Appendix 9.B. Submerged Aquatic Vegetation (SAV) in the Lower St. Johns River and the Influences of Water Quality Factors on SAV.

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1. Lower St. Johns River SAV Distribution and Abundance

SAV has been a dominant component of shallow water (<1m) areas in oligohaline and freshwater regions the St. Johns River Estuary (LSJR) for several hundred years (Bartram 1791, DeMort 1991, Sagan 2001, 2003a, 2007). Detailed transect surveys have identified up to eleven species of these aquatic angiosperms growing in beds along the littoral zone extending from 2 to over 350 m from shore (Table 1; Sagan 2007). These include: *Micranthemum sp.* (baby tears), *Ceratophyllum demersum* (coontail), *Sagittaria subulata* (dwarf arrowhead), *Vallisneria americana* (wild celery or freshwater eelgrass), *Zannichellia palustris* (horned pondweed), *Hydrilla verticillata* (hydrilla), *Chara sp.* (muskgass), *Eleocharis sp.* (spikerush), *Najas guadalupensis* (southern naiad), *Potamogeton pusillus* (slender pondweed), and *Ruppia maritima* (widgeon grass). By far the dominant species has been *V. americana*, which Sagan 2007 found to comprise approximately 63% of the total SAV cover from 1998 through 2007. This was followed by *N. guadalupensis* (16%) and *R.maritima* (10%). All other species comprised approximately 11% of the total cover over that period.

The lower 131 km of the LSJR may be divided into typical estuarine zones based upon salinity conditions and water residence times. Sagan 2003a, 2007 has summarized the abundance of SAV in three sections or ecozones defined as: oligohaline-mesohaline (Zone 1 station between river kilometers 43-61); freshwater lacustrine (Zone 2 stations between river kilometers 69 and 126); freshwater riverine (Zone 3 station from kilometer 137 to upper limits of SAV). Salinity levels are influenced both by patterns of precipitation (McGrail et al. 1998) and tide and wind driven events (Sagan 2007). SAV were recorded from river kilometer 43 to 169. Total SAV coverage in the LSJR has been estimated from aerial photography as 866 ha for 2003 and 2004 (Dobberfuhl and Hart 2006). The most downriver polyhaline and lower mesohaline section of the river system (river kilometers 0-43) have not been known to support SAV (DeMort 1991). SAV growth there may be limited by a combination of high salinity, seasonal extremes in temperature and high turbidity (Brody 1994) although the exact causes are unknown. High salinity (>10-15) areas typically limit SAV growth a very few number of salt tolerant seagrass species compared to low salinity or freshwater areas where more species can survive (Green and Short 2003, Dennison et al. 1993). Of the two dominant seagrass species found along the Atlantic coast of the United States, *Zostera marina* (eelgrass) is limited by high summer temperatures and is not found south of North Carolina. *Thalassia testudinum* (turtle grass) is limited by low winter temperatures and has not been reported north of Sebastion Inlet (Eiseman 1980). Shoal grass (*Halodule wrightii*) is one species that may be able to grow in this region and tolerate the physiological constraints of salinity and temperature Montague and Ley (1993). However, it generally grows in very shallow areas with high light availability and Brody (1994) has suggested that high turbidities in this region may be limiting its success here.

Of the three dominant SAV species found in the LSJR, wild celery comprised not only the greatest system-wide cover (Sagan 2007, Dobberfuhl 2007) but greatest mean maximum depth (0.79m) and was found along all three Zones of the river system from kilometer 43 to the upriver limits of SAV growth at kilometer 161. *N. guadalupensis* typically occurred in all three Zones in shallower water with a mean maximum depth of 0.68m (Sagan 2004a, 2007) and when it co-occurred with wild celery it generally had greatly reduced cover (Sagan 2004a). Widgeon grass grew to the shallowest depths with a mean maximum depth recorded of 0.53m (Sagan 2007). It has been usually observed in the shallowest nearshore areas of the beds in Zones 1 and

2 with cover typically below 50% (Sagan 2003a, 2007). All three species are found throughout the year within the system, but reach greater water depths and broader bed width distributions in the summer and fall compared to the winter and spring (Sagan 2004a). SAV biomass at the deepest depths has been found to be generally low compared to shallower areas and has been characterized by sparse, small plants, less that 5 cm in length and usually comprised of wild celery (Sagan 2004a).

2. Life Histories of Dominant SAV Species in the LSJR

V. americana is one of two species of the genus *Vallisneria* found throughout the world. It consists of two varieties, var. *americana* found in the Americas, East and Southeast Asia, Oceania and Australia, and var. *biwaensis* found in Japan, Hispaniola and Venezuela (McFarland 2006). The second species, *V. spiralis* var. *spiralis* is found in Europe and southwest Asia and var. *denseserrulatae* in Africa, Asia, Oceania and Australia. *V. americana* var. *americana* ranges from Canada southward to Texas and Florida and has been recorded in 40 states in both tidal and non-tidal regions (McFarland 2006). It is a perennial, submersed aquatic plant with ribbon-like leaves up to 2 m or more in length growing in individual ramets expanding vegetatively by rhizomes and stolons (Korschgen and Green 1988). Individual plants are either male or female and capable of sexual and vegetative reproduction. McFarland (2006) provides a recent overview of the reproductive ecology of the species. There are both narrow-leaved and wide leaved variants (Lowden 1982). In northern areas of the U.S. the plants will die back in the winter and produce winter buds that will lie dormant throughout the winter. In the spring as water temperatures warm the winter buds elongate and produce a stolon which will reach the sediment surface and produce new plants through lateral expansion. In southern populations such as those found in LSJR the plants typically do not die back and no winter buds are formed (Haller 1974, Dawes and Lawrence 1989, Clark and Stout 1995, Smart and Dorman 1993, Bortone and Turpin 2000). Flowering in temperate areas typically occurs in the summer (McFarland 2006), however Sagan (2004b) and Dobberfuhl (2007) reported flowering and fruit production in all seasons in the LSJR in studies from 2000 to 2002.

N. guadalupensis (southern naiad or bushy pondweed) is one species of the genus *Najas* of the Najadaceae family. Its distribution ranges from Oregon to Quebec and from California to Florida in both tidal and non-tidal habitats (Hotchkiss 1972). It is a submersed plant characterized by slender branched stems with simple, linear, flattened opposite leaves with no teeth and sheathed bases (Radford et al. 1964). The genus does not have rhizomes or tubers as do most other freshwater SAV and the roots are simple and small with a radicle that is ether short-lived or undeveloped (Stevenson and Confer 1978). Sexual reproduction is the most common method of re-growth and in northern areas it is considered an annual (Schulthorpe 1967). Flowers are inconspicuous at the base of the leaves and pollination takes place underwater (Hutchinson 1975) with production of seeds in the leaf axils (Stevenson and Confer 1978).

Ruppia maritima or widgeon grass of the family Ruppiaceae is a highly variable, slender branching herb with linear leaves opposite leaves 2 to 20 cm long and 1 to 2 cm wide (Radford et al. 1964, Weldon et al. 1969, Stevenson and Confer 1978). It occurs worldwide in coastal bays and other areas subject to tidal influence, but can be found in non-coastal areas including hypersaline palustrine and lacustrine wetlands (Kantrud 1991). It is considered a freshwater plant with a pronounced salinity tolerance (Zieman 1982) but is found with many true seagrass species such as eelgrass, turtle grass and others (Orth and Moore 1988). It occurs in two forms: upright and highly branched in appearance with flowers standing several feet tall and shorter; and creeping, with basal leaves that can be present throughout the year (Bergstrom et al. 2006). It reproduces both vegetatively through rhizomes and sexually through seeds. A typical plant can produce 2-10 rooting nodes along the rhizome each producing a vertical stem with leaves (Kantrud 1991). Sexual reproduction requires elongation of the peduncle upwards to the air-water interface. Once on the surface pollen is release and it floats on the surface until it contacts the floating stigma and pollination occurs. The fertilized flowers produce black, oval-shaped fruits with pointed tips. It can also have an annual or perennial growth from. In deeper more stable environments it reproduces asexually with new stems emerging from the root-rhizome system. In habitats subject to drought or other extreme stresses the vertical shoots or ramets will die after production of seeds and revegetation with occur via seedlings (Bigley and Harrison 1986, Kantrude 1991).

3. Water Quality Factors Influencing SAV

3.1 Salinity Effects on SAV

The ability of underwater plants to tolerate salt is determined by multiple biochemical pathways that facilitate retention and/or acquisition of water, protect chloroplast functions, and maintain ion homeostasis. Many salt-tolerant species accumulate metabolites, amino acids or sugars which play crucial roles regulating osmotic conditions and serve other protective functions at the cellular level (eg. Rout and Shaw 2001a, b, Tripathi et al. 2007, Van Diggelen et al. 1987). The capacity of individuals of each SAV species to adapt to salinity is dependent on both the concentration level of salinity and rate of salinity increase over baseline conditions. Adapting to increased salinity levels requires that the particular SAV species first have the capacity to detoxify the salt effect and/or reduce the osmotic stress, and then have the time and resources to produce these protective mechanisms. Temperature and light can play crucial interactive roles in the development of this adaptive tolerance. For example, during active growth periods (Pinnerup 1980) found that eelgrass (*Zostera marina*) growing at differing salinities was less affected at cold temperatures when metabolic activity was low than at warmer temperatures when metabolic activity and growth potential was high. French and Moore (2003) demonstrated that light

requirements for wild celery were approximately 50% greater for plants grown at salinities of 5 compared to 0, due to decreased photochemical efficiency. Typically acclimatization of SAV to salinity change will only occur within a certain range and at some level lethality will occur regardless of the adaptability of the species (Kantrud 1991). Salinity can have other indirect effects on SAV. For example oxidized sulfate has a much higher concentration in seawater compared to freshwater. When these higher concentrations diffuse into sediment the sulfate is rapidly reduced by bacteria to sulfide. This sediment sulfide, in turn, can be rapidly taken up by the roots and distributed throughout the SAV by their lacunae (Pederson et al. 2004, Borum et al. 2005). These internal concentration of sulfide can affect plant nutrient uptake (Koch and Erskine 2001), photosynthesis and respiration (Goodman et al. 1995, Erskine and Koch 2000, Koch et al. 2007) and ultimately interfere with many cellular enzymatic functions (Koch et al. 1990) affecting plant growth and survival.

Natural events and man-induced supply changes can have significant impacts on salinity and other impacts to freshwater SAV in coastal areas (Bayley et al. 1978, Orth and Moore 1983, Mataraza et al. 1999, Doering et al. 1999, Frazer et al. 2001, Frazer et al. 2006). In the Chesapeake Bay a 100-year flooding event caused by Tropical Storm Agnes caused an extensive loss of SAV vegetation throughout the system (Orth and Moore 1983) which has still not recovered (Moore et al. 2000). Short-term storm induced salinity increases in Kings Bay, Florida (Frazer et al. 2006) were observed to increase salinities to levels that were above the salinity tolerances for several species of SAV, resulting significant declines in SAV biomass and cover. They also suggested that the varying salinity tolerances of different SAV species may increase the competitive advantage of more salt tolerant SAV such as wild celery, compared to less salt tolerant *Hydrilla verticillata* in areas where such storm induced salinity intrusions are common. Eleuterius (1987) similarly observed declines in SAV due to intrusions of seawater during Hurricane Camille in 1969. Frequent subsequent openings of a man-made spillway allowing freshwater to enter wetland systems created brackish conditions that permitted the extensive re-growth of widgeon grass. Similar expansions of the low salinity tolerant widgeon grass, with corresponding reductions in less freshwater tolerant species such as *Halodule wrightii* and *Syringodium filiforme*, were observed in the Banana River in Florida during a 10-year period of reduced salinities (Provancha and Scheidt 2000). Doering et al. (2002) were able to develop relationships between salinity in the estuary and discharge from the Caloosahatchee River in Florida using a hydrodynamic-salinity model to estimate discharge rates that would produce low enough salinities in upstream regions suitable for freshwater SAV (wild celery) but high enough in downstream regions to support more salt tolerant species such as *Halodule wrightii*.

3.1.1 Salinity Effects on Wild Celery

Wild celery has a broad ranging distribution due to its capacity to grow and reproduce successfully under a wide range of habitat conditions including water of various salinities (Stevenson and Confer 1978, McFarland 2006). Because the salinity tolerance of this, as well as other species of SAV, is dependent on a variety of interacting factors including the exposure duration and rate of salinity increase, its tolerance described in various studies has been found to vary. Bourn (1934) published one of the earliest studies on salinity tolerance of wild celery (*V. spiralis*) and found that growth of wild celery increased slightly at a salinity of approximately 2.8 compared to fresh water grown plants. He also found that plants could be maintained at a salinity of 4.2. Etiolation, or shoot elongation similar to that expressed by plants grown in the dark, was evident at a salinity of 6.6 and growth ceased at 8.4. Boustany et al. (2001) found that plants acclimated to salinities of 1, 8 and 18 at a rate of 1 per day and then held there for 5 months showed continued growth at a final salinity of 1, negative growth at 8 and complete dieback at 18 by 70 days. The recovery of some viable root stock at the highest salinity levels suggested to them that there might be the potential for some recovery of plants under conditions where salinity was pulsed to this level for shorter durations. French and Moore (2003) found, however, that rosettes of plants grown at higher salinities (up to 15) were shorter and narrower and had less leaf area than those in lower salinities. They also found that the effective quantum yield, or the photosynthetic efficiency, decreased with salinity in plants grown at salinities of 0, 5, 10 and15, but photosynthetic capacity was not affected.

Doering et al. have studied the salinity tolerance of wild celery using both monitoring of field populations and mesocosm experiments with wild celery from the Caloosahatchee estuary in Florida (Doering et al. 2001, 2002). He and his colleagues found that the wild celery net growth rates decreased with increasing salinity, with eventual mortality at salinities greater than 15. In three of four experiments there was no difference in growth rates between 0 and 3 salinity treatments. At salinity treatments of 9 and 12 there was plant survival but the net growth of the plants was reduced. Above salinities of 15 there was a 50% loss of shoots in 38d at a salinity of 18 and 50% loss in 16d at a salinity of 20.

A variety of studies have found that wild celery can grow well at average growing season salinities of 3 or less (Haller et al. 1974, Twilley and Barko 1990, Jarvis and Moore (2008). In the LSJR Sagan (2003a) found no change in annual abundances between 1998 and 2003 of wild celery dominated SAV beds in regions where the previous growing season salinities were less than 2 (Figure 1) but there was a rapid decrease in abundance in years when the previous growing season salinities were greater than 3 (Figure 1). Studies have also demonstrated that wild celery has reduced growth at mean seasonal salinities of 5 and above (Haller et al. 1974, Davis and Brinson 1976, Staver 1986, Doering et al. 2002, Twilley and Barko 1990, French and Moore 2003, Adair et al. 1994, Bergstrom et al. 2006) and peak abundance in the field is limited to systems where salinities are typically less than 10. The duration of exposure to high salinity is very important in determining plant survival and possible recovery under more suitable

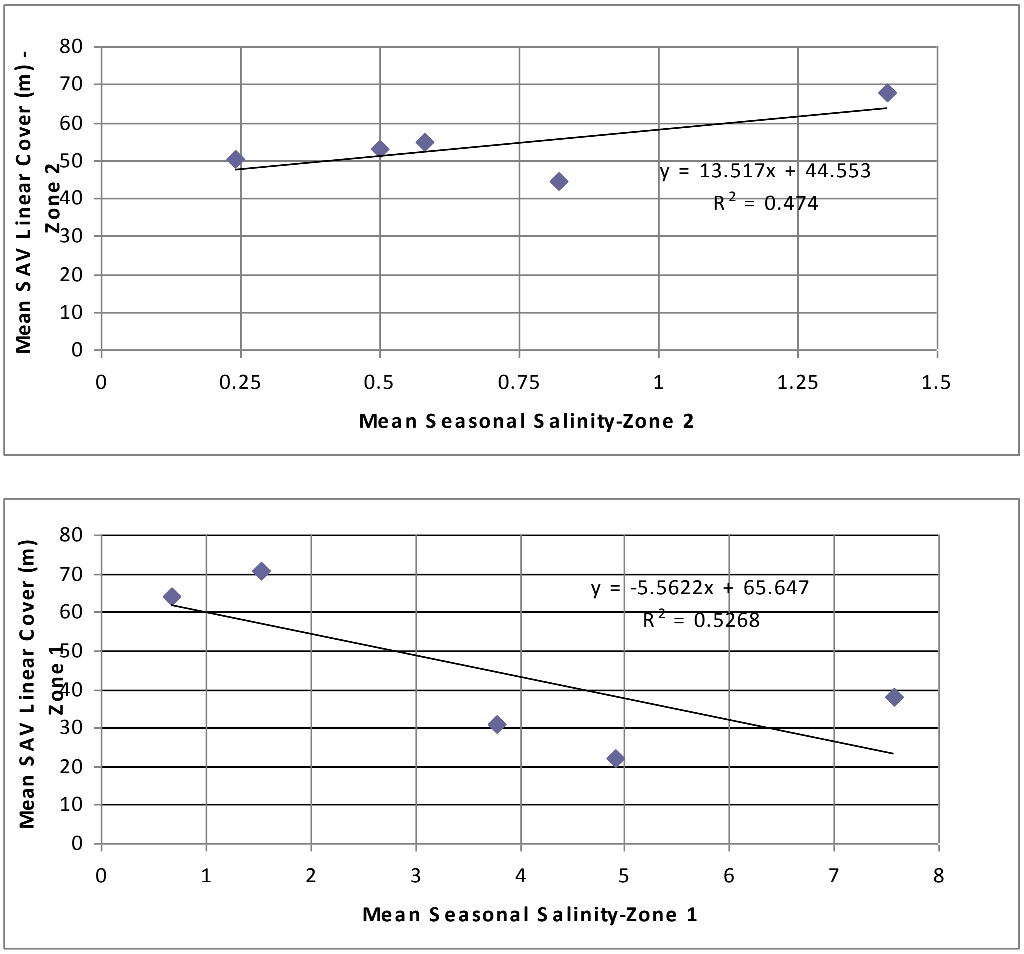

Figure 1. (top panel) Yearly means of SAV transect cover vs. previous year mean salinity for higher salinity Zone 1 (Section 1) in LSJR. (bottom panel) Yearly means of SAV transect cover vs. previous year mean salinity for lower salinity Zone 2 (Section 2) in LSJR. (data from Sagan 2003a).

conditions (Haller et al. 1974, Boustany et al. 2001). Littles (2005) and Frazer et al. (2006) report the effects on wild celery of short term salinities increased to salinities of 5, 15 and 25 for 1, 2 or 7 days compared to freshwater controls. Most measures of growth were reduced with salinity increased to 15 for 1 or 2 days, with mortality by 7 days. Mortality was observed with exposures to 25 for one day and greater.

Table 1 presents a summary of the projected effects of the various combinations of concentration and duration of exposure of wild celery during the growing season to salinity increases based on field information directly from the LSJR (Sagan 2007) and the above referenced field and laboratory studies (Haller et al. 1974, Davis and Brinson 1976, Staver 1986, Doering et al. 1999, 2001, 2002, Twilley and Barko 1990, Adair et al. 1994, French and Moore 2003, Littles 2005, Frazer et al. 2006, Bergstrom et al. 2006, Jarvis and Moore 2008).

Table 1. Summary of relationships between salinity concentrations and duration of exposure on wild celery growth and survival.

	Time (d)			
Salinity	**1**	**7**	**30**	**90+**
25	**Mortality**			
15	**Stress**	**Mortality**		
10	**No Effect**	**Stress**		
5	**No Effect**		**Stress**	
<3	**No Effect**			

"No Effect" indicates that and the concentration of and duration of salinity exposure during the growing season has not been found by itself to adversely affect wild celery under most circumstances. In general, salinity levels of 3 or less are within the short and long term tolerance of wild celery. Seven days or less of exposure to salinities of 5, or 1 day of exposure to 10, will also likely have little long-term effect. "Stress" indicates that photosynthesis, growth, reproduction, or other measures of plant performance will likely be affected by the combination of salinity level and the duration of plant exposure to that level. Therefore one day of exposure to salinity of 10, or 7 days or greater exposure to a salinity of 15, will be stressful to wild celery. "Stressed" populations may be susceptible to interactions with other habitat factors including turbidity (French and Moore 2003) or high sediment organic content (Smart and Barko 1985) that may cause declines or eventual mortality. "Mortality" will likely be experienced by all plants exposed to salinities of 25 for only one day or more, or 15 for 7 days or more.

3.1.2 Salinity Effects on Southern Naiad

The salinity tolerance of southern naiad has received only limited study as it is essentially a freshwater species for most of its distribution with restricted brackish water occurrence (Hotchkiss 1972, Martin and Uhler 1939, Stevenson and Confer 1978). Stevenson and Confer

(1978) report that southern naiad was historically common in areas of the Chesapeake Bay with salinities of 3 and Martin and Uhler (1939) found southern naiad in areas of the Potomac River with salinities ranging from 6 to 9. Haller et al. (1974) found maximum growth at a low salinity of 0.17 with decreasing growth at increased salinities. Mortality was observed after exposure to a salinity of 10 for four weeks. Bergstrom et al. 2006 describe *Najas* spp. in the Chesapeake Bay with a best growth salinity range of 0-5 and a full growth range of 0-10. In summary, southern naiad appears to grow best at salinities less that 3 with decreasing growth up to salinities of 10. Exposure to salinities of 10 for a month or more are likely to result in mortalities.

3.1.3 Salinity Effects on Widgeon Grass

The genus *Ruppia* tolerates a wider range of salinity than other species of freshwater SAV (Kantrud 1991) with a salinity range for widgeon grass observed from 0 to 390. These very high levels of salinity were found in lakes where $MgSO_4$ was the principal salt. Steward and Kantrud (1972) found widgeon grass in wetlands with salinities ranging from 0.35 to >100 and Metcalf (1931) found it fruiting in these areas with salinities up to 36. Studies by Bourn (1935) and Verhoven (1979) suggest, however, that NaCl is much more toxic to widgeon grass that other salts and the osmotic effects of MgSO4 may be one half that of NaCl. While McMillan (1974) observed that widgeon grass could be maintained indefinitely in tap water or distilled water. A number of studies demonstrate that flowering occurs in seawater of salinities from 1.8-28 (Bourn 1935, Mayer and Low 1970, McMillan 1974, McRoy and McMillan 1977, Verhoeven 1979). Seed germination has been found to decrease with increasing salinities (Mayer and Low 1970). Seeds from Florida and North Carolina were tested for germination up to salinities of 30 by Koch and Dawes (1991) and best germination was found at salinities of 15 or less. Similarly, Kahn and Durako (2005) tested germination at salinities up to 70 but germination was only observed at salinities of <20.

Anderson (1974) found a salinity tolerance of plants up to 40, and McMillan and Moseley (1967) found growth up to a salinity of 70. Scott et al. (1952) observed that widgeon grass beds did not die back in a South African estuary until salinity exceeded 69 and, amazingly, survived for two months in evaporating seawater up to a salinity of 35.8. Berns (2003) tested growth at salinities from 0-60. Highest growth was at a salinity of 20 with significant growth from 0-40 and lowest growth at salinities >40. Joanen and Glasgow (1965) found no differences in widgeon grass growth in Louisiana waters that ranged from 3.7 to 33.4. It was also observed to grow in both hypo- and hyper-saline areas in Texas lagoons where waters ranged from nearly fresh to salinities of over 60 (Conover 1964). In the Chesapeake Bay widgeon grass best growth range is described between salinities of 5 and 15 with a full growth range between 0 and >20 (Bergstrom et al. 2006). In Florida Phillips (1960) found widgeon grass growing in areas with salinities ranging from 0 to 33 and in Florida Bay it was found more abundant at lower salinity sites (10-30) compared to higher salinity sites (30-40) by Adair et al. (1994) and at sites with mean annual salinities of 15-25 by Montague and Ley (1993). In the Indian River Lagoon region, including the Mosquito Lagoon and Banana River it has been reported growing in areas with salinities ranging from 20-40 and 15-30, respectively, and expansion of growth in the latter area was related to periods of reduced salinities between 1985 and 1996 (Provancha and Scheidt 2000).

Widgeon grass is tolerant of variable salinity levels but can be impacted if the fluctuations are too rapid. In most estuarine systems variable salinity conditions are common. In the Chesapeake Bay daily salinity variations in areas vegetated by widgeon grass are typically less than 5 (Moore and Jarvis 2008). Verhoeven (1979) observed in the Netherlands that *Ruppia* died out when salinity increased in coastal habitats by 18 in a few weeks. Van Vierssen (1982), also in the Netherlands, found the best growth of widgeon grass in areas where salinities were <22.6 and varied less than 18 in one year. However Richardson (1980) did not see any effect of salinity decreases of 14 in 24 hours in a New Hampshire salt marsh habitat. La Peyre and Rowe (2003) compared plant growth at a constant salinity of 10 to salinity conditions that fluctuated up to 20 or 30 and back. Growth was greatest under constant conditions. Slight increases in salinity can be beneficial to widgeon grass growth. Sagan (2003a) found that widgeon grass abundance increased from 3% to 42%of total SAV cover in the higher salinity areas of the LSJR between 1998 and 2000 when mean annual salinities increased from 0.68 to 4.91. This abundance remained high through 2001 and 2002 when mean annual salinities were 7.58 and 3.78 respectively. The abundance dropped off to 8.3% relative cover in 2003 when salinities decreased to 1.52. In upper regions of the system where salinities remained below 1 few increases were measured. La Peyer and Rowe (2003) also observed decreased growth rates in plants grown under salinities that fluctuated from 10 to 0 and back compared to plants grown at a constant 10. Similarly Chesnes (2002) found that plants grown under salinities that fluctuated from 0-36 around a mean of 18 had reduced performance as the frequency and magnitude of the salinity fluctuation increased. Adaptation of the photosynthetic efficiency of widgeon grass plants over time was observed by Murphy et al. (2003) by two days after transfer from control salinities of 20 to a range of salinities from 0-40. While efficiency rebounded at salinities of 0, 10 and 20, plants transferred to salinity of 40 remained low. Salinity interactions with temperature were tested by Lazar and Dawes (1991)

In summary, widgeon grass is tolerant of very high salinities, exceeding full seawater strength, and will generally not be affected by high salinity water, especially if the salinity fluctuations are less than 10-20 per year. It is responsive to salinity changes and its abundance can actually increase in low salinity regions with slight increases within the 5-15 salinity range.

3.2 Water Column Light Attenuation Effects on SAV

The availability of light for photosynthesis, growth and reproduction is one of the most important factors affecting SAV persistence and survival (Dennison et al. 1993, Kirk 1994), and reductions in available light have been implicated in numerous declines worldwide (den Hartog and Polderman 1975, Peres and Picard 1975, Orth and Moore 1983, Kemp et al. 1983, Cambridge and McComb 1984, Giesen et al. 1990, Batiuk et al. 1992, Dennison et al. 1993, Stevenson et al. 1993, Batiuk et al. 2000). Short-term temporal changes in SAV abundance have also been associated with changes in turbidity and light attenuation levels and these relationships may be related to light thresholds and can be non-linear (Carter et al. 1994). The maximum depth penetration of SAV in both freshwater and marine systems has been directly related to light limitation (Canfield et al. 1985, Chambers and Kalff 1985, Vant et al. 1986, Duarte and Kalff 1987, Duarte 1991, Dennision et al 1993, Abal and Dennison 1996, Olesen 1996, Batiuk et al. 2000, Carter et al. 2000, , Steward et al. 2005, Dobberfuhl 2007), while the upper limit is limited by physical conditions such as waves, exposure and desiccation, UV radiation, high temperatures and/or freezing (Dawson and Dennison 1996, Leuchner et al. 1998, Bjork et al. 1999, Seddon et al. 2000, Koch 2001, Koch and Erskine 2001, Duarte 2002, Moore and Jarvis 2008).

Light availability through the water column to the SAV leaf canopy is attenuated by the water itself, as well as dissolved substances, and suspended organic and inorganic particles in the water (Kirk 1994). In shallow water coastal systems with SAV, it is primarily the dissolved substances and particulate matter that absorb or scatter the solar radiation (Gallegos 1994, Zimmerman 2003, Gallegos 2005). Dissolved substances are effective absorbers of light, while particulate matter will absorb and scatter downwelling radiation (Kirk 1994, Gallegos 1994). Scatter increases the effective path length of the light through the water column, further increasing the rate of attenuation with depth (Kirk 1994). Attenuation through the water column is exponential and is calculated as a negative exponential decay function of downwelling light ($-K_d$). Assuming only a small fraction of incident light is reflected at the water surface the percent of light reaching the SAV leaf surface through the water (PLW) is defined in accordance with the standard Lambert-Beer relationship,

$$PLW = 100 \exp [(-K_d) (Z)],$$

Where Z = water depth in meters.

The downwelling attenuation coefficient K_d can be further partitioned into its components including attenuation from water, dissolved substances (color), suspended sediments or phytoplankton (Gallegos 2001). The SAV plant canopy also attenuates light through the water column as a function of the canopy structure, biomass and density (Titus and Adams 1979, Zimmerman 2003). However, as the deepest edges of beds are approached biomass and density of SAV decreases (Moore 2004) and self shading is decreased.

A variety of studies have found that light levels at the maximum depth of SAV growth in freshwater and marine areas can range from 10-35% of surface irradiance (Batiuk et al. 2000, Kemp et al. 2004). Differences can be related to a variety of factors including: the species of SAV community studied (Batiuk et al 2000), the duration of the integration period (Moore et al. 1997), salinity (French and Moore 2003), temperature (Moore and Jarvis 2008), light quality (Gallegos 1994) as well periphyton, and other fouling organic and inorganic material on the leaf surface (Kemp et al. 2004). Moore et al. (1997) observed that relative short-term (20d) periods of light at or below temperature dependent, physiological compensating light levels for eelgrass in light stressed habitats, were enough to cause SAV death, even if the average seasonal light levels were only minimally affected. Gallegos (1994) found that dissolved organic components in natural waters effectively reduced the photosynthetically useable radiation (PUR) available for plant photosynthesis compared to the broader spectrum photosynthetically active radiation (PAR) or visible light commonly measured at wavelengths between 400-700 nm. Moore et al. 1997 measured the change in spectral qualities of submersed light with distance upriver in the Chesapeake Bay and reported relatively greater attenuation in the blue wavelengths that are particularly important for SAV photosynthesis (Kirk 1994).

Gallegos (2005) measured the absorption and scattering characteristics of light in the LSJR and found that colored dissolved organic matter (CDOM) contributed significantly to the light attenuation of the water column in addition to phytoplankton and non-algal suspended particulates. CDOM was the dominant contributor to light absorption and he found that color absorption in some upstream area was the highest reported for any natural water (Kirk 1984). During dry periods when CDOM levels become reduced due to lower inputs from tributary creeks, Gallegos suggested that increased light availability combined with high nutrient levels in the system may contribute to phytoplankton blooms which would further deprive the SAV of light for growth. Thus, the combination of highly colored and nutrient enriched waters is problematic for SAV growth in this system.

In general, freshwater communities have been found to have slightly lower minimum light requirements compared to marine communities (Kemp et al. 2004). Batiuk et al (2000) found that minimum light requirements during the growing season (April-October) for SAV growth in freshwater and oligohaline areas of the Chesapeake Bay was 9% with SAV always abundant when average levels were at 18% or greater. In contrast, minimum light levels (March-November) for continued SAV growth in mesohaline and polyhaline regions was15%, with SAV always abundant in areas where average light levels were 40%. Similarly Duarte (1991) observed that the maximum depth penetration of the seagrass *Z. marina* approximated 15% of surface irradiance at a range of sites with maximum colonization depths ranging from <1m to >6m worldwide. Dixon (2000) observed that the maximum depth of the seagrass *T. testudinum* colonization in Tampa Bay averaged about 22% of surface irradiance. Batiuk et al. 2000 reviewed a range of studies relating maximum SAV growth in freshwater lakes to light availability. They found that SAV colonization to 1m depths would occur when secchi depths were between 0.4 and 0.7m.

Difference in the light requirements between freshwater and marine species, especially in shallow and turbid areas, may be related to the potential for canopy forming species commonly found in freshwater regions to develop relatively shallow optical depths compared to colonization depths (Batiuk et al 2000, Kemp et al 2004). Under low-light conditions, these canopy-forming species can exhibit increased vertical growth by stem-elongation, and they retain only their uppermost leaves near the water surface (Goldsborough and Kemp 1988; Maberly 1993). Canopy-formation and stem-elongation are two shade-adaptation mechanisms observed for freshwater SAV (Stross 1979, Barko and Smart 1981, Barko et al. 1982, Vermaat et al. 1997, Middelboe and Markager 1997). French and Moore (2003), Barko et al. (1982, 1991) found that *V. americana*, the non-canopy forming SAV which is the dominant SAV species in the LSJR compensated for reduced light availability by increasing leaf length. Additionally, when under light stress *V. americana* was also observed to compensate for reduced light by shifting resources away from rosette and biomass production and total leaf area to elongation of leaves to near the water surface, thus maximizing light capture per unit of production (French and Moore 2003). This capacity decreased as light was reduced below 8% of surface insolation indicating a diminished capacity for morphometiric compensation at very low light levels. Reproduction, including flowering and winter bud formation was also siginificantly reduced or eliminated under long-term light reduction. Again this represents a shift in resources to light capture at the expense of other important components of survival.

The relatively higher light requirements for SAV growing under higher salinity conditions may be related to potentially greater physiological demands and/or non-photosynthetic respiratory demands (including roots and rhizomes; Pregnall et al. 1984, Goodman et al. 1995, Koch and Erskine 2001). Among freshwater species capable of growing under variable salinity conditions French and Moore (2003) found that photosynthesis, growth, and reproduction of the typically freshwater *V. americana* were directly affected by salinity and the light requirements for comparable performance of the species increased nearly 50% as salinity increased from 0 to 5. Dobberfuhl (2007) was able to observe changes in SAV bed (dominated by *V. americana*) distribution and abundance throughout the LSJR Basin and

Crescent Lake region from 1998 through 2004. This period included a period of drought (beginning in1999) followed by more average flow conditions. This drought resulted in differences in response between the downriver, higher salinity region and the upriver, freshwater region. While light in the downriver region increased due to decreases in color, the dominant component of light attenuation in the system (Gallegos 2005), no response in SAV was observed. He attributed this to the concomitant increase in average salinities from 1 to 6 which increased the relative light requirements of the SAV. Following the drought, although light conditions decreased the SAV increased in direct relation to decreases in salinity. In contrast, in the upstream Crescent Lake region where there was no salinity increase during the drought, but was a decrease in color, the SAV greatly expanded during the drought. Overall, Dobberfuhl (2007) concluded that SAV in the LSJR in regions with highest salinities had a mean light threshold of 14% compared to 9% at completely freshwater sites. This approximately 50% increase in light requirements with salinity parallels, almost exactly, the increase in light requirements observed by French and Moore (1993) and Kemp et al. (2004) for Chesapeake Bay freshwater SAV populations subject to salinity stress.

3.3 Nutrient Effects on SAV

The negative effects of nutrient enrichment on SAV are typically indirect, and are usually related to the increased growth of algal competitors compared to the SAV (Valiela et al. 1997). Algal blooms have been demonstrated to results in direct losses of SAV by greater increasing water column light attenuation (Dennison et al. 1993). In addition the growth of epiphytes and periphyton of the photosynthetic surfaces of SAV has been related to reduced photosynthesis and growth. In some studies, direct toxicity of water column nitrate on marine SAV species such as eelgrass has also been suggested as a potential mechanism for stress (Burkholder et al. 1992, Boedeltje et al. 2005). However in studying the comparative effects of water column nitrate enrichment on *Z. marina*, *H. wrightii* and *R. maritima* Burkholder et al. (1994) found that *R. maritima* was, in fact, highly stimulated by nitrate enrichment. Batiuk et al (1992) found no definite correspondence between dissolved inorganic nitrogen (DIN) concentrations in water and freshwater SAV abundance and therefore did no not set dissolved inorganic nitrogen habitat requirements for SAV growing in freshwater regions. They did find correspondence between dissolved inorganic phosphate (DIP) concentrations and SAV presence and set habitat concentrations of <0.02 mg/l. Neundorfer and Kemp (1993) observed that the negative growth response of *Potomogeton perfoliatus* growing in brackish waters to epiphyte growth was related to the ratio of DIN to DIP enrichment . When this ratio was >16:1 DIN was considered limiting to algal growth and when <16:1 DIP was considered limiting. Light was also found to be an important factor affecting epiphyte growth on SAV, and in both marine, and freshwater systems increased light availability can increase algal abundance given adequate nutrient availability (Neckles et al. 1994, Moore et al 1996, Moore and Wetzel 2000).

The negative effects of epiphytes on SAV, especially in marine regions have been well documented (Phillips et al. 1978, Sand-Jensen 1990, Orth and Van Montfrans 1984, Ozimek et al. 1991, Tomasko and Lapointe 1991 Lapointe et al. 1994, Neckles et al 1994, Moore and Wetzel 2000, Duffy et al. 2001). The epiphytic growth can both attenuate light reaching the leaves of the SAV (Sand-Jensen 1977, Bulthuis and Woelkerling 1983, Sand-Jensen and Borum 1984, Twilley et al. 1985) as well as reducing gas exchange to the leaf surfaces (Sand-Jensen 1977). The growth of epiphytes also can serve as a structure for the attachment on non-photosynthetic sediments, animal and other materials, further increasing the fouling material

(Kemp et al. 2004). Light attenuation across accumulated epiphytic material has been estimated to cause a additional 15 percent to 25 percent reduction of transmitted light to polyhaline and mesohaline species (e.g.,Bulthuis and Woelkerling 1983; Staver 1984; Twilley et al.1985; Kemp et al.2004; van Dijk 1993; Vermaat and Hootsman 1994).

Few studies have reported the light attenuation effects of epiphyte material on freshwater SAV. Chen et al. (2007) noted decreased photosynthetic performance in *Potamogeton crispus* exposed to reduced ephytic grazing pressure. Moore et al. (2003) used artificial strips and transplanted shoots of *V. americana* to measure the epiphyte accumulation rates in a freshwater region of the James River in Virginia where historically SAV once grew. They found very low rates of epiphyte accumulation. Kemp et al. (2004) modeled the potential epiphyte and other fouling accumulations on SAV in freshwater and oligohaline regions of the Chesapeake Bay as a function of water column nutrients, total suspended solids and light availability and predicted 20-60% additional attenuation at the leaf surface above that observed through the water column. Sagan (2003b) measured periphyton levels on *V. americana* leaves in the LSJR. She found that periphyton abundance increased from June through September, reaching a maximum dry weight of 0.25g g^{-1} leaf tissue. This was considerably below the 7g g^{-1} observed, without any apparent deleterious growth effects, by Moore and Wetzel (2000) on *Z. marina*. Sagan did observe considerable macroalgal biomass accumulations within the SAV beds of up to nearly 300 gdw m^{-2} at certain locations. This compares to 100 to 214 gdw m^{-2} for *Cladophora glomerata* algae observed in Lake Erie (Lorenz and Herdendorf 1982). She observed apparent effects on the SAV in the LSJR which she hypothesized, in part, was due to the temporal nature of the drifting algae over the SAV at any one area. Dunn et al. (2008) conducted a survey of the epiphytic algal community of *Vallisneria americana* in the LSJR over a 17-month period. A total of 122 taxa was collected at four sites along a 93-km stretch of the river, yielding 32 diatoms (Bacillariophyta), 42 green algae (Chlorophyta), 45 blue-green algae (Cyanobacteria), 2 euglenoids (Euglenophyta), and one dinoflagellate (Pyrrophyta). However, only diatoms and cyanobacteria were seen at all sampling dates, and only a *Cocconeis* sp. was identified at all sites on all dates. They suggested that while epiphytic algae may be responsible for a significant amount of primary productivity in the SAV beds in this system they also reduce available light for the SAV, compete for nutrients, and increase drag on the leaves.

4. Literature Cited

Abal, E. and W.C. Dennison. 1996. Seagrass depth range and water quality in southern Moreton Bay, Queensland, Australian Journal of Marine and Freshwater Research 47:763-771.

Adair, S.E., J.L. Moore and C.P. Onuf. 1994. Distribution and status of submerged vegetation in estuaries of the upper Texas coast. Wetlands, 14: 110- 121.

Anderson, R.R. 1972. Tentative outline for inventory of submerged aquatic vascular plants: *Ruppia maritima* L. (ditchgrass).Chesapeake Science, 13:S172-S174.

Barko, J.W., D.G. Hardin and M.S. Matthews. 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. Canadian Journal of Botany, 60: 877-887.

Barko, J.W. and R.M. Smart. 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. Ecological Monographs, 51: 219-235.

Barko, J.W., R.M. Smart and D.G. McFarland. 1991. Interactive effects of environmental conditions on the growth of submersed aquatic macrophytes. Journal of Freshwater Ecology, 6: 199-207.

Bartram, W. 1791. Travels through North and South Carolina, Georgia, east and west Florida. Literary Classics of the United States, New York.

Batiuk, R., R. Orth, K. Moore, J. C. Stevenson, W. Dennison, L. Staver, V. Carter, N. Rybicki, R. Hickman, S. Kollar, and S. Bieber. 1992. Submerged aquatic vegetation habitat requirements and restoration targets: a technical synthesis. USEPA Chesapeake Bay Program, Annapolis Maryland.

Batiuk, R., P. Bergstrom, M. Kemp, E. Koch, L. Murray, C. Stevenson, R. Bartleson, V. Carter, N. Rybicki, J. Landwehr, C. Gallegos, L. Karrh, M. Naylor, D. Wilcox, K. Moore, S. Ailstock, and M. Teichberg. 2000. Chesapeake Bay submerged aquatic vegetation water quality and habitat-based requirements and restoration targets: A second technical synthesis. CBP/TRS 245/00. EPA 903-R-00-014, U.S. EPA, Chesapeake Bay Program,

Bayley, S., V.D. Stotts, P.F. Springer and J. Steenis. 1978. Changes in submerged aquatic macrophyte populations at the head of Chesapeake Bay, 1958-1975. Estuaries, 3: 78-84.

Bergstrom, P.W., R.F. Murphy, M.D. Naylor, R.C. Davis and J. Reel. 2006. Underwater grasses in Chesapeake Bay and mid-Atlantic coastal waters: guide to identifying submerged aquatic vegetation. UM-SG-PI-2006-01, College Park, MD. 76p.

Berns, D.M. 2003. Physiological responses of *Thalassia testudinum* and *Ruppia maritima* to experimental salinity levels. M.S. Thesis, University of South Florida, Tampa, FL. 63 pp.

Bigley, R.E., and P.G. Harrison. 1986. Shoot demography and morphology of *Zostera japonica* and *Ruppia maritima* from British Columbia, Canada. Aquatic Botany, 24:69-82.

Bjork, M, J. Uku,, A. Weil and S. Beer. 1999. Photosynthetic tolerances to desiccation of tropical intertidal seagrasses. Marine Ecology Progress Series, 191: 121-126.

Boedeltje, G., A. J. P. Smolders, and J. G. M. Roelofs. 2005. Combined effects of water column nitrate enrichment, sediment type, and irradiance on growth and foliar nutrient concentrations of *Potamogeton alpinus*. Freshwater Biology 50: 1537-1547.

Bortone, S.A. and R.K. Turpin. 2000. Tapegrass life history metrics associated with environmental variables in a controlled estuary. In: Bortone, S.A. (ed.), Seagrass Monitoring, Ecology, Physiology and Management. CRC Press, Boca Raton, 65-79 pp.

Borum, J., O. Pedersen, T.M. Greve, T.A. Frankovich, J.C. Zieman, J.W. Fourqurean, and C.J. Madden. 2005. The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. Journal of Ecology, 93: 148-158.

Bourn, W.S. 1934. Sea-water tolerance of *Vallisneria spiralis* L. *and Potamogeton foliosus* Raf. Contributions from Boyce Thompson Institute, 6: 303-308.

Bourn, W.S. 1935. Sea-water tolerance of *Ruppia maritima* L. Contributions from Boyce Thompson Institute, 7: 249-255.

Boustany, R.G. T.C. Michot and R.F. Moss. 2001. Interactive effect of variable light and salinity on biomass and growth of *Vallisneria americana* in Lower St. Johns River, Florida. USA. Final Report to the St. Johns River Water Management District, Palatka, Florda.

Brody, R.W. 1994. Volume 6 of the Lower St. Johns River Basin Reconnaissance: Biological Resources. St. Johns River Water Management District, Technical Report No. SJ94-2. Palatka, Florida.

Bulthuis, D. A., and W. J. Woelkerling. 1983. Biomass accumulation and shading effects of epiphytes on leaves of the seagrass, *Heterozostera tasmanica*, in Victoria, Australia. Aquatic Botany, 16: 137-148.

Burkholder, J.M., K.M. Mason, H.B. Glasgow.1992. Water column nitrate enrichment promotes decline of eelgrass *Zostera marina*: evidence from seasonal mesocosm experiments. Marine Ecology Progress Series, 81: 163–178.

Cambridge, M. L. and A. J. McComb. 1984. The loss of seagrass in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. Aquatic Botany, 20: 229-243.

Canfield, D.E., K.A. Langeland, S.B. Lindea and W.T. Haller. 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. Journal of Aquatic Plant Management, 23: 25-28.

Carter, V., Rybicki, N. B., Landwehr, J. M., and Turtora, M., 1994, Role of weather and water quality in population dynamics of submersed macrophytes in the tidal Potomac River. Estuaries, 17: 417-426.

Carter, V., N. Rybicki, J. Landwehr, and M. Naylor. 2000. Light requirements for SAV survival and Growth. *In* R. Batiuk et al. (eds.) Chesapeake Bay submerged aquatic vegetation water quality and habitat-based requirements and restoration targets: A second technical synthesis. CBP/TRS 245/00. EPA 903-R-00-014, U.S. EPA, Chesapeake Bay Program, Annapolis, MD. pp. 11-34.

Chambers, P.Q. and J. Kalff. 1985. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. Canadian Journal of Fisheries and Aquatic Sciences, 42: 701-709.

Chen, C., D. Yin, B. Yu, and H. Zhu. 2007. Effect of epiphytic algae on photosynthetic function of *Potamogeton crispus*. J. Freshwater Ecology 22(3): 411-420.

Chesnes, T.C. 2002. Responses of subtropical seagrasses to fluctuations in salinity within an experimental facility. Ph.D. Dissertation, University of Florida, Gainesville, FL. 93 pp.

Clark, R. and J. Stout. 1995. Reproductive ecology of *Vallisneria americana* in an estuarine environment. In: 13th Biennial Inetrnational Conference, Estuarine Research Fedeeration, November 12-16, 1995, Corpus Christi, TX.

Conover, J.T. 1964. The ecology, seasonal periodicity, and distribution of benthic plants in some Texas lagoons. Botanica Marina, 7:4-41.

Davis, G.J. and M.M. Brinson. 1976. The submersed macrophytes of the Pamlico River estuary, North Carolina. Raleigh, N.C.: Water Resources Research Institute Report No. 112.

Dawes, C.J. and J.M. Lawrence. 1989. Allocation of energy resources in the freshwater angiosperms *Vallisneria americana* Michx. and *Potamogeton pectinatus* L. in Florida. Biological Sciences, 52: 58-63.

Dawson, S.P. and W.C. Dennison. 1996. Effects of ultraviolet and photosynthetically active radiation on five seagrass species. Marine Biology, 125: 629-638.

DeMort, C.L. 1991. The St. Johns River System. *In*: Livingston, R.J. (ed.) Rivers of Florida. Springer-Verlag, Inc,. New York, pp. 97-120.

Den Hartog, C. and P.J.G. Polderman. 1975. Changes in the seagrass populations of the Dutch Waddenzee. Aquatic Botany, 1: 141-147.

Dennison, W.C., R.J. Orth, K.A. Moore, J.C. Stevenson, V. Carter, S. Kollar, P.W. Bergstrom, and R.A. Batiuk. 1993. Assessing water quality with submersed aquatic vegetation: Habitat requirements as barometers of Chesapeake Bay health. Bioscience, 43: 86-94.

Dixon, L.K. 2000. Establishing light requirements for the seagrass *Thalassia testudinium*: an example from Tampa Bay, Florida. *In* Seagrasses: Monitoring, Ecology, Physiology and Management.. CRC Press. S.A. Bortone (ed.). pp. 9-32.

Dobberfuhl, D.R. 2007. Light limiting thresholds for submerged aquatic vegetation in a blackwater river. Aquatic Botany, 86: 346-352.

Dobberfuhl, D.R. and Hart, D. 2006. Distribution of Submerged Aquatic Vegetation in the Lower St. Johns River: 2004 Atlas. St. Johns River Water Management District. Professional Paper SJ2006-PP3.

Doering, P.H., R.H. Chamberlain and A.D. Steinman. 1999 Effects salinity on the growth of *Vallisneria americana* Michx from the Calooshatchee estuary Florida. Florida Scientist, 62: 89-105.

Doering, P.H., R.H. Chamberlain and J.M. McMungal. 2001 Effects of simulated saltwater intrusions on the growth and survival of Wild Celery, *Vallisneria americana*, from the Calooshatchee estuary (South Florida). Estuaries, 24: 894-903.

Doering, P.H., R.H. Chamberlain and D.E. Haunert. 2002. Using submerged aquatic vegetation to establish minimum and maximum freshwater inflows to the Caloosahatchee Estuary, Florida. Estuaries, 25: 1343-1354.

Duarte, C.M. 1991. Seagrass depth limits. Aquatic Botany, 27: 15-26.

Duarte, C.M. 2002. The future of seagrass meadows. Environmental Conservation, 29: 192-206.

Duarte, C.M., and J. Kalff. 1987. Latitudinal influences on the depths of maximum colonization and maximum biomass of submerged angiosperms in lakes. Canadian Journal Fisheries and Aquatic Sciences, 44: 1759-1764.

Duffy, J.E., K. S. Macdonald, J.M. Rhode and J.D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: An experimental test. Ecology, 82: 2417-2434.

Dunn, A. E., D.R. Dobberfuhl, and D.A. Casamatta. 2008. A survey of algal epiphytes from *Vallisneria americana* Michx. (Hydrocharitaceae) in the Lower St. Johns River, Florida. Southeastern Naturalist, 7: 229-244.

Eiseman, N.J. 1980. An Illustrated Guide to the Sea Grasses of the Indian River Lagoon of Florida. Technical Report No. 31. Harbor Branch Foundation. Ft. Pierce, Florida.

Eleuterius, L.N. 1987. Seagrass ecology along the coasts of Alabama, Louisiana, and Mississippi. Florida Marine Res. Publ., 42: 11-24.

Erskine, J.M., M.S. Koch. 2000. Sulfide effects on *Thalassia testudinum* carbon balance and adenylate energy charge. Aquatic Botany, 67: 275-285.

Frazer, T.K., S.K. Notestein, M.V. Hoyer, J.A. Hale and D.E. Canfield, Jr. 2001. Frequency and duration of pulsed salinity events in Kings Bay. Final Report. Southwest Florida Water Management District, Brooksville, Florida.

Frazer, T.K., S.K. Notestein, C.A. Jacoby, C.J. Littles, S.R. Keller and R.A. Swett. 2006. Effects of storm-induced salinity changes on submersed aquatic vegetation in Kings Bay, Florida. Estuaries and Coasts, 29: 943-953.

French, G.T. and K.A. Moore. 2003. Single and Interactive effects of light and salinity stress on the growth, reproduction and photosynthetic capabilities *of Vallisneria americana*. Estuaries, 26: 1255-1268.

Gallegos, C.L. 2001. Calculating optical water quality targets to restore and protect submersed aquatic vegetation: Overcoming problems in partitioning the diffuse attenuation coefficient for photosynthetically active radiation. Estuaries, 24: 381-397. Jun 2001.

Gallegos, C. L. 1994. Refining habitat requirements of submersed aquatic vegetation: role of optical models. Estuaries, 17: 198-219.

Gallegos, C.L. 2005. Optical water quality of a blackwater river estuary: the Lower St. Johns River, Florida, USA. Estuarine, Coastal and Shelf Science 63, 57-72.

Giesen, W. B. J. T., M. M. van Katwijk and C. den Hartog. 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. Aquatic Botany, 37: 71-85.

Goldsborough, W.J. and W.M. Kemp. 1988. Light responses of a submersed macrophyte: Implications for survival in turbid tidal waters. Ecology, 69: 1775-1786.

Goodman, J., K.A. Moore and W.C. Dennison. 1995. Photosynthetic responses of eelgrass (*Zostera marina*) L. to light and sediment sulfide in a shallow barrier island lagoon. Aquatic Botany, 50: 37-47.

Green, E.P. and F.T. Short. 2003. World Atlas of Seagrasses. University of California Press. Berkeley, California. 298p.

Haller, W.T. 1974. The photosynthetic characteristics of the submersed aquatic plants *Hydrilla*, southern naiad, and *Vallisneria*. Ph.D. dissertation. Gainsville, Florida. University of Florida.

Haller, W.T., D.L. Sutton and W.C. Barlowe. 1974. Effects of salinity on growth of several aquatic macrophytes. Ecology, 55: 891-894.

Hicks, S. D. 1964. Tidal wave characteristics of Chesapeake Bay. Chesapeake Science, 5: 103-113.

Hotchkiss, N. 1972. Common Marsh, Underwater, and Floating-Leaved Plants of the United States and Canada Courier Dover Publications, 223 p.

Hutchinson,, G.E. 1975. A Treatise of Limnology, Limnological Botany. Vol. III. John Wiley and Sons, New York.

Jarvis, J.C. and K.A. Moore. 2008. Influence of environmental factors on the seed ecology of *Vallisneria americana*. Aquatic Botany, 88: 283-294.

Joanen, T., and L.L. Glasgow. 1965. Factors influencing the establishment of wigeongrass stands in Louisiana. Proceedings of the Southeastern Association of Game and Fish Commission, 19:78-92.

Kahn, A.E. and M.J. Durako. 2005. The effect of salinity and ammonium on seed germination in *Ruppia maritima* from Florida Bay. Bulletin of Marine Science. 77:453-458.

Kantrud, H.A. 1991. Widgeongrass (*Ruppia maritima* L.): a literature review. U.S. Fish and Wildlife Service, Fish and Wildlife Research 10. 58 p.

Kemp, W.M., R. Batiuk, R. Bartleson, P. Bergstrom, V. Carter, C. Gallegos, W. Hunley, L. Karrh, E.W. Koch, J. Landwehr, K. Moore, L. Murray, M. Naylor, N. Rybicki, J.C.

Stevenson and D. Wilcox. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water quality, light regime, and physical-chemical factors. Estuaries, 27: 363-377.

Kemp, W.M., W.R. Boynton, R.R. Twilley, J.C. Stevenson and J.C. Means. 1983. The decline of submerged vascular plants in upper Chesapeake Bay: summary of results concerning possible causes. Marine Technology Society Journal, 17: 78-89.

Kemp, W. M., S. Puskaric, A. Faganeli, E. Smith and W. Boynton. 1999. Pelagic-benthic coupling and nutrient cycling. *In,* T. Malone, A. Malej, L. Harding, N. Smodlaka and R. Turner (eds.). Ecosystems at the Land-sea Margin: Drainage Basin to Coastal Sea. American Geophysical Union Publication, Washington, DC. pp. 295-339.

Kirk, J.T.O. 1994. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, Cambridge.

Koch, E. W. 2001. Beyond light: Physical, geological and geochemical parameters as possible submersed aquatic vegetation habitat requirements. Estuaries, 24: 1-17.

Koch E.W. and C.J. Dawes. 1991. The influence of salinity and temperature on the germination of *Ruppia maritima* L. from the North Atlantic and Gulf of Mexico. Aquatic Botany, 40:389-391.

Koch, M. S. and J. M. Erskine. 2001. Sulfide as a phytotoxin to the tropical seagrass *Thalassia testudinum*: interactions with light, salinity and temperature Journal of Experimental Marine Biology and Ecology, 266: 81-95.

Koch, M.S., I.A. Mendelssohn and K.L. McKee. 1990. Mechanism for the hydrogen sulfide-induced growth limitation in wetland macrophytes. Limnology and Oceanography, 35: 399-408.

Koch, M.S., S.A. Schopmeyer, C. Kyhn-Hanse and, C.J. Madden. 2007. Synergistic effects of high temperature and sulfide on tropical seagrass. Journal of Experimental Marine Biology and Ecology, 341: 91-1-101.

Korschgen, C.E. and W.L. Green. 1988. American wildcelery (Vallisneria americana): Ecological considerations for restoration. U.S. Fish and Wildlife Service, Fish and Wildlife Technical Report 19.

La Peyre, M.K. and S. Rowe. 2003. Effects of salinity changes on growth of *Ruppia maritima* L. Aquatic Botany, 77:235-241.

Leuchner, C., S. Landwehr and U. Melhig. 1998. Limitation of carbon assimilation by intertidal *Zostera noltii* and *Z. marina* by dessication at low tide. Aquatic Botany, 62: 171-176.

Lapointe, B.E. D.A. Tomasko and W.R. Matzie. 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. Bulletin of Marine Science, 54: 696-717.

Lazar, A.C. and C.J. Dawes. 1991. A seasonal study of the seagrass *Ruppia maritima* L. in Tampa Bay, Florida. Organic constituents and tolerances to salinity and temperature. Botanica Marina, 34:265-269.

Littles, C.J. 2005. Effects of rapid salinity change on submersed aquatic plants. M.S. Thesis, University of Florida, Gainesville, Florida.

Lorenz, R.C. and C.E. Herdendorf. 1982. Growth dynamics of *Cladophora glomerata* in western Lake Erie in relation to some environmental factors. Journal of Great Lakes Research, 8: 42-53.

Lowden, R.M. 1982. An approach to the taxonomy of *Vallisneri*a L. (Hydrocharitaceae), Aquatic Botany, 13: 269-298.

Maberly, S.C. 1993. Morphological and photosynthetic characteristics of *Potamogeton obtusifolius* from different depths. Journal of Aquatic Plant Management, 31: 34-39.

Martin, A.C. and Uhler, F.M. 1939. Food of game ducks in the United States and Canada. U.S. Department of Agriculture Technical Bulletin 634. Washington, D.C. 308 pp.

Mataraza, L.K., J.B. Terrell, A.B. Munson and D.E. Canfield, Jr. 1999. Changes in submersed macrophytes in relation to tidal storm surges. Journal of Aquatic Plant Management, 37: 3-12.

Mayer, F.L., Jr. and J.B. Low. 1970. The effect of salinity on widgeongrass. Journal of Wildlife Management,34:658-66.

McFarland, D.G. 2006. Reproductive Ecology of *Vallisneria americana* Michaux. ERDC/TN SAV-06-4. Vicksburg, MS: U.S. Army Engineer Research and Development Center. 27p.

McMillan, C. 1974. Salt tolerance of mangroves and submerged aquatic plants. In: Ecology of Halophytes, R.J. Reimold and W.H. Queen (eds). Academic Press, NY pp. 379-390.

McMillan, C. and F.N. Moseley. 1967. Salinity tolerances of five marine spermatophytes of Redfish Bay, Texas. Ecology: 8503-506.

McGrail, L., K. Berk, D. Brandes, D. Munch, C. Neubauer, W. Osburn, D. Rao, J. Thomson, and D. Toth. 1998. St. Johns River Water Management District, pp. 214-237. In: Fernald, E.A. and Purdum, E.D. (ed.), Water Resources Atlas of Florida. Florida State University, Tallahassee, Florida.

McRoy, C.P. and C. McMillan. 1977. Production ecology and physiology of seagrasses. In: C.P. McRoy and C. Helfferich, eds. Seagrass Ecosystems, a Scientific Perspective. Marcel Dekker, New York.

Millelboe, A.L. and S. Markager. 1997. Depth limits and minimum light requirements of freshwater macrophytes. Freshwater Biology, 37: 553-568.

Montague C.L. and J.A. Ley. 1993. A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in northeastern Florida Bay. Estuaries, 16: 703-717.

Moore, K.A. and R.L. Wetzel. 2000. Seasonal variations in eelgrass (*Zostera marina* L.) responses to nutrient enrichment and reduced light availability in experimental ecosystems. Journal of Marine Biology and Ecology, 244: 1-28.

Moore, K.A., D.L. Wilcox and R.J. Orth. 2000. Analysis of abundance of submersed aquatic vegetation communities in the Chesapeake Bay. Estuaries, 23: 115-127.

Moore, K.A. 2004. Influence of seagrasses on water quality in shallow regions of the lower Chesapeake Bay. Journal of Coastal Research, 45: 162-178.

Moore, K.A. B.A. Anderson and B.B. Neikirk. 2003. Restoration of Submerged Aquatic Vegetation (SAV) in the Tidal Freshwater James River 2002-2003. Special Report No. 384 in Applied Marine Science and Ocean Engineering. Virginia Institute of Marine Science, Gloucester Point, Va. 45p.

Moore, K.A. and J. C. Jarvis. 2008. Environmental factors affecting recent summertime eelgrass diebacks in the lower Chesapeake Bay: Implications for long-term persistence. Journal of Coastal Research, 55: 135-147.

Moore, K.A., R.L. Wetzel and R.J. Orth. 1997. Seasonal pulses of turbidity and their relations to eelgrass (*Zostera marina* L.) survival in an estuary. Journal of Marine Biology and Ecology, 215: 115-134.

Murphy, L.R., S.T. Kinsey, and M.J. Durako. 2003. Physiological effects of short-term salinity changes on *Ruppia maritima*. Aquatic Botany, 75: 293-309.

Neckles, H.A., R.L. Wetzel and R.L. Orth. 1993. Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina* L.) dynamics. Oecologia, 93: 285-295.

Neundorfer, J. V. and W. M. Kemp. 1993. Nitrogen versus phosphorus enrichment of brackish waters: Response of *Potomogeton perfoliatus* and its associated algal communities. Marine Ecology Progress Series. 94: 71-82.

Olesen, B. 1996. Regulation of light attenuation and eelgrass *Zostera marina* depth distribution in a Danish embayment. Marine Ecology Progress Series,134: 187-194.

Orth, R.J., and K. A. Moore. 1983. An unprecedented decline in submerged aquatic vegetation (Chesapeake Bay). Science, 22: 51-53.

Orth R.J. and K.A. Moore. 1988. Distribution of *Zostera marina* L. and *Ruppia maritima* L. sensu lato along depth gradients in the lower Chesapeakee Bay, U.S.A. Aquatic Botany 32: 291-305.

Orth, R.J. and J. van Montfrans. 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: A review. Aquatic Botany, 18: 43-69.

Ozimek, T., E. Pieczynska and A. Hankiewicz. 1991. Effect of filamentous algae on submerged macrophyte growth: A laboratory experiment. Aquatic Botany, 41: 309-315.

Pedersen, O., T. Binzer and J. Borum. 2004. Sulphide intrusion in eelgrass (*Zostera marina* L.). Plant, Cell and Environment, 27: 595–602.

Peres, J.M. and J. Picard. 1975. Causes of decrease and disappearance of the seagrass *Posidonia oceanica* on the French Mediterranean coast. Aquatic Botany, 1: 133-139.

Phillips, R.C. 1960. Observations on the ecology and distribution of the Florida seagrasses. Florida Board of Conservation Profession Paper Series, 72 pp.

Phillips, G.L. D. Eminson and B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwater. Aquatic Botany, 4: 103-126.

Pinnerup, S.P. 1979. Leaf production of *Zostera marina* L. at different salinities. Symposium of the Baltic Marine Biologists : relationship and exchange between the pelagic and benthic biota. pp. 219-224.

Pregnall, A.M; R.D. Smith, T.A. Kursar and R.S. Alberte. 1984. Metabolic adaptation of Zostera marina (eelgrass) to diurnal periods of root anoxia. Marine Biology , 83: 141-147. 1984.

Provancha, J.A. and D.M. Scheidt. 2000. Long-term trends in seagrass beds in the Mosquito Lagoon and Northern Banana River, Florida. In: Bortone, S.A. (editor), Seagrasses: Monitoring, Ecology, Physiology and Management. CRC Press, Boca Raton, FL, 177-193.

Radford, A.E., H.E. Ahles and C.R. Bell. 1964. Manual of the Vascular Flora of the Carolinas. University of North Carolina Press, Chapel Hill. 1183 pp.

Richardson, F.D. 1980. Ecology of *Ruppia maritima* L. in New Hampshire (U.S.A.) tidal marshes. Rhodora, 82:403-439.

Rout N.P. and B.P. Shaw. 2001a. Salt tolerance in aquatic macrophytes: Ionic relation and interaction. Biologia Plantarum, 44: 95-99.

Rout N.P. and B.P. Shaw. 2001b. Salt tolerance in aquatic macrophytes: Possible involvement of the antioxidative enzymes. Plant Science, 160: 415-423.

Sagan, J. J. 2007. SAV Monitoring Project: Interim Reports I-V. Interim reports associated with quarterly sampling and groundtruth surveys for the St. Johns River Water Management District, Palatka FL.

Sagan, J. J. 2006. Hurricane effects on submerged aquatic vegetation within the Lower St. Johns River, Northeast Florida, U.S.A. Final Report for the St. Johns River Water Management District, Palatka, FL.

Sagan, J. J. 2005. *Hydrilla verticillata* Propagule Density and Viability in Crescent Lake. A report for the St. Johns River Water Management District, Palatka, FL.

Sagan, J. J. 2004a. SAV Bed Architecture: Water Depth Distribution and Cover of *Najas guadalupensis*, *Ruppia maritima*, and *Vallisneria americana*. Final Report for the St. Johns River Water Management District, Palatka, FL.

Sagan, J. J. 2004b. The Potential for Submerged Aquatic Vegetation Recolonization of Crescent Lake: The Role of Seeds and Vegetative Propagules. A Report for the St. Johns River Water Management District, Palatka, FL.

Sagan, J. J. 2003a. Distribution of Submerged Aquatic Vegetation within the Lower St. Johns River: 1998 - 2003. Final Report for the St. Johns River Water Management District, Palatka, FL.

Sagan, J. J. 2003b. Assessment of Littoral Zone Periphyton Biomass in the Lower St. Johns River: A Pilot Study. A report for the St. Johns River Water Management District, Palatka FL.

Sagan, J. J. 2002. Lower St. Johns River Basin Submerged Aquatic Vegetation (SAV) Final Report for the St. Johns River Water Management District, Palatka, FL.

Sagan, J. J. 2001. Lower St. Johns River Basin Submerged Aquatic Vegetation (SAV) Monitoring: 1998 - 2001. Final Report for the St. Johns River Water Management District, Palatka FL.

Sagan, J. J. 2000. Lower St. Johns River Basin Submersed Aquatic Vegetation (SAV) Monitoring. Final Report for the St. Johns River Water Management District, Palatka FL.

Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. Aquatic Botany, 3: 55-63.

Sand-Jensen, K. 1990. Epiphyte shading: Its role in resulting depth distribution of submerged aquatic macrophytes. Folia Geobotanica et Phytotaxonomica, 25: 315-320.

Sand-Jensen, K. and J. Borum. 1984. Epiphyte shading and its effect on photosynthesis and diel metabolism of *Lobelia dormanna* L. during the spring bloom in a Danish lake. Aquatic Botany, 20: 109-119.

Schulthorpe, C.D. 1967. The biology of aquatic vascular plants. Edward Arnold Ltd., London. 610p.

Scott, K.M.F., A.D. Harrison, and W. Macnae. 1952. The ecology of South African estuaries. Part II. The Klein River Estuary, Hermanus, Cape. Transactions of the Royal Society of South Africa, 33:283-331.

Seddon, S., R.M. Connolly and K.S. Edwane. 2000. Large-scale seagrass dieback in northern Spencer Gulf, South Australia. Aquatic Botany, 66: 297-310.

Smart, R.M. and J.W. Barko. 1985. Laboratory culture of submerged freshwater macrophytes on natural sediment. Aquatic Botany, 21: 251-263.

Smart, R.M. and J.D. Dorman. 1993. Latitudinal differences in growth strategy of a submersed aquatic plant: Ecotype differentiation in *Vallisneria americana*? Bulletin the Ecological Society of America,74 (Suppl.): 439.

Staver, K. 1984. Responses of epiphytic algae to nitrogen and phosphorus enrichment and effects on productivity of the host plant, *Potamogeton perfoliatus* L., in estuarine waters. M.S. Thesis, University of Maryland, College Park, MD.

Staver, L.W. 1986. Competitive interactions of submerged aquatic vegetation under varying nutrient and salinity conditions. M.S. Thesis. University of Maryland, College Park, Maryland.

Stevenson, J.C. and N.M. Confer. 1978. Summary of available information on Chespeake Bay submerged Vegetation. FWS OBS – 78/66 Annapolis, Maryland. 335p.

Stevenson, J.C., L.W. Staver and K. Staver. 1993. Water quality associated with survival of submersed aquatic vegetation along an estuarine gradient. Estuaries, 16: 346-361.

Steward, J.S, R.W. Virnstein, L.J. Morris, and E.F. Lowe. 2005. Setting seagrass depth, coverage, and light targets for the Indian River Lagoon system, Florida. Estuaries 28: 923–935.

Stewart, R.E. and H.A. Kantrud. 1972. Vegetation of prarie potholes, North Dakota, in relation to quality of water and other environmental factors. U.S. Geological Survey Professional Paper. 585-D. 36 pp.

Stross, R.G. 1979. Density and boundary regulations of the *Nitella* meadow in Lake George, New York. Aquatic Botany, 6: 285-300.

Titus, J.E. and M.S. Adams. 1979. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx. Oecologia, 40: 273-286.

Tomasko, D.A. and B.E. Lapointe. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: Field observations and experimental studies. Marine Ecology Progress Series, 75: 9-17.

Tripathi, S.B., K. Gurumurthi, A.K. Panigrahi and B.P. Shaw. 2007. Salinity induced changes in proline and betaine contents and synthesis in two aquatic macrophytes differing in salt tolerance. Biologia Plantarum, 51: 110-115.

Twilley, R. R., W. M. Kemp, K. W. Staver, J. C. Stevenson and W. R. Boynton. 1985. Nutrient enrichment of estuarine submersed vascular plant communities: I. Algal growth and effects on production of plants and associated communities. Marine Ecology Progress Series, 23:179-191.

Van Diggelen, J., J. Rozema and R. Broekman. 1987. Mineral composition of and proline accumulation by Zostera marina L. in response to environmental salinity. Aquatic Botany, 27: 169-176.

Van Vierssen, W. 1982. The ecology of communities dominated by *Zannichellia* taxa in Western Europe. III. Chemical ecology. Aquatic Botany, 14:259-294.

Valiela, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnology and Oceanography 42: 1105-1118.

van Dijk, G. M. 1993. Dynamics and attenuation characteristics of periphyton upon artificial substratum under various light conditions and some additional observations on periphyton upon *Potamogeton pectinatus* L. Hydrobiologia, 252: 143-161.

Vant, W.N., R.J. Davies-Colley, J.S. Clayton and B.J. Coffey. 1986. Macrophyte depth limits in North Island (New Zealand) lakes of differing clarify. Hydrobiologia, 137: 55-60.

Verhoeven, J.T.A. 1979. The ecology of *Ruppia*-dominated communities in Western Europe. I. Distribution of *Ruppia* representatives in relation to their autecology. Aquatic Botany, 6:197-268.

Vermaat, J.E, N.S.R. Agawin, M.D. Fortes, J.S. Uri, C.M. Duarte, N. Marba, . Enriquez, W. Van Vierssen. 1997. The capacity of seagrasses to survive increased turbidity and siltation: The significance of growth form and light use. Ambio, 26: 499-504.

Vermaat, J. E. and M. J. M. Hootsmans. 1994. Periphyton dynamics in a temperature-light gradient. In W. van Vierssen, M. Hootsmans and J. Vermaat (eds.) Lake Veluwe, a macrophyte-dominated system under eutrophication stress. Kluwer Academic Press, Dordrecht, pp. 193-212.

Weldon,, L.W., R.D. Blackburn and D.S. Harrison. 1969. Coom aquatic weeds. U.S. Department of Agriculture, Agriculture Handbook No. 352. Washington, D.C.

Zieman, J.C. 1982. The Ecology of the Seagrasses of South Florida: a Community Profile. U.S. Fish and Wildlife Service, FWS/OBS-82/25. 123 p.

Zimmerman, R.C. 2003. A bio-optical model of irradiance distribution and photosynthesis in seagrass canopies. Limnology and Oceanography, 48: 568-585.