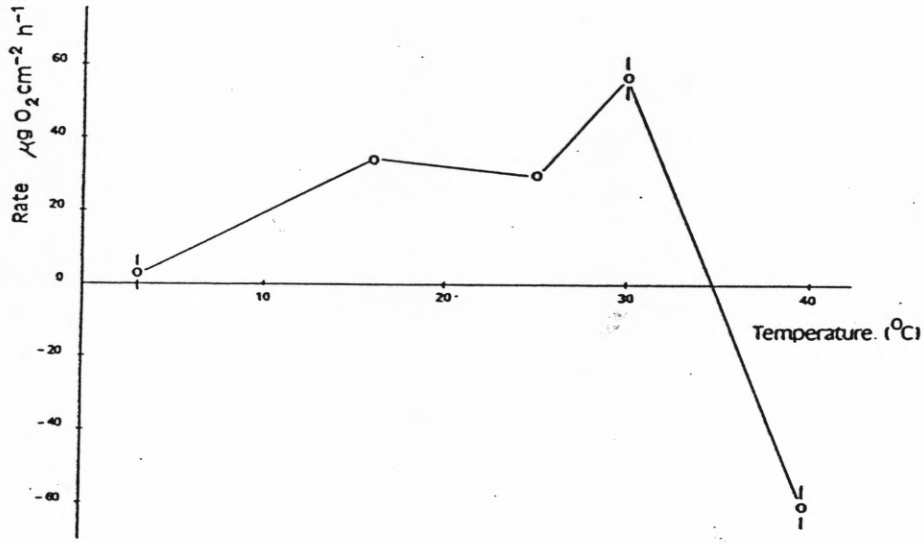

Figure 19b. Relationship between apparent photosynthesis and temperature in *Zostera muelleri* at an irradiance of 47 ± 2 μmol m^{-2} s^{-1}. From Kerr and Strother 1985.

temperature can have a pronounced effect on the P_{max} (Bulthuis 1987). Several investigations have examined the response of P vs. I characters to changes in temperature. As part of his study, Drew (1979) examined the effects of temperature on the rates of photosynthesis and respiration. Measurements of photosynthesis and respiration were made at six temperatures between 10 and 40°C (Figure 20). Photosynthesis increased linearly with increased temperature (r^2= 0.99 to 1.00). For some species (*Posidonia* and *Cymodocea*) temperatures greater than 30°C caused thermal damage and resulted in decreased photosynthesis. At temperatures lower than normally encountered in their natural habitat, all species maintained a moderately low rate of respiration. Bulthuis (1983b) examined the effects of temperature on the P vs. I curve of *Heterozostera tasmanica*. He measured the P vs. I parameters at 8 temperatures ranging from 5 to 40°C (Figure 21). At 25 and 30°C photosynthesis was not light saturated even at the highest intensities (955 μmol m^{-2} s^{-1}). P_{max} increased by a factor of 2.5 between 5 and 30°C and decreased sharply between 30 and 35°C. The rate of dark respiration increased by a factor of 2 between 5 and 20°C with small increases above 20°C. Evans (1984) examined the physiological response of Chesapeake Bay populations of *Zostera marina* and *Ruppia maritima* to temperature. For both species the lowest P_{max} was at 8°C. The highest P_{max} occurred for *Zostera* at 19°C and for *Ruppia* at 26 and 30°C. At temperatures between 8 and 19°C *Zostera* had a higher P_{max} than *Ruppia*. I_k for *Zostera* ranged from 46 μmol m^{-2} s^{-1} at 26°C to 28 μmol m^{-2} s^{-1} at 30°C, while for *Ruppia* the range at the same temperatures was greater (39-72 μmol m^{-2} s^{-1}). In general, *Ruppia* had a higher I_k than *Zostera* at all temperatures. Evans (1984) suggested that at lower temperatures *Zostera* has the competitive edge over

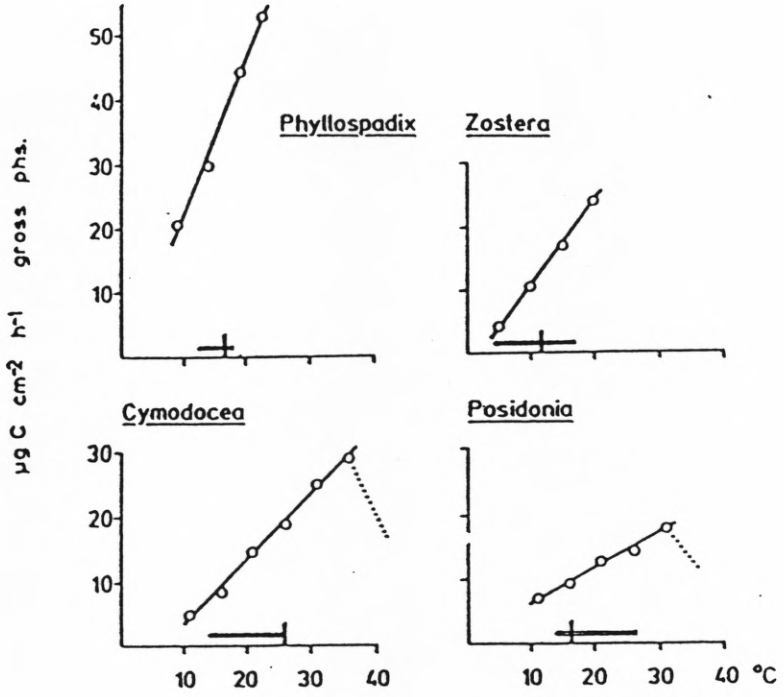

Figure 20. Effect of temperatures both above and below ambient on the rates of gross photosynthesis in four seagrasses. Horizontal bar is the range of environmental temperatures normally encountered by the plant; open circles reflect the incubation. From Drew 1979.

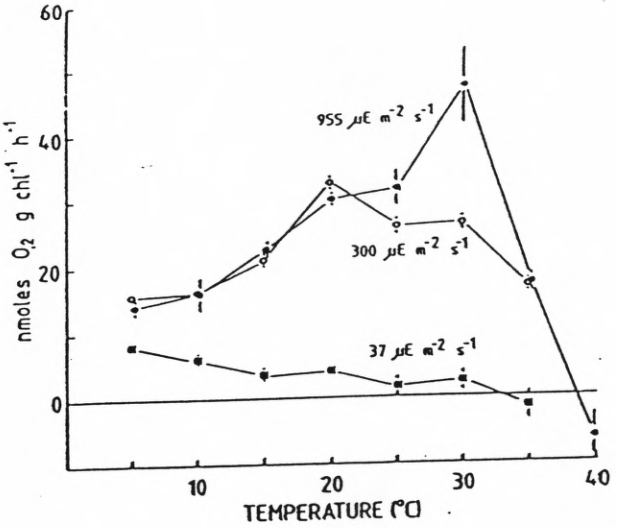

Figure 21. Temperature vs. apparent photosynthesis in *Heterozostera tasmanica* at three irradiance levels. Mean ± 1 SE (n = 3-9) for plants collected from Crib Point, Australia. From Bulthuis 1987.

Ruppia, while at higher temperatures *Ruppia* has the advantage. Thus temporal resource partitioning may allow the coexistence of these species. Kerr and Strother (1985) examined the photosynthetic rate of *Z. muelleri* at light levels of 47 μmol m^{-2} s^{-1} and a range oftemperatures. Photosynthesis increased with temperature from 5 to 30°C and showed a marked decrease at temperatures greater than 30°C (Figure 19).

Marsh *et al.* (1986) examined the effects of temperature on photosynthesis and respiration in *Zostera marina*. They developed P vs. I curves for plants grown at 20-22°C and subjected to various temperatures between 0°C and 35°C (Figure 22). Light saturated net photosynthesis increased with temperature to an optimum around 25-30°C and decreased at 35°C. The initial slopes of the P vs. I curve (α) were greatest at 0°C and least at 35°C. Kerr and Strother (1985) suggest that in winter, low temperatures and low light conditions enable the plants to maintain a positive carbon balance; however, high temperatures (>30°C) and low light would result in a negative carbon balance. Bulthuis (1987) reviewed the effects of temperature on seagrasses. He found compensation irradiance increases with temperature; therefore, to maintain a positive carbon balance, seagrass plants require a greater irradiance during summer than during winter. The literature indicates temperature optima for light saturation of photosynthesis is generally between 25 and 35°C; however, there tends to be a rapid loss of photosynthetic capacity at temperatures above the optimum. Bulthuis (1987) suggests that the seasonality of I_c may have important implications for seagrasses living at or near their minimum light requirements. Madsen and Adams (1989) found that *Potamogeton pectinatus* exhibited optimal photosynthetic production at 30°C and that photosynthesis at 10°C was 63% lower

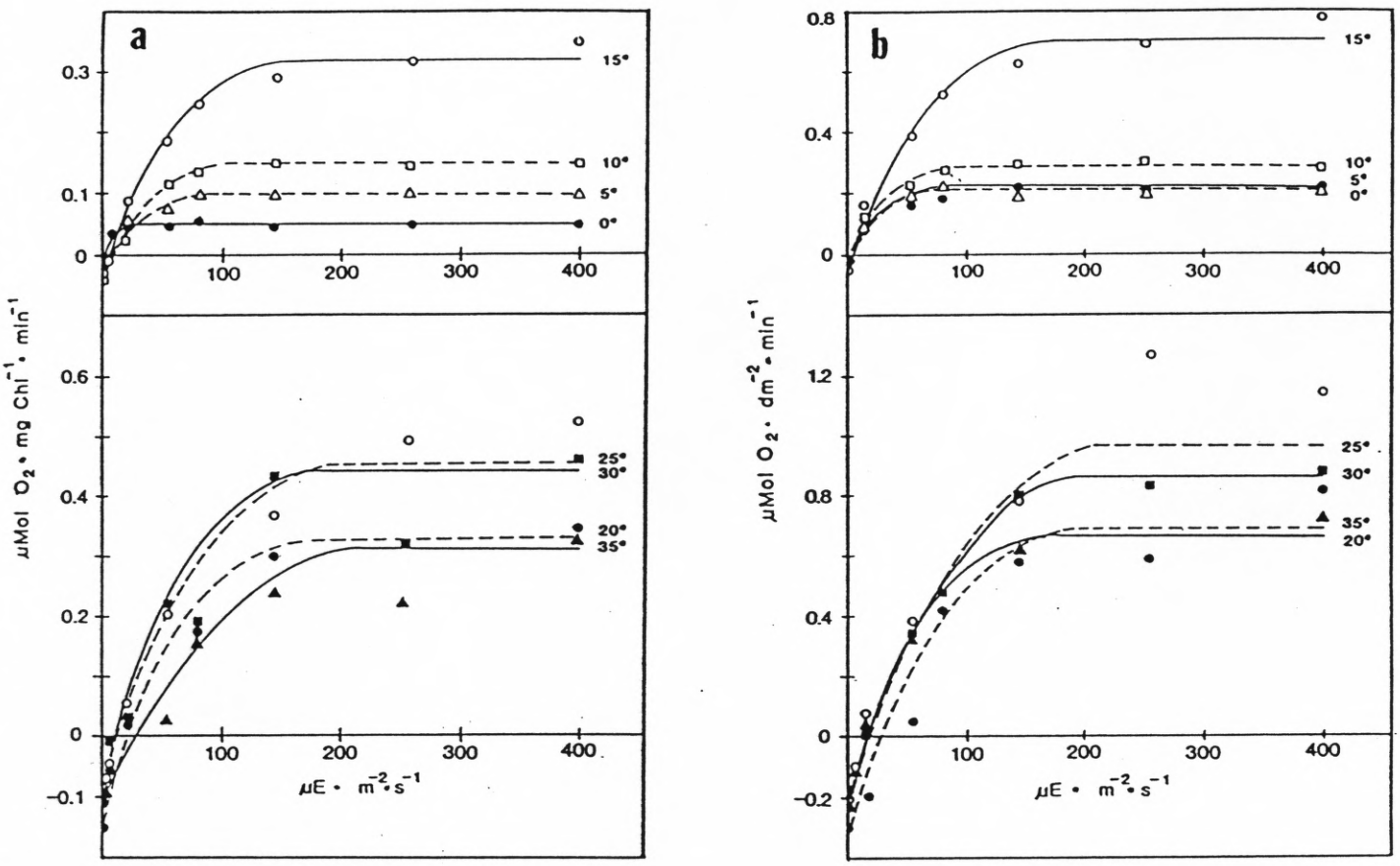

Figure 22. P vs. I relationships of *Zostera marina* leaf segments measured at different temperatures. Leaf tissue was grown at 20-22°C in the field was incubated at the given temperatures for 15 minutes prior to measurement; a, photosynthesis expressed per mg Chlor.$^{-1}$ min^{-1}; b, photosynthesis expressed per dm^{-2} min^{-1}. From Marsh *et al.*, 1986.

than that at 30°C. Perez and Romero (1992) examined the photosynthetic response of *Cymodocea nodosa* to light and temperature. The P vs. I curves showed seasonal variation, with P_{max} and I_k higher during summer than during winter(Figure 23). I_c did not exhibit any seasonality. *Cymodocea* showed no indication of photoinhibition at light levels up to 2500 μmol m^{-2} s^{-1}. Rates of light saturated photosynthesis and dark respiration increased significantly with increasing temperature. Perez and Romero (1992) also suggested the control of seagrass seasonality may be more complex than previously thought.

As with most other fields of science there are some controversies with regard to seagrasses and photosynthesis. One of the biggest difficulties is standardizing units of light energy. Through the years a bewildering variety of units have been used to measure light energy, everything from Langleys (Williams and McRoy 1982) to milliWatts cm^{-2} (Drew 1979) to μEinsteins (Kerr and Strother 1985, Perez and Romero 1992). Although there are numerous conversion factors in the literature, most do not take into account the selective absorption of specific wavelengths of light by water (Lüning 1990; Megard and Berman, 1989). Thus, most calculations that employ conversion factors between units are relatively poor estimates of light energy at depth. The best method for estimating underwater light availability is to measure it *in situ* (Dunton, submitted).

One of the other controversies in the literature is the validity and/or usefulness of carbon budgets based on P vs. I curves developed from leaf segments (Fourqurean and Zieman 1991a). The I_c value developed for leaf tissue does not take into account the large respiratory demands of the below-ground tissue. Thus, whole plant carbon budgets based on leaf tissue probably underestimate the true carbon budget of the whole plant

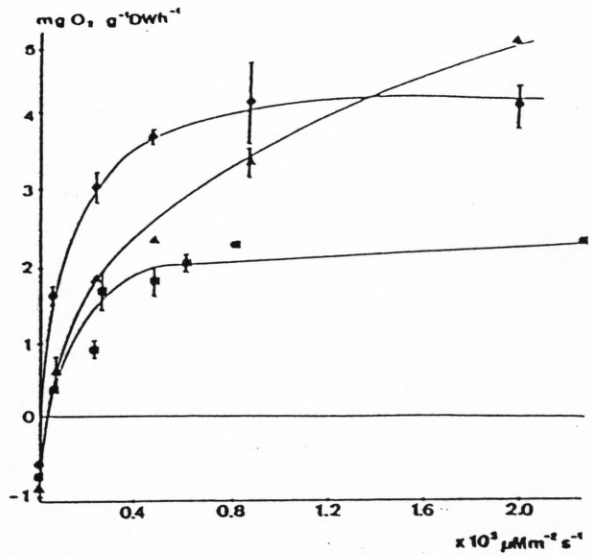

Figure 23a. Seasonal trends in P vs. I curves in *Cymodocea nodosa* for November (boxes), June (triangles), and August (circles). From Perez and Romero 1992.

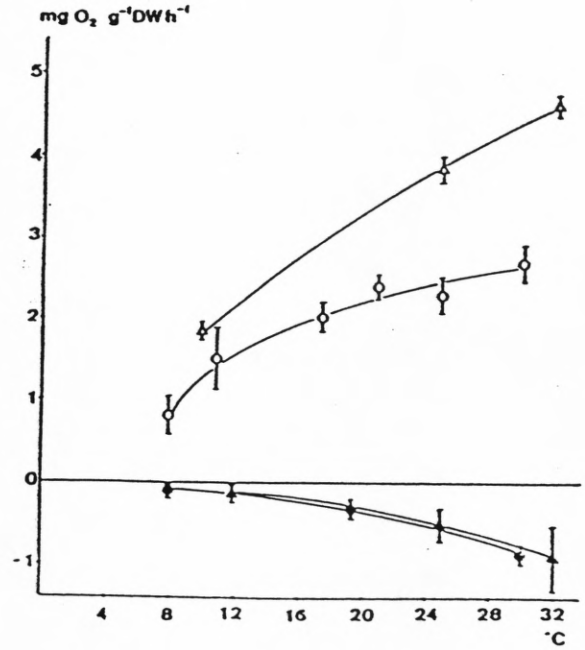

Figure 23b. Response of both net photosynthesis (open symbols) and dark respiration (black symbols) to temperature in August (triangles) and February (circles). From Perez and Romero 1992.

(Fourqurean and Zieman 1991 b). Fourqurean and Zieman (1991a) used a P vs. I chamber that allowed them to develop P vs. I curves for whole plants in a more natural orientation to the light field. They found that leaves account for less than 50% of the total plant respiration. Knowledge of the above- to below-ground apportionment and the factors that control this ratio are critical to modelling carbon budgets of seagrasses. In addition, the question of using whole plant vs leaf tissue P versus I data in models of plant carbon budgets must still be addressed.

Measurements of photosynthesis in seagrasses suggest that light and temperature are the factors that control the rate of photosynthesis and respiration. In general, photosynthesis at a given light level increases until the optimum temperature is reached. At temperatures above the optimum, photosynthesis decreases. Compensation irradiance also varies with increased temperature as a result of increased respiration. Thus, at elevated temperatures plants require greater irradiance to maintain a net carbon balance. The observed seasonal pattern in P vs. I parameters is probably a result of seasonal temperature changes.

Seasonal changes in seagrasses

Seagrasses, like most plants, exhibit seasonal changes in production, P vs. I parameters and organic constituents. Odum (1963) examined the productivity of Texas *Thalassia testudinum* and reported a marked seasonal cycle in productivity with considerable interannual variation (Figure 24). Zieman (1975b) examined the seasonal variation of Florida *Thalassia* with reference to temperature and salinity. Maximum productivity, standing crop, leaf length and blade density occurred by early summer. He found that

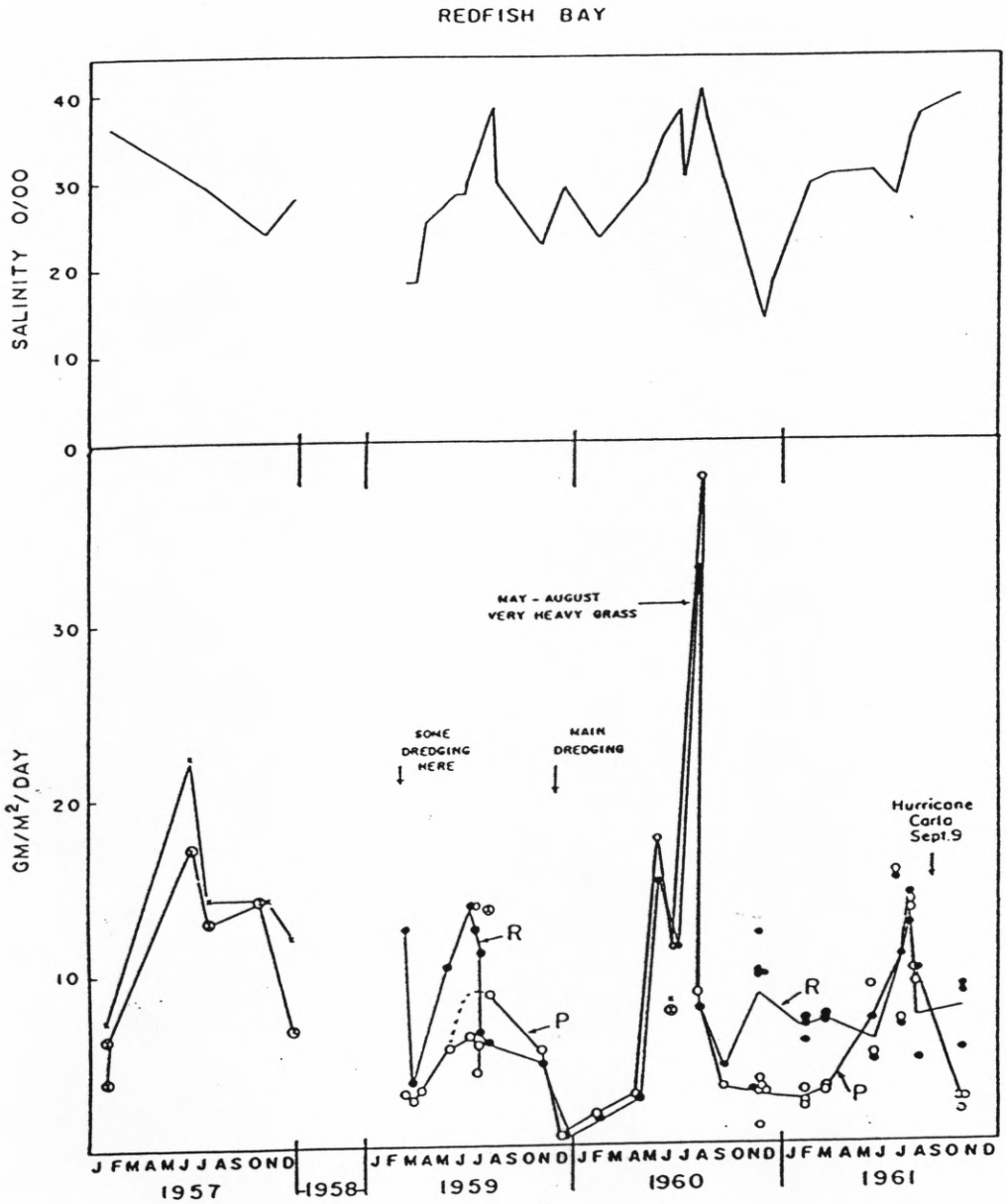

Figure 24. Record of salinity, gross photosynthesis and total respiration 1957-1961 for *Thalassia testidinum* in Texas. From Odum 1963.

although *Thalassia* undergoes marked seasonal variation, blade density during winter was about 50% of maximum blade density during summer. Maximum blade density occurred during late April and May and leaves were carried until October. Minimum blade densities occurred from December through March. Zieman (1975b) concluded that temperature and salinity were the major factors controlling the seasonal variation of *Thalassia* in Florida. Walker and McComb (1988) examined the seasonal variation of *Amphibolis antarctica* and *Posidonia australis* in Shark Bay, Western Australia. *Posidonia* showed no clear seasonal pattern of production or standing stock for the duration of the study (1982-1983). *Amphibolis* had maximum production during summer, coincident with highest light and temperatures. Although seasonal variation was evident for *Amphibolis*, it was not very pronounced, while *Posidonia* did not exhibit a seasonal pattern. In general, it appears that seagrass biomass and density increase with increasing light and temperature during late spring and early summer (Figure 25). Dunton (1990) examined the production ecology of *Ruppia maritima* and *Halodule wrightii* in two estuaries along the Texas coast. The species differed with respect to seasonality of growth, time of flowering and persistence of overwintering populations. In both estuaries *Ruppia* was a strict opportunist colonizing bare areas yearly (i.e. no overwintering populations) and completing its growth cycle in four months. *Halodule* was absent from the Guadalupe Estuary (San Antonio Bay), but in the Nueces Estuary (Corpus Christi Bay) it produced overwintering populations with year-round growth. Dunton (1990) concluded that in some Texas estuaries *Ruppia* grows as an annual weed, whereas *Halodule* grows as a perennial (Dunton 1990). However, other investigators have documented perennial populations of *Ruppia maritima* in Upper Laguna Madre and

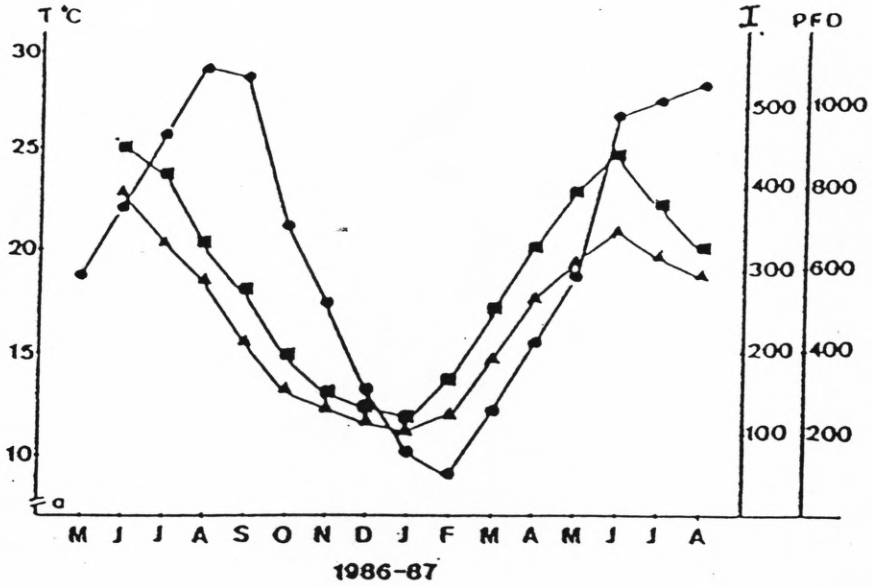

Figure 25a. Some seasonal environmental features of an Australian study site: total irradiance (squares, Wm^{-2}), PAR photon flux density (triangles, $\mu mol\ m^{-2}\ s^{-1}$) and temperature (°C, circles). Values are monthly averages. From Perez and Romero 1992.

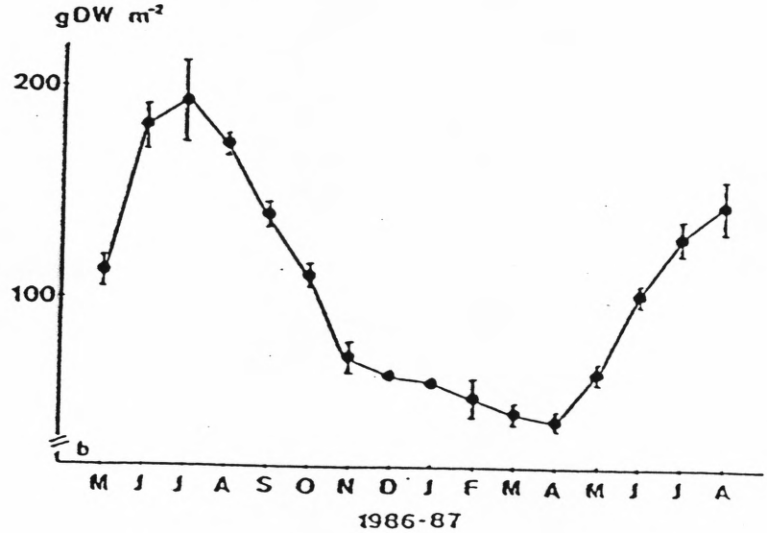

Figure 25b. Seasonal pattern of above-ground biomass. Standard errors are indicated by vertical bars. From Perez and Romero 1992.

Redfish Bay (Pulich 1985). Thus, both annual and perennial stocks of *Ruppia* occur along the Texas coast.

Many investigators have noted that the P vs. I parameters of seagrasses exhibit a seasonal pattern. Drew (1978) examined factors affecting the seasonal variation in photosynthesis of *Posidonia* and *Cymodocea* in the Mediterranean. *Cymodocea* had comparable photosynthetic rates during both spring and summer, while *Posidonia* had higher photosynthetic rates during spring than during summer (Figure 17). Calculation of a carbon balance based on the experimental P vs. I numbers shows that a shallow *Posidonia* community may have a positive carbon balance during spring and a negative carbon balance (due to higher respiratory demands) during summer (Drew 1978). However, it should be noted that the carbon budget calculations based on leaf P vs. I curves do not take into account the respiratory demands of the below-ground tissues. Congdon and McComb (1979) found that *Ruppia* exhibits seasonal changes in above and below-ground biomass, with low crops occurring during late autumn and winter. Although they did not investigate seasonal changes in the P vs. I curves *per se*, they inferred changes in the light requirements based on changes in standing crop (Congdon and McComb 1979). Ott (1979) presented evidence for an annual rhythm in the growth cycle of *Posidonia oceanica*. After two years of growth *in vivo* under conditions of constant light and temperature, the seagrass *P. oceanica* still exhibited a pronounced seasonal growth rhythm. However, changes in photosynthetic capabilities were not examined in this study. Bulthuis (1983b) reported that temperature dramatically influenced the P vs. I curve of *Heterozostera tasmanica*. Bulthuis suggested that *Heterozostera* has higher light requirements during summer than during winter due to

increased respiration associated with high summer temperatures. Thus, this species exhibits seasonal changes in its light requirements due to changes in the rate of respiration. It was also suggested that these plants are more susceptible to decreased light availability during summer than during winter (Bulthuis 1983b). Macauley *et al.* (1988) examined seasonal changes in standing crop and chlorophyll content of *Thalassia testudinum* in the Northern Gulf of Mexico. *Thalassia* exhibited seasonal variation in standing crop and chlorophyll content; standing crop was strongly correlated with temperature and moderately correlated with incident irradiance. They suggested that temperature was the controlling factor for *Thalassia* productivity along the Northern Gulf of Mexico (Macauley *et al.,* 1988). Perez and Romero (1992) found that *Cymodocea nodosa* exhibits some photoadaptation to the yearly light cycle. During summer, when there is high irradiance, the plants have high I_k and P_{max} values and do not exhibit photoinhibition; however, during the winter these plants shift toward shade-adapted characters (Table 12). It is suggested that winter photosynthetic rates may be limited by low temperatures rather than low light. The mechanisms causing these adaptations are not well understood and may involve short-term light adaptation and internal rhythms keyed to changes of the seasons.

Researchers have also investigated seasonal changes in the organic constituents of seagrasses. Dawes and Lawrence (1979) investigated how blade removal influenced the proximate composition of the rhizome of *Thalassia testudinum.* They concluded that the rhizome acts as a storage organ which supports blade regeneration as well as seasonal growth. Soluble carbohydrate was the primary reserve and was actively mobilized through the rhizome. Rhizomes had the largest carbohydrate reserves exhibiting a seasonal rise

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Table 12. Seasonal variation in the P-I parameters of *Cymodocea nodosa*. P_{max} and R expressed in mg O_2 per d dry h^{-1}; I_{sat} and I_{comp} expressed as μmol m^{-2} s^{-1}. From Perez and Romero 1992.

Month	P_{max}	R	I_{sat}	I_{comp}
February	2.31	0.41	69	10
April	2.64	0.14	238	12
June	5.48	0.47	398	31
August	4.37	0.56	88	10
November	2.51	0.73	160	36
December	3.22	1.00	127	30

during late spring and summer and a decrease during winter. Carbohydrate levels in the rhizome were lowest in early spring. Dawes and Lawrence (1980) made a seasonal examination of the proximate constituents of *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme* (Table 13). They found that in the rhizomes soluble carbohydrate levels were highest during the fall and lowest during spring. They suggest that soluble carbohydrates sustained the plants through the winter when productivity was low. Calorific levels were similar between species with the highest levels occurring in the rhizomes. Of the three species, the rhizomes of *Thalassia* had the highest level of organic material, suggesting that this species may be more tolerant of adverse conditions. Dawes and Lawrence (1983) suggest that *Thalassia* is better adapted to year round growth, while the other species (*Halodule* and *Syringodium*) are more opportunistic.

Pirc (1985) examined the growth dynamics of *Posidonia oceanica* with respect to the seasonal changes of soluble carbohydrates, starch and other organic compounds in different parts of the plant. He concluded that winter leaf growth was supported by the mobilization of starch from the rhizomes. Pirc (1985) hypothesized that subsidized winter leaf growth enabled the plant to take maximal advantage of increased light during the spring. During summer and autumn large quantities of carbohydrates were found in both the leaves and the rhizomes. Plants utilize summer and fall energy influx to compensate for low production during winter and spring. Ralph *et al.* (1992) examined the distribution of extractable carbohydrate reserves in the rhizome of *Posidonia australis*. Carbohydrate levels were significantly higher in the stele tissue than in the cortex. Lower carbohydrate reserves were found in juvenile tissue and near the apical meristem, while unexpanded internodes had

Table 13. Seasonal variation of protein, soluble carbohydrate and kilocalories for blades and rhizomes of three seagrass species. From Dawes 1987.

		January	April	July	October
Thalassia testudinum					
Blades	Protein	8	9	22	13
	Carbohydrate	6	9	9	7
	Kilocalories	2.4	3.0	3.1	2.6
Rhizome	Protein	9	8	16	7
	Carbohydrate	12	21	24	36
	Kilocalories	3.2	3.4	3.0	2.8
Syringodium filiforme					
Blades	Protein	9	8	13	13
	Carbohydrate	22	16	18	20
	Kilocalories	3.1	2.4	3.2	3.1
Rhozome	Protein	9	5	12	16
	Carbohydrate	36	38	50	46
	Kilocalories	3.6	3.7	3.6	3.5
Halodule wrightii					
Blades	Protein	19	18	19	14
	Carbohydrate	14	19	15	13
	Kilocalories	3.1	3.5	3.3	3.3
Rhizome	Protein	9	7	8	8
	Carbohydrate	43	40	43	54
	Kilocalories	3.7	3.7	3.4	3.6

[1]Percent dry weight
[2]Per gram dry weight

relatively large carbohydrate reserves. It was suggested that stored carbohydrates are used for winter maintenance and support early spring blade growth.

Seagrasses can also adjust the concentration and distribution of chlorophyll within their tissues. Mazzella *et al.* (1979) concluded that the photosynthetic activity of *Zostera marina* leaves was regulated by four factors: age of tissue, light intensity, exposure and presence of epiphytes. For young parts of leaves, light intensity and tissue maturity were most important. For older leaves, the presence of epiphytes was more important than the other factors. Wiginton and McMillan (1979) examined the chlorophyll composition of seagrasses under controlled light conditions. Chlorophyll concentrations in both *Thalassia* and *Halodule* were correlated with chlorophyll content increased with decreasing light in both the field and lab. Chlorophyll *a*:*b* ratios were correlated with different depth ranges and may affect depth distribution of seagrasses. The similarities in light levels at the maximum depth of seagrasses in both St. Croix and Texas suggests that the seagrass populations were restricted by similar light relationships at each locale. In general, seagrasses are responding mainly to changes in light quantity, not light quality (Wiginton and McMillan 1979). Mazzella *et al.* (1980) found that *Zostera* had a gradient of leaf pigmentation and photosynthetic activity. The initial slope of the P vs. I curve increased from leaf base to leaf tip. Light saturation occurred at 100-150 μmol m^{-2} s^{-1} for all leaf types. Czeczuga (1986) examined the effect of light quality on the photosynthetic pigments of the green alga *Chara*. In freshwater *Chara* forms meadows that may have the same functions as seagrasses in estuarine waters. Highest chlorophyll *a*,*b* and carotenoids were found when green and yellow filters were placed over the light source, while the lowest

pigment concentrations occurred when blue and red filters were used. Enriquez *et al.* (1992) examined how light was absorbed by *Posidonia oceanica*. Their results indicate the amount of light absorbed increases linearly with increased pigment packaging in the leaves. Thus, increasing chlorophyll results in increased light absorption per unit leaf weight. The increasing absorption per unit weight should increase the photosynthetic and growth rates of a light-limited plant.

Changes in the chlorophyll concentration may allow a species to survive in a particular habitat. Several studies have investigated the physiological ecology of seagrasses in relation to light and photosynthesis. Dennison *et al.* (1981) concluded, based on shading and reflecting studies, that *Zostera marina* adjusts to light conditions by changes in leaf area production. Under low light the plants increase their leaf area to intercept more photons. Jimenez *et al.* (1987) examined the response of *Zostera noltii* and *Z. marina* to high light under stressed conditions. *Zostera marina* had higher chlorophyll levels at low light, with maximum chlorophyll concentrations occurring at 150 μmol m^{-2} s^{-1}. *Zostera noltii* chlorophyll increased with light intensity and were constant at light levels above 150 μmol m^{-2} s^{-1}. *Zostera noltii* was light saturated at 3600 μmol m^{-2} s^{-1} showing no evidence of photoinhibition, while *Z. marina* was light saturated at 1100 μmol m^{-2} s^{-1} with significant photoinhibition above this light intensity. For both species I_c was 30-35 μmol m^{-2} s^{-1}. They concluded that *Z. noltii* was more photosynthetically efficient, especially at high irradiances. Dawes *et al.* (1989) compared the physiological ecology of *Halophila decipiens* and *H. johnsonii* from Florida. With respect to P vs. I characters, *H. decipiens* was strongly photoinhibited at irradiances above 300 μmol m^{-2} s^{-1} while *H. johnsonii* was photoinhibited

at irradiances above 1000 μmol m^{-2} s^{-1}. *Halophila decipiens* had an I_c value of 29 μmol m^{-2} s^{-1} compared to about 50 μmol m^{-2} s^{-1} for *H. johnsonii*.

Although interannual variation may be large, most seagrass species exhibit very pronounced seasonal trends. In general, plant biomass increases rapidly during spring and early summer and is maintained through the summer. During fall, biomass decreases as the blades senesce and slough off of the plant. The P vs. I characters of most seagrass species follow a similar trend. The plants appear to be "sun adapted" during the summer and "shade adapted" during the winter. Generally, P_{max} is lower during the winter than during the summer; presumably, this is due to reduced enzymatic activity at lower temperatures. The concentration of organic constituents also varies seasonally. During summer, when production is greatest, the plants store large amounts of carbohydrate in the rhizomes. During the fall and winter, when light levels are low, the plants draw upon these reserves. During late winter (very early spring) the plants put forth a new crop of leaves, supported at least in part by stored carbohydrate. During this time the plants are probably most susceptible to prolonged periods of reduced irradiance.

CHAPTER 5: RECOMMENDATIONS FOR FURTHER RESEARCH

Texas estuarine systems are remarkably diverse, as examplified from the hypersaline Laguna Madre to the freshwater dominated estuaries of the northern Texas coast. As a consequence, the potential problems faced by resource managers with respect to water quality and water clarity (transparency) is unique to each estuary. Estuarine systems dominated by freshwater inflow are more likely to experience the effects of eutrophication than estuaries where evaporation exceeds inflow (e.g., Laguna Madre). Conversely, systems that are flushed frequently are less likely to experience the long-term effects of chronic phytoplankton blooms, as is now occurring in Laguna Madre (the brown tide). Setting water quality criteria to maintain the current level of productivity in these systems will therefore be estuary specific. The immediate challenge is to thoroughly define hydrographic characteristics common to each system before they begin to respond negatively to anthropogenic inputs. The goal will then be to use this database to establish water quality standards to maintain the health of each system. With very few exceptions, Texas is fundamentally different than most other East Coast and Gulf Coast states which have lost much of their valuable coastal habitat; in Texas the goal is still to preserve the natural habitat, not to restore or create what has been lost.

The extensive development of submerged aquatic vegetation in south Texas bays and estuaries is primarily related to reduced freshwater inflows and lower levels of inorganic nutrients. Light attenuation is *the* major problem that must be addressed in these systems. Although increasing urban and agricultural development do present an alarming potential

for eutrophication, dredging and other construction activities clearly present the greatest immediate danger to seagrass beds. These activities significantly increase turbidity which reduces the amount of light reaching the bottom.

Our failure to largely prevent the loss of seagrass beds now and in the past has largely resulted from an inadequate knowledge of:

(1) the minimum light requirements needed to maintain a positive carbon balance and net growth for the various species,

(2) the amount of light actually reaching the plants on the seabed.

Although some effort has been made to address the photosynthetic light requirements of seagrasses through laboratory experiments, these measurements often cannot be extrapolated into the field. *In situ* measurements using entire plants are thus highly recommended and potentially the most useful for management purposes.

Currently, we have information on the light requirements and underwater light fields for only one of five Texas seagrasses (*Halodule wrightii*). *In situ* photosynthetic parameters need to be measured for both *Syringodium filiforme* and *Thalassia testudinum*, which along with *Halodule*, constitute the majority of the approximate 850 km^2 of seagrass meadows in Texas. Without the knowledge of the minimum light requirements for growth and photosynthesis of these plants, the development of water quality and water transparency standards will be extremely difficult.

Compilation of published nutrient and water chemistry data for each estuary with information on the *in situ* light requirements and underwater light fields of Texas seagrasses

can be used to develop water quality criteria to preserve seagrasses in Texas estuaries. The contributions of suspended solids, chlorophyll *a* and dissolved inorganic nitrogen to the diffuse light attenuation coefficient (k) for each estuary can then be used in carbon budget models for seagrasses within each estuary to maintain the current productivity and distribution of seagrasses. This approach is similar to that used in Chesapeake Bay (Batuik *et al.*, 1992; Dennison *et al.*, 1993) but incorporates quantitative data on underwater light fields and the light requirements of the plants. Recent studies suggest that the physiological light requirements of the seagrass *Halodule wrightii* in Texas is similar among estuaries (Dunton, submitted and unpub. data); if this is true for other species then the strategy described above is not unnecessarily complex, and our goal of establishing water quality standards to protect seagrasses in Texas coastal environments is attainable.

Based on the arguments presented above, our recommendations for further work to achieve this goal are:

1. Determine the *in situ* photosynthetic requirements of Texas seagrasses, including (by priority): *Thalassia testudinum, Syringodium filiforme, Halophila engelmanni* and *Ruppia maritima* (this work on *Halodule wrightii* is complete).
2. Collect *in situ* continuous measurements of underwater PAR in conjunction with nutrient and chlorophyll measurements in Texas estuaries containing seagrasses for calculation of diffuse light attenuation coefficients (k). (This work has been in progress in both Upper Laguna Madre and Corpus Christi Bay since 1990/1991; see Dunton, submitted).

3. Evaluate the contributions of suspended solids, water column chlorophyll *a*, inorganic nitrogen and dissolved matter to the diffuse light attenuation coefficient (k) for specific Texas estuaries based on available data and field sampling.
4. Develop seasonal and annual carbon budgets for predominant Texas seagrasses. This information can be used to: (a) assess the impacts of chronic light reduction, (b) minimize loss of habitat by temporal or seasonal restriction of construction activities and, (c) determine the feasibility of mitigation (creation or restoration) projects.

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