ABSTRACT

Title of Dissertation / Thesis: INTERACTIONS OF SEAGRASS BEDS AND
                                   THE WATER COLUMN: EFFECTS OF BED
                                   SIZE AND HYDRODYNAMICS

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Beds of seagrass and other submersed angiosperms have been shown to reduce water velocities and water-column dissolved nutrient and seston concentrations. In eutrophic waters, these effects could reduce algal biomass, enhancing light availability to the surface of the leaves and therefore, increasing seagrass growth. Small seagrass beds (1-10m diameter) should have little influence on water flow and water quality, but there is little research on the effect of bed size on these factors. To investigate the effects of seagrass bed size on these interactions, I developed a numerical ecosystem simulation model and used a spatial simulation model. I also conducted mesocosm and field measurements to determine if the expected relationships were evident in reality. I measured water quality, sediment characteristics, epiphyton mass, and hydrodynamic characteristics across beds of the seagrass *Ruppia maritima* L. in mesohaline Chesapeake Bay. I also measured net community nutrient uptake in mesocosms. Field measurements of water transport and

nutrients were used to calibrate a spatial model of water and nutrient flow through *Ruppia* beds. This model was used to determine the potential effects of water flow velocity and bed size on nutrient gradients. An ecosystem simulation model was constructed and used to investigate the effects of nutrient supply rates and grazer densities on epiphytic algae and macrophyte growth. Simulation model results showed the controlling effect of nutrient loading rate on epiphytic algal and *Potamogeton perfoliatus* L. biomass. *Potamogeton* growth rate was highest at low nutrient loading rates, which allowed the angiosperms to reduce nutrients to levels that reduced algal growth. Grazer effects were greatest at intermediate loading rates. Spatial modeling simulations showed the potential influence of bed size and current velocity on water quality changes in shallow water. In the field, ammonium and dissolved inorganic carbon (DIC) decreased, and dissolved oxygen increased with distance into large (> 300 m diameter) beds of one meter tall, moderate density *Ruppia*. Water quality was little changed in beds smaller than 100 m wide. Epiphyton mass was generally variable, but decreased with distance into beds under low dissolved nutrient conditions in the fall of 2001. Epiphyton dry weight was related to total suspended solids. Large, dense, seagrass beds in shallow water, may have a gradient of trophic conditions from outside to inside, while the surrounding water should dictate conditions in small beds.

INTERACTIONS OF SEAGRASS BEDS AND THE WATER COLUMN:
EFFECTS OF BED SIZE AND HYDRODYNAMICS

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Dedication

This work is dedicated to my family and friends who I have neglected in the process.

Acknowledgements

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Chapter 1: Introduction

Background

Effects of nutrients on SAV communities

Eutrophication is known to lead to reduced submersed aquatic vegetation (SAV) by causing decreased light availability due to planktonic (Phillips et al. 1978, Sand-Jensen and Borum 1983) and epiphytic algal shading (Sand-Jensen 1977). Though this paradigm makes sense, the quantitative relation between nutrients and their negative consequences is not well understood. This may be due to numerous interactions and feedback effects, including the uptake of nutrients by SAV and variable influences of epiphytic grazers (Figure 1.0). Mesocosm experiments have shown negative effects of nutrient enrichment on seagrass growth (e.g., Short et al. 1995) and biomass (e.g., Twilley et al. 1985) associated with increases in algal growth (e.g., Sand-Jensen 1977, Taylor et al. 1995). Some studies have failed to detect negative influences on growth or biomass, which may be due, in part, to the influence of grazers but may also be due to neglecting to scale nutrient loading rate to the seagrass biomass.

One microcosm study (Boustany et. al 1999) used a "high" loading rate of 1 μmol N l^{-1} d^{-1} that, considering the nutrient demand of the angiosperms, could have been used as the "low" treatment instead. Other systems have been flushed with 1600% exchange per day (Neckles et al. 1993), which allows little chance for leaf uptake to alter nutrient concentrations. In enclosed systems, epipyhte grazers, including fish, can have an unrealistically large effect on epiphyton mass (e.g., Heck

Figure 1.0 Feedback diagram of seagrass bed and water column. The diagram shows effects of seagrass on water column nutrients and algae resulting in positive feedback for seagrass growth. DBL is the diffusive boundary layer thickness. Plus signs denote positive effects and minus signs denote negative influences. The effect of one parameter on another is determined by counting plus and minus signs in between them. If there is an odd number of minus signs, the influence is negative and if there are all plus signs or an even number of minus signs, the influence is positive.
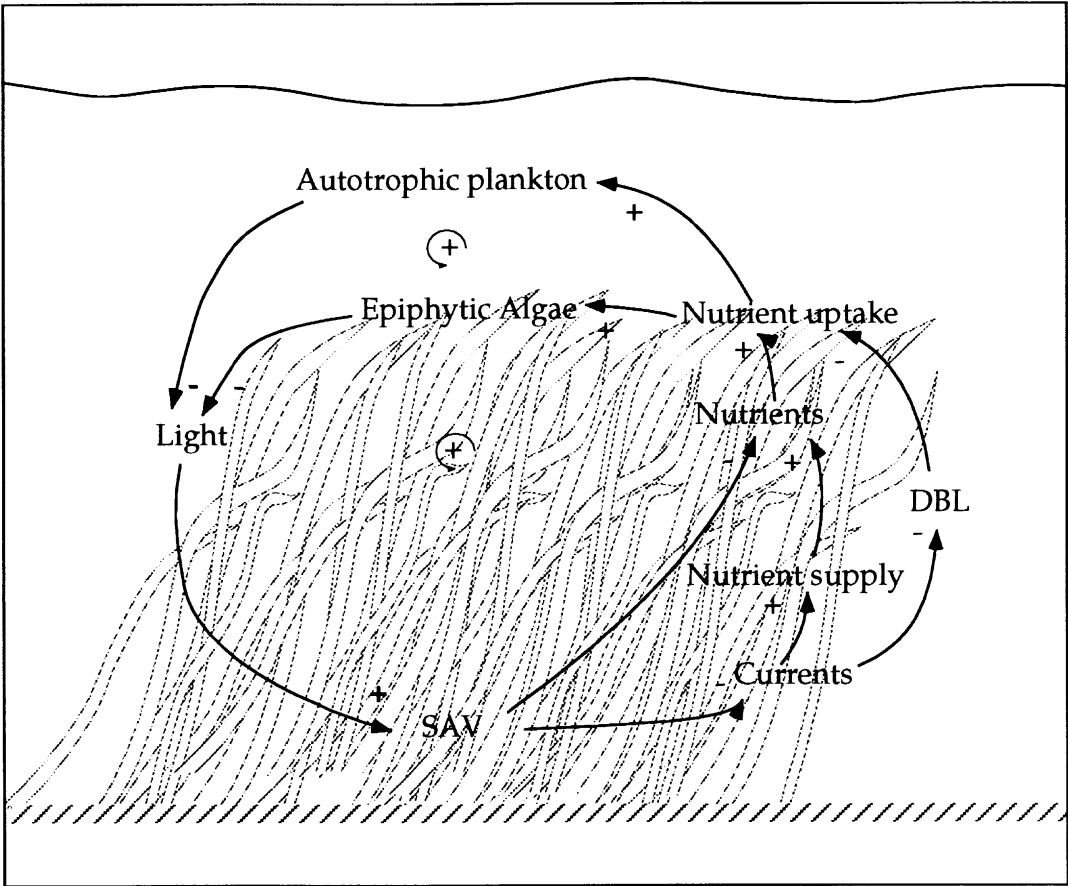
et al. 2000). Correlative studies (Stevenson et al. 1992, Dennison et al. 1993) showed that nutrient concentrations below 10 µmol N l^{-1} and 1µmol P l^{-1} are required for survival of SAV in most of Chesapeake Bay. Though it is useful to have a round figure to go by, 10µmol N l^{-1} is five times higher than the half saturation constant for N uptake of algae, so there may be a reason that SAV are not shaded out at that concentration.

Model simulations and mesocosm measurements (Chapter 2) reveal that nutrient reductions caused by SAV uptake can reduce local nutrient concentrations to levels that limit epiphytic algal growth at low rates of water exchange. In the simulations, epiphytic algal biomass increased with exchange rate as the nutrient loading rate and local concentration increase. Ammonium uptake by *Thalassia testudinum* and its epiphytic algae was shown to be mass-transfer limited (Cornelisen and Thomas 2002) in a flume study. Coral reef algal turf productivity has similarly been shown to be limited by mass-transfer and diffusion boundary layer (DBL) thickness (Carpenter et al. 1991, Carpenter and Williams 1996). Effects of water exchange and loading rates have rarely been considered in relation to SAV community responses to eutrophication. The nutrient loading rate will vary with water mixing and flushing rates, as well as SAV bed size, configuration, and productivity.

Two models of Chesapeake Bay seagrass communities (Kemp et al. 1995, Madden and Kemp 1996) did not include sediment nutrients. Several submersed angiosperm models have simulated responses to nutrient addition but did not include epiphytic algae (e.g., Zimmerman et al. 1987). A shallow lake ecosystem model (Zhang et al. 2003a, Zhang et al. 2003b) that did examine nutrient loading rate effects

on submersed angiosperms may have overestimated leaf nutrient uptake because it was not affected by sediment nutrient concentration.

Effects of SAV on hydrodynamics

SAV alters water flow at several length scales. With large scales (meters or greater), water flow is diverted around dense SAV patches, which act as flow obstructions (Machat-Wenninger and Janauer 1991, Rybicki et al. 1997). At intermediate scales (centimeters), the drag due to individual shoots reduces water flow within beds, especially within the canopy (e.g., Jackson and Winant 1983, Gambi et al. 1990, Carpenter and Williams 1993). And, at smaller scales (millimeters), the friction due to SAV leaves will result in a transformation of flow energy to turbulent energy, blade-induced turbulence (e.g., Ackerman and Okubo 1997), and altered diffusion boundary layer thicknesses (e.g., Koch 1993, 1994), which affect exchange of nutrients and carbon.

The allocation of SAV biomass horizontally and vertically (e.g., Vermaat et al. 2000) in the water column will influence SAV effects on water flow. If plant canopy height is less than the water column depth, water flow rate will be higher than if the shoots extend to the surface and will be faster above the canopy than within it (e.g., Gambi et al. 1990). Increased water velocities were found beneath an *Amphibolis* canopy (van Keulen and Borowitzka 2002). Koch (1996) found higher water velocities near the sediment surface than in the canopy due to lower turtlegrass (*Thalassia testudinum*) surface area as a result of reduced surface area of leaf sheaths. When compared to free-stream velocity, water flow is generally found to be reduced

near the sediment surface in meadow-forming seagrass beds, resulting in an increased roughness height (Fonseca et al. 1983, Bartleson 1988).

The drag coefficient of seagrass should be related to leaf surface area, but the current can alter the orientation of shoots, resulting in reduced surface area exposed to the current. Dense wild celery (*Vallisneria americana*) in high current had a low drag coefficient similar to bare sand, while intermediate density turtlegrass in lower currents had a higher drag coefficient (Bartleson, unpublished data). A decreasing drag coefficient with increasing water flow velocity was shown for several species of submersed plants by Sand-Jensen (2002). Leaf drag has the effect of reducing the contact of SAV and external water, and therefore, the potential for interaction between SAV and external dissolved and particulate substances. It should also reduce current energy towards the center of large beds, where wind-derived energy (Koch and Gust 1999) may be the dominant source of turbulence.

A number of studies have quantified a series of effects of SAV or seagrass density and spatial distribution on water flow and wave energy. Gambi et al. (1990) showed in a flume that fluid flux decreased with distance into a patch but found no effect of *Zostera marina* (eelgrass) density on water flow. Water flowed over ("skimming flow") a continuous eelgrass bed but flowed through a patchy bed (Worcester 1995). Leaf surface area per m^2 accounted for 70% of the water flow reduction in macrophyte beds in Lake Memphremagog (Petticrew and Kalff 1992), but no spatial information was provided by the authors. Wave energy was reduced by 40% per meter of vegetation in a wave tank (Fonseca and Cahalan 1992). Sear (1977) used a flume to determine the effects of submersed plants on vertical diffusion and

found a 36% decrease in water flux in the littoral zone. Water velocities inside dense stands of *Callitriche cophocarpa* Sendtner slowed by 11 fold within two meters of the bed edge (Sand-Jensen and Mebus 1996), while other species had little influence. Macrophyte biomass was not quantified in this study. A detailed study of current velocity across a 30 meter-wide *Groelandia densa* meadow showed sharp (10 fold) reductions in velocity within meters of the bed edge, especially on edges parallel to the flow (Machat-Wenninger and Janauer 1991). Entrainment of sediment decreased sharply within one meter of the edge of seagrass plots in a flume (Fonseca and Fisher 1986). Water velocities were higher outside macrophyte beds in the flume studies of Gambi et al. (1990), in a stream (Sand-Jensen and Mebus 1996), and in rivers (Machat-Wenninger and Janauer 1991, Rybicki et al. 1997). This occurrence is expected since the flow must be conserved, but differences in flow through open water areas may be more gradual. Consequences of these effects on water flow also include: altered sedimentation and resuspension (Ginsburg and Lowenstam 1958, Ward et al. 1984, Fonseca and Fisher 1986, Bartleson 1988, Koch 1999b, Gacia and Duarte 2001, Granata et al. 2001, Agawin and Duarte 2002, Schultz et al. 2003), exchange volume reduction (Rybicki et al. 1997), and wave attenuation (Fonseca and Cahalan 1992).

Several studies have reported on the effect of submersed macrophytes on turbulence and the DBL. A tidal marsh study showed that turbulence intensity decreased hyperbolically with stem density and with distance from the creek edge (Leonard and Luther 1995), with much of the turbulence (65%) dissipated within three meters of that edge. Mean velocity was reduced, and turbulence intensity was

increased from the edge to the center of a kelp bed (Koehl and Alberte 1988). Vegetation mimics were found to reduce vertical dispersion and enhance turbulence in a flume (Nepf et al. 1997a).

Models of hydrodynamics in shallow water usually neglect the effect of submersed macrophytes on water flow (e.g., Kuo and Park 1995), and attempts at modeling the effects of vegetation are few. The effect of vegetation on pelagic-littoral water exchange was modeled in a lake (Weiler 1978). A one dimensional, steady state model was developed using flexible vegetation (Kutija and Hong 1996). More recently, the effect of a seagrass morphology on water flow was shown in a ten layer model (Verduin and Backhaus 2000), and an air flow model was adapted for water flow through a seagrass bed (Abdelrhman 2003). Nepf et al. (1997b) used detailed Laser Doppler Velocimeter (LDV) measurements of water flow between cylinders to produce a model of diffusion. This model may be used with water flow and stem density measurements to estimate canopy diffusivity after characterization of the wake structure of a particular macrophyte species. These results would vary to some degree in SAV beds since shoots are flexible in comparison to cylinders.

A model was developed for water flow through emergent vegetation (based on rigid cylinders) that takes into account macrophyte density and stem Reynolds' numbers (Nepf 1999). This method seems useful for modeling water flow through SAV beds of various densities, but more information is needed about the drag coefficients of relevant SAV species, and how their orientation is affected by current speed, in order to quantify how water flow changes across beds under a variety of densities, bed sizes, and flow conditions. One simple way to model the water flow

would be to assume the flow is the same as in a pipe, as has been done for coral reefs (Bilger and Atkinson 1992), with drag reducing water flow.

Effects of hydrodynamics on SAV communities

Hydrodynamics can, in turn, influence SAV communities. At all spatial scales, water movement supplies nutrients and organic matter and removes waste. At intermediate scales, currents and waves cause blade movement that could affect epiphytic solids accumulation and light availability. At small scales, non-directional water movement (turbulence) affects the diffusive boundary layer thickness at the leaf surfaces and controls flux of carbon and nutrients to the macrophytes.

Currents bring dissolved N and C into SAV and seagrass beds, reducing the potential for nutrient limitation of the angiosperms and algae. Some studies have shown positive correlations of nutrient uptake, photosynthesis, or macrophyte growth with current speed without determining whether transport limitation or uptake limitation was relieved. Koch (1994) found that *Thalassia testudinum* collected from calm environments was C saturated at low current velocities (blade friction velocities of 0.25 cm s^{-1}). Nitrate uptake by *Macrocystis integrifolia* increased with velocity up to 6 cm s^{-1} (Hurd et al. 1996). In a flume study, Cornelisen and Thomas (2002) found that mass transport limited uptake of ammonium by seagrasses and epiphytic algae. Thomas and Cornelisen (2003) found that ammonium uptake of *Thalassia testudinum* communities was much higher under oscillatory flow than steady flow, showing that diffusive uptake was limiting.

Currents, both steady and oscillating, and turbulence can affect the boundary layer thickness. As current speed and turbulence intensity decrease within a bed, the

diffusive boundary layer (DBL) thickness on leaves is increased, slowing the flux to

the plant surface and, as a result, also slowing leaf uptake of dissolved nutrients and

carbon (Munk and Riley 1952) and potentially reducing photosynthesis of

angiosperms (e.g., Fonseca and Kenworthy 1987, Koehl and Alberte 1988, Koch

1994) and algae (e.g., Wheeler 1980, Koch 1993). Photosynthesis of *Ulva latuca*

increased up to friction velocities of 0.3 cm s^{-1} (Koch 1993). At low ammonium

concentrations, turbulence enhanced growth of *Ulva latuca* (Parker 1981). *Vallisneria*

americana growth was shown to increase with mean flow speed up to 7 cm s^{-1} in

mesocosms (Merrell 1996). Stirring increased the leaf area of *Aponogeton elongatus*

grown in aquaria (Crossley et al. 2002). Thus, advection as well as the diffusion-

reaction process (Sanford and Crawford 2000) can control the uptake of nutrients by

angiosperms and algae.

　　　High current speeds or wave motion in general may alter the sediment load

and physically reduce epiphytic algal biomass (Horner et al. 1990). Seagrass beds can

trap and stabilize sediments (Ginsburg and Lowenstam 1958, Harlin et al. 1982).

Enhanced sedimentation can result in increased light availability (Moore 1996, Moore

et al. 1996), as well as altered sediment biogeochemistry through increased organic

input (Bartleson 1988) and alteration of sediment grain size (Wanless 1981). The

degree of water motion may influence gradients of oxidized and reduced sediments

and affect processes, such as nitrification/denitrification, nitrogen fixation, as well as

porewater flux. Stagnant water could result in hydrogen sulfide buildup, which could

be deleterious to rooted plants (e.g., Koch 1999). Currents may interact with

protrusions from the bottom (Huettel and Gust 1992), including seagrasses (Koch and Huettel 2000) altering porewater exchange.

Since SAV beds influence water flow, the effects of flow on SAV communities should change over space, with shoot density, current speed, or wind conditions. It is hypothesized that turbulence should decrease from the outer edge to the interior of an SAV bed, but the relationships between SAV biomass, distance into the bed, current energy, and turbulence are not known. In support of this, turbulent kinetic energy was lower 50 m into a turtlegrass bed than just outside of it (Koch 1996).

Questions that should be addressed include: How large a bed is required to have significant effects on water flow? Does patchiness facilitate water flow through beds (e.g., Worcester 1995)? Since the characteristics of water motion can influence nutrient cycling (e.g., Thomas and Cornelisen 2003), they should be quantified in experimental systems and be in the range of field measurements to properly interpret experimental results (Sanford 1997).

Influence of SAV on the water column and ecological feedback effects

a). Effects of SAV on nutrient and TSS concentrations:

SAV communities can absorb nutrients from the water column (McRoy and Barsdate 1970, Howard-Williams 1981, Iizumi et al. 1982, Thursby and Harlin 1984, Kemp et al. 1984, Moore 1996) and reduce current speeds (e.g., Gambi et al. 1990), resulting in increased sedimentation and increased water clarity (Ginsburg and Lowenstam 1958, Ward et al. 1984). The length of time that nutrients are sequestered in macrophyte tissue should be relatively long compared to microalgae due to the

lifespan of the macrophyte tissue, the high biomass, and the formation of structural tissue (Twilley et al. 1986). By sequestering nutrients until the end of the growing season (Landers 1982), submersed macrophytes may relieve eutrophication stresses that cause phytoplankton blooms and hypoxia. The rate of nutrient uptake by leaves may be quite significant, even though roots may account for most of the uptake. The NH_4^+ uptake by *Ruppia maritima* leaves was up to 230 µmols g dry wt.$^{-1}$ h^{-1} (Thursby and Harlin 1984). At this rate, 43 grams of dried leaves could reduce the NH_4^+ concentration in one m^3 of still water from 10 µmol l^{-1} to limiting levels in an hour. Though SAV leaf uptake can not account for the entire water column nutrient demand, at high biomass, it can be the largest sink. Epiphytic algae growth will increase total nutrient demand (e.g., Howard-Williams and Allanson 1981) even further.

b). Feedbacks and ecosystem responses:

The nutrient reduction caused by SAV uptake could result in reduced epiphytic algal growth and enhanced SAV growth due to the reduction of light limitation. This positive feedback eventually results in even greater nutrient reductions as SAV biomass increases. If epiphytic algae are light-limited, however, the reduction in TSS may cause increased growth. The effects of SAV that are best documented are those on their immediate environment. Light extinction (e.g., Westlake 1964), temperature (Dale and Gillespie 1977), water flow (Ginsburg and Lowenstam 1958), nutrients, TSS, oxygen, substrate, DOC, DIC, and biota are

affected by SAV (see Carpenter and Lodge 1986 for review), though these effects are

not always quantified in a manner that is useful for modeling.

c) Spatial variations in nutrient concentrations alter feedback effects:

The effects of SAV on nutrient and TSS concentrations may not be uniform

over space and may be affected by water exchange conditions and bed sizes. Edges of

beds and patches will experience higher nutrient and TSS loads than centers of large

beds. The width of the edge effect will depend on the current and biomass allocation.

Spatial plankton community changes could result from the reduction of nutrients and

TSS in beds as well as due to altered fish and zooplankton biomass. Quantification of

these changes is necessary in order to predict the effect of large seagrass beds on the

pelagic-benthic ecosystem.

The influence of spatial characteristics of SAV beds on ecosystem responses

a)*. Scale in ecology, and applications in seagrass beds:*

Landscape ecology involves the study of effects of large-scale (km) patterns

on ecosystem processes (e.g., Turner 1989). Though the spatial scale had been

ignored by most submersed plant researchers, recently interest has been increasing

(Bell and Hicks 1991, Irlandi et al. 1995, Irlandi 1996, Robbins and Bell 1994,

Fonseca and Bell 1998, Frankovich and Fourqurean 1997, Bell et al. 2001, Hovel et

al. 2002, Fourqurean et al. 2003). Physical processes, such as wave exposure and

current speed, were found to influence seagrass bed attributes, such as perimeter to

area ratio and sediment organic content (Fonseca and Bell 1998). Patch size and

macrophyte density may then affect recruitment, growth and survival of bed

inhabitants, such as bivalves (Irlandi 1996). Other parameters that have not been

examined for their effect on processes and patterns are size and relative location within a bed. These may have significant influences on variables measured and processes within beds. For example, the center of a large, dense bed may have a much lower particulate matter supply than that of a small or sparse bed. A study on the effect of spatial configuration on the growth of the bay scallop was conducted in beds of various degrees of patchiness (Irlandi et al. 1995), but no details were given about factors affecting the food supply, such as the overall bed size or the current energy. Many studies have been done without regard to, or without noting location in a bed size of bed, or rates of water exchange, even though the findings depend on these factors.

b). Effect of SAV on spatial patterns of nutrient and TSS concentration:

The influences of SAV on water column nutrients and TSS cannot be extrapolated from test tubes or mesocosms to larger scales (e.g., Short and Short 1984) or to models of SAV-water column interactions due to the effects of SAV beds on water flow, and due to the changes in biomass, hydrodynamics and water column concentrations across space. Mass transfer, diffusion, and uptake kinetics can limit nutrient uptake by a seagrass bed. Mass transfer to estuarine submersed angiosperms is controlled by tidal currents and influenced by the vertical distribution of leaf biomass in the bed. As water moves across a shallow, photosynthesizing bed, the current speed decreases due to drag while the nutrient concentration decreases due to uptake. The slowing of advection in a bed can result in enhanced declines in nutrient concentrations, and hence, reduced nutrient uptake. Thus, large, dense beds could reduce local nutrient concentrations to a greater degree than sparse beds and small

patches. This is illustrated in Figure 1.1 by a spatial calculation of how tidally averaged nutrient concentrations may be affected over space by patchy or continuous seagrass beds. Although nutrient concentrations are lower within the large bed, average concentrations over the total area are higher due to the reduced uptake rates within the large patch. Figure 1.2 shows how nutrient concentrations along a flow axis may be influenced by a combination of uptake, drag, and transport rates, and how water flow is affected by drag. Local nutrient reductions have been shown in a variety of SAV beds (e.g., Moore 1996). The slowing of currents within seagrass beds has been documented as well (e.g., Rybicki et al. 1997). The combination of nutrient uptake and water exchange reduction can result in a zone of slow-moving, nutrient depleted water. Mulholland et al. (1994) measured nutrient uptake of benthic algae in flumes and found trapping of water near the bottom when biomass was high. This allowed reduction in nutrients within the trapped layer but reduced overall nutrient reduction. Hydraulic characteristics and nutrient cycling processes were found to be closely coupled (Mulholland et al. 1994). SAV in large, dense beds may have less influence on the average nutrient concentration over a wide area than dispersed macrophytes due to flow diversion induced by the drag of the dense bed.

Further affecting nutrient uptake by SAV beds is diffusion, which is a function of the diffusive boundary layer thickness (e.g., Koch 1994). Since current speed, turbulence, leaf biomass, and their interactions affect the boundary layer thickness, the thickness should vary across space, increasing in thickness towards the center of large, dense beds. To accurately predict uptake of submersed macrophyte beds, it would be necessary to have measures of small-scale turbulence and water

Figure 1.1 Hypothetical tidally averaged relative nutrient reductions in small, large, and patchy seagrass beds.

Seagrass Distribution

Nutrient concentrations

Nutrient s

High

Low

Tide direction
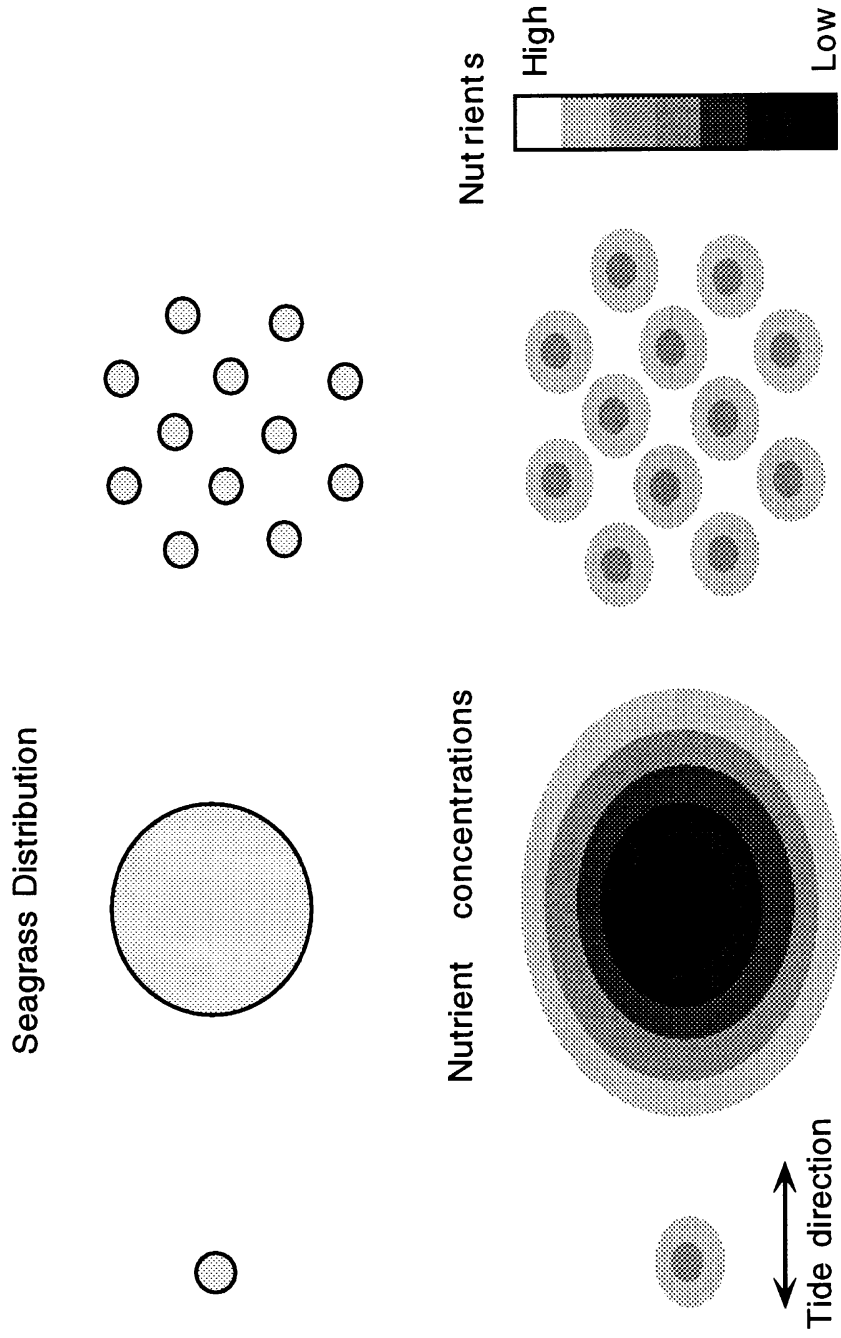
Figure 1.2 Hypothetical relative changes in water quality and hydrodynamics and subsequent changes in photosynthetically available radiation (PAR) epiphytic algal and SAV growth. DIN stands for dissolved inorganic nitrogen, TSS for total suspended solids, DBL for diffusive boundary layer. Small, medium and large are SAV bed sizes.
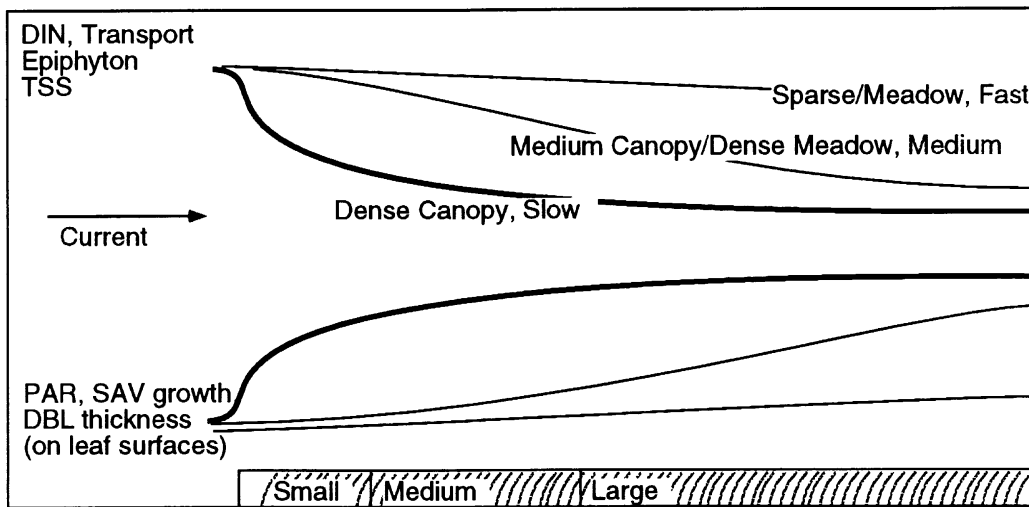
flow in different size beds. Calculation of the ratio of macrophyte nutrient uptake to the rate of advection (Stanton number) will determine if mass transport or diffusion limits uptake (e.g., Atkinson and Bilger 1992). Turbulent diffusion may be the dominant form of transport for nutrients at low flow, while advection would dominate at higher flow/bed size ratio. A diffusion-reaction model could be used to determine nutrient flux at low flow; but at high flows, uptake rate and concentration alone would determine flux.

Spatial nutrient information within beds is necessary to model effects of nutrients on SAV ecosystems because nutrients can affect epiphytic algal growth, and hence, light availability to leaves. Though within-bed effects have been documented, the effect of SAV on nutrients in surrounding waters is poorly documented. Large beds in shallow water, such as Florida Bay, could have a large influence on water quality in adjacent waters. Predicting effects of nutrients on nearby pelagic systems requires knowledge of the water flow and uptake characteristics of a bed. This topic is addressed in Chapter 3.

Total suspended solids (TSS) concentrations within beds can decrease due to SAV effect on water flow (e.g., Ginsburg and Lowenstam 1958). Modeling the influence of TSS on SAV can only be done with a spatial model that allows changes in TSS to occur spatially. This model needs to be calibrated to a range of shoot densities and water flow rates. This is an important factor in determining the light available to SAV communities as well as adjacent pelagic-benthic communities (Bulthuis et al. 1984). If water is cleared of TSS as it passes through a bed, it may

result in a shift of producer biomass from the water column to the benthos in surrounding areas, as more light can reach the bottom.

c) Ecosystem effects of bed size to water exchange ratio:

Interiors of dense, shallow SAV beds with high biomass and low water exchange rates may experience drastically lower nutrient concentrations than exist in the surrounding water (e.g., Moore 1996). Therefore, production of other autotrophs (epiphytic algae and phytoplankton) may be inhibited if nutrients are reduced below saturating levels, and recycling may become more important for continued algal production (e.g., Mullholland et al.1992). Epiphyte biomass has been correlated with nutrient gradients over large spatial scales (Frankovich and Fourqurean 1997), and the reduction of nutrients in bed interiors may result in a similar pattern. Most SAV species can obtain much of their nutrients from the sediments (e.g., Thursby and Harlin 1984, Hensel 1992), so the nutrient supplies in overlying waters are not as important to their survival.

Reduced water exchange and flow in bed interiors may also cause reductions in epiphytic biomass, if concentrations fall below saturating levels. This is illustrated indirectly in Figure 1.3, where SAV biomass is positively correlated with nutrient supply until the supply exceeds uptake; then, epiphytic algae are released from nutrient limitation and increasingly reduce SAV growth by shading. Since epiphytic algae attenuate light and may be partly responsible for the loss of SAV with eutrophication, large, dense beds may be more resistant to eutrophication than small or sparse beds due to this localized nutrient reduction. The size of a bed needed to reduce nutrients sufficiently to reduce epiphyte growth is not known. The increased

Figure 1.3 Effect of water exchange rate on maximum SAV leaf biomass at a range of inflow N concentrations.
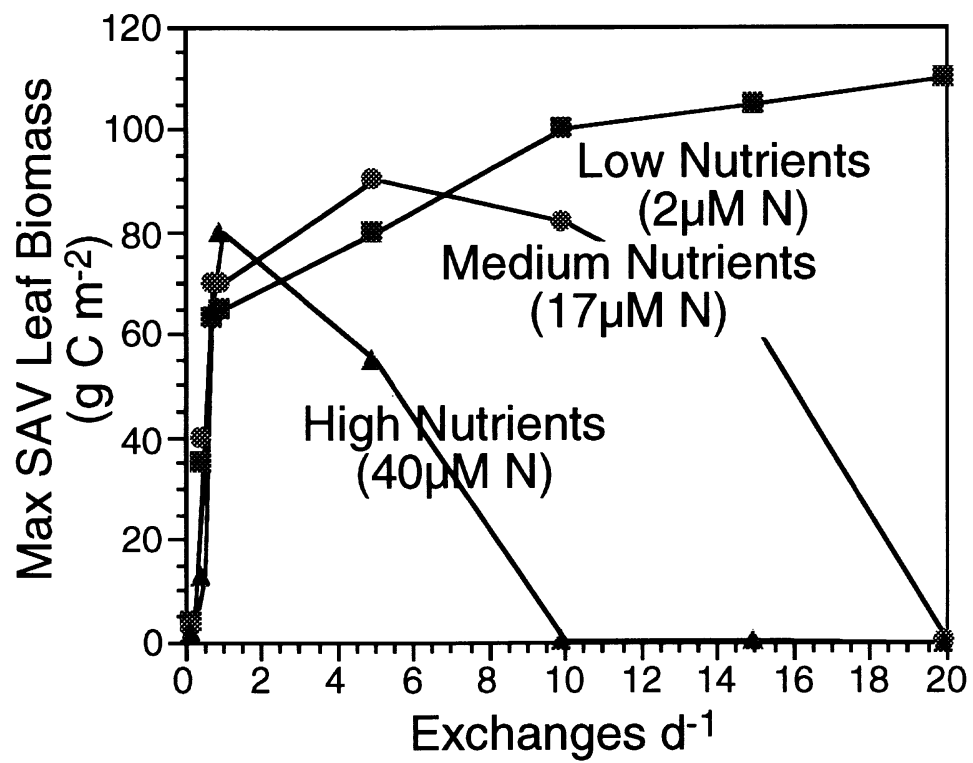
light availability could increase epiphytic algal growth in cases where they are light-limited, however. Epiphytic algae biomass may not be noticeably different if grazer densities are lower within beds, as may happen because of increased fish densities. A complicating factor is the low percentage of algae in some epiphytic assemblages. This effect, in conjunction with decreased TSS concentrations, could permit large, dense beds to survive eutrophic conditions by allowing more light to reach the leaves. Fouling of leaves by epiphytic fauna may also be reduced due to reduced POM supply.

Phytoplankton within beds can be reduced both by sedimentation and nutrient reduction (Brammer 1979) as well as grazing by zooplankton and fish (Schriver et al. 1995). Phytoplankton abundance was lower in SAV beds than in open water in the freshwater portion of the Potomac River (Jones 1990). Phytoplankton species composition may change due to reduced nutrients, decreased turbulence, allelopathy (Jasser 1995), and humic exudation (Stoecker, pers. comm.). Flagellates may be dominant in dense beds, due to their lack of dependence on turbulence. Abundance of dinoflagellates was found to increase in the presence of macrophytes in lake enclosures (Schriver et al. 1995). Of course, senescence of macrophytes will conversely cause increases in nutrients and phytoplankton (e.g., Landers 1982).

SAV production may also vary spatially within beds due to changes in nutrient conditions. Interiors of large SAV beds may become starved even for sediment nutrients as water flowing toward mid-bed is stripped of dissolved and particulate nutrients. Nutrient limitation of seagrasses has been reported for many sites (e.g., Agawin et al. 1996), and the spatial variation in nutrient limitation should

be examined. Primary production in SAV systems is much greater than in unvegetated areas (Mann 1982). As a result, large differences in pH, CO_2, O_2, and nutrients between SAV beds and surrounding waters can result. An SAV system may draw materials and energy from the surrounding unvegetated systems, reducing their productivity and changing the energy flow of the ecosystem. Carbon and nitrogen are stored in macrophyte tissue, epiphytic algae and sediments, changing the base of the pelagic food chain.

Shoot surface area per m^2 was correlated with surficial sediment composition in a Canadian lake (Petticrew and Kalff 1992). Silt-clay, organic matter, ammonium, and total nitrogen were found to increase from non-vegetated to patchy and to dense beds, with an increase also seen towards the center of a bed (Kenworthy et al. 1982). Several other studies show the effects of SAV on sediment biochemistry (e.g., Boon and Sorrell, 1991, Wigand et al. 1997) but do not correlate them with SAV biomass, and no effect on surrounding sediments has been noted. Export of detritus was inversely correlated with SAV biomass in a stream (Fisher and Carpenter 1976). Sedimentation within the bed can drastically alter light levels (Rybicki et al. 1997), which can further affect production of angiosperms and algae. Some studies (Bell et al. 1994, Murphey and Fonseca 1995) report differences in seagrass bed fauna and flora with respect to energy regime. Since the energy regime changes across beds, the biotic community is expected to vary along this gradient as well.

d) Effect of SAV on secondary production, bacterioplankton and community structure:

Differential flow, uptake and sedimentation as water moves over a bed can result in differences in pH, nutrients, TSS, and light across beds that can affect production, nutrient uptake, and sediment geochemistry. Little quantitative information is available on the effects of SAV on planktonic community structure. Bacterioplankton are correlated with SAV production (Tornblom and Søndergaard 1999), but there is no information about how much SAV is needed to see an effect. Zooplankton may be positively correlated with SAV biomass as it offers protection from predation (Timms and Moss 1984, Schriver et al. 1995). Decreased phytoplankton biomass in dense beds may not be a food problem for zooplankton, since other algal sources could take its place.

Epifauna and infauna may be affected by the current changes in a bed. The current reduction near the sediment surface may reduce food supply to suspension feeders (Frechette et al. 1989). Both water movement and the presence of vegetation were found to affect the densities of infaunal communities in *T. testudinum* and *Halodule wrightii* beds (O'Gower and Wacasey 1967) and attached scallop larvae (Eckman 1987). Many studies have found higher faunal densities within SAV beds (e.g., Lubbers et al. 1990), but some of these differences may be due to spatial differences in food supply, and the average densities over a bed may not be different from those in non-vegetated areas. The results of a study on influence of seagrass patch size and energy regime on the hard clam (Irlandi 1996) are difficult to interpret because of the large-scale effects of SAV patches on water flow.

e) Modeling SAV ecosystems:

A numerical ecosystem simulation model can be used to estimate the effects of nutrients on SAV growth at a range of nutrient concentrations, supply rates, and grazer densities. This can help define the mechanisms involved in the nutrient/growth relationship and allow better designed mesocosm experiments. A model is also a way to relate results from mesocosm experiments to field conditions. Several simulation models of SAV production have examined SAV responses to nutrient enrichment and grazing regulation of epiphytic algal growth (Wetzel and Neckles 1986, Kemp et al. 1995, Madden and Kemp 1996). These models have simulated neither the dynamics of the grazers themselves nor the feedback interactions among grazers, epiphytic algae and SAV. In addition, no experiments or models have explicitly considered how resident predator populations may control herbivorous grazing. At least one model of an SAV ecosystem was designed to show the feedback effects of SAV biomass on nutrient and POM concentrations (Bartleson 1988), but this model is insufficient for this problem due to the lack of spatial detail. This model shows that SAV reduces current speed and enhances sedimentation, but in a downstream cell, water inflow rate and water quality are changed, so the response of that cell may be different from the modeled cell. Models of Chesapeake Bay water quality have not addressed the effects of SAV beds on water column properties, though much of the water in an estuary with large areas of shallow water could flow over and be affected by SAV beds. When meadow size was increased in a simulation of a littoral zone, water column nutrients were decreased (Buzzelli et al. 1998), but there were no adjustments made for effects of increased SAV on water flow. The presence of SAV in areas targeted

for reduced nutrient inflows may result in greater improvements in water quality than would be expected by reduction of nutrients alone.

A simple model can be used to estimate the effects of nutrients on SAV communities under different exchange rates (Chapter 2). Spatial models may allow examination of the effects of pattern, hydrography, and bathymetry on the basic interactions. A model of nutrient transport through an SAV bed is needed. The simplest model may be a diffusion-reaction model. This model will result in spatial nutrient fluxes based on diffusion rate and uptake alone and may be appropriate for some dense canopy-forming beds that experience gentle currents. Another model that may be useful is an advection-dispersion model that incorporates a transient storage zone (e.g., Bencala and Walters 1983). This method may be more useful in meadow-forming beds that have a large over-canopy flow and a zone of stationary water within the bed. Though modeling may be inappropriate for making quantitative predictions, the influence of SAV on water column nutrients is so strong that it is within reason to run scenarios relating to nutrient changes. A spatial model will make a good tool for visualizing the role of water exchange and bed size (Chapter 3) and for examining specific sites.

To fully understand how SAV beds interact with nutrient cycles and ecosystem dynamics, we need to quantify the effects of SAV bed size on hydrodynamics in the field (Chapter 4). We need to know the proportion of water flowing past a SAV bed that is affected by it to determine the effect on the adjacent, benthic-pelagic system. A hydrologic model influenced by spatial differences in drag would allow estimation of water flow characteristics in SAV beds.

Benefits of this research would include: 1) improved ability to interpret field data from SAV beds, 2) increased understanding of effects of nutrients on SAV systems, and 3) increased knowledge for guiding restoration efforts. The above text presents the reasons for taking a large-scale view, looking at spatial relationships, and examining hydrodynamics in SAV beds.

Research questions and approaches

The above background and rationale lead to questions, such as: 1. How do bed size, shoot biomass and water exchange rate (or residence time) affect water column nutrient concentrations? 2. Do these interactions subsequently affect epiphytic algal coverage and other ecosystem components? The attempt to address these questions is found in the following chapters. Chapter 2 examines the response of a model SAV ecosystem to changes in nutrient loading per unit biomass. Chapter 3 demonstrates the effect of spatial scale and water flow on water column nutrients, using a simplified spatial model and some field measurements. Chapter 4 gives examples of cross-bed differences in dissolved oxygen, pH, epiphyton coverage, and sediment characteristics.

Chapter 2: Use of a simulation model to examine effects of nutrient loading and grazing on *Potamogeton perfoliatus* L. communities in microcosms

Abstract

I constructed a numerical simulation model of an enclosed, submersed macrophyte ecosystem to examine the effects of nutrient supply rates, grazer densities and initial conditions, such as marcrophyte biomass, on macrophytes and epiphytic algae. The model included an internal nutrient pool that controlled root and leaf nutrient uptake and was calibrated to literature values and mesocosm experiments. Simulations were run to examine how initial conditions, nutrient supply rates and the presence of grazers may affect the outcome of nutrient addition experiments. Simulations revealed that the outcome of an experiment could be largely controlled by the initial conditions or by biomass changes during the experiment. For example, high initial macrophyte biomass reduced light and nutrients available for algae, which prevented the overgrowth of algae, even at high nutrient addition rates. Epiphytic algae biomass increased with water exchange rate regardless of inflow nutrient concentration. Submersed macrophytes grew best at lower exchange rates that allowed nutrient concentrations to be drawn down, slowing algal growth. Simulations showed that the effect of grazers on epiphytic algal biomass was greatest at intermediate nutrient addition rates. When grazers were absent, macrophyte biomass could be highest with low or high inflow nutrient concentrations, depending on the water exchange rate. Model analysis also revealed that it is essential to consider

nutrient loading rate per unit macrophyte biomass, not just nutrient concentration, when quantifying the effects of eutrophication on submersed macrophytes. These results show the utility of using a simulation model together with ecosystem experiments. They also show how water exchange rates, or residence times, which can depend on bed size, could affect eutrophication responses of submersed macrophyte ecosystems.

Introduction

Declines in submersed macrophyte populations in Chesapeake Bay and worldwide have been attributed in part to nutrient enrichment (Christensen and Andersen 1958, Orth and Moore 1983, Cambridge and McComb 1984). Nutrients from agricultural runoff, sewage, etc., can cause epiphytic algal (Phillips et al. 1978, Harlin and Thorne-Miller 1981) and phytoplankton growth (Boynton et al. 1982), which reduce light availability and, consequently, the growth rates of submersed macrophytes (e.g., Short et al. 1995). The relationship between water column nutrient concentrations and macrophyte growth or health has been documented by some field studies (e.g., Stevenson et al. 1993), controlled experiments (e.g., Neckles et al. 1993) and simulation models (e.g., Wetzel and Neckles 1986), but guidelines for nutrient levels that prevent loss of seagrasses are still not easy to justify.

The effect of eutrophication on epiphytic coverage of leaves is still in question because many factors can affect epiphyton composition, growth (e.g., Cattaneo 1987) and accumulation (e.g., Jewett-Smith 1991, Strand and Weisner 1996). Water column nutrient concentrations, light, temperature and hydrologic conditions can be very dynamic, complicating the determination of the correct parameter values to be

correlated with measured epiphyton biomass. Variability over large and small spatial scales is also common.

Predicting effects of nutrients on submersed macrophytes and of macrophytes on the ecosystem is also difficult due to changing interactions of macrophytes with the water column (hydrodynamics and nutrients) across space. Submersed macrophyte communities can reduce nutrient concentrations when their biomass is high in relation to the volume of water exchanged with the adjacent system (e.g., McRoy and Barsdate 1970, Moore 1996, Moore et al. 1996). Localized reductions in nutrients could result in reduced algal growth and improved light transmission to macrophytes, resulting in positive feedback for growth. The magnitude of the interactions between macrophytes and the water column could be related to the area of macrophyte coverage, and, most likely, density (Ward et al. 1984, Moore 1996) and spatial pattern as well, since these may influence water exchange. Because of these factors, it is difficult to determine the nutrient loading rate or even the experimental enrichment levels to a submersed macrophyte bed in an estuary. For example, some studies used slow release fertilizer as a nutrient addition (Williams and Ruckelshaus 1993, McGlathery 1995, Wear et al. 1999), so neither the water column nutrient concentrations nor the loading to the macrophytes could be calculated. Controlled experiments allow for the opportunity to track and quantify effects of all important variables.

Microcosm and mesocosm experiments have been used to examine the effects of nutrients on epiphytic algae (Neckles et al. 1993) and submersed macrophyte growth (Twilley et al. 1985, Neundorfer 1990, Short et al. 1995, Taylor et al. 1995).

These experiments have generally shown an inverse relationship between water column nutrients and macrophyte growth (e.g., Twilley et al. 1985, Neckles et al. 1993), but results have been variable, partly due to the large number of factors involved. Investigators generally use high and low nutrient inflow concentrations but do not always consider the nutrient loading rate per unit of macrophyte biomass. For example, one study found little difference in macrophyte biomass between loading rates (Taylor et al. 1999), but the highest loading rate was not high enough to supply the demand of the macrophytes and epiphytic algae. One microcosm study compared responses to two different water exchange rates at the same nutrient loading rate, but the different responses may have been due to the two experiments being run in different seasons (Sturgis and Murray 1997). When an experiment is initiated with low macrophyte biomass, a low nutrient addition rate may result in the same water column nutrient concentrations as high addition rates when biomass has increased later in the experiment.

In some locations, invertebrate grazing may effectively reduce the effects of epiphyton on macrophytes (Hootsmans and Vermaat 1985, Howard and Short 1986, see Hughes et al. 2004 for review). However, the relative ability of herbivorous grazing to control epiphyton accumulations can vary with season, region and feeding mode of the grazer populations (Howard 1982, Brönmark 1985, Neckles et al. 1993). In addition, significant changes in the mortality of these grazers that may result from predation or altered environmental conditions (e.g., Lubbers et al. 1990) can influence the ability of grazers to control epiphytic algal growth.

Ultimately, differences in trophic structure of the community associated with submersed macrophytes can radically alter the responses to changes in nutrient levels. Grazers were shown to keep algal biomass from increasing at eight times ambient nutrient concentrations in artificial streams (Pan and Lowe 1994). Cyanobacteria on eelgrass, however, were not affected by grazing in microcosms (Neckles et al. 1994). Results of one experiment showed improved seagrass growth with grazers present, even at a high water exchange rate, but inflow nutrient concentrations were not reported (Hootsmans and Vermaat 1985). In another study with a single nutrient addition rate and predator treatment, results were confounded by the predator feeding on epiphytic algae as well as the grazers (Heck et al. 2000).

When nutrient loading per unit macrophyte biomass is not considered in microcosm experiments, results may only be relevant for specific water exchange rates used. As a consequence of not considering how macrophyte communities reduce nutrient concentrations, experiment results could either be difficult to interpret or counterintuitive. For example, if a nutrient loading rate is high enough, grazers may not be able to keep up with epiphytic algal growth, and a grazer effect will not be detected.

Other problems that may confound results of enclosure experiments are "founder effects" (Gamble and Davies 1982) and other artifacts such as wall effects (see Dudzik et al. 1979). For example, an initial colonist in one or more tanks may exclude other species. Initial SAV biomass may also strongly influence results. If macrophyte biomass is high at the start of an experiment, its effect on light and nutrients may reduce the production of phytoplankton even at high nutrient loading

rates. Simulation models can be used to examine these relationships and help us understand the experiment results.

Models are used to help management agencies set goals for the management of nutrient inputs to estuaries (e.g., Cerco and Cole 1993), but their formulations are not really appropriate for addressing the interactions of macrophytes and nutrients over space. Published simulation models have not fully examined the interactive effects of submersed angiosperms, nutrients, epiphytic algae and grazers. For instance, though the eelgrass models of Ferguson and Adams (1979), van Montfrans et al. (1984) and Wetzel and Neckles (1986) examined epiphytic algal - grazer interactions, they did not include nutrients. In these studies, grazing reduced epiphytic algal biomass, resulting in increased light availability and macrophyte growth.

Other published models considered, (Kemp et al. 1995, Madden and Kemp 1996) did not include sediment nutrients. These would not show realistic effects of rooted macrophytes on dissolved nutrients and consequent community effects. The nutrient absorption ability of rooted macrophyte leaves is influenced by the sediment nutrient content, which is also affected by macrophyte uptake (e.g., Thursby and Harlin 1984).

Though the concept of submersed angiosperm feedback effects is well known, the mechanisms representing the feedbacks are not found in seagrass models. The kilometer scale used in some models may be inappropriate when macrophyte-water column interactions occur since water column concentrations may change over tens of meters. By showing the water column changes that can occur in one m^2, this model can be used to illustrate this insufficiency.

A numerical ecosystem simulation model can also be used to show the effects of nutrients on macrophyte growth at a range of nutrient concentrations, supply rates and grazer densities. This can help explain the mechanisms involved in the nutrient/growth relationship, thus allowing better-designed microcosm experiments.

A model is also a tool to relate results from enclosed experimental systems to field conditions and may also help explain apparently conflicting results of experiments. Simulation models also allow experimenters to examine the possible effects of initial conditions. Here I develop and use a model of a submersed macrophyte ecosystem to examine effects of water residence time and trophic interactions, which are important in determining the consequences of nutrient enrichment on submersed macrophytes in microcosms and in natural systems.

Methods

The model equations were developed from empirical relationships based on laboratory and field data from mesohaline Chesapeake Bay, other estuaries and theoretical functions. I built upon components of previous seagrass and benthic pelagic models (Bartleson 1988, Bartleson and Kemp 1991). The model structure is shown in Figure 2.1. Equations are shown in Table 2.1 and Table A1 and coefficients and documentation are shown in Table A2. I designed the model to track nitrogen (N), oxygen (O) and carbon (C) through the system. It has 17 state variables: *Potamogeton perfoliatus* L. leaves, *P. perfoliatus* roots, *P. perfoliatus* non structural N, phytoplankton, epiphytic algae, macroalgae, benthic algae, bacterioplankton, amphipods, labile dissolved organic matter, water column dissolved inorganic N and O_2, sediment porewater dissolved oxygen and dissolved inorganic N, deposit feeders
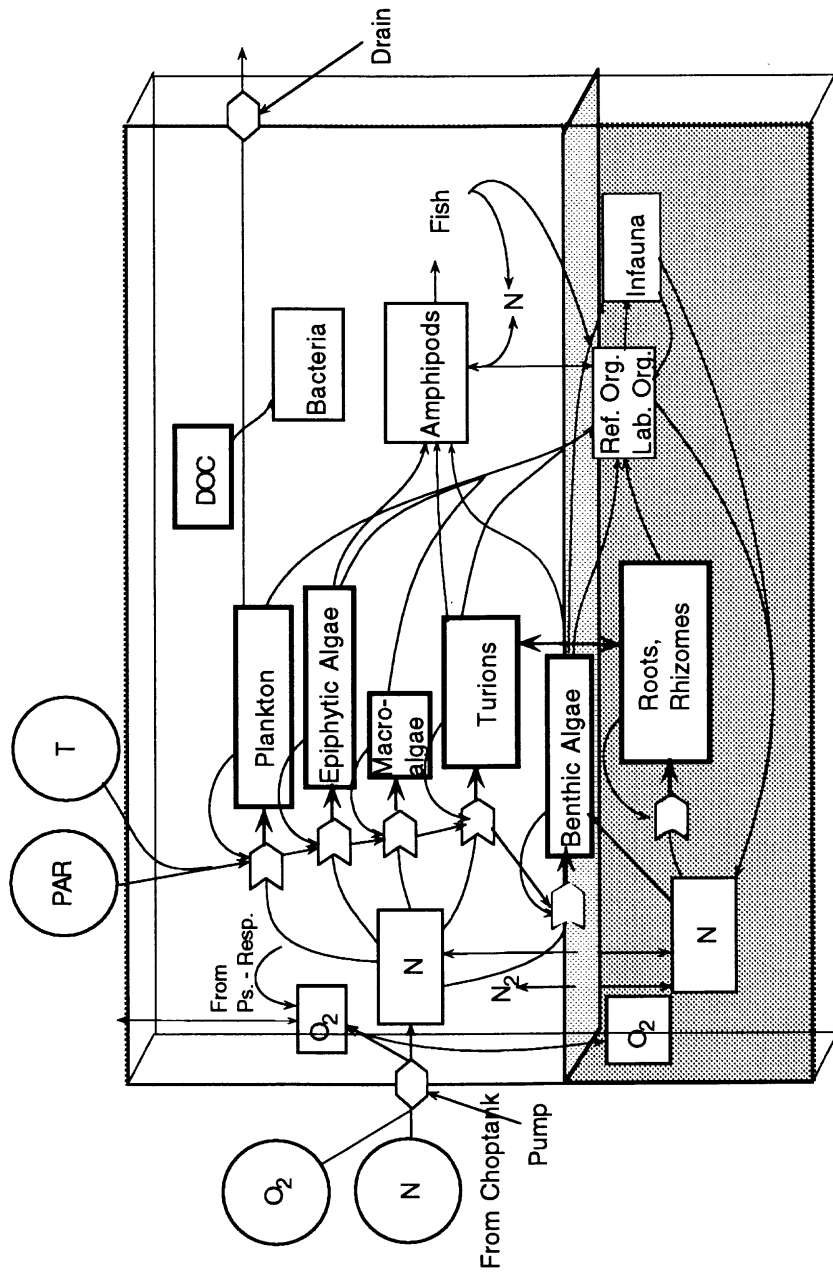
Figure 2.1. Model state variables and selected material and information flows. Some flows are left out for simplicity and are described in the text. Nitrogen concentration (N) is modeled in stoichiometry with C except in macrophytes and sediments where internal non-structural N is modeled separately. PAR is photosynthetically available radiation, T is temperature, DOC is dissolved organic carbon, N_2 is nitrogen gas, and O_2 is oxygen.

Table 2.1
Model differential equations

Potamogeton perfoliatus above-ground C

$$\frac{dSL}{dt} = Ps_{SL} - In_{SL} - Tr_{SL,SR} - Rs_{SL} - Ex_{SL} - Mn_{SL}$$

Potamogeton perfoliatus below-ground C

$$\frac{dSR}{dt} = Tr_{SL,SR} - Rs_{SR} - Ex_{SR} - Mn_{SR}$$

Potamogeton perfoliatus non-structural N

$$\frac{dSN}{dt} = Up_{SL} + Up_{SR} - R_{NC} \cdot \left(\sum Ls_{SL} + Ls_{SR} \right) + K_{NC} \cdot Ps_{SL}$$

Phytoplankton

$$\frac{dPO}{dt} = Ps_{PO} + Fl_{PO} - Gr_{PO} - Sk_{PO} - Mn_{PO} - Rs_{PO} - Ex_{PO}$$

Epiphytic Algae

$$\frac{dEA}{dt} = Ps_{EA} - Rs_{EA} - Ex_{EA} - Mn_{EA} - In_{EA}$$

Macroalgae

$$\frac{dMA}{dt} = Ps_{MA} - Rs_{MA} - Ex_{MA} - Mn_{MA}$$

Benthic Algae

$$\frac{dAB}{dt} = Ps_{AB} - Gr_{AB} - Mn_{AB} - Rs_{AB} - Ex_{AB}$$

Bacterioplankton

$$\frac{dBP}{dt} = Up_{BP} - Rs_{BP} - Mn_{BP} - Fl_{BP}$$

Amphipods

$$\frac{dAM}{dt} = In_{EA} + In_{SL} + In_{BA} - Rs_{AM} - Ex_{AM} - Mn_{AM} - In_{FI}$$

Labile dissolved organic matter

$$\frac{dCD}{dt} = K_{81} \cdot Mn_{PO} + K_{83} \cdot Mn_{BP} + \sum Ex_{SL,EA,MA,OP} - Fl_{CD} - Up_{BP}$$

Dissolved inorganic nitrogen

$$\frac{dNW}{dt} = K_{70} \cdot \sum Rs + Df_{NS} + Fl_{NW} - \sum Up_{NW}$$

Oxygen

$$\frac{dOW}{dt} = K_{89} \cdot \sum Ps + Fl_{OW} + Df_{OW} - K_{r14} \cdot \sum Rs - Df_{OS}$$

Sediment dissolved inorganic nitrogen

$$\frac{dNS}{dt} = K_{r15} \cdot Rs_{BD} - Df_{NS} - Ni_{NS}$$

Sediment oxygen

$$\frac{dOS}{dt} = A_{sod} - \left[K_{r14} \cdot (Rs_{BD} + Up_{CR} + Up_{CL}) \right] - \left(K_{92} \cdot Ni_{NS} \right)$$

Deposit Feeders

$$\frac{dBD}{dt} = In_{BD} - Rs_{BD} - Eg_{BD} - Mn_{BD}$$

Labile sediment carbon

$$\frac{dCL}{dt} = Sd_{CL} + Ex_{SR} + K_{a12} \cdot (Mn_{AB} + Mn_{BD} + Eg_{BD}) - Up_{CL}$$

Refractory sediment carbon

$$\frac{dCR}{dt} = Sd_{CR} + K_{a16} \cdot (Mn_{AB} + Mn_{BD} + Eg_{BD}) - Up_{CR} - Bu_{CR}$$

Model state variables and their differential equations. P. perfoliatus = Potamogeton perfoliatus, Bu = burial, C = carbon, Df= diffusion, Eg = egestion, Ex = excretion, Fl = upstream import-export downstream, Mn= natural mortality, In = ingestion, Ps = photosynthesis, Rs = respiration, Sd = sedimentation, Up = uptake.

(infauna), sediment labile organic C and sediment refractory organic C. I calibrated the model to data from a 1993 *P. perfoliatus* experiment conducted in 10 liter microcosms (Sturgis and Murray 1997). The model used a time step of 15 minutes to capture diel effects of light on nutrients, production and respiration. I used fourth order Runge-Kutta numerical integration.

Potamogeton perfoliatus L., (Redhead Pondweed, Redhead Grass, Perfoliate Pondweed) used to be widely distributed in the Chesapeake Bay region and experienced declines in response to eutrophication (Southwick and Pine 1975, Brush and Hilgartner 2000). It has an apical meristem, as do other canopy-forming species, which allows more exposure to light than basal meristem species. In the model, *Potamogeton* growth was dependent on photosynthetically available radiation (PAR) at the top of the canopy. Integrated light (e.g., Talling 1957) is more appropriate for calculating the light available for meadow-formers, such as eelgrass (*Zostera marina*). The microcosms used to calibrate the model were small (120 liters) and would allow canopy formation (leaves spreading at the water surface) even by meadow-forming species. The model uses parameter values from studies of a variety of species and may be more appropriate for canopy-forming species. Differences in nutrient absorption, growth rate, etc., vary more between measurements than between species. Since temperatures were fairly constant in the microcosms, it was unnecessary to use more species-specific coefficients.

Sensitivity analyses were conducted to examine the model's limitations, identify sensitive coefficients and to determine the suitability of the model for our use. Model coefficients or initial values (which could possibly have large effects on

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output) were increased or decreased 25%, and the resulting change in maximum

macrophyte biomass during a growing season (eight months) was determined for a

low nutrient input run and a medium nutrient input run with and without grazers.

Sensitivity of the model to initial conditions was also determined by starting the

model with high epiphtye biomass and then high macrophyte biomass with and

without grazers. For this analysis, the water exchange rate was 1 d^{-1}, and inflow

dissolved inorganic nitrogen (DIN) concentration was 40 μmol l^{-1}.

Microcosm experiments were conducted in 1995 and 1996 at an indoor

facility at Horn Point Laboratory to examine the effects of water exchange and

trophic complexity on SAV response to nutrient enrichment. The microcosms were

120 liter aquaria with 10 cm of sediment from a protected area in the Choptank River

under fluorescent light (~120 μM photons m^{-2} s^{-1} PAR). Inflow water was pumped

from the Choptank into a pond (containing *Potamogeton pectinatus*) for dissolved

nutrient reduction before being filtered (through sand and 2μm filters) and supplied to

the tanks at a water exchange rate of 1 d^{-1} (see Severn 1998 for detailed description).

These aquaria were larger than those used in experiments for model calibration. The

1995 experiment had low and high grazer biomass treatments, an exchange rate of 1

d^{-1} and an inflow DIN concentration of approximately 30 μmol l^{-1}. I compared the

data from this experiment to the model, and the model underestimated the

Potamogeton biomass. This may have been due to the tanks having a larger surface

area than the calibration tanks, which allowed less light to reach the interior leaves. I

slightly increased the *Potamogeton* self-shading coefficient so that modeled biomass

was close to the data from the low grazer treatment and compared the other modeled state variables with the data.

I then ran simulations using low and high water exchange rates (1 and 12 day^{-1}), an inflow DIN concentration of 10 µM and a constant epiphytic algal grazing rate to show how exchange rate could affect DIN concentrations and autotroph biomass. Simulations were also run at a range of water exchange rates and inflow DIN concentrations with constant grazing to demonstrate how the interaction of DIN inflow concentration and water exchange rate could affect epiphytic algal biomass accumulation.

In another set of model runs, I examined how the combined effects of grazers, inflow DIN concentrations and water exchange rates affected macrophyte biomass. In these simulations, I varied inflow DIN concentrations from 2 to 40 µM and the water exchange rate from 1 to 16 times per day. These analyses helped us understand subsequent microcosm experiments where inflow rates also varied between treatments (not described here). Simulations were also run to determine appropriate levels of predators to use and how the interaction of nutrient loading, grazers and fish would affect standing stocks prior to a 1996 trophic complexity microcosm experiment. In these simulations, three different inflow N concentrations were used (2, 17 and 40 µM) at an exchange rate of one per day. The model state variables and equations are described below.

Potamogeton perfoliatus

Potamogeton perfoliatus was modeled as three compartments: above-ground (SL), below-ground (SR) and non-structural N (SN). Carbon fixation was a function

of biomass, light and nutrients. Maximum photosynthetic rate for *P. perfoliatus* was 30 mg C $g^{-1}h^{-1}$ in experiments by Goldsborough and Kemp (1988). The effect of light on maximum photosynthesis was calculated by using average saturating irradiance (I_k) and half saturation (K_m) values (from Harley and Findlay 1994, Goldsborough and Kemp 1988) of 350 and 150 $\mu E\ m^{-2}\ d^{-1}$. The effect of dissolved nitrogen (mainly NH^+_4 in our systems) on photosynthesis was modeled as a hyperbolic function of both sediment and water column nitrogen with a half-saturation coefficient (K_s) of 20 mg l^{-1} for sediment N and 14 mg l^{-1} for water column N (Thursby and Harlin 1984). Light available to leaves is affected by water column attenuation, epiphyton coverage, macroalgae shading and self-shading. Epiphytic algal shading was biomass specific (a coefficient of 0.11 mg C^{-1} mg leaf C^{-1} was used, which assumes 0.15 μg Chl a cm^{-2}, 5 μg Chl a mg epiphyton C^{-1}, and 3.7 cm^{-2} mg leaf C^{-1}). Light attenuation due to epiphytic biomass is variable, and a portion of the photosynthetic area of the macrophytes may not be covered, so I used a value slightly less than 3 mg C $1cm^{-2}$ (e.g., Staver 1984). This converts to 3.7 mg C^{-1}mg leaf C^{-1} (@ 0.75 mg C cm^{-2}).

Because shoots grew to be longer than the water was deep, they spread out on the surface, making a canopy that was largely uncolonized by algae due to exposure to air. This also occurs in estuaries among a variety of species with apical meristems (a feature that may increase survival in turbid waters). I accounted for this by reducing the shading coefficient for epiphytic algae at the leaf biomass level where the canopy forms (30 g C m^{-2}). *Potamogeton* may maintain positive carbon balance even with high epiphyton biomass due to this factor. Self-shading was assumed to be an exponential function of leaf biomass.

Leaf and root losses include respiration and senescence. The influence of temperature on respiration was assumed to be exponential with a Q_{10} of 2 (Bulthuis 1987). This function was used for all biotic components based on enzyme kinetics. Enzymes also degrade as temperatures rise, but I assumed that the biota were adapted to seasonal temperatures. When grazers were added, allometric relations were used to estimate grazing rates (Cattaneo and Mousseau 1995).

Inflows to non-structural nitrogen depended on N concentrations in the sediments and water column (Monod formulations) and *Potamogeton* biomass with the internal N pool providing negative feedback. The N pool was allocated to above and below-ground biomass based on the photosynthetic rate and an average C:N ratio. Other losses were in stoichiometric proportion to C losses.

Algal components - phytoplankton, epiphytic mass, macroalgae, benthic algae

Algal carbon fixation was modeled as a function of temperature, light and nutrients. The effect of temperature was assumed to be exponential with a Q_{10} of 2. This formulation was used by Kremer and Nixon (1978) and supported by several published values (Bannister 1974, Fasham et al. 1983). Enzyme inhibition is known to occur at high temperatures in single species, but I assumed that it does not occur among the whole assemblage of phytoplankton at the normal summer temperatures. Although the photosynthesis-temperature relationship is based on short-term response, since phytoplankton size varies inversely with temperature in Chesapeake Bay (Malone et al. 1991), there is an allometric basis for this formulation. Maximum growth rates and temperature coefficients for phytoplankton (PO) were calibrated within the range of reported values (Talling 1957, Eppley 1972, Ojala 1993, etc.).

The effect of light on maximum photosynthesis was calculated by using the formulation of Talling (1957) modified for the effect of self-shading. The half saturation coefficients were averages of measured values in spring and summer. Talling's expression does not incorporate photo-inhibition, which was not a factor in the microcosms. An attenuation coefficient for self-shading of 0.002 per mg phytoplankton C was used (Steeman-Nielsen 1962). PAR is absorbed in the water column by phytoplankton and sediments, and self-shading occurs at the sediment surface for benthic algae (BA). The light half-saturation coefficient for benthic algae was assumed to be lower than for phytoplankton (Cahoon et al. 1993). The effect of dissolved N on photosynthesis was modeled as a hyperbolic function with a half-saturation coefficient of 15 mg m^{-3} (Scavia 1980, Goldman and Glibert 1983). I assumed a ratio of 70 mg C mg Chl^{-1} (Malone 1982). Ammonium uptake by BA was assumed to be from the sediments (e.g., Krom 1991).

Losses of PO were assigned to respiration, sinking, exudation, natural mortality, grazing and export. Respiration was modeled as a function of temperature (Scavia et al. 1976), biomass and production. Reported specific respiration rates range from 0.02 to 1.2 d^{-1} (Geider 1992), or about 10% of P_{max} (Parsons et al. 1984). Respiration rates of flagellated species may be high relative to the diatoms due to their active nature (Geider and Osbourne 1989). Grazers of phytoplankton in the Chesapeake Bay include copepods, protozoa and menhaden. The grazing loss rate was assumed to be 20 % of carbon fixation for simplicity (e.g., Ryther and Sanders 1980). Sinking is a percentage (15% d^{-1}) of biomass. Sinking rates of phytoplankton assemblages are determined by their composition (Pitcher et al. 1989), with diatoms

sinking faster than dinoflagellates and microflagellates. Although sinking rates of individual diatoms are usually less than 1 m d^{-1}, gelatinous aggregations formed may sink 100 m d-1 or more (Smetacek 1985). Phytoplankton-dissolved organic carbon (DOC) release was significantly correlated (slope of 0.15) with production (Malone and Ducklow 1990). Other measurements showed rates ranging from zero to 15% of biomass (Eppley and Sloan 1965). Death, or density-dependent mortality, was an exponential function of biomass. Viral infection rates, for example, may increase with density (Sieburth et al. 1988). Outputs of BA, MA and EA were to grazing, respiration and sediment organic carbon, where consumption by microorganisms, meiofauna and macroinfauna occurs. I used a formula that presumed grazers preferred epiphytic algae over benthic and macroalgae.

Bacterioplankton

Growth of bacterioplankton (BP) depends on dissolved organic carbon (DOC), dissolved nitrogen (NW), dissolved O_2 (OW) and temperature. Although assimilation rates of 1.2 g C g C^{-1}h^{-1} have been measured (Wetzel and Christian 1984), specific production in the bay ranges from 0.5 to 2 per day (Ducklow and Hill 1985). Production ranged from 52 to 680 mg C m^{-2} d^{-1} from September to November 1984. The Monod formulation was used and expresses growth as a function of dissolved and particulate organic matter. Half-saturation values of eutrophic bacteria ranged from 112 mg C m^{-3} to over 100 g C m^{-3} for glucose (Semenov 1991), which may be about the same as phytoplankton-derived, dissolved organic carbon (DOC). No good estimates were available for naturally occurring organic matter. Vmax for glucose uptake ranged from 78 µg to 50 g l^{-1} (Semenov 1991). The effect of DOC on

growth depends on the percentage of DOC derived from phytoplankton. The equation for uptake adjusts the rate depending on the percentage derived from phytoplankton exudation. Nitrogen does regulate DOC uptake, however. The K_s for NW was assumed 2 mg m^{-3}.

Wheeler and Kirchman (1986) documented the uptake of dissolved nitrogen by bacterioplankton. I modeled the effect of temperature on uptake as exponential, with a Q_{10} of 2.7 (Shiah 1993). The percentage of bacterioplankton that is active is also affected by temperature (Sommaruga and Conde 1997). The effects of dissolved nitrogen (DIN) and O_2 on growth were assumed to be hyperbolic. Though the half-saturation coefficient for O_2 is possibly below 0.2 (Shiah and Ducklow 1994), I used 1 in the model to be conservative.

Outflows included respiration, lysis and excretion and grazing and sedimentation of bacteria attached to detritus. Respiration was modeled as a linear function of uptake (Azam et al. 1983) and, to a lesser degree, a function of biomass and temperature. Respiration was not modeled solely as a function of biomass due to the ability of some species to survive long periods of starvation (Novitsky and Morita 1978).

The effect of temperature on respiration may vary significantly and may depend on substrate concentration (Pomeroy et al. 1991). I chose to use a small value that allowed biomass to increase with temperature and allowed an adequate food supply for protozoans. Lysis was modeled as an exponential function of biomass to account for density-dependent mortality (Proctor and Fuhrman 1990, Heldal and Bratbak 1991). Bacterial excretion rates were negligible in one study (Azam et al.

1983), so a small percentage (5% d^{-1}) of biomass was assumed to be lost to DOC. I assumed that sedimentation was a linear function of biomass.

Consumers

The dominant epiphytic algae grazers in these experiments were gammarid amphipods (AM), mainly *Leptocheirus* sp. These are also dominant in the shallow mesohaline portion of the Bay (Marsh and Tenore 1990). Concentrations used were in the mid-range (5 g C m^{-2}) of those reported from shallow-water systems (e.g., Virnstein et al. 1983, Fredette et al. 1990). Individuals were at least 7 mm long at the beginning of the experiment. They were modeled as biomass for simplicity by regressing length with dry weight and assuming a C:dry weight ratio of 0.4 (Kennish 1987). Ingestion was modeled as a function of algal and macrophyte biomass (with a preference for epiphytic algae) and an allometric function of average amphipod size.

Outflows were to respiration, excretion and mortality. Respiration and excretion were linear functions of ingestion. Mortality was both natural and due to predation by fish, if present. The trophic complexity experiment used two fish (*Fundulus heteroclitus*) of approximately 10 g total wet weight for 4-8 hours/week in the fish treatments. Predation rates for the model were determined by weighing a collection of amphipods, adding them to a bowl containing a fish and weighing the remaining amphipods after 1 day. Outflows from fish in the model were to respiration and excretion, which were linear functions of ingestion.

Dissolved organic matter

The major constituents of dissolved organic carbon (DOC) in estuaries are humic acids of terrestrial origin that are relatively refractory to microbial

decomposition (Mantoura 1981). A smaller proportion of total DOC is from direct release from phytoplankton and indirect release from grazing and excretion of zooplankton (Lancelot 1979, Roman et al. 1988). Only the labile fraction was modeled here. Surface water values of labile DOC averaged 270 mg C m^{-3} in spring and 420 mg C m^{-3} in summer (Jonas and Tuttle 1990), although total DOC ranges from 1.5 to 6.5 mg l^{-1}.

Inflow to DOC includes phytoplankton exudation and leaf excretion, and a percentage of lysed phytoplankton and bacteria. DOC exudation from phytoplankton was assumed to be 100% dissolved, while dead phytoplankton was assumed to be 25% dissolved. Production rates of DOC in 1988 averaged 72 and 120 mg m^{-3} d^{-1} in spring and summer respectively (Malone et al. 1991). Loss was to bacterial uptake.

Dissolved nitrogen

Water column dissolved nitrogen (NW) included NH^{+}_{4}, NO^{-}_{3}, and NO^{-}_{2}. Inflows to dissolved nitrogen were from the header tank and regeneration. Regeneration was a percentage of all except phytoplankton respiration terms. NW was assumed to be regenerated at a ratio of 106C:16N. This ratio may be high; for example, the C:N ratio of copepods is higher than that of phytoplankton, so they must be conserving N relative to C. The C:N ratio of organic state variables and flows, except phytoplankton respiration, were assumed to be 6.625:1. Respiration of bacteria was coupled to N regeneration to keep a balance, although, at high C:N ratios (>15:1), ammonium was not regenerated from natural assemblages of freshwater bacteria (Tezuka 1990). N excreted by fish was assumed to be 30% of ingestion (e.g., Nemazie et al. 1993).

The loss terms included outflows and uptake by autotrophs and bacterioplankton. Phytoplankton take up NW in proportion to the amount of carbon fixed. Redfield's ratio (106C:16N) was used for the proportionality constant. To maintain Redfield's ratio, the uptake ratio N:C was adjusted to the ratio of respiration and exudation to gross production. Bacterioplankton take up NW in proportion to the percentage of phytoplankton exudation in the DOC pool. Since phytoplankton include some partially heterotrophic forms, DOC exudation was assumed to have some amino acids as well as nitrogen-free molecules, such as glycolic acid.

Dissolved oxygen

Inflow to dissolved oxygen (DO) was from diffusion and phytoplankton production. Atmospheric diffusion was a function of the concentration difference, salinity and temperature (see Kemp and Boynton 1980). A photosynthetic quotient of 1.3 (Valiela 1984) was used as the ratio for oxygen produced per carbon fixed.

Outflow was to water column respiration and sediment oxygen demand. Flows were in stoichiometric relation to carbon flows (using a respiratory quotient of 0.9). Oxygen units were mg l^{-1}.

Sediment-dissolved inorganic nitrogen

Inflow to sediment-dissolved nitrogen (NS) was from ammonification of organic nitrogen, including aerobic and anaerobic decomposition and infauna excretion. A C:N ratio of 6.6:1 was assumed for all deposited organic matter. Five percent of the nitrogen from buried refractory material was assumed to enter the dissolved pool (to stabilize the deep sediment C:N ratio).

Outputs of the sediment NS pool were nitrification-denitrification and diffusion. Nitrification was modeled as a hyperbolic function of NS and sediment oxygen concentration and an exponential function of temperature. The reported half-saturation coefficients range from 0.1 to 700 μM NH^+_4 (to 500 mg m^{-2}) and <1 to 16 μM O_2 (Henriksen and Kemp 1988). The effect of temperature on nitrification fits the Arrhenius equation with a Q_{10} between 2 and 3.3 (see Henriksen and Kemp 1988 for review). Nitrification rates in various estuaries, including Chesapeake Bay, range to greater than 30 mg m^{-2} d^{-1} (Henriksen and Kemp 1988). Denitrification was coupled with nitrification. Diffusion was a percentage of ammonium concentration.

Sediment oxygen

The amount of oxygen in the sediment is affected by sediment oxygen demand, infaunal activity and the oxygen concentration in the overlying water. Inputs included diffusion/flux from the overlying water. The maximum diffusion rate was adjusted to equal the maximum summer oxygen uptake (~45 mmol m^{-2} d^{-1}, or 1.44 g). Sediment reworking and burrow irrigation increased the exchange of water with the water column (Aller 1982). This effect was modeled by using a term that hyperbolically increases sediment oxidation with the respiration of infauna. Apparent diffusion coefficients can be 10-100x molecular diffusion coefficients (Aller 1982) because of bioturbation.

Outputs were to respiration of deposit feeders, other aerobic respiration and nitrification. The stoichiometric molar ratio of O_2 consumed per NH^+_4 oxidized to NO^-_3 in nitrification is 2:1 (Christensen and Rowe 1984) or 4.57 grams per gram. Wezernak and Gannon (1968) suggested 3.22 g O_2 g $ammonia^{-1}$ oxidized to nitrite

and 1.11 g O_2 g nitrite^{-1} oxidized to nitrate, due to CO_2 fixation by nitrifiers. Denitrification does not release O_2. Sediment oxygen consumption averaged between 0.54 and 1.57 g O_2 m^{-2} d^{-1} at mid-bay stations in 1989 (0.36-1.32 in 1990). Though sulfur was not modeled here, sulfide oxidation can account for much of this demand based on a 2:1 stoichiometry of oxygen consumed to sulfide diffusion (Roden 1990). Deposit feeders' O_2 consumption is in balance with respiration.

Infaunal deposit feeders

Major infaunal (DF) taxa include the polychaetes *Heteromastus filiformis*, *Scolecolepides viridis* and *Nereis succinea* (Kemp and Boynton 1981). Ingestion was an exponential function of temperature and a hyperbolic function of dissolved oxygen and sediment POC concentration. Maximum ingestion rates of labile and refractory carbon were 4 and 2% day^{-1} respectively before the temperature correction. Temperature controls survival and growth in the polychaetes *Polydora ligni* (Rice and Simon 1980), *Capitella capitata* and *Neanthes arenaceodentata* (Oshida and Reish 1974). The temperature coefficient for ingestion gives a Q_{10} of 2. The half-saturation coefficient for oxygen was assumed to be 2 mg l^{-1}. Food supply influenced brood size of *S. benedicti* (Levin and Creed 1986), fecundity and size of *Polydora ligni* (Zajac 1985) and population growth in *Capitella* spp. (Tenore and Chesney 1985). The half-saturation coefficients for refractory and labile carbon were calibrated.

Outflows were to respiration, defecation and mortality. Respiration and excretion were linear functions of ingestion. *Abarenicola pacifica* respiration was about 2% d^{-1} and was not related to feeding (Taghon 1988). I assumed that 5% of

ingested C was excreted (Grémare et al. 1989), and 10% was respired (Taghon 1988). Resting respiration was assumed to be 0.2 % d^{-1} (Taghon 1988).

Sediment organic carbon

Sediment organic carbon was separated into labile (CL) and refractory (CR) fractions based on ease of decomposition (Billen et al. 1989). For calibration, pool sizes were estimated from measurements of chlorophyll in the surface sediments and measurements of decomposition rates (Burdige 1991) using the "G model" approach (Berner 1972).

Inputs included sedimentation and infauna excretion. Carbon was deposited to the sediments from phytoplankton, amphipod excretion and microalgal and macrophyte senescence and was divided 50:20 into the two sub-compartments, the remainder being considered recalcitrant. Sedimentation of particulate organic matter (POM) was not considered since the inflow water was filtered. All deposited material was assumed to have the same ratio of labile to refractory carbon.

Sediment POM is consumed by meiofauna, both aerobic and anaerobic bacteria and by deposit-feeding infauna. Aerobic respiration of meiofauna and bacteria was simulated as an exponential function of temperature ($Q_{10} = 2$), a linear function of OS and a hyperbolic function of carbon. The hyperbolic function was used because something besides oxygen (e.g., pH) may limit aerobic respiration at high carbon concentrations. The rate coefficients for biological utilization of labile and refractory fractions were based on geochemical experiments (e.g., Westrich and Berner 1984), which found decomposition rates ranging from 0.01-0.05 day^{-1} for CL and from 0.0002-0.001 day^{-1} for CR.

Aerobic respiration consumes up to six mmoles C m^{-2} d^{-1} during periods when the bottom water is oxygenated (72 mg m^{-2} d^{-1}). Metabolizable POC pools at mid-bay sites were 24.84 and 36.84 g C m^{-2} respectively (Roden 1990). Seasonal sediment organic carbon concentrations in the top one cm of sediments in 8-11 m of water range from 2.5 to 3.5% dry weight (Boynton et al. 1988). Chlorophyll content in the top cm ranged from near 0 to 0.025 % dry weight (0 to 1.25%). This corresponds to 12.5 g metabolizable carbon m^{-2}. Denitrification consumes labile carbon (at a ratio of 0.96 C:N) and is equal to nitrification. Anaerobic decomposition was a function of temperature and carbon and was a negative power function of oxygen, while aerobic respiration was an exponential function of temperature, a hyperbolic function of carbon and was positively correlated with oxygen.

Photosynthetically available radiation

PAR (I) measured at the top and sides of the microcosms averaged 120μE m^{-2} d^{-1}. PAR was reduced by attenuation in the water column by water molecules, phytoplankton and by benthic algae at the sediment surface.

Results

Sensitivity analysis and initial conditions

The effects of increasing selected parameters by 25% on maximum *Potamogeton* biomass in a low nutrient, medium nutrient and medium nutrient / grazer run are shown in Table 2.2. At the low N inflow rate, *Potamogeton* biomass was only sensitive to factors affecting its growth, such as maximum growth rate. At medium nutrients with grazers, macrophyte biomass was also sensitive to factors

Table 2.2
Sensitivity analysis of selected parameters affecting maximum SAV biomass during a growing season.

Parameter	Change in maximum macrophyte biomass (%)		
	Low None	Med. Grazer	Med. None
SAV growth rate	+6	+54	+122
Initial SAV leaf C	+2	+3	+16
SAV PAR half saturation coefficient	-21	-32	-52
Epiphyte growth rate	0	-34	-13
Epiphyte light extinction	0	-2	-32
Initial Epiphyte C	0	0	-3
Inflow Nitrogen	0	-22	-32
Grazer mortality	-	-24	-

Inflow rate for all scenarios was 1 exchange per day. Dissolved nitrogen inflow concentrations were 2 and 15μM. None refers to grazers.

influencing algal accumulation. With medium N inflow without grazers, increased *Potamogeton* growth rate allows the macrophytes to outgrow epiphytic algae. The epiphytic algal light extinction coefficient also becomes a factor since epiphytic algal biomass is high.

The modeled macrophyte response to nutrient additions was highly dependent on initial conditions. For example, in Figure 2.2, the left panels show the results of model runs with high initial epiphytic algal biomass and low *Potamogeton* biomass, with and without grazers present. When initial epiphytic algal biomass was relatively high and grazers were present, *Potamogeton* biomass was held in check until epiphytic algae biomass was reduced to an equivalent level by grazing (Panel a). Epiphytic and macroalgae reduced nutrients and shaded the macrophytes when no grazers were present (Panel b). The panels on the right show the result of higher initial macrophyte biomass with and without grazers present. High macrophyte biomass reduced the available nutrients and light, resulting in slower algal growth when grazers were present (Panel c). When grazers were absent, epiphytic algae grew, but biomass remained low, relative to *Potamogeton* (Panel d). Nutrient concentrations remained low due to the combined uptake of plants and algae, and light availability for the algae is low due to leaf shading.

1995 Baseline simulation

After adjusting the *Potamogeton* self-shading coefficient so that modeled biomass matched the data, cumulative measures of ecosystem behavior (dissolved N and community production and respiration) were comparable to microcosm experimental data. But measured biomass of epiphytic algae and grazers diverged
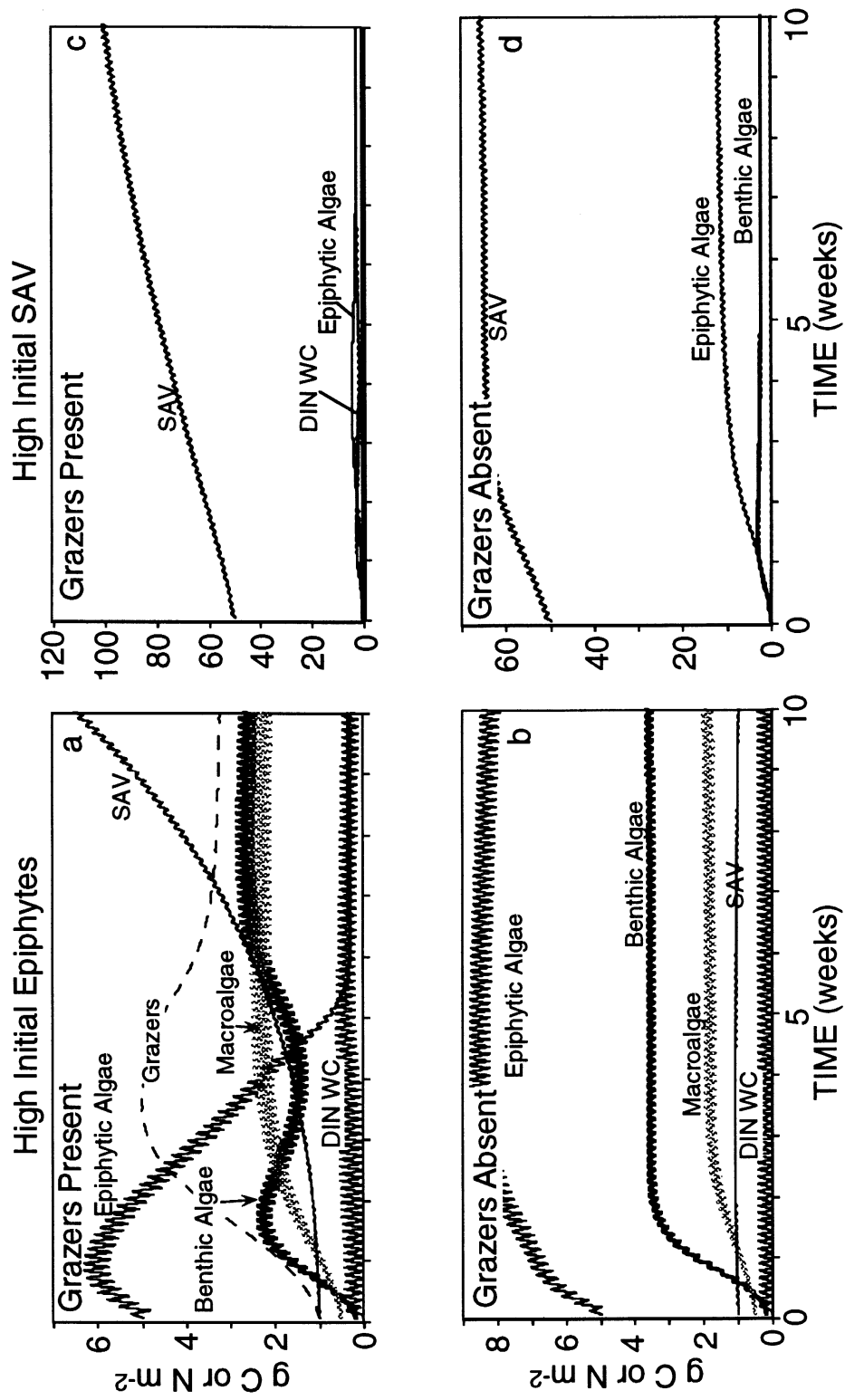
Figure 2.2. Effects of initial SAV and algal biomass on selected state variables over the course of simulated experiments with and without grazers present. Note scale differences between panels.

from model results in the high-grazer run (Figure 2.3). The model predicted that grazers would control epiphytic algal biomass in the high-grazer treatment, and that epiphytic algal biomass would be higher in the low-grazer treatment. Measured epiphytic algal biomass, though, was not significantly different between treatments. The pattern of the simulated grazer biomass followed the data but was also slightly lower for the low grazer run than in the experiment, and the peak biomass was almost double the modeled number for the high-grazer run.

Nutrient loading rate per unit macrophyte biomass

The effect of water exchange rate on *Potamogeton* and epiphytic algal growth is shown in Figure 2.4. At the low exchange rate ($1 \, d^{-1}$), DIN concentrations are reduced, epiphytic algae biomass is low and macrophyte biomass increases linearly. When the exchange rate is increased to $12 \, d^{-1}$, the DIN concentration stays above limiting levels, and epiphytic algae grow and affect macrophyte biomass, though not very much. The effect of the interaction of water exchange rate and inflow nutrient concentration on epiphytic algal biomass is shown in Figure 2.5. Epiphytic algal biomass increases with exchange rate most quickly at the highest concentrations, but high biomass accumulations are possible even at inflow concentrations of $5 \, umol \, l^{-1}$ when the exchange rate is high.

Figure 2.6 shows how the presence of grazers affects *Potamogeton* response to different water exchange rates and inflow nutrient concentrations. Leaf biomass increases with exchange at first as *Potamogeton* is nutrient-limited. At low inflow concentrations, leaf biomass continues to increase with exchange as macrophytes are nutrient-limited and epiphytic algal growth is low. With grazers present, higher leaf
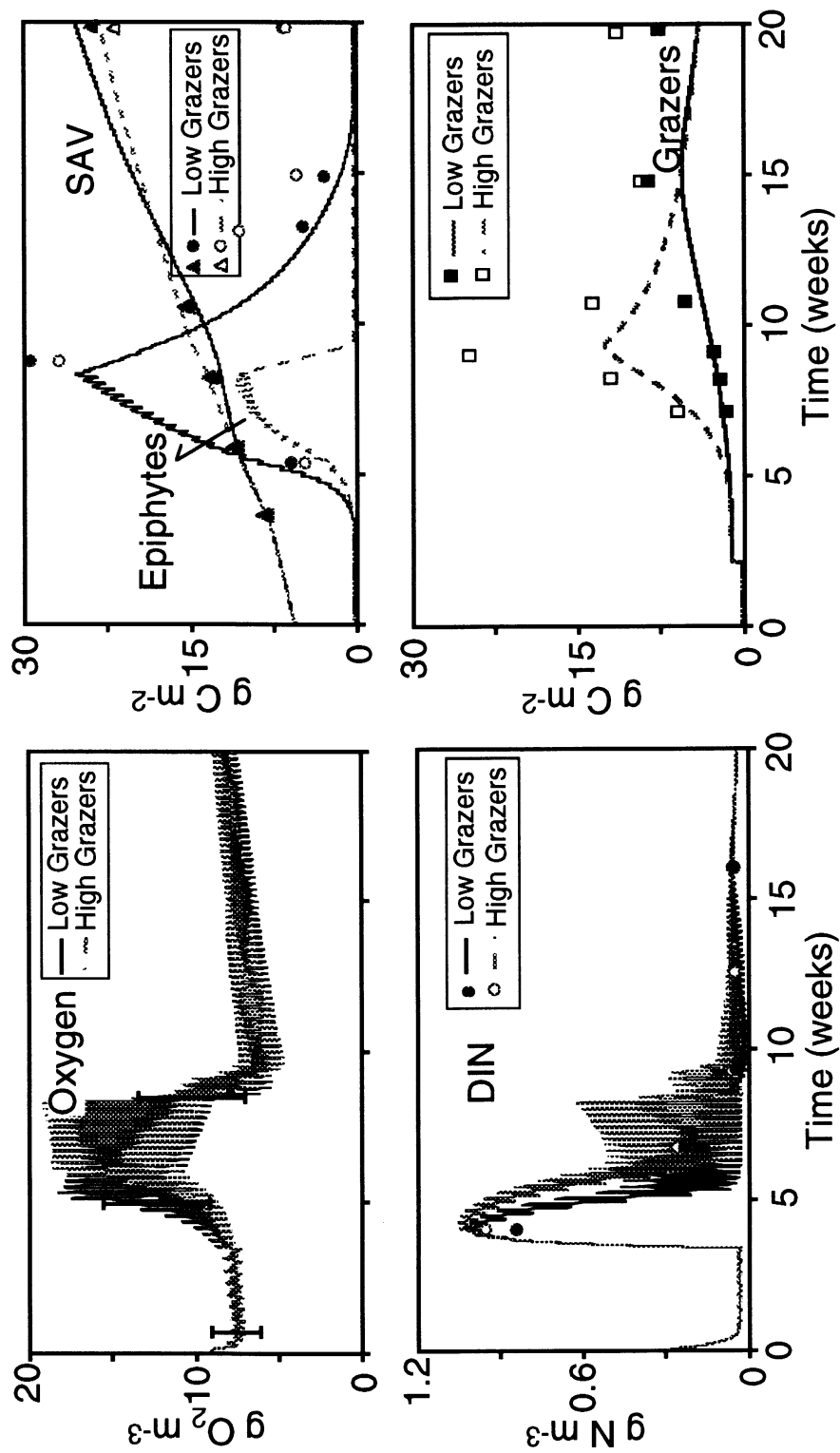
Figure 2.3. Model results (lines) with data (symbols) from 1995 mesocosm experiment. Filled and open points are from low and high grazer experiments, respectively. SAV above ground biomass only is plotted.
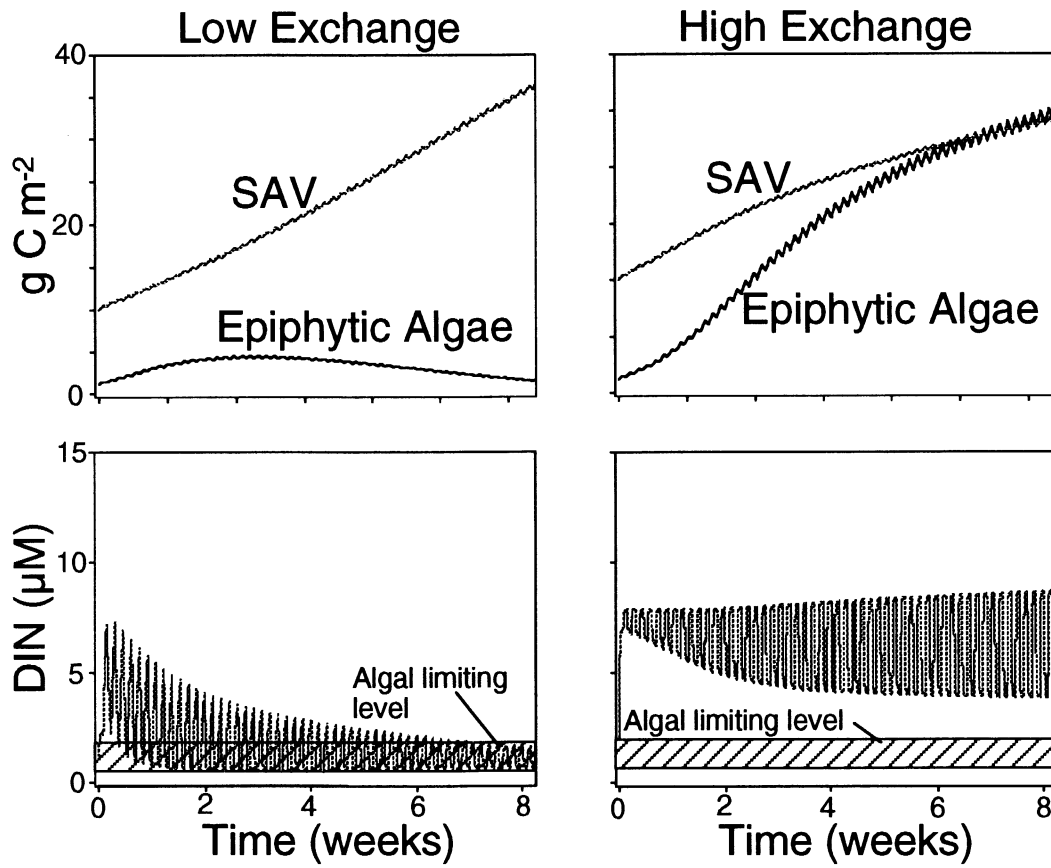
Figure 2.4. Simulation model output with low exchange (left panels) and high exchange (right panels) of water with the same input DIN concentration (10μmol l^{-1}). Hatched area denotes approximate limiting level of DIN for algae. SAV above ground biomass is plotted.
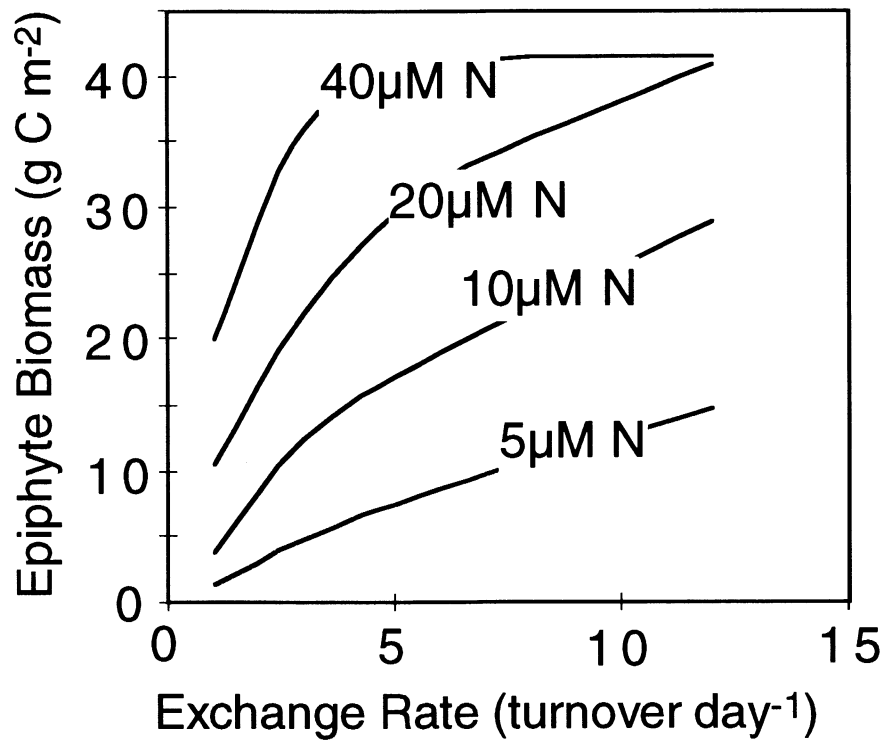
Figure 2.5. Effect of exchange and nutrients (loading/unit biomass) on epiphytic algal biomass. Plotted biomass is maximum attained during a 20 week run.
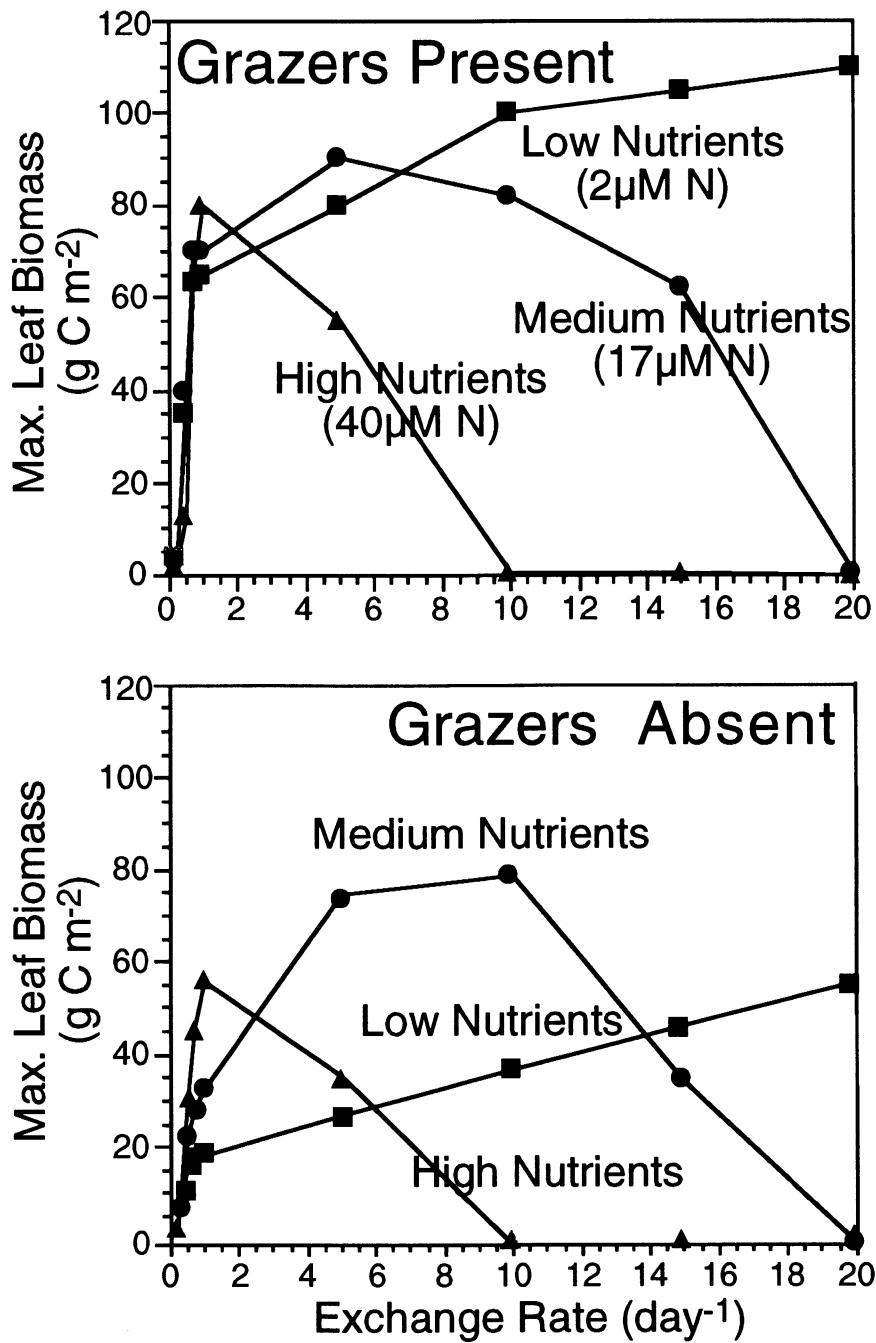
Figure 2.6. Effect of interaction of exchange rate, nutrients and grazers on above ground (leaf) biomass. Leaf biomass is plotted vs exchange rate with grazers present in the upper panel and absent in the bottom panel.

biomass is obtained before reductions begin due to algal overgrowth at higher inflow concentrations.

Trophic complexity simulations

Simulation results of the effects of interactions of nutrient loading, grazers and fish on the macrophyte community are shown in Figure 2.7. The effect of nutrient loading on epiphytic algal and macrophyte aboveground biomass with no grazers is shown in the left column of panels. As nutrient loading increases, epiphytic algae increase, and *Potamogeton* biomass decreases. The positive effect of grazers on *Potamogeton* biomass increased with nutrient loading rate (middle column). At the low nutrient inflow level, algae biomass remains low, and organic N is slightly decreased due to grazing. At the moderate level, epiphytic algae are decreased, and organic N is increased due to the stimulating effect of grazers on primary production, until the grazer biomass starts to decline. The organic N then declines due to the inability of the algal community to sequester the inflowing DIN. Macrophyte leaf biomass increases due to the reduction in epiphytic algae. When nutrient inflow is high, epiphytic algae biomass is not reduced as much, and organic N increases due to continual transformation of inflowing N into biomass and then into detritus. Macrophyte biomass is reduced compared to the moderate inflow but is higher than when there were no grazers.

Adding fish (right column) increased algal growth and nitrogen cycling at moderate nutrient addition rate (shown by the larger variation in DIN in Panel f than in Panels d and e) and decreased nitrogen cycling at high nutrient addition rate compared to the grazer scenario. At moderate N inflows, the epiphytic biomass was

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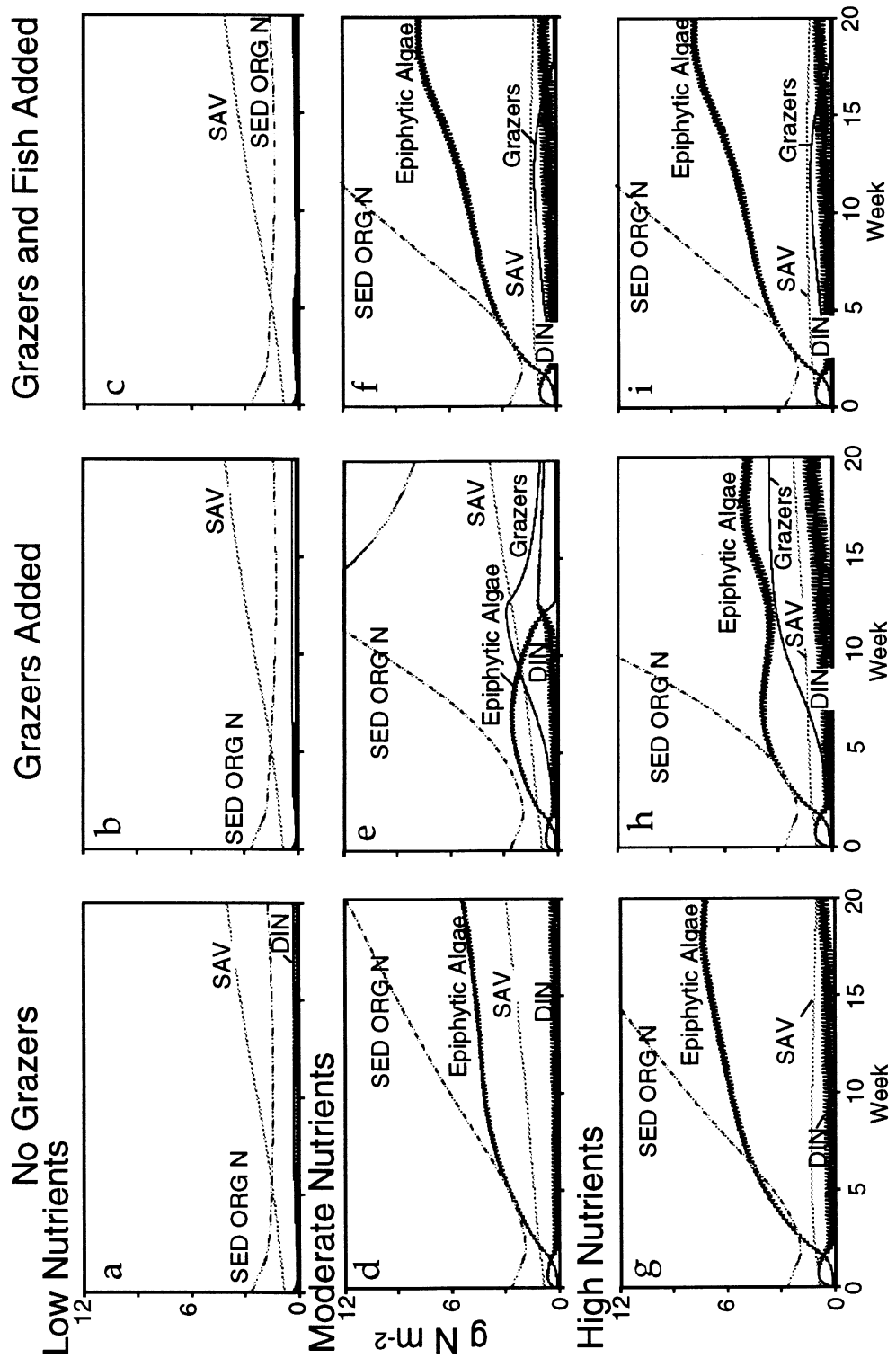
Figure 2.7. Model results of nutrient addition to SAV mesocosms containing no grazers (left panels), grazers (middle panels), and grazers with fish (right panels). All output is shown in units of g N m⁻². DIN is dissolved inorganic nitrogen, and SED ORG N is sediment organic nitrogen. SAV represents above ground biomass only.

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highest with grazers and fish due to the increased N availability due to regeneration. This resulted in lower macrophyte biomass than without grazers. At the highest N loading rate, epiphytic algal biomass was highest without grazers or fish and lowest with only grazers. There was no stimulatory effect of fish and grazers on epiphytic algal biomass at this loading rate because nutrients were not limiting. The effect of fish on macrophyte biomass was negative due to shading by increased algal biomass.

Discussion

Model suitability, sensitivity analysis and initial conditions

As with most models, this mathematical representation is not designed to perfectly predict the behavior of an ecosystem in a microcosm or an estuary but to give a qualitative or heuristic account of system behavior that may be better than what I could estimate from our own intuition or "back of the envelope" calculations. The equations are only representations of our thoughts on how the system works, and the coefficients are fixed, whereas, in nature, they are variable. The coefficients used came from measurements using a variety of species, not just *P. perfoliatus*, and the measurements of the coefficients may only be representative under certain conditions.

Though some of the coefficients may have come from tropical or marine species, the errors induced were not likely to qualitatively affect the model behavior of most interest to us, which might be, for example, rooted macrophyte response to light. Of more concern to us was deciding on equation formulations or coefficients from within the range of reported values that were appropriate for this system. For example, the shoots formed a canopy making epiphytic algal shading less important, so I reduced the epiphytic algal shading coefficient. Also, if I had more information

on cyanobacterial nitrogen fixation to calibrate the model, it may have increased

model accuracy, but I felt increasing model complexity would further reduce

accuracy (see Costanza and Sklar 1985). Despite the lack of precision in the

predictive ability of a model such as this, if it keeps track of our assumptions about

how the system works, then it serves a purpose. While it may be more expedient to

use a published model, there is a strong likelihood that the model will not adequately

describe the relevant processes, or that the model user will not understand all of the

assumptions inherent in the model.

Some variables, including dissolved organic nitrogen (DON) and ammonium

regeneration, were not measured in the experiments. Because the inflow water was

filtered from ponds used to draw down the dissolved nutrients, DON may have been a

significant nitrogen source. Regeneration may be a large part of the nutrient

requirement, although root uptake and benthic algae may reduce N available for

epiphytic algae and phytoplankton growth. Ammonium uptake by algae was tied to

photosynthesis in the model, causing large diel fluctuations in DIN. Ammonium is

probably taken up more continuously by algae as a function of internal concentrations

and stored for later use (Droop 1983). This may be an important factor controlling the

concentration of DIN and the growth of epiphytic algae at low nutrient levels because

high macrophyte biomass may hold DIN concentrations below the half-saturation

level of epiphytic algae.

The response of the model to changes in the coefficients and settings was

reasonable, and no variables were overly sensitive to changes. This is not to say the

coefficients chosen were optimal, but only that they were within a reasonable range. I

decided that even if the model erred on the side of insensitivity, it could be relied upon qualitatively. The sensitivity analysis shows that I should use at least a moderate inflow nutrient concentration in experiments designed to see nutrient effects on *Potamogeton* biomass. Using a high water exchange rate with a low inflow nutrient concentration (2 µmol l^{-1}) would not allow effects to be seen, even though the loading rate may be moderate to high.

The initial condition simulations illustrate the importance of using models in the experimental design process. For example, if an experiment is designed to examine the effects of epiphytic algae and grazers on growth, and was started with a high macrophyte biomass, nutrient inflow would have to be adjusted upwards to stimulate the epiphytic algae in order to see a grazing effect. Starting an experiment with low macrophyte biomass may result in overgrowth of epiphytic algae even at low nutrient inflow levels. They also illustrate a mechanism potentially contributing to the "clear water state" of shallow lakes (discussed in Scheffer et al. 1993b). Once a macrophyte bed is established, its ability to draw nutrient concentrations down to levels that limit production of algae could help the bed withstand eutrophication. The bed size required for this would, of course, be larger in an estuary with higher current velocities.

1995 Baseline simulation

The lack of effect of grazers in the experiment could have been due to growth of species of "epiphytic" algae that were not consumed by the amphipods. Macroalgae represent the less preferred algal group in the model and its biomass increased so that the sum of macroalgae and epiphytic algae in the model output was

closer to the measured epiphyte biomass. "Epiphyton" can be a monoculture or a diverse assemblage of taxa and can include inorganic and detrital particles. The epiphyton mass in these microcosms was not strictly algal, and the algal species changed with nutrient addition. These factors and others make modeling epiphytic algae as one or two compartments (*EA* and *MA*) problematic. It has been shown in other studies that grazers can have little or no effect on accumulation rates of certain algal species. In one study, blue-green algae dominated the epiphytic algal community when amphipods and isopods were present in a nutrient-enriched eelgrass microcosm (Neckles et al. 1994). Mayfly larvae, *Baetis tricaudatus*, had no effect on the biomass of a diatom, *Cocconeis placentula,* in a stream microcosm (Pan and Lowe 1994). If a variety of grazers are present, however, the likelihood of an epiphytic algal species being ungrazed should decrease.

The model's underestimation of grazer biomass may be explained by either low growth rate or high loss rate coefficients. The amphipods had a short life-cycle, a high reproductive rate and no predators in this experiment. I was satisfied with the effect the grazers had on epiphytic algal biomass and did not make further modifications to make the model fit the data. Since the amphipods reproduced so quickly and were so omnivorous (including cannibalism), their feeding behavior and reproductive cycle should be investigated further if they are to be used in longer experiments. In the estuary, predation or migration may keep their biomass in check.

Nutrient loading rate per unit macrophyte biomass

Figure 2.4 shows, at low water exchange rates, net community nutrient uptake exceeds supply, so nutrient concentrations are reduced to where they limit algal

growth. The drawdown of nutrients is a function of nutrient loading rate per unit autotroph biomass. At high biomass to loading ratios, significant reductions in nutrients can occur that could influence algal, and, thus, macrophyte growth.

As long as the inflow nutrient concentration is above limiting levels, increases in flow (or decreases in residence time) allow epiphytic algal biomass to increase (Figure 2.5). Thus, epiphytic algal biomass accumulation does not depend solely on the nutrient concentration and can be higher at low concentration and high water exchange than at high concentrations with low exchange.

Grazing can alter the effect of nutrient supply on epiphytic algal biomass. Figure 2.6 shows that grazers have the greatest effect at low nutrient loading rates, when they can remove the epiphytic algae faster than they can grow, leaving more nutrients and light for the macrophytes. Nutrient excretion by grazers may also enhance macrophyte growth at low loading rates. These figures illustrate how the choice of water exchange rate in an experiment may result in a counterintuitive outcome. If an experiment is designed with too low an exchange rate, macrophyte response may overlap. With grazers present, there is little difference between the low and medium nutrient treatments until exchange is more than 10 times per day. With grazers absent, the greatest leaf biomass is obtained with high inflow nutrient concentrations at the low exchange rate, with medium nutrients at an intermediate exchange rate and with low nutrients at the highest exchange rate.

 The residence time of water within a macrophyte bed depends on the current velocity and the bed size. A large, dense bed (1 km^2) in shallow water will have a much slower water exchange rate than a small patch, and it will have much more time

to interact with the water. Interiors of large, dense macrophyte beds under low-flow conditions may experience lower nutrient concentrations than the edges (e.g., Moore 1996). Water exchange rate decreases from the bed edge to the interior as the time for interaction increases. If interior nutrient concentrations are reduced below saturating levels, production of other autotrophs (phytoplankton, epiphytic and benthic algae) within a bed may be reduced, and recycling may become more important for algal production (e.g., Mulholland et al. 1994). Most submersed macrophyte species can obtain most of their nutrients from the sediments if that is where they are more available (e.g., Thursby and Harlin 1984), so low water column concentrations will not necessarily reduce their growth. Benthic algae may also derive much of their nutrient requirements from the sediments (e.g., Vadeboncoeur and Lodge 1998), but filamentous and foliose forms could still be limited by low water column nutrients. Smaller beds or beds in high flow environments are less likely to influence water quality and should have little positive feedback, similar to our high exchange scenarios.

The nutrient uptake ability of submersed macrophyte communities depends on the amount of nutrient regeneration within the community. Regeneration rates in estuaries will vary depending on the supply and lability of organic material. Eutrophic systems should have relatively high particulate organic concentrations, higher sediment nutrients and, thus, low leaf uptake rates. Since this model and the microcosm experiments had no particulate organic inflow, our net nutrient uptake rate would be more representative of an oligotrophic estuary.

Though the idea that the effects of nutrient loading on shallow communities should be dependent on autotroph biomass seems intuitive, it may not be that well understood. Models of submersed macrophyte interactions with water quality do not take this into account, as I have mentioned. Asaeda et al. (2001) showed effects of nutrient loading and water retention time on submersed macrophyte communities but attributed differences in nutrient concentrations to phytoplankton uptake. Brinkman et al. (1994), however, examined the influence of loading rate with a pelagic-benthic mesocosm and a model, although they found no effect of loading on oxygen dynamics.

Extrapolating results from microcosms or models to larger spatial scales should be done with great caution. Factors that make this difficult include the effect of macrophytes on suspended matter, the effect of macrophyte density on feedback effects and variable physical, chemical and biotic factors. The grazer and fish populations in the shallows of the Bay are seasonal and not well documented. If grazer populations are low due to predation, pesticides or natural cycles, the effect of nutrients on epiphytic algae will be greater. Pesticides such as Chlorpyrifos (O,O-diethyl O-3,5,6-trichloro-2-pyridyl phosphorothioate), Permethrin (3 phenoxybenzyl(1RS)-cis,trans-3-(2,2-dichlorovinyl)-2,2 dimethylcyclopropanecarboxylate), and Naled (1,2-dibromo-2,2-dichloroethyl dimethyl phosphate) currently in use for mosquito control kill crustaceans in concentrations far below those obtained following application rates on the labels (Mayer 1987). Since mosquito control is practiced in populated areas, this may be a factor affecting submersed macrophyte response to eutrophication. The feeding

behavior of small fish species in macrophyte beds needs to be understood since they may also reduce epiphytic algal biomass and reduce macrophyte response to nutrient loading.

Trophic complexity simulations

The model results showed that our initial conditions, including the proposed fish biomass addition and N addition rates, should be appropriate for examining the interactions of nutrients, grazers and fish on epiphytic algal biomass, nutrient availability and macrophyte biomass in microcosms. The model results suggest that an experiment designed to show grazer effects on submersed macrophytes should use a high loading rate and run for an extended period. Little difference in *Potamogeton* biomass is evident at the end of 20 weeks. Though the model did not reveal anything that was not intuitive, it served a purpose in keeping track of all our assumptions and verifying that the loading rates would allow differences to be seen between treatments.

The model showed that fish addition increased epiphytic algae and decreased *Potamogeton* biomass in medium to high nutrient runs. Fish also increased epiphytic algal biomass in high nutrient-treated ponds (Moss 1976). Fish predation on grazers increased epiphytic algae and decreased macrophyte biomass in exclosure experiments (Brönmark 1994). The presence of fish may not always result in increased epiphytic algal biomass. Pinfish (*Lagodon rhomboides*) fed on epiphytic algae in one trophic complexity experiment (Heck et al., 2000). In open systems, a great deal of variability would be expected due to the dynamics of the system, including the seasonality of grazers and the mobility of predators.

The behavior of amphipods and fish can make a microcosm experiment diverge from a numerical model. Amphipods may change their behavior in the presence of predatory fish by spending more time in the sediment. In order for the model to work, the type of algae that grows on the leaves has to be something the amphipods will eat. They did not consume the filamentous green algae in the 1995 experiment (modeled as macroalgae), and may not eat some other epiphytic algal species. If the amphipods select certain algae, then other types may continue to grow, negating the positive effect of grazers on light availability to the macrophytes. Fish may kill more amphipods than they can digest and may also disturb the sediment or eat epiphytic algae.

Conclusions

The model behaved well in the sensitivity analysis, and, though it did not correctly predict the values of all state variables in a baseline simulation, the behaviors were similar, and the reasons for differences could be explained simply. It proved useful in exploring the effects of initial conditions and how they could determine the outcome of an experiment. It was also useful for showing effects of interactions of inflow nutrient concentrations, water exchange rates and grazers on microcosm experiments. The model keeps track of secondary processes, such as regeneration, which may not be considered in an experimental design but may contribute to the outcome of an experiment. Models could also be used to help determine the length of an experiment or the appropriate sampling interval. There are many things that can occur in a microcosm that there may be no mechanisms for in the model, which could reduce the model's ability.

The feedback effect of macrophytes reducing nutrients and increasing available light is important to consider in experiments and possibly when determining maximum nutrient discharges to estuaries. Our simulations show that using nutrient concentrations to predict habitat quality for submersed macrophytes (e.g., Batiuk et al. 2000) in shallow water may not be as accurate as using a nutrient loading rate. Nutrient concentrations can change due to macrophyte community uptake, and how they change over space is a function of the interaction of the nutrients with the macrophyte community. Although the effect of grazers on epiphytic algal biomass has been shown experimentally, the model demonstrates how their effect on macrophyte growth may be most important in areas with high flow rates (short residence times) or high nutrient loading per unit biomass.

Chapter 3: Effect of seagrass bed size and flow regime on water quality

Abstract

Seagrass communities have been shown to reduce current velocities and water-column dissolved nutrient and seston concentrations. These effects could reduce algal biomass, enhancing light availability to the leaf surface and therefore, increase seagrass growth. I hypothesized that gradients in nutrient concentration would be found across large seagrass beds due to the interaction of the plant community and the water column. I measured water flow characteristics and nutrient concentration gradients across seagrass beds and community nutrient uptake rates in mesocosms. I used these measurements to calibrate a groundwater flow model (MODFLOW/MT3D) to demonstrate the effects of water flow velocity and bed size on nutrient gradients. The maximum nutrient concentration change (from 10 μmol NH^+_4 l^{-1} up-current to 1 μmol NH^+_4 l^{-1} inside) was measured at the edge of a very dense mixed species macrophyte bed in the Potomac River. The average net NH^+_4 reduction in Widgeon Grass (*Ruppia maritima* L.) beds was much lower than this (<1 μmol N l^{-1} hr^{-1}) and much lower than the uptake rate measured in the mesocosm. Ammonium concentrations were significantly lower inside the seagrass beds than upstream, though the average difference was minimal. Water flow reduction in large, dense Widgeon Grass beds averaged 48% and was the main cause of nutrient flux reduction to bed interiors. Both flow intensity and the ratio of steady flow to flow

variance decreased approximately 50% inside *Ruppia* beds resulting in reduced nutrient supply rates by diffusion. A flow model accurately describes the effect of water flow velocity, seagrass bed roughness, and nutrient uptake in creating gradients in nutrient supply across large, shallow, dense, canopy-forming seagrass beds. The model shows that while in slow currents, nutrient concentration differences could occur over a 1 m flow path in the seagrass bed, under the general flow conditions of our study sites, changes occur over tens of meters. In conclusion, at least in shallow waters, large, dense seagrass beds have gradients of water and nutrient supply from edge to center that may cause gradients in trophic state, as well as faunal density and diversity.

Introduction

Eutrophication indirectly reduces bottom coverage of seagrasses by limiting light as a result of planktonic (Sand-Jensen & Borum 1983) and epiphytic algal shading (Sand-Jensen 1977, Phillips et al. 1978, Stevenson 1988). Conversely, seagrasses have been shown to partially moderate some eutrophication effects by sequestering nutrients and carbon, increasing water clarity, and producing dissolved oxygen (e.g., Moore 1996, Rybicki et al. 1997). High biomass of seagrasses can lead to reduced local nutrient concentrations (Howard-Williams 1981) that could, in turn, increase light availability to seagrasses by reducing planktonic and epiphytic algal biomass (Sand-Jensen 1977). The ability of the seagrass communities to damp pulsed nutrient inflows may be particularly important, as these can stimulate phytoplankton blooms, which in turn may increase organic sedimentation and subsequently, oxygen depletion from bottom waters. Seagrass beds also reduce current speeds (e.g.,

Fonseca et al. 1982, Madsen and Warncke 1983), resulting in increased sedimentation of total suspended solids (Ginsburg & Lowenstam 1958, Ward et al. 1984) and increased water clarity. Several studies show the effects of seagrasses or other submersed angiosperms on hydrodynamics (e.g., Fonseca et al. 1982, Sand-Jensen & Mebus 1996, Koch 1996), but measurements at intermediate scales (meters) may not be applicable at larger scales (100's of meters), as velocities may decrease with seagrass bed size and density. The information reported in the seagrass literature (e.g., Fonseca et al. 1982, Sand-Jensen & Mebus 1996) does not allow calculation of total flow reduction per unit seagrass biomass, or the water flow across a bed. Some atmospheric and terrestrial studies (e.g., Pitlo & Dawson 1990) do consider the function of vegetation increasing bottom friction. These studies calculate roughness coefficients useful for determining large scale (kilometers) water flow patterns.

The amount of nutrient uptake by a seagrass bed, and the effect of nutrients on the community, will depend on the residence time of water in the bed. In turn, this will depend on the bed size and water flow rate. Water flow rates in seagrass communities are modified by the leaf surface area, seagrass spatial distribution (Nepf 1999), and bed size. Nutrient uptake by a seagrass bed is dependent on conditions such as temperature and light, but will also depend on hydrodynamic conditions (Koch 1994) and on water column and sediment nutrient concentrations (Thursby & Harlin 1984). These environmental conditions may change across large seagrass beds as nutrients are absorbed and flow energy is dissipated. I hypothesize that relations between seagrass beds and the water column should be related to the area of seagrass coverage, the water volume exchanged, and most importantly, seagrass density and

spatial pattern, because these can exert strong influence on exchange and trapping of nutrients. Thus, large canopy-forming beds in slow currents should have gradients in water quality from up-current to inside beds. Small, sparse seagrass beds in fast currents should have little effect on water quality with less potential for feedback effects such as decreased algal biomass and increased light availability (Figure 3.1).

Conceptually, we can think of water flow in a seagrass bed in a depth-integrated sense. Under these conditions, flow can be determined by the hydraulic gradient and drag, which is a function of shoot surface area and spacing and water velocity (e.g., Burke and Stolzenbach 1983). From a shallow water frictional balance, assuming that flow is barotropic and depth-averaged, we know that a balance exists between the surface slope and drag, so in the two horizontal directions

$$gh\frac{\partial h}{\partial x} = C_D u^2 \quad \text{and} \quad gh\frac{\partial h}{\partial y} = C_D v^2 \tag{1}$$

where g is the gravitational acceleration constant, h is the water surface height, C_D is the drag coefficient, u is velocity in the direction of mean flow (x), and v is velocity in the direction perpendicular to flow (y). If the distributions of $h(x,y)$ and $CD(x,y)$ are known, eq. 1 may be solved for the flow velocity distributions u(x,y) and v(x,y).

Nutrients flow along with water and are affected by net community uptake. Assuming steady state, the change in dissolved nitrogen concentration (N) is due to the divergence of horizontal N transport,

$$\frac{\partial N}{\partial t} = -\frac{1}{h}\frac{\partial}{\partial y}(vhN) - U(N, B_s) \tag{2}$$

Figure 3.1 Hypothetical relative changes in water quality and hydrodynamics and subsequent changes in photosynthetically available radiation (PAR) epiphytic algal and SAV growth. Dark lines show the expected interaction at low transport, or dense canopy, thin line for medium canopy and transport, and dotted for low plant density and fast currents. DIN stands for dissolved inorganic nitrogen, TSS for total suspended solids, DBL for diffusive boundary layer. Small, medium and large are SAV bed sizes.

74
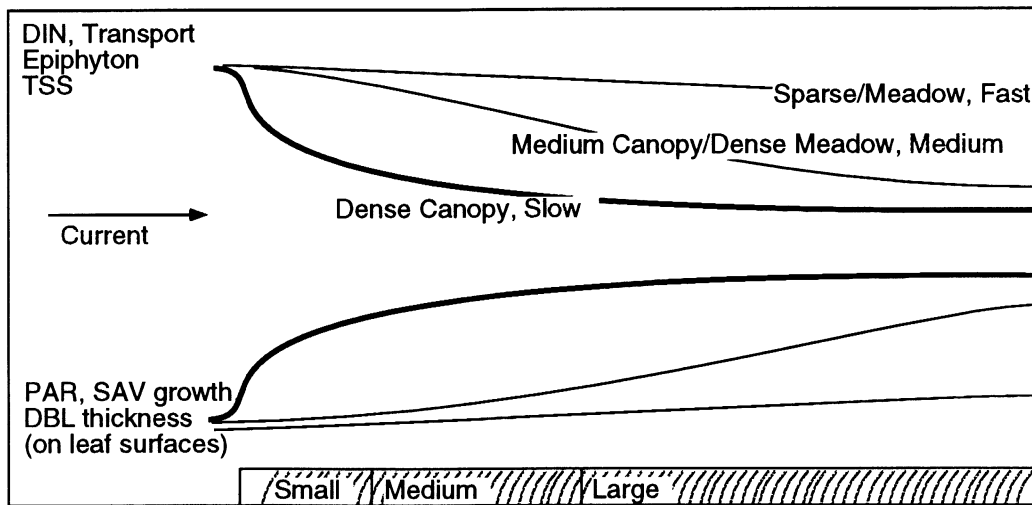
where $U(N, B_s)$ is net seagrass bed uptake which is a hyperbolic function of N and a linear function of seagrass biomass, B_S. Transport ($v\ h$) is divided by h to keep N in concentration units.

The purpose of this study was to evaluate how seagrass beds can affect spatial variations in water quality. I approached this by using field and mesocosm measurements, and a model. Using this perspective improved my ability to: 1) model the effect of anthropogenic nutrients on seagrass ecosystems, 2) model the influence of seagrass ecosystems on adjacent pelagic-benthic systems, and 3) better interpret experimental and monitoring data collected from seagrass ecosystems.

Methods

Field and laboratory measurements

In the growing seasons of 2000 and 2001, I measured flow characteristics, water quality, and seagrass biomass across dense beds in mesohaline Chesapeake Bay and the Potomac River (Figure 3.2). The seagrass beds sampled near the mouth of the Choptank and Little Choptank Rivers (TS, TN, TC, CC and LC) consisted of monospecific *Ruppia maritima* L. (Widgeon Grass) while the Onancock River mouth site (ON) included *Zostera marina*, and the Potomac River site (P1) was a mixed species bed including *Hydrilla verticillata*, *Vallisneria americana*, *Heteranthera dubia*, *Myriophyllum spicatum*, and other freshwater macrophytes. Seagrass bed locations, sampling dates and measurements made are shown in Table 3.1. From July until September, the Widgeon Grass reproductive shoots were up to 1 m long, and formed a partial canopy over the shorter 10-20 cm vegetative shoots, which formed a

Figure 3.2. Selected field sites at the mouth of the Choptank River. Stippled areas are large, dense SAV beds. Not all the SAV coverage is shown.
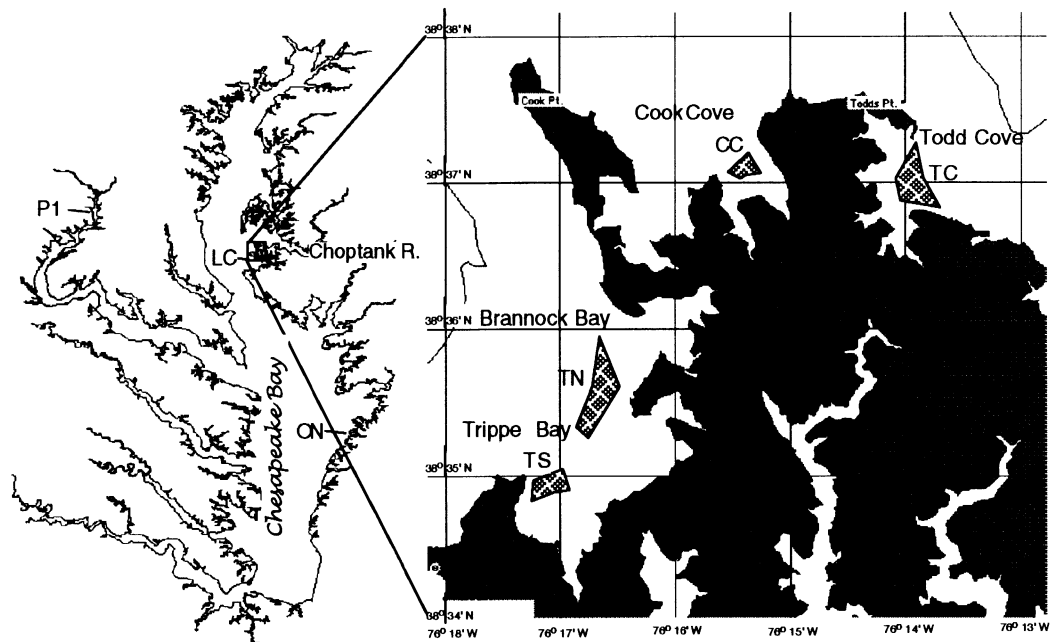
Table 3.1
Sample dates, grass bed size, plant biomass and percent cover, locations and transport measurement dates.

Site	Date	Width (m)	Density (g dwt m^{-2})	Pct. cover	Latitude	Longitude	Transport transect date
TC	06/03/00	340	37 ± 21	40	38° 37.1'	76° 13.5'	
TN	09/17/00	400	81 ± 26	90	38° 35.8'	76° 16.6'	10/15
TS	10/06/00	280	94 ± 12	80	38° 34.8'	76° 17.1'	10/06, 10/12
TS	04/09/01	na	nm	nm	38° 34.7'	76° 16.9'	
TC	04/13/01	na	nm	nm	38° 37.1'	76° 13.5'	
TC	04/14/01	nm	nm	nm	38° 37.1'	76° 13.5'	
TC	05/29/01	340	87 ± 7	95	38° 37.2'	76° 15.4'	
TS	06/20/01	320	82 ± 32	90	38° 34.8'	76° 17.1'	
ON	07/21/01	480	66 ± 39	70	37° 41.7'	75° 50.9'	
LC	08/09/01	280	80 ± 24	80	38° 32.8'	76° 15.9'	
PI	08/11/01	800	328 ± 141	95	38° 46.9'	77° 01.8'	8/11
CC	08/29/01	220	89 ± 25	50	38° 37.2'	76° 15.4'	9/08
TC	09/04/01	300	14 ± 5	30	38° 37.1'	76° 13.5'	
TN	09/17/01	400	102 ± 16	95	38° 35.8'	76° 16.6'	9/18

na: not applicable, nm: not measured

dense meadow. I mapped the beds visually or by aerial photography. Percent cover was determined visually or from the photos using NIH Image software. To determine seagrass coverage, I collected above-ground biomass (0.05 m^2 quadrat) from stratified-random transects in the mapped regions. The nearest dense patch was sampled if the random location was bare so the total areal biomass would not be underestimated after adjusting for percent plant cover. Shoots were removed by hand from each quadrat. The lengths of ~ 25 vegetative leaves and all of the reproductive shoots were measured from each sample. I scrubbed and washed epiphytic material from the leaves and dried them at 60° C to a constant weight to determine dry weights. Average biomass for the bed was determined by multiplying the biomass by the percent cover. The N content of dried, ground (Wiley Mill) September 2001 subsamples from site TN1 was determined (Perkins-Elmer CHN analyzer). I used the leaf dimensions (wet) and dry weights and to calculate average leaf surface area (a_p).

I made water flow measurements on calm (<5 knot) days on the incoming tide. I used a 10 MHz acoustic Doppler velocimeter (ADV, SonTek Inc., San Diego, California) that sampled at 25 Hz for 3.6 to 6.8 minutes per reading (see Voulgaris & Towbridge 1998 for review) to determine water transport, steady flow speed, and turbulence intensity. The ADV probe was clamped to a stainless steel rod that was pushed approximately half a meter into the sediment. Any shoots that would interfere with the acoustic beams were removed or a 0.1 m^2 hardware cloth square was staked to the sediment under the probe in dense vegetation. To determine water transport, I measured 3 to 4 current velocity profiles along a transect from up-current to the inside of the seagrass beds (see example in Figure 3.3), taking about 15 minutes per profile.

Figure 3.3. A map of the spatial extent of dense vegetation at Trippe Bay (TS) showing current direction and locations of ADV profiles.
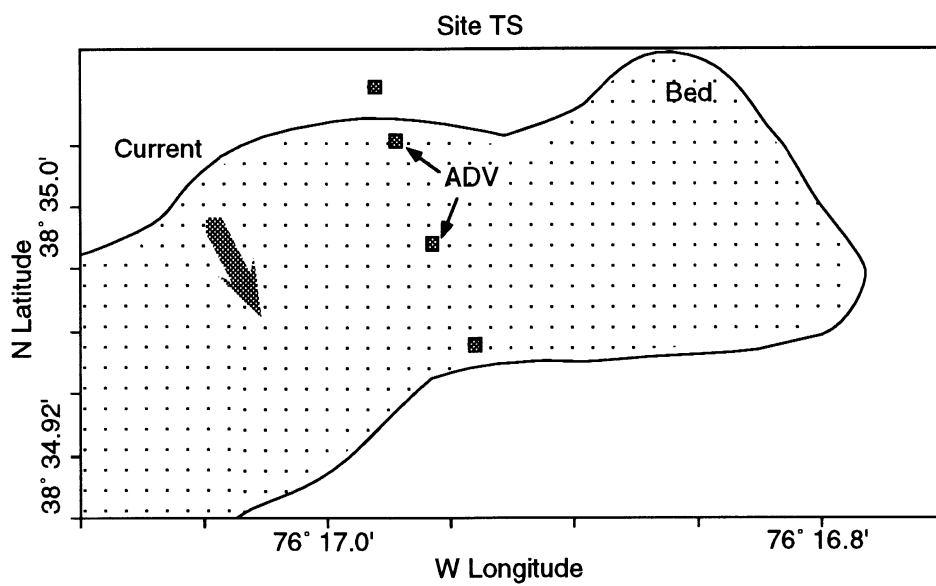
Each profile was integrated by adding the areas of trapezoids formed by the depth and velocity differences between measurements, and the area of the rectangle formed by connecting the upper velocity to the surface.

Steady flow speeds were calculated using:

$$u_{steady} = \sqrt{(U^2 + V^2 + W^2)} \tag{3}$$

where U, V, and W are the average velocities (m s^{-1}) in the vertical and two horizontal directions. Turbulence intensity, a measure of the variance of the velocity components, was determined by:

$$q = \sqrt{\tfrac{1}{3}(u^2 + v^2 + w^2)} \tag{4}$$

where u^2, v^2, and w^2 are each the variance of the respective velocity components (see Tennekes & Lumley 1972).

Flow intensity is the root mean square velocity and combines steady and fluctuating flow:

$$u_{RMS,total} = \sqrt{\tfrac{1}{3}\left[\langle(U+u)^2\rangle\right] + \left[\langle(V+v)^2\rangle\right] + \left[\langle(W+w)^2\rangle\right]} \tag{5}$$

I applied a filter to the data using WinADV (Wahl, 2000) to eliminate interference signals before analyzing the data. Waves jarring the support were the main source of

lost data. Data were not used if $> 3\%$ of the 3.6 minute samples were filtered. The inside and outside (and up-current) bed q and ratio of u_{steady} to q were compared using a Wilcoxon matched-pairs signed-ranks test (Sokal and Rohlf 1981) using Instat (Graphpad Software Inc., San Diego, CA).

To determine net nutrient uptake of the seagrass beds, I measured current velocity, water depth, and dissolved nutrient concentrations from a boat across the beds at each site on incoming tides. Wind speed and wave height were also recorded. I took sub-surface water samples, recorded sample positions using GPS, and measured velocities using ADV or by recording dye movements over time. For dye measurements, a rod was placed into the sediment horizontally and was attached with 2 meters of line to a float. Dye (e.g., Rhodamine) was injected approximately mid-depth adjacent to the rod and the time for the center of the bolus to pass the float was recorded. Ammonium was determined photometrically (Strickland and Parsons 1972). Nutrient uptake rates were calculated from the change in nutrient content m^{-2} per unit distance divided by the time required for the parcel of water to travel that distance. On some days, nutrient samples were taken inside and up-current of seagrass beds without measuring water flow velocity. The inside bed edge and up-current ammonium concentrations were compared using a Wilcoxon matched-pairs signed-ranks test (Sokal and Rohlf 1981) using Instat (Graphpad Software Inc., San Diego, CA).

I measured net nutrient uptake of Widgeon Grass communities and unvegetated systems in mesocosms (Figure 3.4) to determine community uptake rates. I conducted three one-week incubations in September and October 2001. The

Figure 3.4. Mesocosm used for uptake experiments and flow characteristics. Diagram (a) photo (b) and flow velocity profile (c). Pattern of currents generated by paddlewheel shown by arrows. Horizontal current velocity is measured in the center of the tank and some return flow follows the sides.
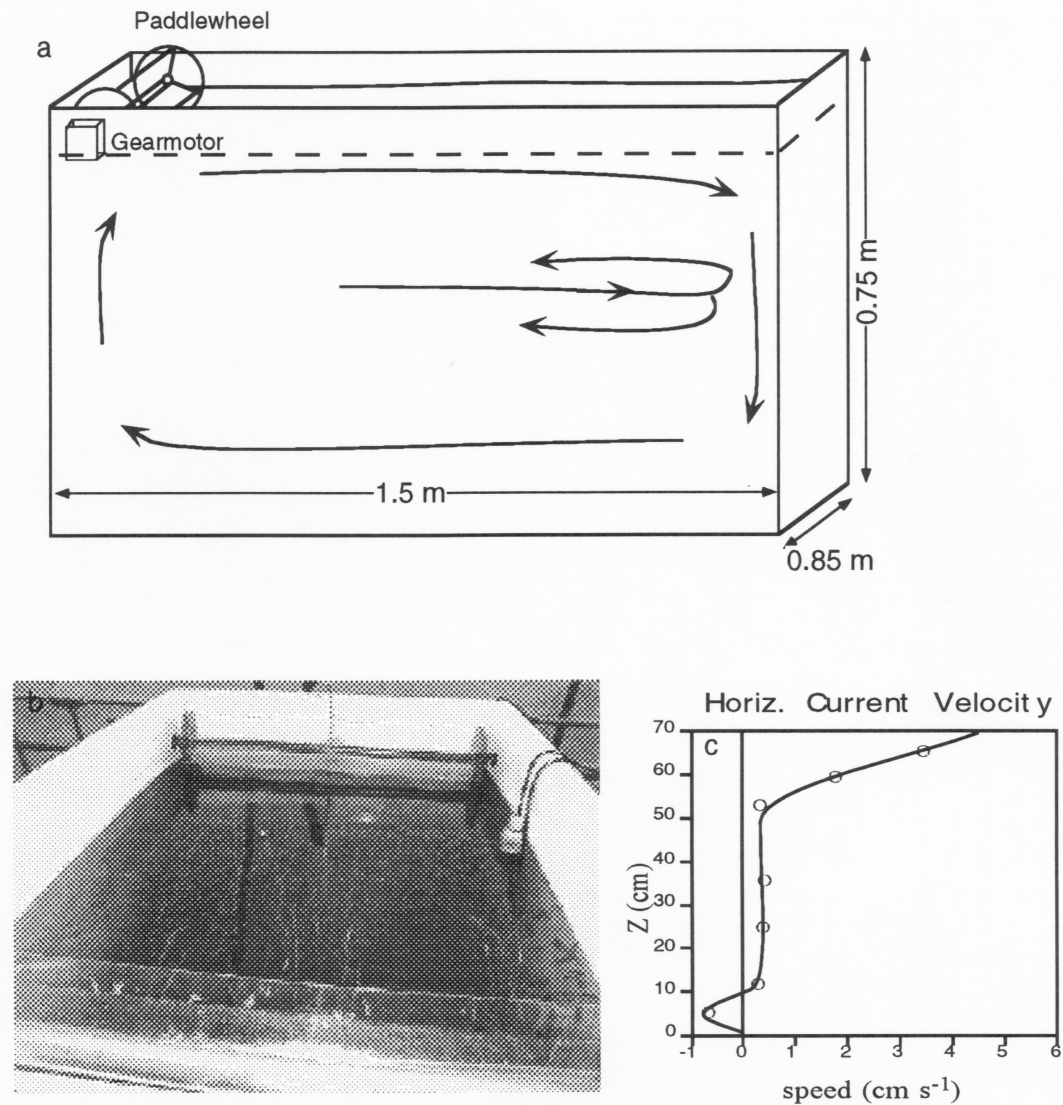
mesocosms were 1.3 m^2 and 0.8 m^3 in volume, with water depth of 70 cm, and 10 cm

of sediment. The sediment had been collected from a shallow Choptank River

location that had supported seagrass growth in the past. Choptank River water (11

psu) was filtered through sand and a 2 µm filter and metered into the tanks. Physical

and chemical parameter ranges during the experiment are shown in Table 3.2. The

tanks were stirred with a paddlewheel that generated velocity profiles and turbulence

characteristics similar to interiors of beds in slow currents (Table 3.3). I determined

net NH^+_4 uptake by sampling over time after addition of ammonium phosphate to

obtain concentrations of 560 µg l^{-1} of dissolved N and P concentrations in

stoichiometric excess (e.g., Redfield 1934). Ammonium concentrations were

determined photometrically (Strickland and Parsons 1972). Photosynthetically

available radiation (measured at the surface with a LI-COR 1000 and spherical

quantum sensor) and temperature were monitored during the experiments, and

biomass of *Ruppia* and sediment porewater nutrients (Hesslein, 1976) were

determined at the end of the experiments. The slope of the averaged data was used to

calculate areal vegetated or unvegetated nutrient uptake rates. The *Ruppia* biomass in

the mesocosm (144 g d wt m^{-2}) was similar to moderately dense beds at our study

sites near the mouth of the Choptank.

Model description

To model the water flow in two dimensions, I used a simple model where

flow is determined by the hydraulic gradient and drag, which is a function of shoot

surface area, spacing between shoots and water velocity. I configured a groundwater

modeling software program, MODFLOW (McDonald and Harbaugh 1988,USGS),

Table 3.2 Mesocosm parameters.

Parameter	Range
photosynthetically available radiation	80-1500 μ E m^{-2} d^{-1}
Salinity	11-12 psu
Ruppia biomass (total)	144 g dry wt. m^{-2}
Temperature	18-27° C
Sediment NH$_4^+$ conc.	0.7 mg l^{-1}
Water column NH$_4^+$ conc.	4 - 40μmol l^{-1}

Table 3.3

Direct measurements of flow characteristics in the vegetated mesocosm and across a *Ruppia maritima* grass bed at Brannock Bay on 10/15/00. Height of each measurement is shown. Measurement abbreviations are: steady current velocity (u_{steady}), turbulence (q), and flow intensity ($u_{RMS, total}$). Selected medium size bed was 400 m in width and plant density averaged 81 g dry wt m^{-2} and over 90% cover. Depths were 85 to 120 cm in the field and 78 cm in the mesocosm. Mesocosm measurements are averaged across the tank.

Bed Description	height (cm)	u_{steady} (cm s^{-1})	q (cm s^{-1})	Ratio (u_{steady}/q)	$u_{RMS, total}$ (cm s^{-1})
Mesocosm					
49 g dwt m^{-2} surface	65	2.09	1.11	1.95	2.27
49 g dwt m^{-2} mid-depth	35	0.65	0.56	1.20	0.49
49 g dwt m^{-2} bottom	8	0.75	0.46	1.60	0.54
188 g dwt m^{-2} surface	68	2.00	0.63	2.89	1.33
188 g dwt m^{-2} mid-depth	35	0.57	0.45	1.30	0.17
188 g dwt m^{-2} bottom	10	0.15	0.31	0.52	0.19
Field Site					
bare sediment, surface	66	7.3	6.07	1.21	2.19
bare sediment, mid depth	40	6.13	4.50	1.36	1.68
bare sediment, bottom	5	4.77	4.05	1.18	0.84
bed edge, surface	88	5.71	2.14	2.67	4.60
bed edge, mid-depth	40	2.59	1.46	1.77	1.56
bed edge, bottom	5	1.3	1.42	1.07	0.68
bed middle, surface	84	3.25	1.51	2.15	3.58
bed middle, mid-depth	51	1.25	1.28	0.98	1.56
bed middle, bottom	9	0.51	1.14	0.44	1.56

with the MT3D99 module (SSP & A Software) to simulate a one layer unconfined

aquifer with a high hydraulic conductivity. The flow of groundwater and solutes

through porous media is analogous to the flow of water and dissolved nutrients

through seagrass beds. Groundwater mean flow is also driven by the hydraulic

gradient and is affected by hydraulic conductivity of the aquifer (Darcy's Law),

$$Q = AK\, h_y \tag{6}$$

where Q is flow rate; A is cross sectional area; K is hydraulic conductivity (m s^{-1}) and

h_y is the water surface slope. Thus, velocity is a function of the forcing head pressure

and a term that incorporates drag; K. K is analogous to the inverse of a linear drag

coefficient.

The MT3D99 module allows the assignment of solute uptake coefficients to

individual cells or groups of cells. In MODFLOW, I specified a one layer, unconfined

aquifer with a grid size of 30 by 30, a cell size of 20 meters and a thickness of 1

meter. I assigned different coefficients for hydraulic conductivity and uptake to

selected "seagrass bed" cells in the grid, and ran the model at a variety of flow rates,

inflow N concentrations, and drag coefficients. Table 3.4 shows coefficient values

used for the groundwater model runs and the corresponding seagrass bed

measurements. The flow equation for MODFLOW (McDonald and Harbaugh, 1988)

is

$$\frac{\partial}{\partial x}\left(K_{xx}\frac{\partial h}{\partial x}\right) + \frac{\partial}{\partial y}\left(K_{yy}\frac{\partial h}{\partial y}\right) + \frac{\partial}{\partial z}\left(K_{zz}\frac{\partial h}{\partial z}\right) + W = S_s\frac{\partial h}{\partial t} \tag{7}$$

Table 3.4

Model coefficients and measured values. Slopes for model runs were adjusted to alter flow rates.

Term	Model	Measurement	Units	Source
Slope	$0.75 - 3.1 \times 10^{-6}$	$0.3 - 2.3 \times 10^{-6}$	$m\ m^{-1}$	calculated
Hydraulic conductivity, unvegetated	590		$m\ s^{-1}$	calculated
Hydraulic conductivity, vegetated	280		$m\ s^{-1}$	calculated
Drag coefficient, unvegetated		0.003	unitless	literature [a]
Drag coefficient, vegetated		0.022	unitless	measured [b]
Maximum N uptake rate, unvegetated	0	13, 19.6	$mg\ m^{-2}\ d^{-1}$	measured, literature [c]
Maximum N uptake rate, vegetated	20	0- 235	$mg\ m^{-2}\ d^{-1}$	measured, literature [d]
Half saturation coefficient, unvegetated	0.420	0.420	$mg\ l^{-1}$	literature [c]
Half saturation coefficient, vegetated	0.128	0.128	$mg\ l^{-1}$	literature [d]

The MODFLOW parameters were set to built-in reservoir settings, with initial hydraulic head = 1.005 in left boundary cells, transmissivity = 1500, layer type was unconfined, and initial concentration was varied from 2 to 40 μmols l^{-1}. The dispersion coefficient (mechanical and molecular diffusion) was set to 0. Bulk density was set to 100 g m^{-3} for the vegetated cells and 0 for unvegetated cells. The duration of the simulations was 12,000 time steps (seconds).

[a] Werner et al. 2003

[b] see Appendix A

[c] Dodds et al. 2002 (~0.04 μmols $m^{-2}\ s^{-1}$ average field measurement Figure 5)

[d] Thursby and Harlin 1984 (V_{max} 9.7 umol h^{-1} gram dry wt^{-1})

where K is hydraulic conductivity along the x, y or z axis, h is the potentiometric head (m), W is the volumetric flux of water into the system (s^{-1}), S_s is specific storage of the media, and t is time. For a vertically integrated situation, with no inputs, and no specific storage, this equation can be simplified to

$$\frac{\partial}{\partial x}\left(K_{xx}\frac{\partial h}{\partial x}\right) + \frac{\partial}{\partial y}\left(K_{yy}\frac{\partial h}{\partial y}\right) = 0 \tag{8}$$

MODFLOW calculates flow from

$$u = -\frac{K_{xx}}{\theta}\frac{\partial h}{\partial x_i} \quad \text{and} \quad v = -\frac{K_{yy}}{\theta}\frac{\partial h}{\partial x_i} \tag{9}$$

where K_{xx} and K_{yy} are the principal components of the hydraulic conductivity tensor (m s^{-1}), and θ is a dimensionless scaling factor. Substituting equation 9 into equation 8 yields a simple statement of flow continuity. Equation 9 is mathematically equivalent to equation 1 if we substitute $\frac{gh}{C_D u}$ for K_{xx}, $\frac{gh}{C_D v}$ for K_{yy}, and set $\theta = 1$, to obtain

$$u = \frac{gh}{C_D u}\frac{\partial h}{\partial x} \quad \text{and} \quad v = \frac{gh}{C_D v}\frac{\partial h}{\partial y} \tag{10}$$

for the two directions. Thus, in principle, we can use MODFLOW to solve for the flow through a seagrass bed if we know $h(x,y)$ along the boundaries of the model domain and we know $C_D(x,y)$.

Using Manning's equation, our velocity measurements and a literature roughness value for sand, I calculated a slope for an unvegetated area and used this slope to set boundary conditions for the model domain. Since the hydraulic conductivity term (K) behaves linearly with respect to velocity instead of

quadratically, I did the following: After initializing the model by setting the K of all cells as a constant based on a representative literature value of C_D and field measurements of u, the model was run and a prediction of $h(x,y)$ was obtained. Then the values of C_D within the seagrass bed were increased to an appropriate value from the literature (Sand-Jensen 2002), new Ks calculated using the initial estimate of u and the new C_Ds, and new solutions for h, u, and v were derived. The new solutions for u and v were combined with the in-bed and outside bed C_Ds to calculate another estimate of $K(x,y)$. The process was repeated until the velocity estimates stopped changing.

The equation used by MODFLOW for the transport of solutes is

$$\frac{\partial N}{\partial t} = \frac{\partial}{\partial x_i}\left(D_{ij}\frac{\partial N}{\partial x_j}\right) + \frac{\partial}{\partial x_i}(v_i N) + \frac{q_s}{\theta}N_s + \frac{\rho_b}{\theta}\frac{\partial \overline{N}}{\partial N}\frac{\partial N}{\partial t} - \lambda\left(N + \frac{\rho_b}{\theta}\overline{N}\right) \qquad (11)$$

where N is the nutrient, the first term on the right represents dispersion (D is the dispersion coefficient), the second term on the right is advection (v is pore water velocity), the third term is volumetric flux (q is flux, θ is a dimensionless rate constant and N_s is the sorbed concentration), the fourth term represents the sorbed material where ρ_b is the bulk density, and the last term is the reaction kinetic term with λ being the reaction rate constant. I specified the Monod formulation for nutrient uptake in MODFLOW, which is commonly used for plant nutrient uptake kinetics. Model runs were made to examine the effect of bed size and velocity on nutrient concentrations and distribution within beds.

Field and laboratory

Ruppia shoot biomass, bed width (parallel to flow), and coverage for the sampling trips are shown in Table 3.1. The biomass was generally high during summer and fall, but cownose rays (personal observation) reduced biomass at site TC during the summer, especially in 2001. The largest dense Widgeon Grass bed was at site TS in 2000, and site TN in 2001. The other Widgeon Grass sites had dense and bare areas, resulting in lower average biomass. The *Ruppia* biomass to surface area measurements averaged 0.25 cm^2 mg dry weight^{-1}. *Ruppia* N content averaged 2.4% of dry weight for one seagrass bed (TN) sampled in September 2001.

Figure 3.5 shows measured gradients in ammonium concentration over seagrass beds for days with high up-current N concentrations. The steepest declines were in the very dense macrophyte bed at site P1 and at site CC where currents slowed with distance into the cove. For most of the up-current nutrient samples, ammonium concentrations were very low. Even so, the difference in NH^+_4 concentrations between all inside bed and up-current sites was significantly different from zero (1.31 vs. 1.81 µmol l^{-1}, P= 0.0025, one tailed Wilcoxon matched-pair signed ranks test), even though it only averaged 0.5 µmol l^{-1} (Table 3.5). At individual sites with the most data (TC and TN) the differences were significant as well (P< 0.05). At site TC when rays were not present, inside bed ammonium concentrations were lower on all but one occasion.

Average net seagrass community nutrient uptake rates determined from concentration gradients across the *Ruppia* beds were less than 1 mg m^{-2} hr^{-1}. In

Figure 3.5. NH_4^+ concentrations from transects across various beds mainly with high up-current concentrations. P1 is an extremely dense canopy-forming bed in the Potomac River. The rest of the samples are *Ruppia maritima* beds of moderate density. Table shows velocities (u) and sample dates.
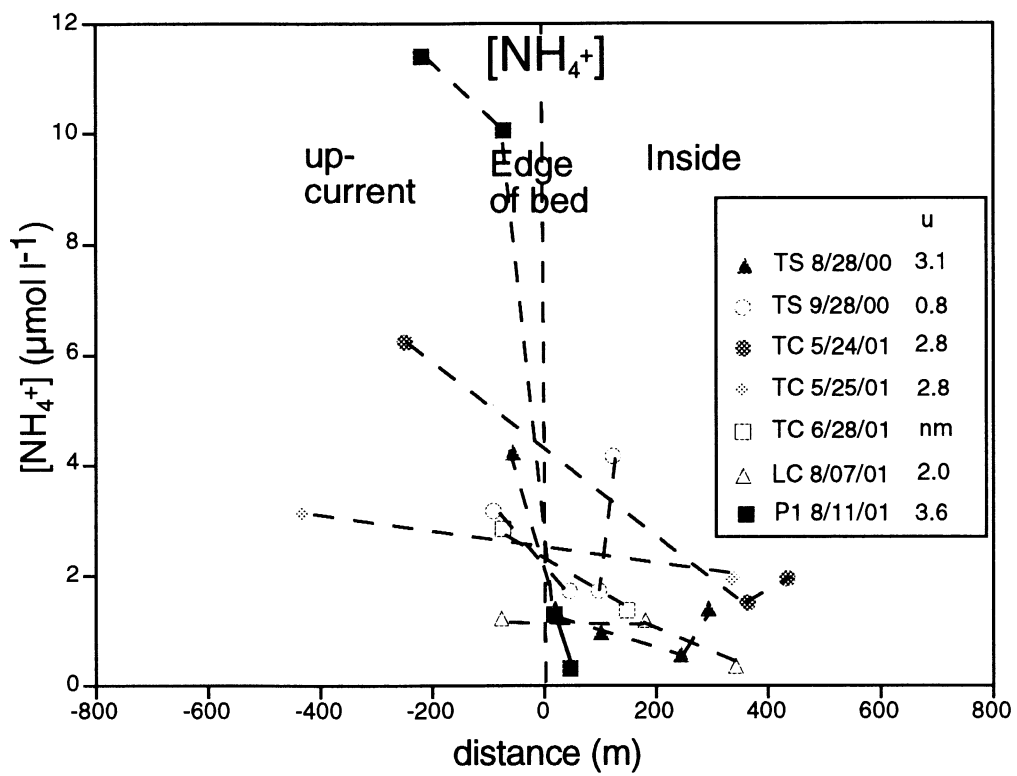
Table 3.5

Ammonium concentrations inside beds and upstream, and flow velocities within beds. Flow velocities were measured near the inside edge of the beds. a denotes depth averaged ADV profile measurement; v stands for visual dye measurements.

Site	Date	NH_4^+ inside (μmol l^{-1})	NH_4^+ upstream (μmol l^{-1})	Flow velocity (cm s^{-1})
TC	6/01/00	3.9	5.12	4 a
TS	8/10/00	1.13	2.4	
TS	8/11/00	12.1	6.73	
TS	8/28/00	4.2	0.95	3.5 v
TS	9/28/00	2.28	3.28	0.8 a
TN	10/15/00	0.23	0.38	4.2 a
TC	5/24/01	1.73	6.20	2.2 a
TC	5/25/01	1.94	3.12	2.1 a
TC	5/31/01	0.82	1.85	2.8 a
TC	6/14/01	1.75	2.63 (R)	
TC	6/28/01	2.83	2.40 (R)	2.5 v
TC	8/01/01	0.38	0.48	
TC	8/02/01	1.03	1.23	2.0 v
TC	8/05/01	0.97	0.33	1.5 a
TC	8/23/01	0.72	0.97	2.9 a
TS	6/20/01	0.43	1.80	
TS	7/13/01	0.45	0.13 (R)	
CC	8/23/01	0.91	0.77	2.9 a
CC	9/13/01	1.01	1.51	2.6 a
LC	8/09/01	0.33	1.21	2.9 a
TN	8/15/01	0.23	0.38	
TN	8/18/01	0.28	1.1	
TN	8/22/01	0.62	0.28	2.4 a
TN	9/17/01	0.56	0.75	3.0 v
TN	9/18/01	1.22	0.82	1.2 a
TN	9/22/01	0.62	1.21	
TN	10/02/01am	0.33	1.16	
TN	10/02/01pm	0.23	0.72	2.0 v
TN	10/03/01	0.47	0.62	
TN	10/04/01	0.72	0.97	2.5 v
TN	10/12/01	0.38	0.43	5.0 v
P1	8/11/01	0.3	10.0	3.4 a

R: Rays present

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comparison, net nutrient uptake measurements in the *Ruppia* mesocosm were substantially (two orders of magnitude) higher (235 mg N m^{-2} hr^{-1}). There was no significant uptake in the unvegetated mesocosms.

Water transport measurements showed a gradual reduction in transport with distance into beds, with $48 \pm 19\%$ (n = 4) reductions on the inside of large, dense, *Ruppia* beds not located in small coves (see Figures 3.6 and 3.7). Larger differences were found at site P1 (96%), which had very high biomass, and at site CC (76%), which was in a protected cove. The flow variance (q), the ratio of u_{steady} to q and the flow intensity ($u_{RMS, steady}$) decreased with depth and with distance into large, dense beds (Table 3.3 and Figure 3.8). The mean differences between inside and up-current q values were significantly different from zero for the *Ruppia* sites (means of 1.15 vs. 1.463 cm s^{-1}, P= 0.031). The mean differences between inside and ratios of u_{steady} to q and zero were also significant (1.40 vs. 2.83, P= 0.031). Flow intensity differences were also significantly different from zero (2.06 vs. 3.90 cm s^{-1}, P=0.031).

Model

Figure A1 shows the effect of size of dense seagrass beds on water surface elevation and speed at a representative velocity (10 cm s^{-1}). The presence of the beds results in increases in water surface elevation on the upstream sides and decreases on the downstream sides. The effect of the beds on velocities extends about one bed diameter in front of and behind the beds. Flow intensification occurs on the outside edges parallel to the flow direction. The model boundaries interfere with the flow patterns out from the large beds. The percentage flow reduction by seagrass beds increased with the initial water surface slope.

Figure 3.6. Spatial variation in current velocity profiles upstream and in the seagrass bed at site TS on 10/06/00 (a). The water surface is indicated by horizontal bars. The canopy height was 70 - 100 cm. Spatial variation in transport due to plant drag (b).
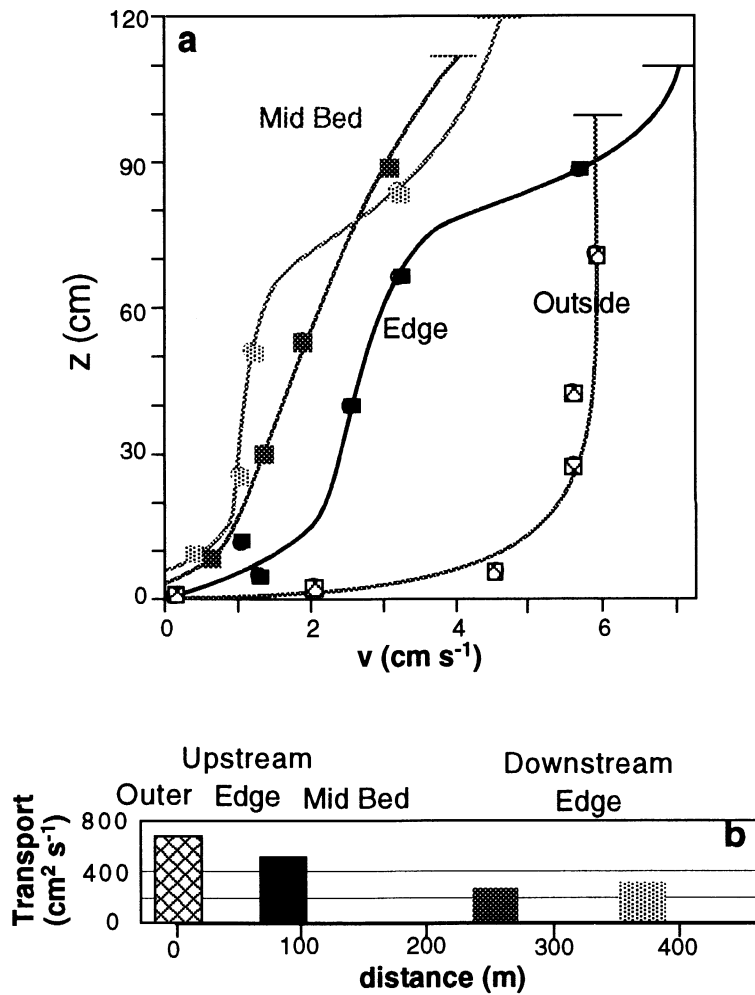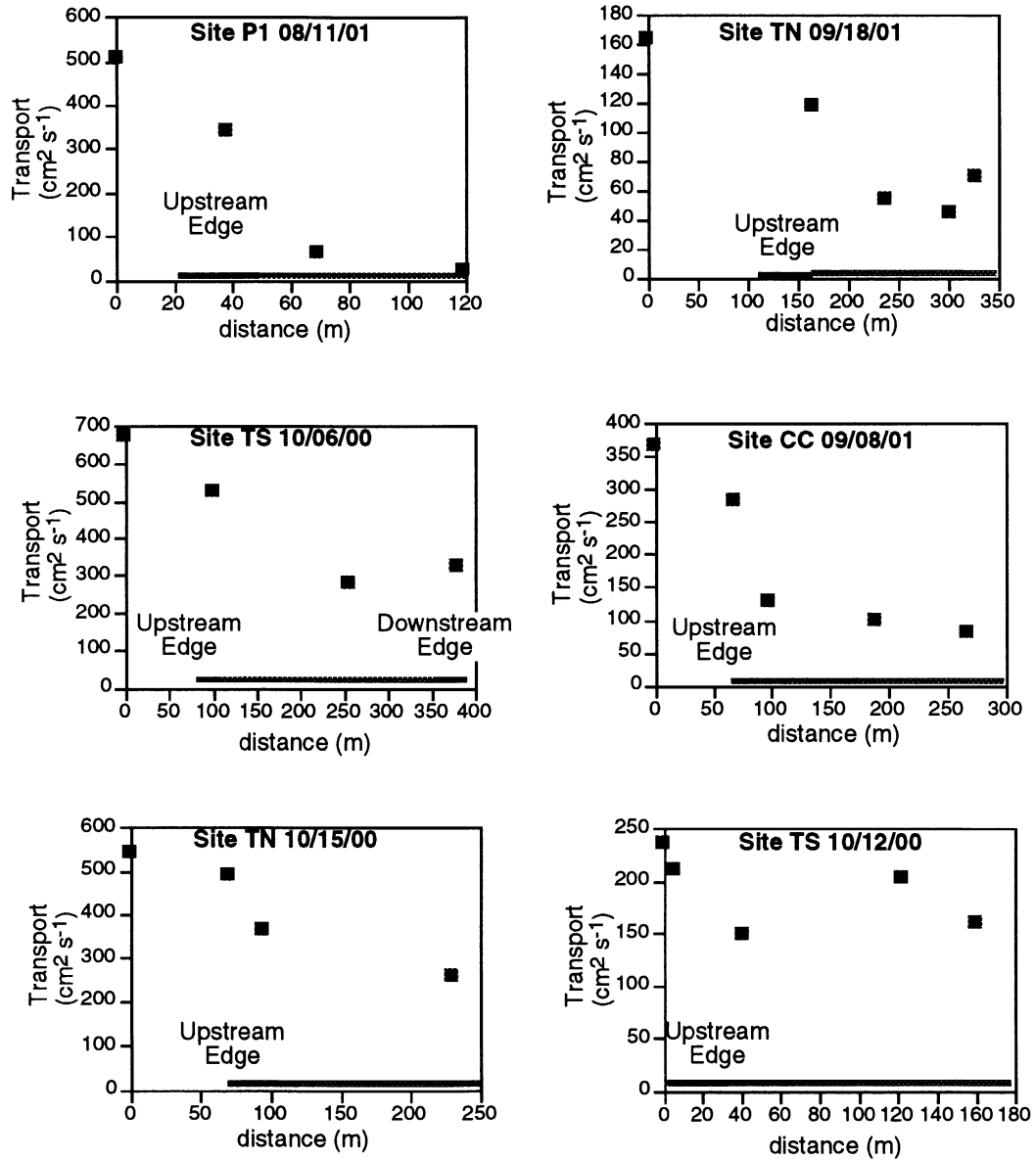
Figure 3.7. Water transport from upstream to bed interior of several sites. The solid line at the bottom is the patchy zone on the edge, and the patterned line is the continuous portion of the bed.

Figure 3.8. Example of spatial variation in hydrodynamic parameters across a large, dense *Ruppia* bed (site TS on 10/06/00) showing both velocity (u, solid lines) and turbulence intensity (q, dotted lines) variations with depth.
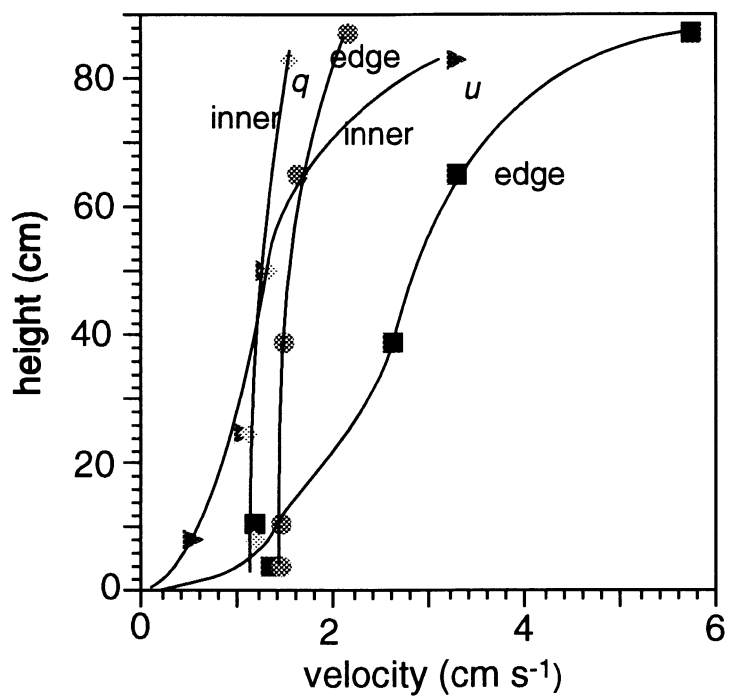
Model output with the water flow speed set at 5 cm s^{-1} (Figure 3.9) shows nutrient concentrations in the large (400 m wide) seagrass bed decrease because the net seagrass community uptake rate exceeds the rate of supply due to advection. Significant changes in N concentration are seen 80 meters downstream of the edge of the large bed under these conditions. As the contours of the intermediate size bed show, downstream nutrient concentrations are affected for a distance greater than the length of the bed. The large bed draws N concentrations down to levels that limit seagrass uptake (~10 µmol l^{-1}, Thursby and Harlin 1984), while the small (60 m^2) bed has little discernable influence on the nutrient concentrations. The average areal nutrient uptake rate of the small bed is higher than that of the larger beds, however, since nutrients are less limiting.

Running the model at a range of velocities and plotting nutrient concentration vs. distance into a seagrass bed shows the relationship between velocity, bed size, and nutrient concentrations (Figure 3.10). The degree of nutrient reduction within the bed is inversely related to flow velocity. The larger and denser the seagrass bed and the slower the current, the greater the volume of water with reduced nutrient concentrations. As drag is decreased, there is less effect on nutrient concentrations (Figure 3.11). From these graphs we can estimate the relevant spatial scale under each set of conditions. Under low flow or high drag conditions, significant differences are seen within the first cell of the bed. At higher flow rates, it takes tens of meters for nutrient concentrations to be reduced. Though the slow current or dense bed conditions have the greatest effect on the nutrient concentrations, the overall effect of the bed on water quality will be greatest at higher flow rates. Contour plots in Figure

Figure 3.9. Output of MODFLOW model showing surface view of N concentrations over a large (400m), intermediate (160m) and small (60m) bed.
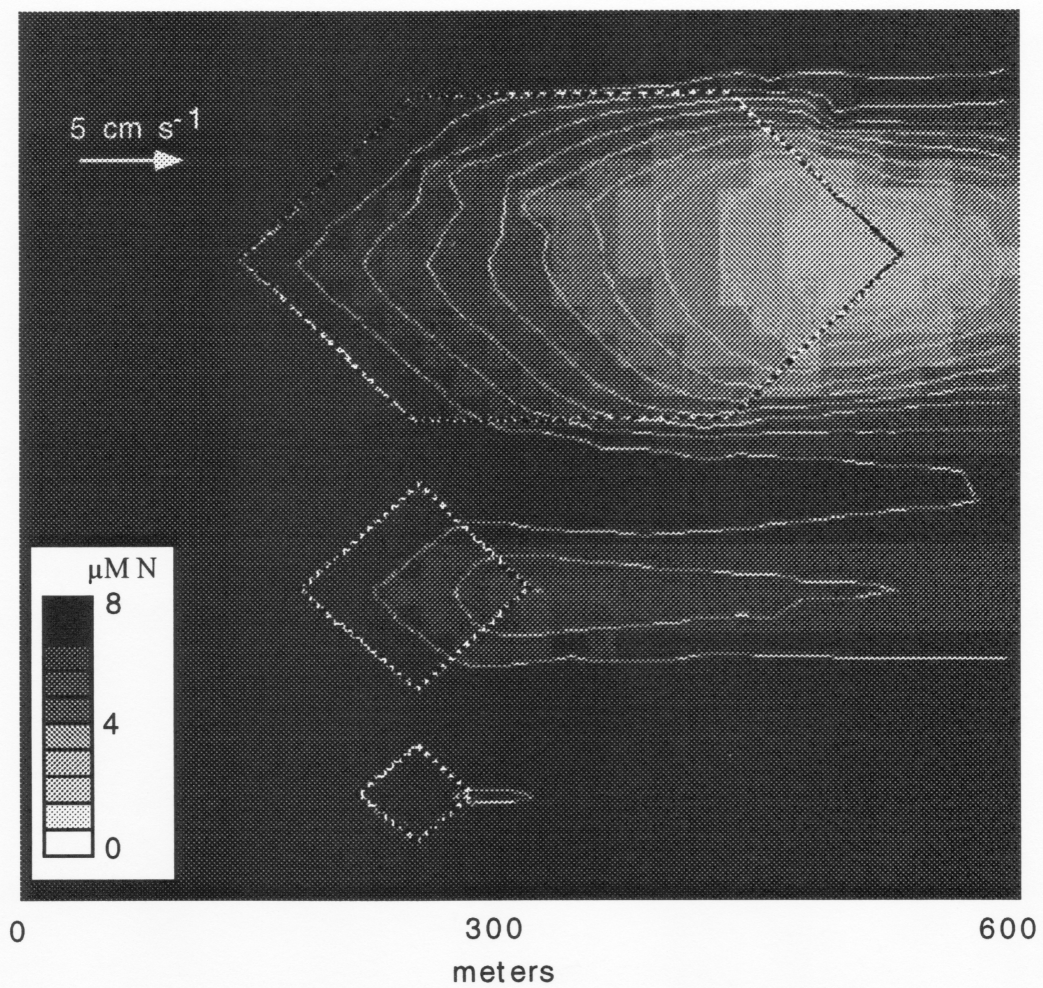
Figure 3.10. Sensitivity analysis showing effect of current velocity on DIN concentrations across a 400 m wide (0.16 km^2) bed.
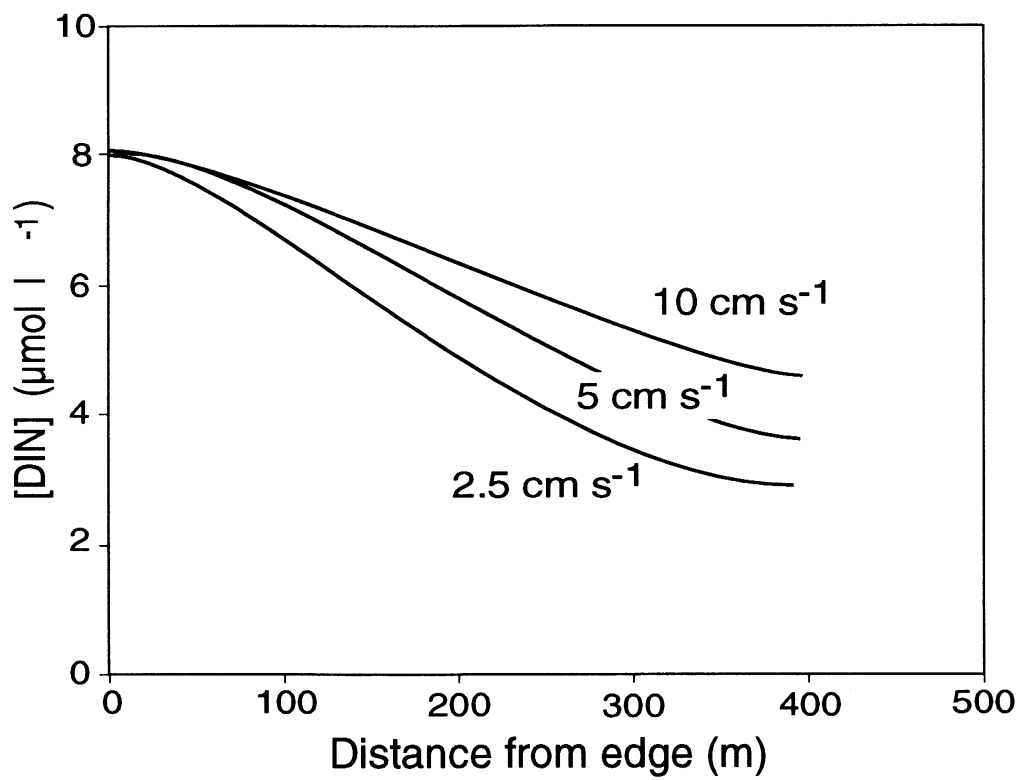
Figure 3.11. Sensitivity analysis showing effect of drag induced flow reduction (in percentages) on DIN concentrations across a 400 m wide (0.16 km^2) bed.
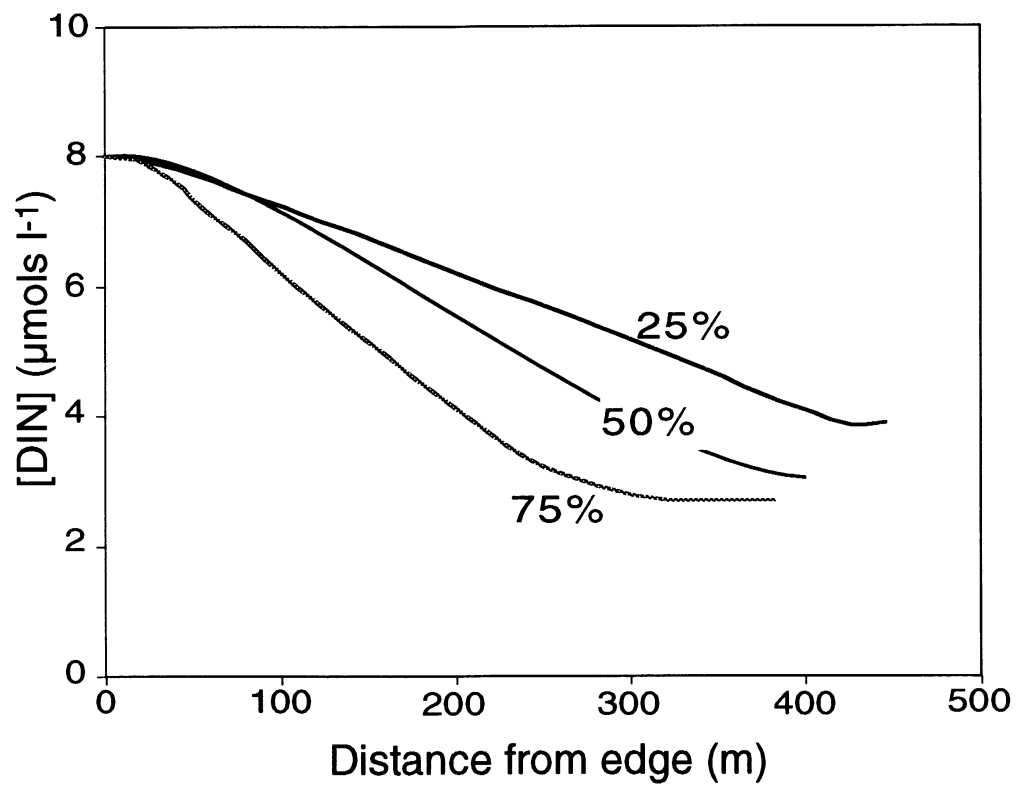
3.12 show the combined influence of current velocity and N concentration on maximum N reduction by seagrass beds. These show that large beds are needed to significantly reduce in-bed concentrations at higher water exchange rates.

Discussion

Transport control of seagrass bed nutrient uptake

Seagrass beds that are small or are in deep or fast flowing waters may have no influence on the nutrient concentrations in the overlying water. Transport of nutrients does not limit production in these beds, and diffusion at the leaf surface may be the limiting factor (e.g., Koch 1994). Seagrass beds that are larger or growing in slower moving water may reduce water column nutrient levels to limiting levels where transport can limit production. Transport into shallow, dense seagrass beds is decreased due to the drag induced by the seagrasses. Because of this, the exchange of nutrients and dissolved inorganic carbon (DIC) is further reduced. If the net water column nutrient uptake rate is high, this could further restrict nutrient supply to bed interiors. If a large bed is transport limited, a transport reduction of ~ 50% could significantly reduce nutrient supply to the bed interior.

The mesocosm experiment showed that a Widgeon Grass community can exert a high N demand at least on a short term basis. The net uptake rates I measured were in the range of literature values for uptake by individual rooted macrophytes (Thursby and Harlin 1984) and communities in situ (Howard-Williams 1981). This nutrient demand easily surpasses the DIN supply rate at moderate current speeds. Though our field measurements show that a significant reduction in nutrient concentrations can occur over a short distance particularly at the edge of a dense
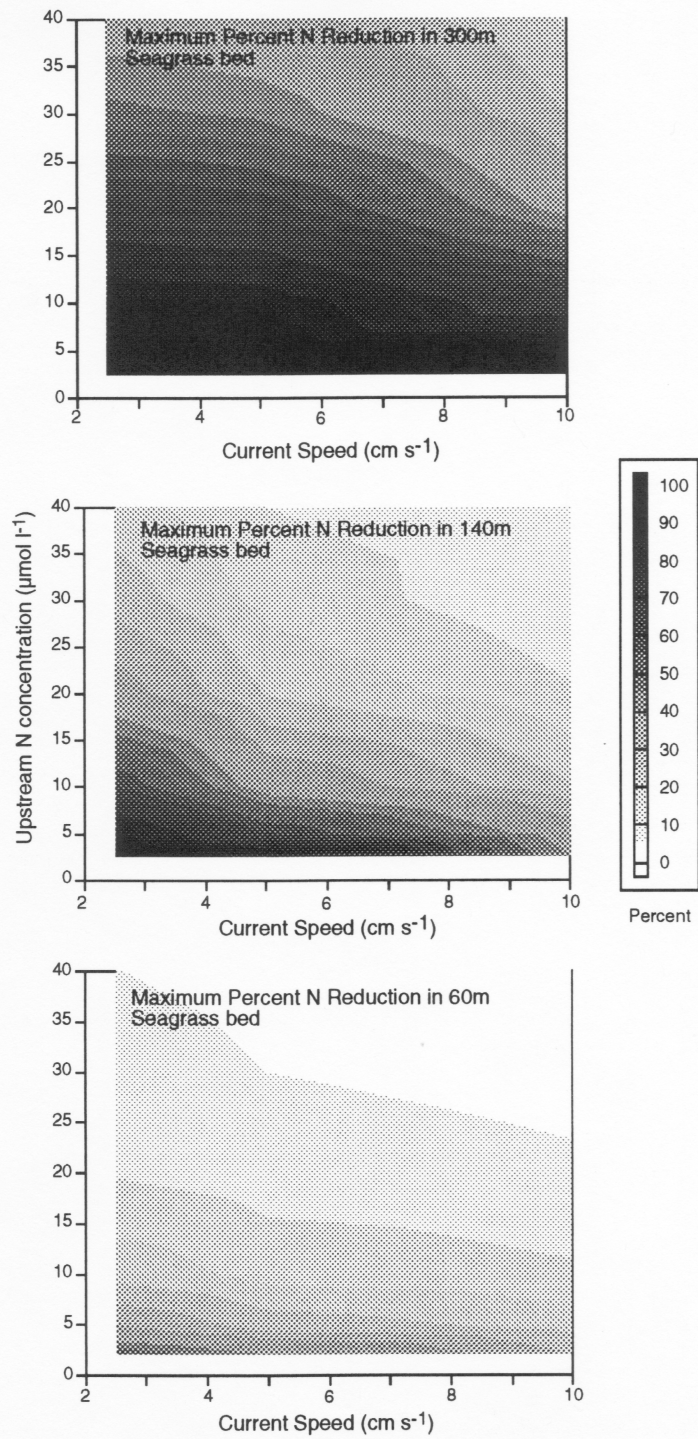
Figure 3.12. Model output of influence of current velocity and upstream N concentration on N concentrations across a seagrass bed.

seagrass bed during the day (Figure 3.6), these net uptake rates were not nearly as high as in the mesocosms, and sometimes indicated net regeneration. On the occasions when up-current nutrient concentrations were high, water transparency was good, and beds were dense, concentrations decreased with distance into beds. Slower net uptake rates in the field than in the mesocosm may have been due simply to lower nutrient concentrations and higher regeneration rates at the field sites. As external ammonium concentrations were usually below the half-saturation coefficient for leaf uptake (Thursby and Harlin 1984) leaf uptake rates were probably very low. On some occasions up-current NH_4^+ concentrations were already in the range of the half-saturation coefficient (~2 µM) for algal uptake (Goldman & Glibert, 1983, Scavia 1980) before being reduced further within the bed. This could have a negative effect on production over the course of a day in the center of the bed, depending on the ability of algae to store nutrients when they are available. Macrophyte production may be affected as well, though sediment nutrients could reduce the need for water column nutrients (Thursby and Harlin 1984, Hensel 1992) especially away from the edge where settling rates and regeneration rates are higher. The N content of *Ruppia* biomass (2.4 %) showed that plants in the dense bed interiors were neither nitrogen-limited nor saturated (see Gerloff and Krombholz 1996).

Though the model runs may under or over-estimate the net nutrient uptake of seagrass beds, they demonstrate qualitatively the effect that bed size, velocity and drag may have on nutrient concentrations. The model results show that under selected conditions, nutrient concentrations can decrease substantially across a large (400 m wide) seagrass bed. The positive feedback mechanism where seagrass communities

decrease nutrient concentrations, subsequently decreasing algal biomass and increasing available light, may occur in larger beds (> 400 m wide) at moderate flow rates (5-10 cm s^{-1}), but is only expected with very low flow rates (1-2 cm s^{-1}) in small (<100 m wide) beds. If we model a shallow bed using a 1 km square grid size, a nutrient uptake rate based on up-current nutrient concentrations may greatly overestimate the actual uptake since uptake is reduced at lower in-bed concentrations. If we integrate the nutrient concentrations over a large bed with the small-scale spatial model, we can modify uptake rates in a kilometer scale model.

The model sensitivity analyses can be used to quantify the effects of variables controlling nutrient concentration over a bed. By adjusting current velocity, bed roughness, and uptake rate, the model can be used to make predictions about the interactions of nutrients and seagrasses at a variety of shallow water sites. The steepest nutrient gradients should be found in dense, canopy-forming beds at slow current velocities. Beds in coves or near-shore where currents are slowed may reduce nutrient concentrations over shorter distances. At exposed sites like outer Trippe Bay (Figure 3.2), nutrient concentrations should be reduced significantly within 50 meters of bed edges.

Though net nutrient uptake by macrophytes beds has been documented in the Chesapeake Bay (Stevenson et al. 1981) and elsewhere (Howard-Williams 1981) and nutrient concentration gradients across seagrass beds have been reported (Casey and Westlake 1974, Moore 1996) gradients may depend on the bed location, net seagrass growth rates, recent turbidity, and the sediment nutrient concentration. Protected beds or interiors of large beds in areas with high turbidity may trap large amounts of

suspended organic matter that can serve as a nutrient source as it decomposes. Also, as water flow decreases with distance into a bed, more organic matter can settle, resulting in increased regeneration of nutrients. If the sediment nutrient concentration is lower near the bed edge due to water motion and lower organic content, the macrophytes there may remove more nutrients from the water column. Decreases in nutrient concentrations across a bed may be more likely to occur while submersed angiosperm biomass is accumulating. This occurred in a stream, where aquatic angiosperm accumulation accounted for the difference between up and downstream nutrient concentrations (Casey and Westlake 1974). As a bed matures and leaf density increases, sediment organic nutrients may accumulate due to increased deposition of leaves (e.g., Hemminga et al. 1999) as well as allochthonous matter (Ginsburg and Lowenstam 1958, Ward et al. 1984, Fonseca and Fisher 1986, Bartleson 1988, Koch 1999b, Gacia and Duarte 2001, Granata et al. 2001, Agawin and Duarte 2002, Schultz et al. 2003). Then, decomposition (regeneration) may supply much of the community nutrient requirements (e.g., Landers 1982). Whether macrophyte beds are a source (e.g., Prentki et al. 1979, Carpenter 1980) or a sink (Mickle and Wetzel 1978) of dissolved nutrients over the long term may only be decided by measurements of nutrient burial rates in sediments. In oligotrophic areas, beds that are nutrient-limited (e.g., Short et al. 1985, Barko and Smart 1986, Terrados et al. 1999) may be limited in size due to submersed angiosperm community uptake. Similar bed size effects or cross-bed gradients should be found in suspended solids and DIC. Reductions in DIC could also result in decreased photosynthesis of the submersed angiosperms or of algae.

Both nutrient supply and turbidity could be reduced within coves due to reduced wave energy and water exchange. Most beds in eutrophic areas of the Chesapeake Bay such as the Choptank River and Eastern Bay are found in coves (Figure 16 and 18 in Orth et al. 1995), while less eutrophic areas to the south (Tangier Sound, Figure 21 and 24 in Orth et al. 1995) have exposed beds. Consequently, coves should be considered as preferred seagrass restoration sites in eutrophic areas if there are not high nutrient loads from the immediate watershed or groundwater. Resources may be best spent by restoring one large bed instead of several small ones.

Transport reduction by seagrass beds

As the MODFLOW results indicate (Figure A1), dense seagrass beds affect water flow in the surrounding area as water is diverted around the bed. Flow velocities slow to a minimum in the first model cell and stay uniform across the central portion of the large beds. While this behavior was shown in field data at other sites (e.g., Madsen and Warncke 1983, Machata-Wenninger and Janauer 1991), this was not what I found at my field sites. Submersed angiosperms lack the lignified structural material of terrestrial rooted plants and so, resist flow only due to their buoyancy. Their flexibility that I observed, can lead to a greater degree of bending, and consequently lower drag (Sand-Jensen 2002) at the higher current speeds near the bed edge. Fonseca and Kenworthy (1987) also noted greater deflections of leaves at the edge of a seagrass bed. This flexibility allows the current energy to be transmitted (see Denny 1988) farther into seagrass beds. Because of this, a more gradual reduction in flow than the model suggests may be expected. This phenomenon would reduce the effect of small beds on water flow, and reduce the effects of all bed sizes

on water column nutrients at high flow speeds. Further measurements of the change in stem bending angles across the seagrass beds would allow model calibration that could result in a more gradual slowing of water into the seagrass beds.

Some plants (terrestrial, marsh or kelp) may be inflexible enough that a single plant, or row of plants may cause a significant flow reduction. The small reduction in transport I measured at the bed edges compared to mid-bed is evidence that the flow energy is attenuated with distance into the bed. Large flow reductions induced by an extensive seagrass bed are very dependent on the canopy height in relation to the water depth. When water depth exceeds the canopy height, flow over the canopy can compensate for the flow reduction within the canopy. The ratio of canopy height to water depth was approximately 1:1 at our sites, though reproductive shoot density was not as high as the vegetative shoot density.

The water flow profiles show that a lens of water near the bottom can be temporarily trapped by dense seagrass beds. This was also shown in other studies (e.g., Mullholland et al. 1994, Koch and Gust 1999). This will enable a large degree of interaction of the *Ruppia* community and the water column within the trapped layer, while reducing the interaction with the surface layer (e.g., Koch and Gust 1999). The large roughness height indicated by the profiles will also increase the potential for net sedimentation because resuspension is prevented (Fonseca and Fisher 1986, Bartleson 1988). It could also reduce pressure-induced porewater fluxes (e.g., Huettel & Gust 1992, Nepf & Koch 1999, Koch and Huettel 2000) since drag induced lift forces will be higher in the water column (away from the sediment).

Though blade density is commonly considered as a factor affecting water velocity and transport, bed size is not usually taken into account. Differences in flow reduction have been noted between dense and sparse *Zostera marina* beds (Eckman 1987, Worcester 1995). Though the relation between distance into the bed and flow conditions has been noted in reference to pollination (Ackerman 1986) it has not been fully examined by any means in the field. Some investigators have reported findings from flumes or from one location within a bed and made conclusions about the effect of the seagrass bed on water flow without considering that conditions will change across a bed. Small flume measurements can only simulate the edge of a bed (e.g., Gambi et al. 1990). Our measurements demonstrate the cross-bed differences in flow conditions due to the interaction of the water flow with the bed, and that conclusions about water flow within large beds should not be made from single point measurements or flumes. Location within beds, bed size, proximity to shore, depth, exchange rates, etc., can influence measurements of flow, nutrient cycling, seagrass growth, and food supply.

Balance between transport and diffusion supply of nutrients

Daytime reductions of dissolved nutrients within beds have been reported previously (e.g., Ozimek et al. 1990, Moore 1996). There have been few estimates of the degree of mass transport limitation experienced by seagrass beds, however, and estimates of nutrient loading per unit seagrass biomass are rarely mentioned in field or mesocosm macrophyte bed studies. Mass transport may limit productivity within beds, especially in oligotrophic waters, by reducing uptake of N and possibly carbon. Flow reductions and increased DBL thicknesses within beds could cause further

nutrient limitation. This may limit bed size or density in oligotrophic or quiescent

waters and result in highest algal productivity on the edge of beds.

Dissolved nutrient supply to seagrass communities depends on mass transport,

diffusion, regeneration and uptake kinetics. The relative importance of transport and

diffusion depends not only on the bed size but also location within the bed. Inside

large, shallow beds, with reduced nutrient transport and increased thicknesses of the

DBL, autotrophs could be limited by both mass transfer and diffusion. Rooted plants

appear to be less nutrient-limited than algae since they have access to sediment

nutrient pools, which often increase with distance into a bed (see Chapter 4). If

seagrass growth rates are higher inside beds due to higher sediment nutrients, and

epiphytic algae growth is decreased, this should accentuate differences in epiphytic

algal biomass from the up-current to the inside of a bed. Because of these processes,

small beds or edges of large beds may be more susceptible than bed interiors to algal

overgrowth due to elevated nutrient concentrations.

The reduced flow intensities ($u_{RMS, total}$), and u_{steady}/q ratios within the beds,

especially near the bottom, will result in increased diffusive boundary layer (DBL)

thicknesses, and further decreased nutrient and CO_2 exchange. Decreases of these

measures within the bed are significant for nutrient uptake, because it will be limited

by lower supply of N as well as increased DBL thickness (e.g., Koch 1994). The ratio

of u_{steady} to q has a large influence on the effect of flow intensity on potential

diffusion rates (see Porter et al. 2000). A change in $u_{RMS, total}$ will produce an order of

magnitude greater change in diffusion rate in mixed flow ($1 < u_{steady}/q < 4$) than in

steady flow ($4 < u_{steady}/q$) conditions. Since our sites fell into the mixed flow category,

small changes in $u_{\text{RMS, total}}$ result in large changes in potential diffusion rate. The combined effect of an average 50% reduction in the ratio of u_{steady}/q, and the 47% decrease in $u_{\text{RMS, total}}$ result in diffusion rate reductions of substantially greater than 50%. Mid-bed, near bottom values of u_{steady}/q indicated a switch to a fluctuating flow environment ($u_{\text{steady}}/q < 1$), where diffusion rates should be very slow (equal to plaster dissolution rates of 0.1 g h^{-1}).

Caveats

Because this is a simple model, there are many processes that it cannot capture, but it is useful for the goal of predicting nutrient concentrations over a large (400 m), dense (> 50% cover), shallow canopy-forming bed with slow-moving currents. However, since complete mixing within each cell is assumed, the model may overestimate the uptake of nutrients. Turbulent diffusion measurements and vertical oxygen profiles show that the mixing occurs over short distances (meters) (See Appendix). When the canopy height is less than the water depth, water will flow over the bed. In this case, over-canopy flow is not affected by leaf drag, and shear at the top of the canopy results in momentum transfer to the canopy (Kouwen & Unny 1973). This can also occur in a canopy-forming bed at high tide and at high current velocities. Though this could be represented by using more layers and increasing drag with depth, momentum transfer between layers does not occur in the simple model, so it would not be accurate. Water will preferentially flow through bare sections of a bed that is not uniform, and again, only a very detailed model will show this. It may also be more appropriate to adjust the cell sizes for bed density or velocity. At slow flow rates or high densities, nutrient reductions will occur in a shorter distance.

Due to the dynamics of estuarine systems a large amount of data may have to be collected to validate this model. For example, leaf nutrient demand may be reduced by high sediment nutrient concentrations (Thursby & Harlin 1984) and low light levels, so under turbid, eutrophic conditions, there may be little water column uptake by seagrasses or the attached epiphytic algae. Net community nutrient uptake should also vary with other conditions as well, and a bed could be a nutrient source instead of a sink. Thus, our model formulation is best for large (400 m), shallow (1 m), canopy- forming beds in low to moderate currents (1-10 cm s^{-1}) and moderate nutrient conditions (< 20 µM DIN). Under eutrophic conditions, with high organic sedimentation rates, leaf uptake rates may be negligible, but dense epiphytic algae populations may still reduce water column nutrient concentrations. Simultaneous measurements with current profilers up-current and inside the bed would improve the accuracy of the transport reduction measurements.

Conclusions

Seagrass bed size and biomass can influence the interaction of the seagrass community and the water column and cause gradients in nutrient concentrations. The model results and the gradients in nutrient concentration and hydrodynamics found over dense beds, demonstrate this. Interiors of large, dense beds may have lower water column nutrient availability due to lower mass transport rates and thicker boundary layers for diffusion. Gradients in suspended solids can also be found across large beds as incoming particles settle out with the reduced water motion. As a result, interiors of large beds may have much lower sediment nutrient regeneration rates than areas near the bed edges. Concentrations of larvae or eggs of aquatic animals, as well

as their food supply can also be greater at bed edges (Irlandi 1994, Bologna and Heck 2002). Since gradients in water quality and hydrodynamics may exist across shallow seagrass beds, researchers studying these beds should consider this when designing their experiments or monitoring projects.

Though the model used here is highly simplified, it provides a way to visualize and quantify the relationship between factors such as seagrass biomass, water exchange and nutrient reduction across beds. The interactions should be greatest in large, dense, canopy-forming beds with low exchange rates, such as those found within coves. Because nutrient reductions within these beds may result in decreased algal growth and increased light availability, models of canopy-forming seagrass systems with high seagrass biomass should use a grid size small enough to capture these interactions (0.5 km or less), or adjust coefficients to compensate. With some exceptions (e.g., Bell and Hicks 1991, Robbins and Bell 1994, Fonseca et al. 2002), seagrass researchers have generally ignored large-scale landscape patterns that terrestrial researchers have found important. This may result in misinterpretation of results at a small scale and therefore inaccurate conclusions of models at a larger scale.

Chapter 4: Importance of bed size in determining water quality gradients and epiphyton distribution across *Ruppia maritima* L. beds in mid Chesapeake Bay

Abstract

I investigated the hypothesis that *Ruppia maritima* L. communities can improve water quality and hence, withstand eutrophication provided the bed size is large and dense enough to buffer nutrient inputs. Parameters such as plant density and current velocity affect the interaction of seagrasses with the water column but these effects have not been quantified and are often ignored. Understanding these relationships is important for determining water quality standards and restoration goals, particularly in coastal waters where eutrophication has been documented. I measured water column TSS and ammonium, water flow profiles, sediment characteristics, epiphyton mass and chlorophyll *a*, and *Ruppia maritima* biomass across seagrass beds in the mesohaline Chesapeake Bay. Dissolved oxygen and pH increased with distance into the beds during daylight hours reflecting high rates of areal net primary production. Measured pH changes indicated up to 31% reductions in dissolved inorganic carbon (DIC) in the interior of beds over 200 meters wide. The reduced DIC availability and increased oxygen in bed interiors could reduce bed productivity because of C limitation and O_2 inhibition of photosynthesis. Water column ammonium concentrations were slightly lower within beds, but did not decrease in stoichiometric relation with DIC. Based on this, N demand by the seagrass bed communities was met mainly by sediment regeneration. Overall, there was no significant difference between total suspended

solids (TSS) inside and up-current from seagrass beds. Epiphyton dry mass (all biotic and sediment material attached to leaves) per cm^2 of leaf surface was lower in bed interiors except when cownose rays were not present and increased with TSS concentrations, which were often higher near shore. Epiphyton chlorophyll *a* showed no consistent pattern across beds except in the fall of 2001 when it was highest on the edges of all beds sampled. Sediment grain size decreased with distance towards bed interiors and from the source of wave energy. Large beds appear to have a gradient of trophic conditions from up-current to inside, while conditions in small beds are dictated by the surrounding water and bed location. Due to its influence on the water column, seagrass bed size and location affects the ability of seagrasses to compete for light and carbon as well as the growth of resident fauna and flora in brackish, eutrophic waters.

Introduction

While submersed angiosperm communities are qualitatively important for their high primary productivity (Zieman 1982), providing habitat for aquatic fauna (Heck and Thoman 1984), improving water quality (Howard-Williams 1981), and for their function in erosion control (Thorhaug 1986), quantification of key ecological processes has been elusive. Eutrophication indirectly reduces bottom coverage of seagrasses and other submersed angiosperms by increasing planktonic (Sand-Jensen and Borum 1983) and epiphytic algae (Sand-Jensen 1977, Phillips et al. 1978) thus reducing light availability to the leaves and other benthos. Dense beds of submersed angiosperms can cause local reductions of water column nutrients (Howard-Williams 1981, Van Donk et al. 1993) and dissolved inorganic carbon (Van den Berg et al.

2002), and elevated dissolved oxygen and pH (e.g., Reddy 1981). These water quality changes can have complicated physiological effects on the components of the benthic community. For example, epiphytic algae depend on the water column for nutrients and dissolved inorganic carbon (DIC), so their growth may be reduced if the incoming supply of these critical materials is lowered. This reduction in epiphytic algae could, in turn, increase light availability to submersed angiosperms (Sand-Jensen 1977). Submersed angiosperms also reduce current speeds, resulting in decreased nutrient transport, increased net sedimentation of total suspended solids (Ginsburg and Lowenstam 1958, Ward et al. 1984), and increased water clarity. Several studies show the effect of submersed angiosperms on hydrodynamics (e.g., Fonseca et al. 1982, Sand-Jensen and Mebus 1996, Koch 1996), but these effects may vary with changes in variables such as water flow rates (Fonseca et al. 1982, Koch and Gust 1999), stem density (Nepf 1999). The effect of bed size remains an open question. Though there are some reports of changes in water quality (e.g., Moore 1996) or current velocity (e.g., Fonseca et al 1982, Sand-Jensen and Mebus 1996) with distance into beds, additional field information would facilitate quantification of the effects of bed size and density on spatial variations in water quality. For example, while maximum flow rate changes may take place within cms of the bed edge in a flume, where water is forced through the bed (Fonseca et al 1982), water can flow around beds in the field. This may result in larger vertical gradients in current velocities as leaf friction extracts energy from the overlying water.

A recent report (Kemp et al. 2004) concluded that the suitability of water quality for submersed angiosperms in the Chesapeake Bay could be calculated using

nutrient and total suspended solids (TSS) concentrations. A previous Chesapeake Bay study (Stevenson et al. 1993) correlated the presence of submersed angiosperms with water quality at the up-current edge of seagrass beds. If large beds can significantly alter nutrient and TSS concentrations, then it may be necessary to consider bed size when deciding habitat requirements. Though bed size or location within a bed may influence their results, some studies (e.g., Ward et al. 1984, Jones 1990, Terrados and Duarte 2000, Gacia et al. 2002) compare characteristics of vegetated and unvegetated areas without considering either variable. There may be little difference between the two sites if the seagrass bed is not dense or large enough, or under wave dominated conditions (see Koch and Gust 1999). In large seagrass beds, the measured variables may depend on location within the bed.

I hypothesize that the amounts of nutrient and carbon uptake by a seagrass bed, and the effect of these nutrients on the community, will depend on the residence time of water in the bed. In turn, this will obviously depend on the hydrodynamic regime (tides and waves; Koch and Gust 1999) and water flow rate, which in turn depends on the leaf surface area and plant spatial distribution (Nepf 1999). Again bed size effects remain largely unstudied but nutrient uptake by a bed will depend on environmental conditions such as temperature and light, but will also depend on hydrodynamic conditions (Koch 1994, Cornelisen and Thomas 2002) and on water column and sediment nutrient concentrations (Carignan 1982, Thursby and Harlin 1984, Hensel 1992, Madsen and Cedergreen 2002). These conditions may change across large beds as nutrients are absorbed and hydrodynamic energy is dissipated. Most of the studies that have shown effects of submersed angiosperms on water

quality have been in lakes with slow exchange rates. Estuaries and large lakes will have a range of flow conditions that will influence the degree of physico-chemical interaction.

Relationships between seagrasses and the water column should be related to the degree of water exchange, the area of seagrass coverage (bed size), the shoot density and the spatial pattern; because these influence exchange and particle trapping. Thus, I hypothesize that large, canopy-forming seagrass beds occupying most of the water column in slow currents will have gradients in water column nutrients, DIC and DO from up-current to inside. These water quality gradients should result in a shift toward oligotrophy and increased available light toward the interior of large beds. If interior nutrient and DIC concentrations are below the nutrient half saturation concentration constant for algal uptake, algal biomass may be decreased and light availability to leaves may be increased. TSS gradients should also result in increased light availability and lower epiphyton mass in bed interiors. From a previous work (Frankovich and Fourqurean 1997) I theorize that epiphyton coverage is also correlated with nutrient gradients if they exist. Small, sparse beds in fast currents should have little effect on water quality with less potential for feedback effects such as decreased algal biomass and increased light availability (Figure 4.0). Sediment parameters are also affected by large beds. There should be decreases in particle and increases in %AFDW with distance into beds. I hypothesize that oxygen efflux and sediment Chl a will decrease with distance into beds.

Knowing more about the effects of bed size may give us a better understanding of the manners in which eutrophication affects seagrass ecosystems.

Figure 4.0. Feedback diagram of seagrass bed and water column. The diagram shows effects of seagrass on water column nutrients and algae resulting in positive feedback for seagrass growth. DBL is the diffusive boundary layer thickness. Plus signs denote positive effects and minus signs denote negative influences. The effect of one parameter on another is determined by counting plus and minus signs in between them. If there is an odd number of minus signs, the influence is negative and if there are all plus signs or an even number of minus signs, the influence is positive.
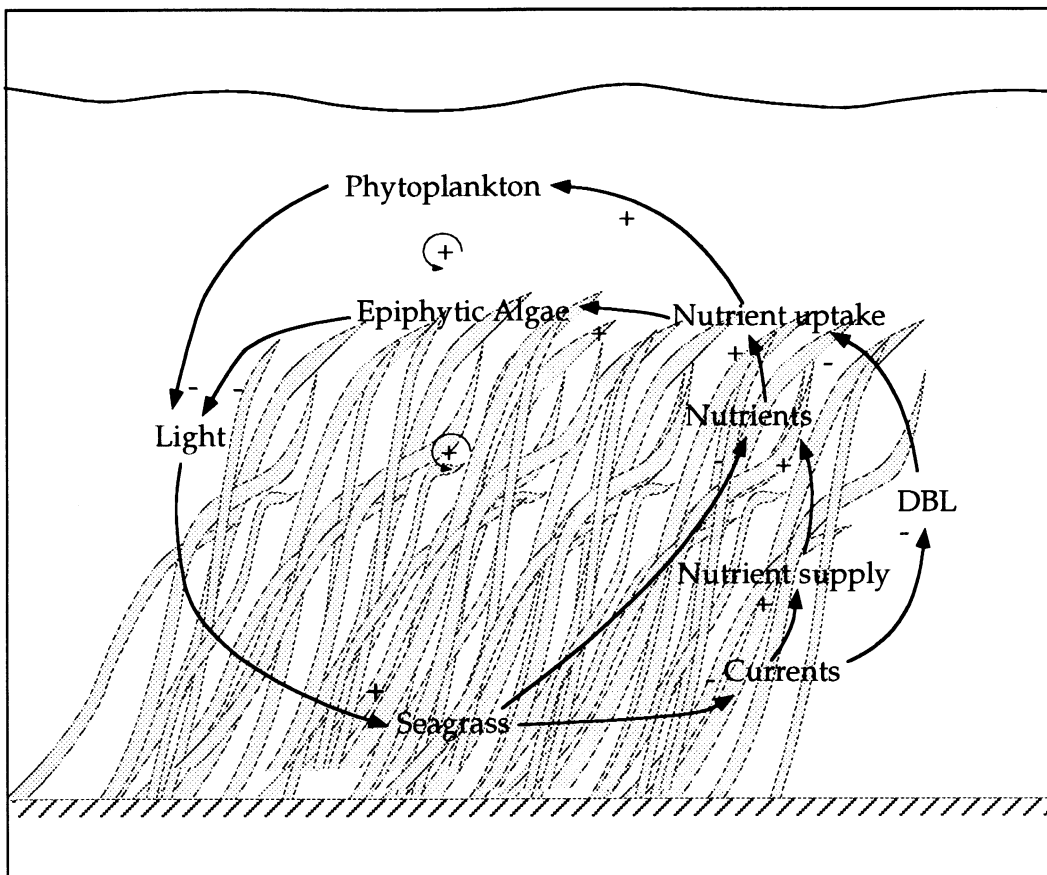
The goal of this study was to increase the ability to predict responses of shallow estuarine ecosystems to nutrient addition by quantifying effects of seagrass biomass and bed size on water quality and to demonstrate how this could feed back and influence macrophyte growth.

Methods

Study areas

I chose vegetated and adjacent unvegetated areas along the mesohaline Choptank and Little Choptank Rivers, Chesapeake Bay, Maryland, USA as primary study sites (Figures 4.1 and 4.2 and Table 4.0). Chapel Creek Cove (HC1) was furthest upriver with Todd cove (TC1 and TC2) and Cook Cove (CC1) down-river. Trippe and Brannock Bay (TN1, TN2, BB1, BB2 and BB3) face the Chesapeake Bay at the river mouth, and LC1 is 2 km from the mouth of the Little Choptank. The sites had a range of Widgeon Grass (*Ruppia maritima* L.) densities and sizes. Sites TC2, BB2 and TN2 were unvegetated areas adjacent to sites TC1, BB1, and TN1. In recent years, this species has been the most prolific in the mesohaline portion of Chesapeake Bay (Orth et al. 1995). Some other sites were only sampled on one or two occasions. One of these sites was north of the Choptank River in Eastern Bay (site EB) and three were south: site TB in Tar Bay, site HO at the mouth of the Honga River and site ON at the mouth of the Onancock River (see Figure 4.14).

In the Chesapeake region, the strongest winds annually are from the north-northwest. On the Choptank River in 2001, the mean wind speed from the northwest quadrant was ~ 9 knots, while the other quadrants averaged ~ 5 knots at the Horn Point weather station (see Figure A2). Each site had different exposures to the

Figure 4.1 Chart of main study sites in mesohaline Chesapeake Bay. BB represents
Brannock Bay sites (BB1, 2 and 3); TN represents Trippe Bay sites (TN1 and TN2);
CC1 marks Cooks Cove; TC is Todds Cove (sites TC1 and TC2); HC1 is Chapel Creek;
and LC1 is the Little Choptank River site.
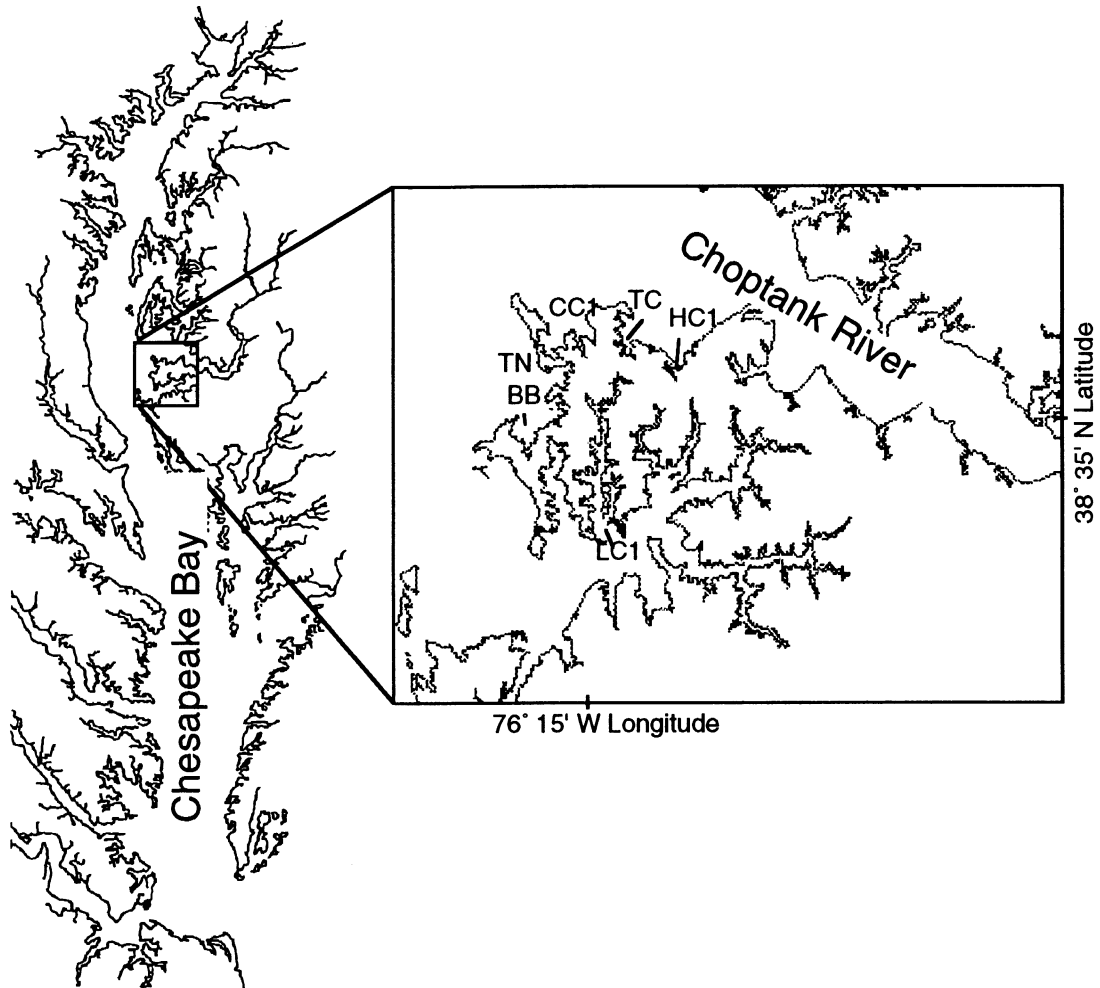
Figure 4.2. Macrophyte beds and depth profile maps of sites in fall 2000. Shaded areas are macrophyte beds and contour lines are depths in meters below mean low water. Site TN1 and BB1 are in Trippe Bay and TC1 is in Todds Cove. Land is stippled or out of the mapped area.

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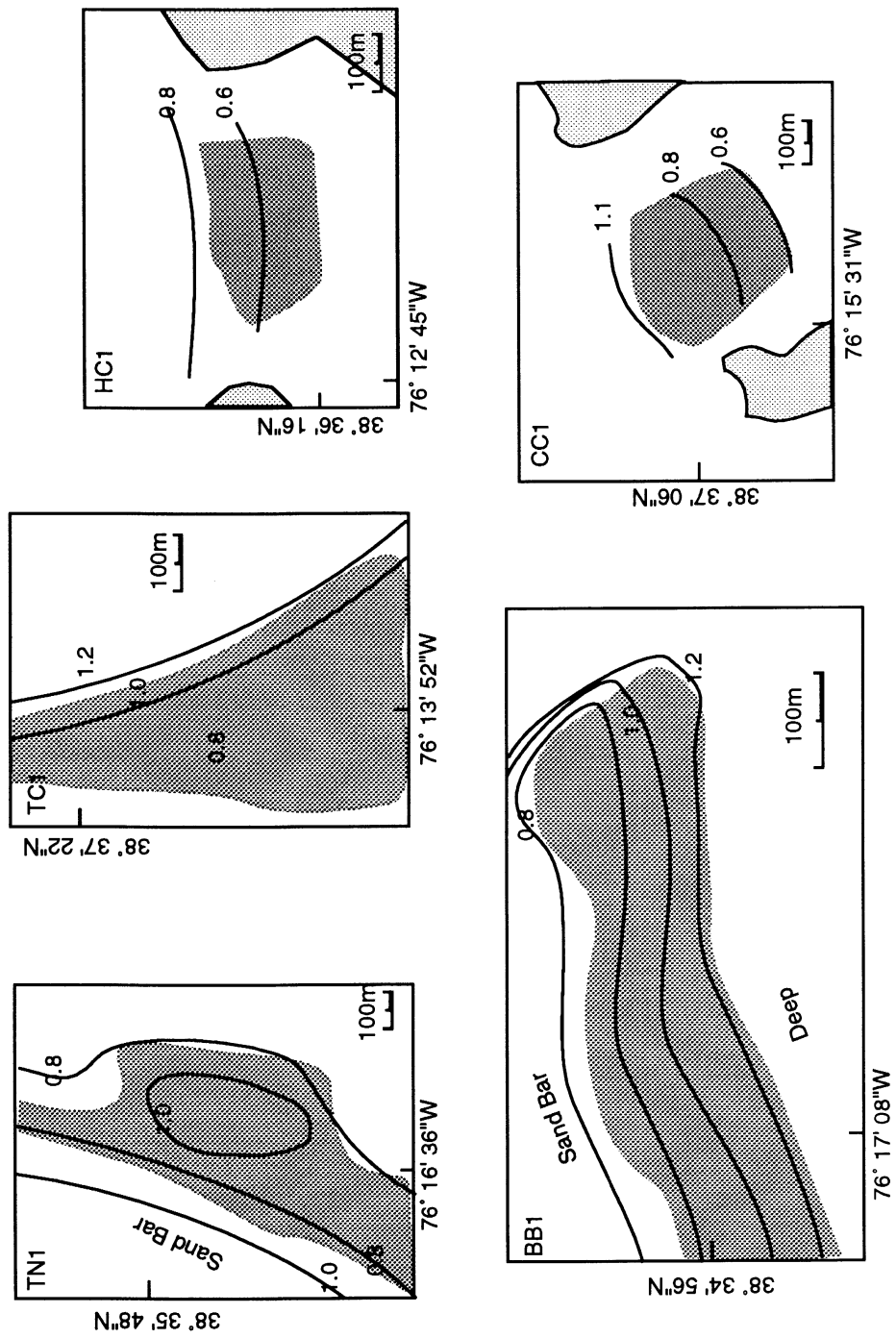
Table 4.0 Location of *Ruppia maritima* bed study sites with bed widths (in relation to flow direction), macrophyte biomass and percent coverage. Densities are mean and 1 *SD*.

Site	Latitude	Longitude	Date	Width (m)	Biomass (g dwt m^{-2})	Percent Cover (%)
TC1	38° 37.1'	76° 13.5'	1999	500	68 ± 22	75
TC1	38° 37.1'	76° 13.5'	06/03/00	340	37 ± 21	40
CC1	38° 37.2'	76° 15.4'	06/08/00	180	42 ± 8	50
HC1	38° 36.4'	76° 12.6'	08/08/00	170	49 ± 18	75
TN1	38° 35.8'	76° 16.6'	09/17/00	400	81 ± 26	95
BB1	38° 34.8'	76° 17.1'	10/06/00	280	94 ± 12	80
BB3	38° 34.5'	76° 17.2'	07/28/00	120	87 ± 7	95
TC1	38° 37.1'	76° 13.5'	05/24/01	340	87 ± 7	95
BB1	38° 34.8'	76° 17.1'	06/20/01	320	82 ± 32	90
TC1	38° 37.1'	76° 13.5'	06/28/01	270	18 ± 11	30
ON	37° 42.9'	75° 50.7'	07/29/01	nm	nm	nm
LC1	38° 32.8'	76° 15.9'	08/09/01	130	80 ± 24	80
BB1	38° 34.8'	76° 17.1'	08/16/01	280	75 ± 20	85
TN1	38° 35.8'	76° 16.6'	09/17/01	400	102 ± 16	95
CC1	38° 37.2'	76° 15.4'	09/13/01	220	89 ± 25	50
HO	38° 14.6'	75° 08.6'	10/15/01	nm	nm	nm
TB	38° 20.5'	76° 14.1'	10/15/01	nm	nm	nm
EB	38° 56.1'	76° 16.0'	10/19/01	nm	nm	nm

nm: not measured

strongest wind and waves. The most wave-exposed sites were at Trippe Bay (TN1 and TN2) and Honga River (HO), and these were exposed to a long NNW fetch (more than 50km). Site BB1 was protected on the west but only sheltered from the open bay by shallow sand bars. Site BB2 and BB3 were just south of and protected by site BB1. Site BB3 was fully protected and near shore. The other Choptank sites (TC1, TC2, and CC1) were upriver and had a maximum exposure to the north with protection from the west. Cook Cove was exposed to the northwest and had sandbars running NE to SW on the north edge of the bed. Todd Cove had no sand bars. The northern fetch there was the width of the river (~10 km). Site LC1 was on the north side of the Little Choptank River and, therefore, was the most protected from the strongest winds from the NNW. Site EB was similarly protected from the north.

Water depth over the beds decreased from 1.9 m to 0.3 m toward shore in Todd and Cook Cove, but depth at sites TN1 and BB1 was shallowest (0.5 m) at the outer edge (a sand bar) and sloped into a shallow basin toward shore. Site BB2 averaged 0.3 m deeper than site BB1. Site TN2 was west of site TN1, and had a similar average depth. Site BB3 is shallow and near shore. Site HO was 1.2 meters deep, with depth increasing offshore. Water depth at site EB was 0.5 m. Salinity in the area of the Choptank River sites ranges from 9 to 15 psu, increasing from spring to fall. Growing season water temperatures range from 15º C in spring to 25º C and then back to 16º C in the fall. Some *Ruppia* plants maintain short vegetative shoots through the winter when temperatures fall below 5º C.

The Choptank River has persistent gradients of water column nutrients and total suspended solids (TSS) decreasing from upstream to downstream due to

watershed and sewage inflows (Stevenson et al. 1993, Staver et al. 1996). Upstream dissolved inorganic nitrogen (DIN) and TSS values are commonly >1.4 and 30 mg l^{-1} respectively and downstream values as low as 0.014 and 6 mg l^{-1}. Water column nutrient concentrations at our sites were generally low, and were lowest in late summer and early fall.

Ruppia biomass determination

I usually made sampling trips on calm (< 7 knot wind) days during the active seagrass growing season: March through November, of 2000 and 2001. I also sampled site TC1 in the summer of 1999. After May, the *Ruppia maritima* reproductive shoots were up to 1 m long, and formed a partial canopy over the shorter 10-20 cm vegetative meadow. In spring, I located and mapped the approximate location of the Choptank River seagrass beds (using GPS receivers) by feeling for vegetation with our feet, and when the water was clear enough, I circled the bed in a boat mapping the bed boundaries and depth using a GPS receiver and measuring staff, respectively. I also took photographs of some seagrass beds from about 250 m with a tethered balloon and a programmable camera (Samsung Maxima Zoom 105). I used commercial photographs (courtesy of Virginia Institute of Marine Science) taken at a scale of 1 to 24,000 to supplement our maps. Percent seagrass cover was determined visually or by analysis of scanned photos using NIH Image software. To determine macrophyte biomass, I collected *Ruppia* biomass across three replicate transects using stratified/random sampling procedure and a 0.05- 0.1 m^2 quadrat. I uprooted the plants, placed them in bags in a cooler for later processing. In sparse beds, I sampled in the nearest patch to our random location and multiplied the resulting macrophyte

biomass by the percent cover to determine average biomass. In the lab, I measured the length of ~ 25 vegetative leaves and all the reproductive stems from some samples. I washed and subsequently dried the plants at 60° C until constant weight.

Epiphyton determinations

To determine epiphyton biomass in 2000, the third node from the growing tip of a given shoot was collected at sites across three stratified random transects in each cove. The third node was chosen as a way to normalize for the progression of epiphytization as leaves age. In 2001, the turions were selected at random, because the younger (first through third) turions were observed to have lower than average epiphyton loadings. Two to three replicates were taken at each site, placed in plastic bags and put in a cooler. The samples were taken back to the lab for analysis. Care was taken to avoid loss of epiphyton but waves may have dislodged some. Even when there was little turbulence, loosely attached material was still lost. The length and width of each seagrass blade was measured in order to calculate the total blade area. I separated epiphyton from the seagrass blades in water using a razor blade. I then filtered portions of the resulting slurry through pre-weighed, pre-combusted glass fiber (GFF) filters. I then dried the filters at 60° C for 24 hours and placed them in a desiccator before re-weighing. Total epiphyton load (mg epiphyton dry weight cm^{-2} seagrass blade area) was determined from the dry weight of the separated epiphyton and the area of the seagrass blades. To determine organic epiphyton biomass, the filters were then combusted by placing them in a muffle furnace at 450° C for one hour. The filters were re-weighed and the percent ash free dry weight (AFDW) was then determined by subtracting the ashed weight from the dry weight, dividing by the

dry weight and multiplying by 100. The inorganic epiphyton load (mg inorganic epiphyton weight cm^{-2} seagrass blade area) was calculated by subtraction from the organic biomass and the area of the seagrass blades.

For the epiphytic algal determination, the same process as described above was followed until filtration. The epiphyton slurry was filtered through unwashed GFF filters. The filters were wrapped in aluminum foil and put on ice. Chlorophyll *a* (Chl *a*) concentrations were determined flourometrically using a Turner Designs model 700 fluorometer (calibrated against a pure chlorophyll standard) immediately after grinding in 90% cold acetone.

Physical and chemical measurements

Most water quality sampling trips coincided with flood tide. On each sampling trip, I measured water depth and current velocity as well as water quality parameters such as turbidity and dissolved oxygen (DO). I measured these parameters by towing a Hydrolab Datasonde (model III or IV) and a YSI DO probe (Model 57) behind a canoe across the beds and adjacent unvegetated areas. I took readings or recorded values from mid-depth every 15 to 60 seconds along with GPS coordinates. Diel measurements of water quality were made inside the seagrass bed at Todd Cove (on 06/14/00, 07/18/00 and 08/02/01) and Brannock Bay (on 08/25/00, 09/08/00) using Hydrolab Sondes and ISCO samplers. DO probes were calibrated daily and checked against each other. The other Sonde sensors were calibrated and DO probes were calibrated to zero twice monthly.

Current velocity was measured on flood tide either before or after water quality measurements either with dye or with an acoustic Doppler velocimeter (ADV,

10 MHz model, SonTek Inc., San Diego, California). Dye measurements were made by injecting dye at mid depth with a large syringe or plastic bottle and timing the passage between rods inserted into the sediment a meter apart. The ADV sampled at 25 Hz for 3.6 to 6.8 minutes per reading (see Voulgaris & Towbridge 1998 for review). The ADV probe was clamped to a stainless steel rod that was pushed approximately half a meter into the sediment. To determine transport, I measured 3 to 4 current velocity profiles along a transect from up-current to the inside of the seagrass beds, taking about 15 minutes per profile (see example in Figure 4.3). Transport was then calculated by adding the trapezoids formed using the average velocity and the depth difference of each pair of measurements and the area of the rectangle formed by connecting the upper velocity measurement from the depth of measurement to the surface. Water depth was measured prior to sampling at a marked site and while sampling along transects.

I sampled water column TSS either at approximately 50 m intervals across selected transects (~ 4 per bed) or mid-bed and up-current from the seagrass beds. I determined TSS concentrations of the water samples by pre-combusting GFF filters at 450° C, filtering an aliquot of the shaken sample, rinsing with DI water, drying at 60°C, desiccating and reweighing the filters. I took sub-surface nutrient samples across transects, filtered them through GFF filters, stored them on ice and analyzed them for dissolved NH_4^+ photometrically (Parsons et al. 1984). Net nutrient uptake was calculated from the change in nutrient concentration with time multiplied by the water volume and divided by the surface area.

Figure 4.3 Horizontal profiles of current velocity across a *Ruppia* bed at Trippe Bay (TN1) on 10/15/00. Each symbol is the result of a 3.6 minute average of ADV data. Solid lines are extrapolated by eye and extend to the surface. In this bed, the vegetative shoots were 15 cm tall and reproductive shoots extended to ~ 70 cm (arrows) above the bottom. The coverage was patchy (60% cover) at the edge, but denser (95%) inside. Measurements made from 12:44 to 14:50 pm.
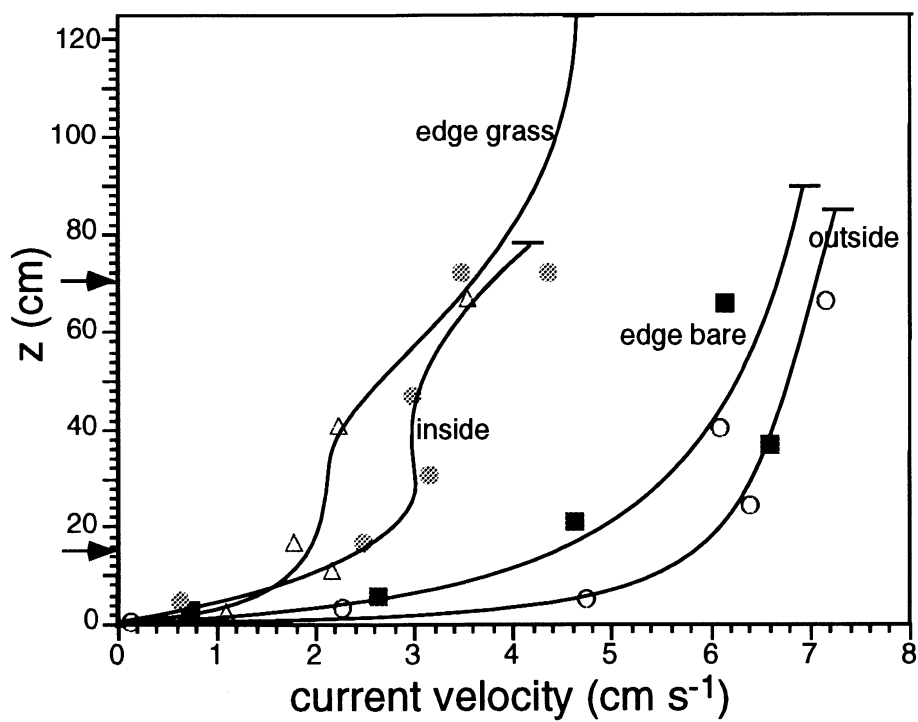
I measured local wind velocities at time of sampling with a Brunton hand held vane anemometer. Chesapeake Bay Observation System buoys recorded regional conditions that I correlated with sampling intervals. Average wave height within beds was estimated using a meter stick.

Sediment sampling and measurements

I took sediment cores along transects in several beds using a 2.5 cm dia. corer. I analyzed either the top 1 cm for percent ash free dry weight (AFDW), or used the top 5 cm for sediment grain size analysis. For AFDW analysis I dried (60º C) and weighed the sample until constant weight prior to combusting at 450º C for 1 hour and re-weighing. AFDW (%) was then determined by subtracting the ashed weight from the dry weight, dividing by the dry weight and multiplying by 100. I washed the sediment from the surface (top 5 cm) cores through sequential sieves and weighed each sediment grain size fraction after drying.

Sediment-water nutrient fluxes were measured on two occasions (08/29/00 and 9/22/00 at BB1). Four cores (10 cm dia.) about 100 m apart (each including up-current, patchy edge, and two mid-bed) were taken along three transects. I took care to avoid including macrophytes in the sample. The cores were enclosed and placed in a water bath with Choptank River exchange water and the overlying water was continuously, gently stirred using stir bars. Water samples were removed every 2 hours until dark and then in the morning. These samples were analyzed for DO. Sediment Chl *a* was determined after the experiment was over (acetone extraction with centrifugation, followed by the fluorescence measurement).

Sediment porewater nutrients were also measured twice at the Trippe Bay site (TN1) in fall 2001. Porewater diffusion samplers (Hesslein 1976) were filled with deionized water that was purged with N_2 gas. The samplers were taken to the site in a bucket of oxygen-free DI water and pushed into the sediment so that the sample chambers were approximately 2 to 6 cm deep. They were left in the sediment for a week before sample collection (removing peepers, withdrawing the sample with a syringe), return to the lab on ice, and subsequent analysis for NH_4^+.

Data analysis

I calculated DIC concentrations using pH, temperature and salinity data and the geochemical software PHREEQC (Parkhurst and Appelo 1999). I adjusted ion concentrations and alkalinity assuming a linear relationship between upstream freshwater measurements at Greensboro MD (USGS) and seawater values. Results were checked using the pH and alkalinity calculation in Millero and Sohn (1992) and calculating alkalinity as A_T (μmol kg^{-1}) = 660 + 47.6 S (Hunter 1998). I assumed that the change in alkalinity due to DIN uptake and change in DIC due to $CaCO_3$ formation were negligible. I used the Wilcoxon matched-pairs signed-ranks test to compare DO, epiphytic algal Chl a, epiphyton dry weight, and TSS between locations. If p values were < 0.05 I considered the results significant. The Mann-Whitney U test was used for non-paired comparisons of epiphytic algal Chl a and sediment parameters. A multiple regression analysis was used to show the relationship between DO change, water velocity, macrophyte biomass and depth. I used Graphpad Instat (Graphpad Software Inc.) for all statistical tests as described in Sokal and Rohlf (1981).

Site characteristics

Site locations and bed characteristics are listed in Tables 4.0 and 4.1. The sites had a range of Widgeon Grass areal coverage, with Trippe Bay site TN1 having the highest (95% cover), and Chapel Creek Cove having the lowest biomass (averaging < 25% cover in 2001). In August of 2001, Site TN1 above-ground biomass averaged 102 g dry wt. m^{-2}. Percent cover and biomass varied greatly over both years at Todd Cove. Schools of large cownose rays (*Rhinoptera bonasus*) were observed digging for infauna mainly in Todd Cove and Chapel Creek Cove during June through November of both years. While feeding, they resuspend the sediment, increasing TSS concentrations. A crab trawler was very active over the Trippe and Brannock Bay sites in 2000, and this substantially reduced the density of reproductive shoots during the summer. Hydraulic clam dredging was intensive near Todd and Chapel Coves during each spring. The dredges completely uproot plants in their path and generate plumes of highly turbid water (> 120 mg l^{-1}). Though the Todd Cove bed was almost completely scoured away by feeding rays in June and July 2000 (to 40% cover), the remaining *Ruppia* plants were able to spread and form a large dense bed (340 m wide) by fall. In 2001, the Todd Cove beds were badly damaged by the rays and did not recover fully. Chapel Creek Cove also experienced large biomass changes due to rays but stayed very sparse (< 10 % cover) through fall of 2001. Site LC1 was very sparse in 2000 but was quite dense (80% cover) in 2001. Mute swans were also occasionally abundant in Trippe Bay, Todd Cove and Chapel Creek Cove. They dug up and ingested Widgeon Grass and their excretion may have affected dissolved

Table 4.1 *Ruppia maritima* bed characteristics and water quality gradients at sites where sufficient measurements were taken. DO change was calculated for two transects on 05/05/01. Means and 1 *SD* are given for *Ruppia* biomass. Bed width is in the direction of flow.

Site	Date	Bed Width (m)	Water Depth (m)	Shoot Density (g dwt m^{-2})	Percent Cover + (height)	Current Speed (cm s^{-1})	DO change (μg l^{-1}m^{-1})	NH$_4^+$ in (μmol l^{-1})	NH$_4^+$ out (μmol l^{-1})	TSS in (mg l^{-1})	TSS out (mg l^{-1})
TC1	1995	500	0.7	68 ± 22	75 (t)	1	16	-	-	-	-
BB1	07/28/00	280	1.0	94 ± 12	95 (t)	6	8	3.18	2.15	12.3	3.2
BB2	07/28/00	-	1.2	0	0	4	0				
BB3	07/28/00	120	1.2	87 ± 7	95 (t)	0.5	24	1.26	0.60	4.6	4.3
HC1	08/08/00									13.5	46.9
TC1	08/24/00	340		37 ± 21	40	2.5		3.9	5.12		
TC2	08/24/00	-	1.1	0	0	4	1				
TN1	09/17/00	400		81 ± 26	90	6		0.23	0.38		
TN2	09/17/00		0.8	0	0	6	2				
TC1	05/05/01	340	0.95	87 ± 7	95 (s)	2.7 (p)	18, 40	0.73	0.96	6.2	8.8
TC1	05/24/01	340	1.05	87 ± 7	95 (t)	2.2 (p)	17	1.73	6.20		
TC1	05/31/01	270	0.92	18 ± 11	30 (t)	3	2	1.23	1.03	3.1	18.3
TC1	06/28/01	270	0.87	18 ± 11	30 (t)	nm	5	2.01	2.53	12.2	8.3
CC1	09/13/01	220	0.8	89 ± 25	50 (t)	1 (p)	9	1.01	1.51		
LC1	08/09/01	130	0.91	80 ± 24	80 (t)	4	8	1.2	0.75		
TN1	09/17/01	400	0.87	102 ± 16	95 (t)	3	17	0.72	0.96	1.7	2.2
TN1	10/04/01	400	0.85	102 ± 16	95 (t)	6	7	0.96	1.68	1.2	3.1
TN2	10/04/01	-	0.8	0	0	6	2				
TN1	10/12/01	400	0.9	102 ± 16	95 (t)	5	12	0.43	0.38	4.1	33.0

t: tall (85-115 cm reproductive shoots), s: short (12-17 cm vegetative shoots), p: ADV profile

nutrient concentrations. Total bed size ranged from 0.25 km^2 (CC1) to over 0.6 km^2 (TN1).

Each location had different characteristics such as water quality and wave exposure, so between-site comparisons of the bed influences on water quality would not be statistically meaningful. Turbidity was generally high near the Choptank River mouth until fall in both 2000 and 2001. Water flow and hydrodynamic conditions of the sites are described in detail in Chapter 3. Water transport measurements showed up to 48% reductions from up-current to inside large, dense beds.

Water quality gradients of DO

The median of the differences between DO concentrations of inside and up-current sites was significantly different from zero (P < 0.0001). Figure 4.4a shows the effect of current velocity and bed biomass on oxygen concentration with distance into beds. The slope of the change in DO was dependent on velocity and macrophyte biomass (y = 8.17 -2.7 x u + 0.144 x biomass, R^2 = 0.65). Depth and TSS did not make significant contributions to the regression. The percentage of a bed that had elevated DO concentrations increased with bed size (Figure 4.4b). The greatest DO changes with distance into beds were found in dense vegetation where velocities were slowest, and near shore. This is illustrated in Figure 4.5a during slack low tide in Todd Cove (average depth 37 cm; canopy height ~ 100 cm). With higher velocities or deeper water, larger beds or greater distances are needed to see effects of seagrass beds on DO (see Table 4.1). Figure 4.5b shows the DO across a dense bed (Site TN1) with an average velocity of 1.2 cm s^{-1}. Elevated DO was not found over beds from 1 to 5 meters wide except near shore where the current was slow. Increases in DO of

Figure 4.4. Dissolved oxygen (DO) concentration changes across beds at different current velocites and shoot biomass (a) and effect of bed size on percentage of bed with elevated dissolved O_2 (b). The diagonal lines are calculated from the regression equation. Each symbol is a separate measurement in one of the grass beds. Bioturbation by cownose rays reduced light availability, decreasing oxygen production in one measurement (panel b).
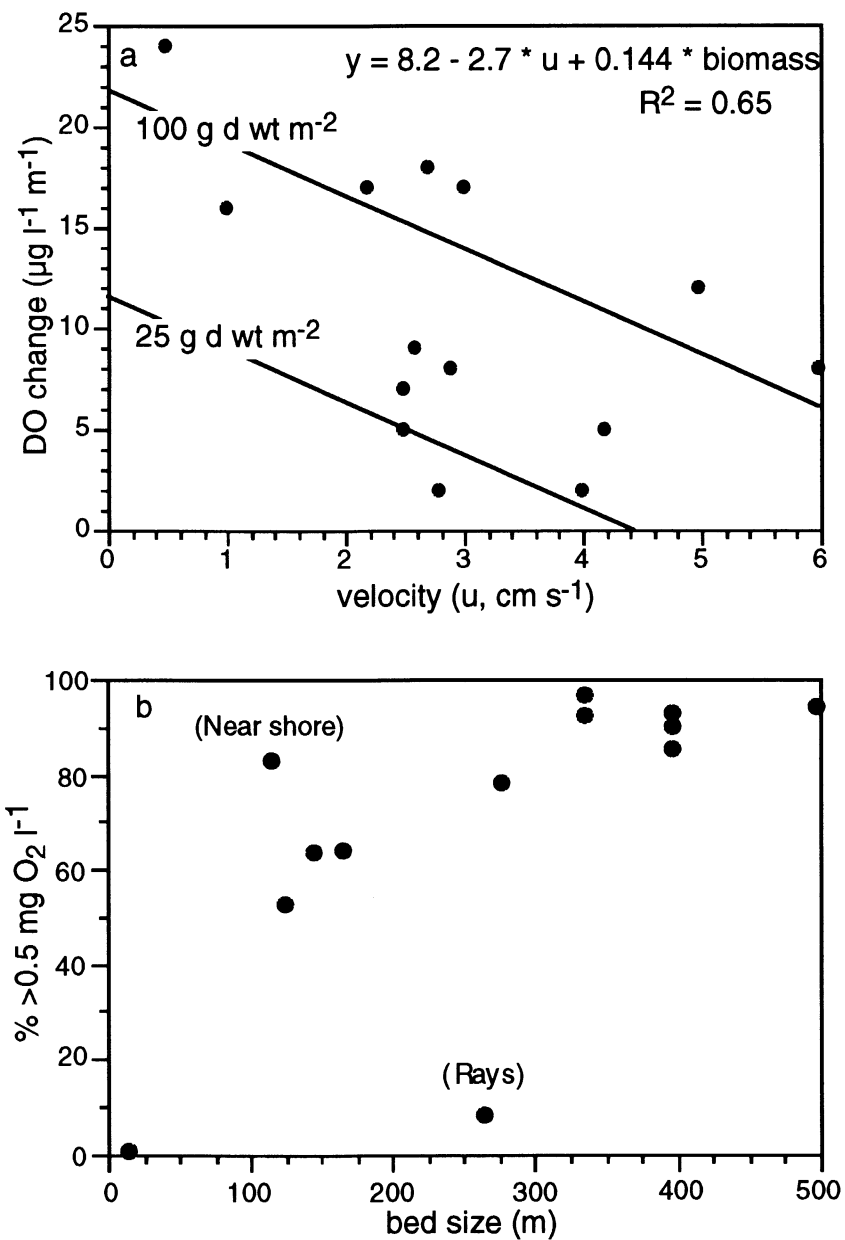
Figure 4.5. Dissolved O_2 contour plot examples. Panel a is Todd Cove in summer 1999 at slack low tide and panel b is site TN1 in fall 2001 on flood tide.
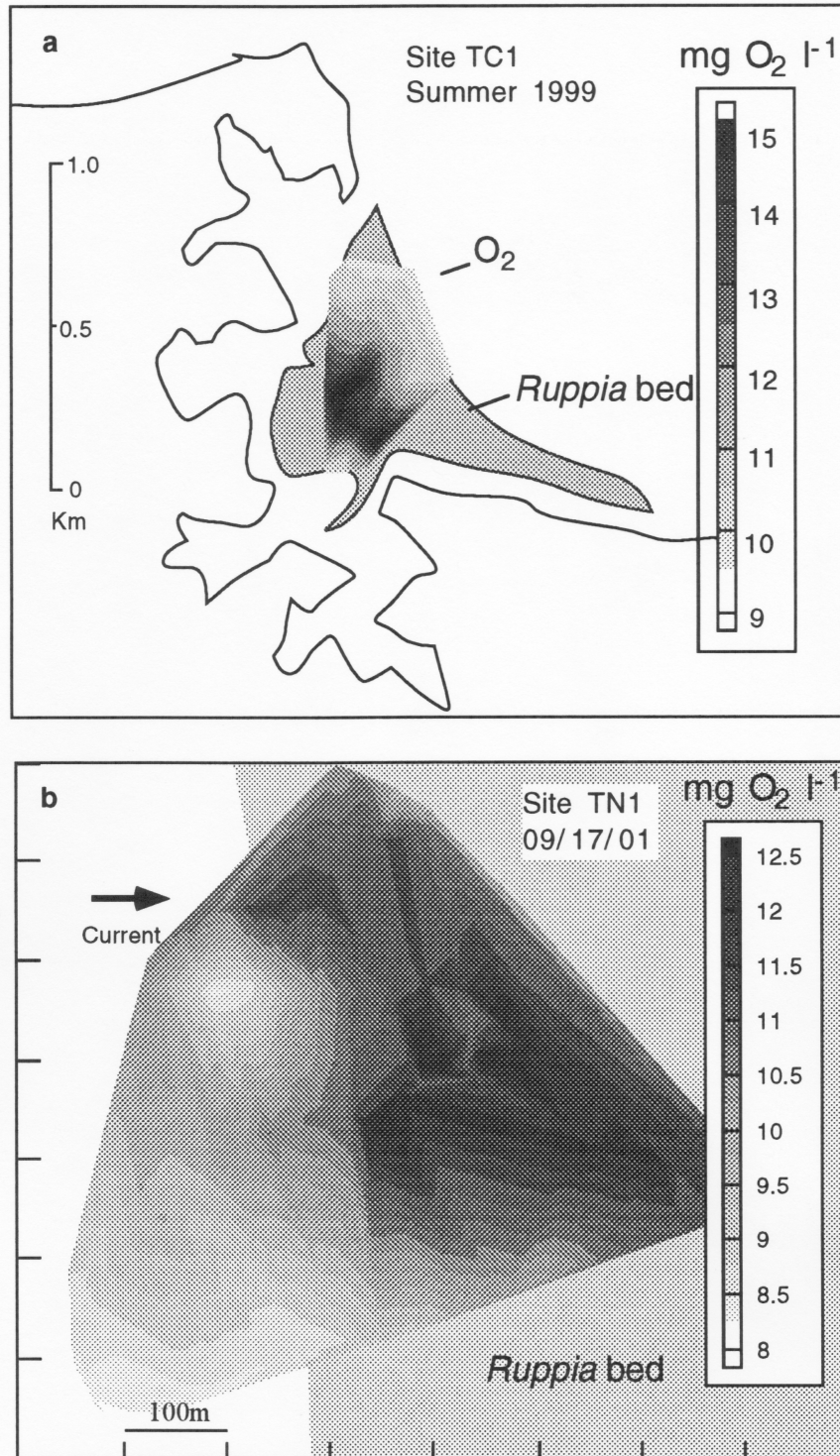
0.1 mg l^{-1} became evident in larger beds (>100 m) and average currents (> 2 cm s^{-1}) within about 10 meters of the upstream edge. Increases of 0.5 mg l^{-1} occurred within about 30 to 60 meters of bed edges in average currents. Though gradients were found outside of beds and in unvegetated areas (e.g., BB2) the gradients were generally much less steep.

Water column ammonium.

Ammonium concentrations inside and up-current of beds are shown in Table 4.1. The difference in ammonium concentrations between all in and up-current sites was significantly different from zero (1.31 vs. 1.81 µmol l^{-1}, $n = 13$, one tailed Wilcoxon matched-pair signed ranks test, $p = 0.0025$). At individual sites with the most data (TC1 and TN1) the differences were significant as well ($P < 0.05$). At site TC when rays were not present, inside ammonium concentrations were lower on all but one occasion.

Water column pH and DIC

Water column pH covaried with DO at all vegetated sites on all sampling trips. A DO change of 3.8 mg l^{-1} and a pH change of 0.65 units were found at site TN1 on 9/17/01 where the pH of the bed interior was 9.1 (Figure 4.6). The average pH increase across a bed was 0.42 units. The lowest pH change (0.28) was recorded at TC1 after ray damage (on 6/28/01). In 2001, the average bed interior pH was 8.63, and interior readings over 9 were recorded on 4 sampling trips. The highest pH recorded was 9.36 at site TN1 on 09/18/01. Sites TC1 and CC1 also had readings over 9 on that day. The largest pH change recorded was 0.77 units at site CC1 on 9/13/01. In 2001, the average DIC reduction by all seagrass beds sampled was 119

Figure 4.6. Correlation of pH and DO for representative trips. and effect of DIC change on pH along a salinity gradient (b). The DIC change of 0.15 mmol is approximately the amount caused by photosynthetic production of 2.5 g C m^{-2}.
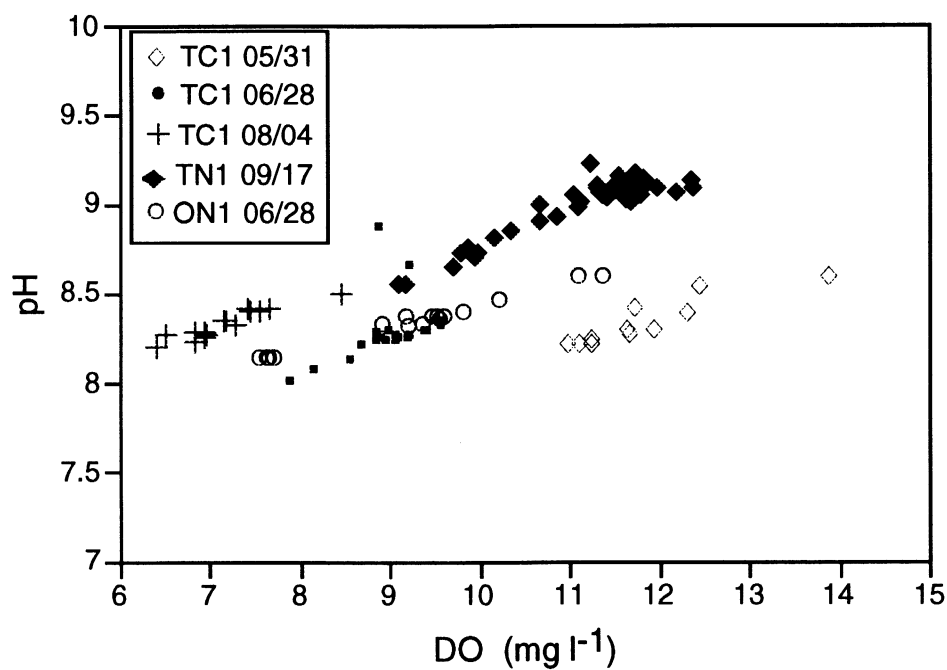
($SD = 84$) µmol l^{-1}. This is equal to 11% of the average up-current DIC concentration. The lowest interior DIC concentrations were below 700 µmol l^{-1}. Site TN1 had the highest average DIC change in 2001 (210 µmol l^{-1}).

TSS

TSS concentrations were often higher near shore due to resuspension, and overall, there was no significant difference between within-bed and up-current samples (Table 4.2, Wilcoxon matchedpairs signed-ranks test, $P > 0.1$). When rays were present in the beds, TSS concentrations within the beds averaged 76 mg l^{-1}, (to over 200 mg l^{-1}) and were significantly higher than up-current from beds (Wilcoxon matched-pairs signed-ranks test, $p = 0.008$). I found decreases in TSS with distance into all beds sampled on at least one occasion (Table 4.2).

Epiphyton vs. water quality.

Epiphyton dry weights were correlated with TSS due to resuspension near shore, or due to cownose rays (Figure 4.7, 4.8, and Table 4.3). Figures 4.7a and 4.8a show high epiphyton accumulations inside beds where cownose rays were abundant and TSS concentrations were 40 mg l^{-1}. Epiphyton accumulation on the leaves at the most ray-impacted site TC1 was almost 100 mg dry weight per cm^2. Accumulations were much lower (~ 1 mg dry weight per cm^2) when rays were less abundant. Figure 4.8b shows the variation in TSS over one day at site TC1 with rays present. Epiphyton dry weight was loosely correlated with TSS (Figure 4.9) over all samples. Figure 4.10 shows examples of epiphytic algal Chl a correlating inversely with cross-bed NH$_4^+$ gradients.

Table 4.2

Total suspended solids concentration (TSS) inside and outside grass beds (mean $\pm$ 1 SD).

Site	Date	TSS in (mg l^{-1})	TSS out (mg l^{-1})
TC1	06/10/00*	27.7 ± 20.0	3.1 ± 0.0
TC1	06/13/00*	79.6	15.1
TC1	06/15/00*	36.9 ± 3.07	23.8 ± 1.08
CC1	06/15/00	15.4 ± 0.0	11.5 ± 1.09
BB1	06/21/00	4.9 ± 0.50	9.6 ± 2.8
BB1	06/23/00	23.8 ± 1.1	18.5
BB3	06/26/00	9.8 ± 0.2	7.6
BB1	07/28/00	12.3	3.2
BB3	07/28/00	4.6	4.3
HC1	08/08/00	13.5	46.9
TC1	05/05/01	6.2	8.8
TC1	05/31/01	3.1	18.3
TC1	06/08/01*	18.3	9.8
TC1	06/09/01*	293	19.8
BB1	06/12/01*	12.8	9.5
TC1	06/14/01*	65.7	18.8
TC1	06/28/01*	12.2	8.3
TN1	09/17/01	1.7	2.2
TN1	10/04/01	1.2	3.1
TN1	10/12/01	4.1	33.0

* Rays present

Figure 4.7. Apparent effects of TSS (due to wind or rays) and water motion on epiphyte dry weight. Bars represent TSS, and squares and error bars are mean and standard deviation of epiphyte dry weight. Distances are from innermost site. Cownose rays were feeding throughout the bed in panel a. Panel b shows the possible influence of nearshore resuspension or water motion on epiphyton dry weight. Panel c shows the influence of high offshore turbidity on epiphyte weight in a protected cove. Panel d shows higher epiphyte mass at the outside edge of an exposed bed.
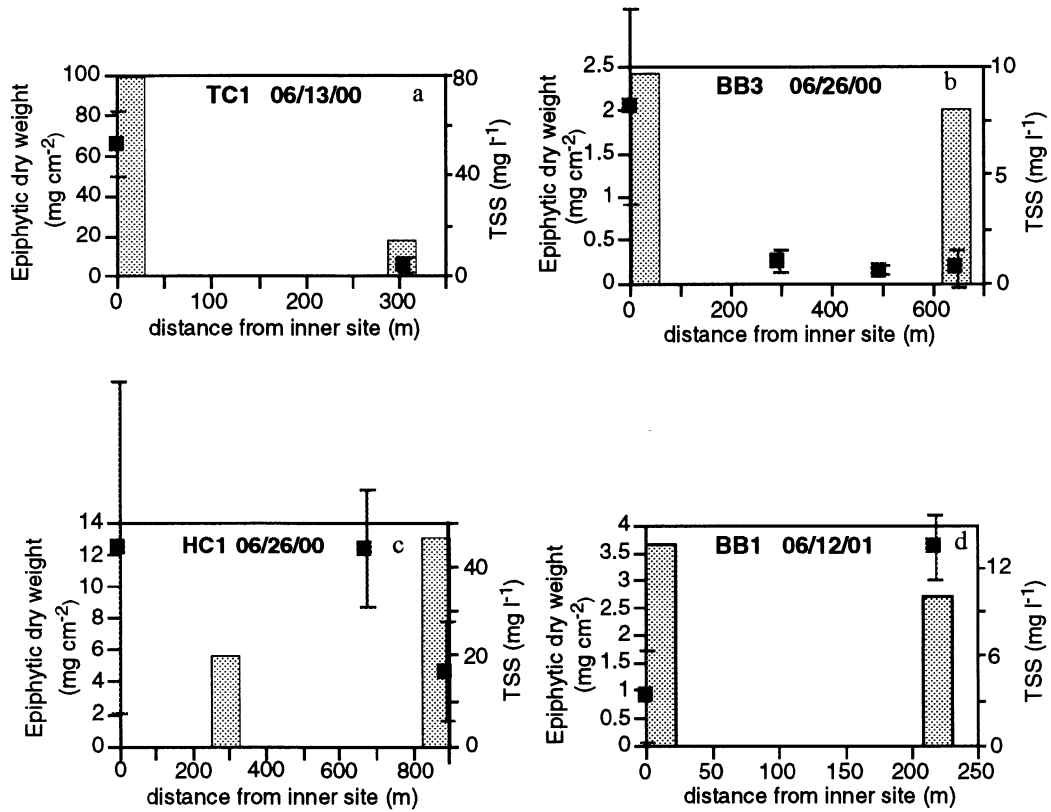
Figure 4.8. Effect of resuspension due to cownose rays on epiphyton (a) and TSS over one day at TC1 with ray schools present (b). Error bars represent 1 *SD*.
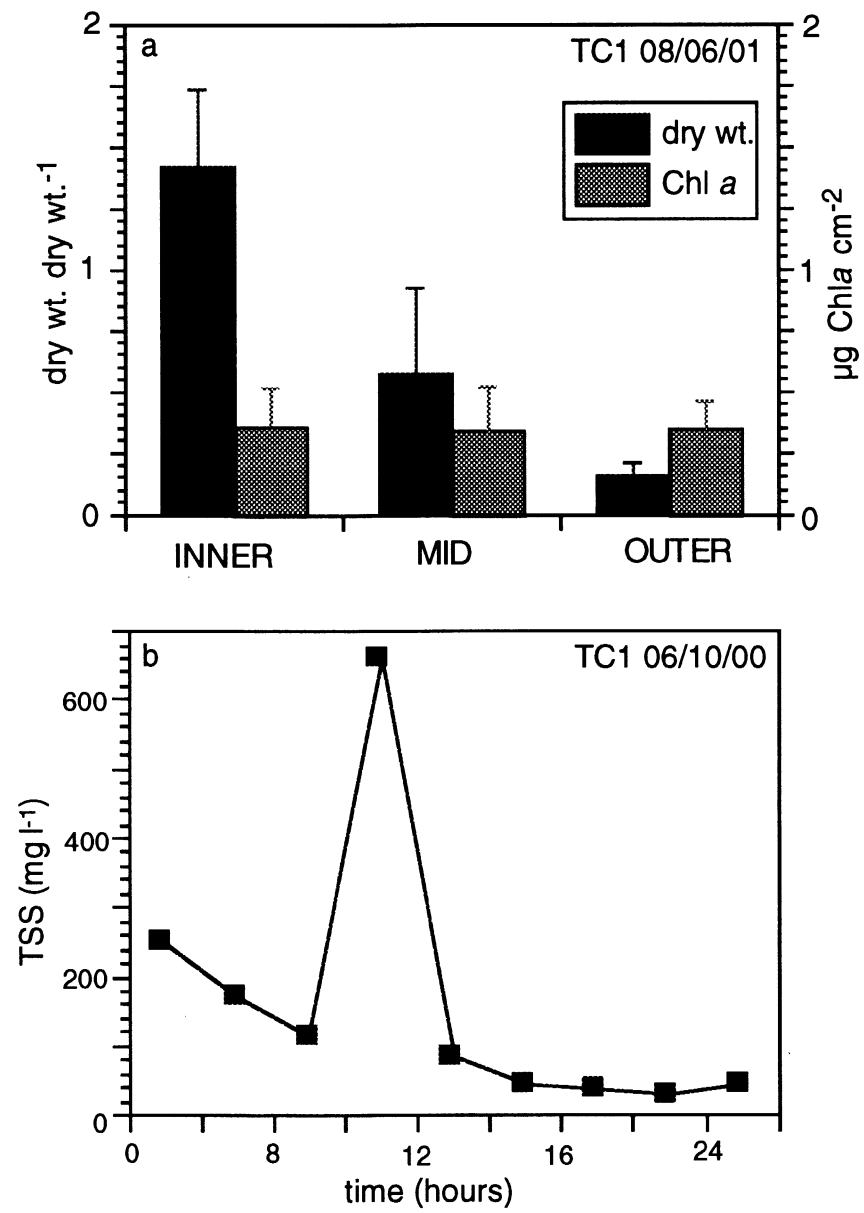
Table 4.3

Epiphyte dry weight inside and on the outside edge of *Ruppia maritima* beds
(mean ± 1 SD).

Site	Date	dry wt. in (mg cm^{-2})	dry wt.edge (mg cm^{-2})
TC1	06/13/00*	1.79 ± 0.57	0.19 ± 0.11
CC1	06/13/00*	8.68 ±2.3	0.29 ± 0.23
CC1	06/19/00*	6.22 ± 2.27	10.49 ± 7.6
BB1	06/19/00	2.01 ± 1.00	2.26 ± 1.17
BB1	06/26/00*	0.14 ± 0.08	0.23 ± 0.06
BB1	07/14/00	2.03 ± 1.17	0.18 ± 0.20
BB1	07/21/00	0.47 ± 0.11	1.14 ± 0.14
BB1	07/21/00	1.19 ± 0.55	0.70 ± 1.04
TC1	05/24/01	1.16 ± 0.93	
TC1	06/05/01*	31.0 ± 1.1	8.8 ± 3.0
BB1	06/12/01	0.89 ± 0.82	3.61 ± 0.59
TC1	06/14/01	0.50± 0.11	3.29 ± 2.97
BB1	06/21/01*	0.45± 0.21	0.06 ± 0.01
TC1	06/28/01*	0.58 ± 0.52	0.45 ± 0.21
TN1	07/13/01	0.15 ± 0.01	0.56 ± 0.20
TC1	07/17/01*	1.0 ± 0.71	
TC1	08/06/01*	2.76 ± 0.64	0.30 ± 0.08
TN1	08/15/01	0.32 ± 0.25	2.14 ± 1.13
TN1	08/16/01	0.42 ± 0.09	0.94 ± 0.36
TN1	08/18/01	0.31 ± 0.12	
TN1	09/17/01	0.13 ± 0.04	0.77 ± 0.07
TN1	09/19/01	0.08 ± 0.03	1.31 ± 0.50
TC1	09/25/01	0.19 ± 0.21	1.01 ± 0.72
CC1	10/04/01	0.26 ± 0.05	1.38 ± 0.72
TC1	10/05/01	1.38 ± 0.08	2.00 ± 0.19

* Denotes ray presence.

Figure 4.9. Total suspended solids vs. epiphyton dry weight for sites and dates with data for both parameters.
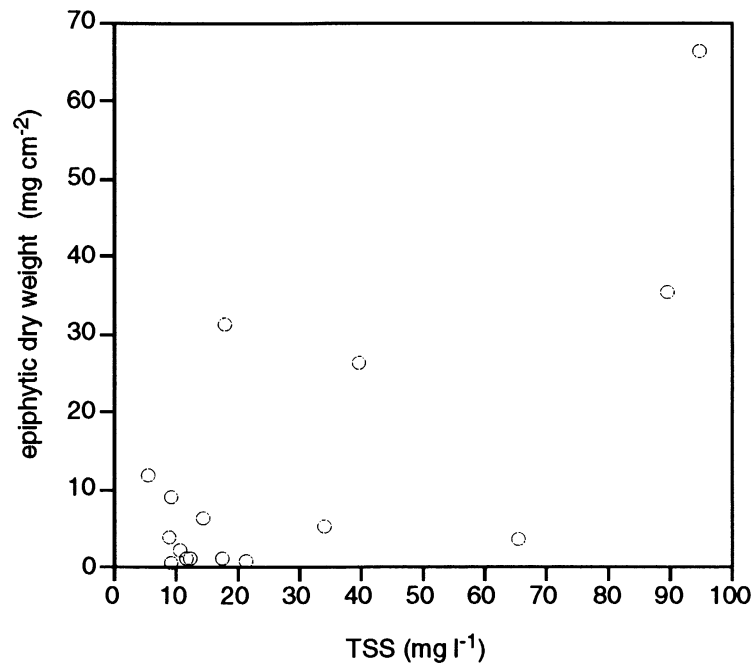
Figure 4.10. Epiphyte Chl a and water column NH_4^+ inside and at the outer edge of *Ruppia maritima* beds. Boxes and error bars are mean and standard deviation of epiphyton Chl a, and squares are NH_4^+ concentrations.
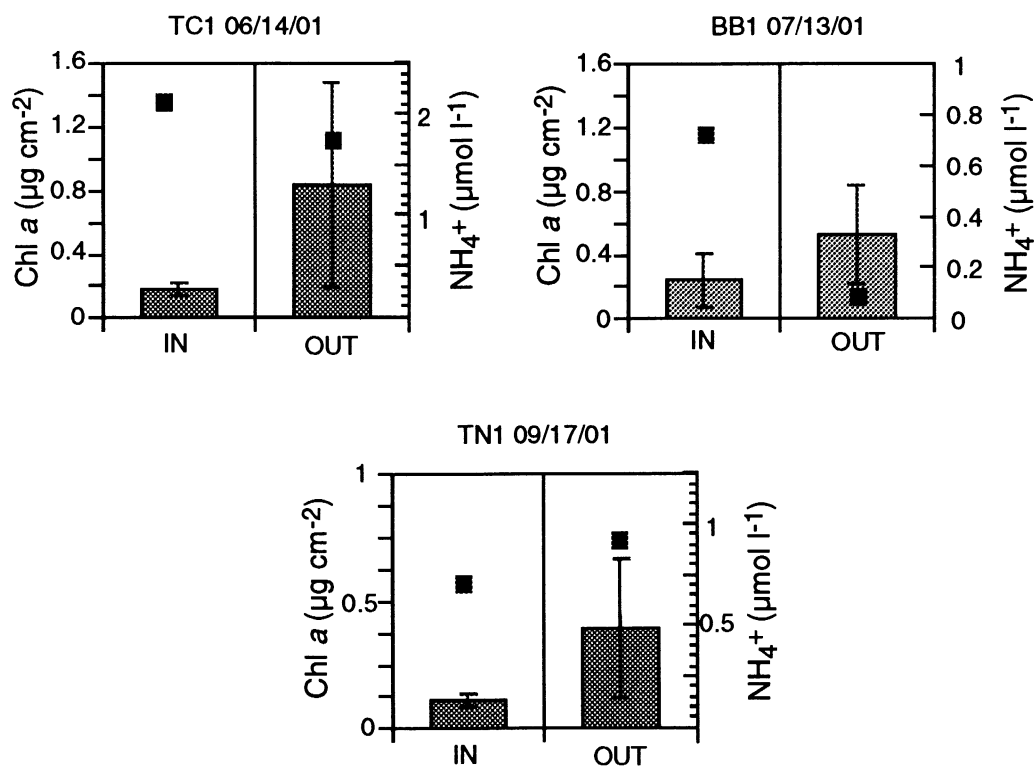
Corresponding to a large scale water quality gradient in the Choptank River (Figure 4.11a), I found significant differences in epiphyton mass measured within the same week between the farthest upstream site and the downstream sites (~ 2 vs. 0.3 mg dry weight per cm^2, Figure 4.11b). Nutrient concentrations at the mouth of the Choptank River were lowest in the summer and fall (Figure 4.12a), and epiphyton dry weight and Chl a declined into fall (Figure 4.12b and c).

Epiphyton vs. bed size, location, in relation to areas of highest DO concentration

Over all sampling trips and sites, epiphyton dry weight per cm^2 leaf (Table 4.3) was not significantly different between inner and outer samples (Wilcoxon matched-pairs signed-ranks test). When sites without rays were removed, the median difference between inner and outer sites was significantly different from zero ($M = 0.67$, $SD = 0.16$, vs. $M = 1.37$, $SD = 0.18$ mg dry weight per cm^2, $n = 16$, Wilcoxon matched-pairs signed-ranks test, $p = 0.0065$). Over the summers of 2000 and 2001, epiphytic algal Chl a was variable spatially within sites (Table 4.4, Figure 4.10) with no significant difference between inside and up-current samples.

Starting in August 2001, I found high epiphytic algal accumulations (dominated by the filamentous diatom *Tabellaria floculosa*) on the outer edge of some beds in the Choptank River. There, algal coverage decreased with distance into the bed. Since the water was clear, I could see and map the highly epiphytized areas. Large areas with high epiphyton mass (equal to the macrophyte above-ground biomass) were found on the up-current edges of beds and away from shore (Figure 4.13). Where beds were narrow and near shore, high epiphyton mass was restricted to the up-current edge of the bed. Samples from south in Little Choptank, and Honga

Table 4.4
Epiphyte Chl *a* inside and outside grassbeds (mean ± 1 SD).

Site	Date	Chl *a* inside ($\mu g\ cm^{-2}$)	Chl *a* out ($\mu g\ cm^{-2}$)
TC1	06/13/00*	1.630 ± 0.748	0.593 ± 0.303
CC1	06/19/00*	0.750 ± 0.130	0.921 ± 0.693
BB3	06/20/00	0.506 ± 0.351	0.691 ± 0.411
BB3	06/20/00	0.068 ± 0.041	0.085 ± 0.041
BB1	07/14/00	0.510 ± 0.115	0.055 ± 0.033
BB1	07/21/00	0.094 ± 0.025	0.091 ± 0.023
BB1	07/21/00	0.169 ± 0.075	0.054 ± 0.006
BB1	07/21/00	0.092 ± 0.010	0.206 ± 0.070
HC1	08/08/00	1.669 ± 0.162	2.465 ± 2.465
BB1	06/12/01*	0.289	0.437 ± 0.146
TC1	06/14/01*	0.181 ± 0.036	0.834 ± 0.645
BB1	07/13/01	0.515 ± 0.306	0.079 ± 0.046
TC1	08/06/01*	0.354 ± 0.157	0.264 ± 0.028
TN1	08/16/01	0.154 ± 0.074	0.326 ± 0.060
TN1	09/17/01	0.065 ± 0.008	0.670 ± 0.272
BB1	09/19/01	0.083 ± 0.029	0.394 ± 0.170
TN1	09/20/01	0.037 ± 0.025	0.412 ± 0.272
CC1	10/03/01	0.034	1.077
TC1	10/05/01	0.016 ± 0.021	0.320 ± 0.209
HO	10/15/01	0.362 ± 0.030	2.560 ± 2.452
ON	10/15/01	0.127 ± 0.046	0.858 ± 0.227
EB	10/19/01	0.074 ± 0.063	1.928 ± 0.577
LC1	10/20/01	0.030 ± 0.007	0.711 ± 0.244

* Denotes ray presence.

Figure 4.11. Choptank River water quality gradient (panel a) and epiphytic mass gradient (panel b) at sites with submersed plants. TN1 is in Trippe Bay, TC1 is in Todds Cove, and HP is at Horns Point.
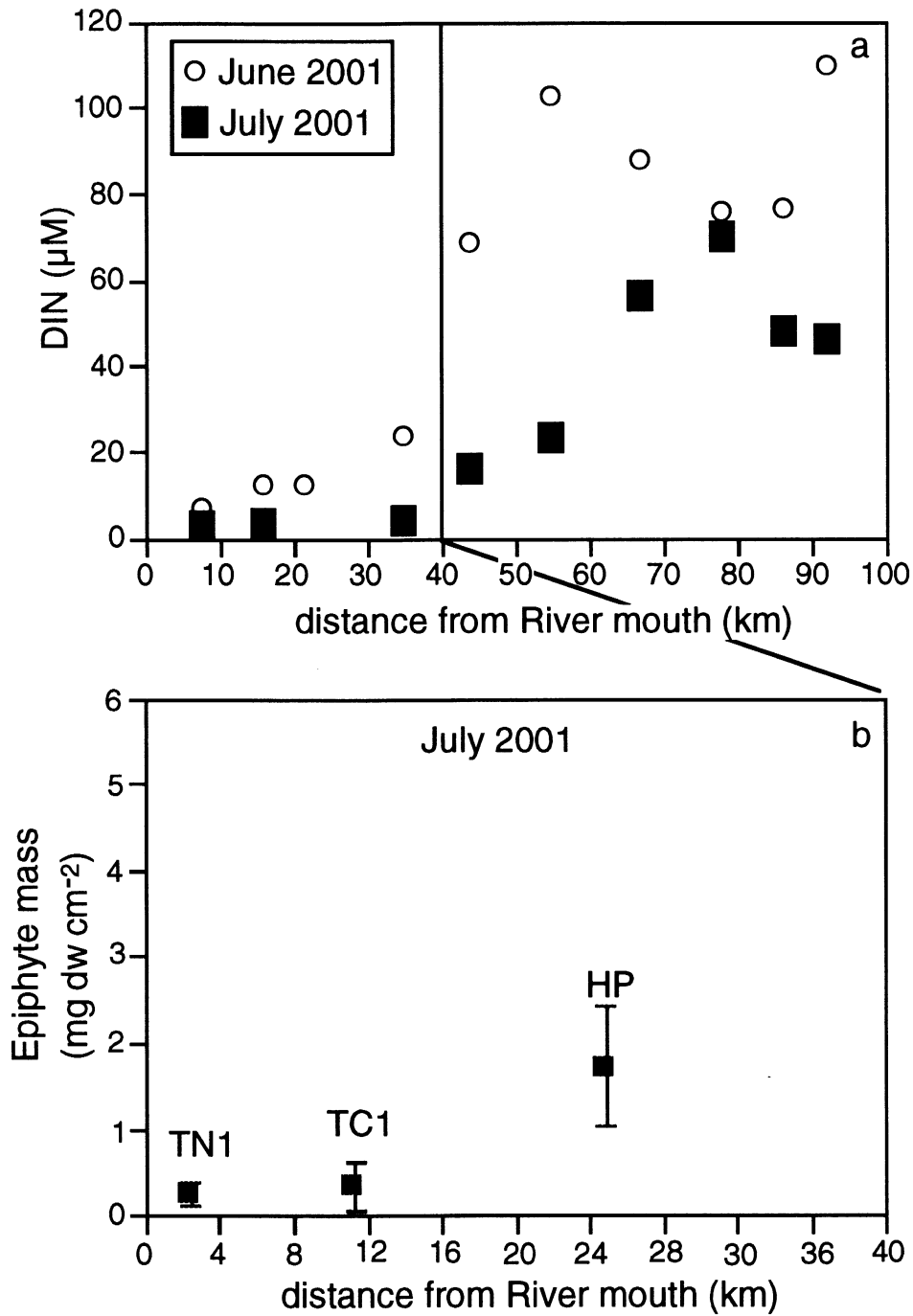
Figure 4.12. Seasonal water quality near site TC1 (a) and epiphyte dry weight (b) and Chl *a* (c) at Choptank River sample sites inside beds in 2001. Error bars represent 1 S.D.
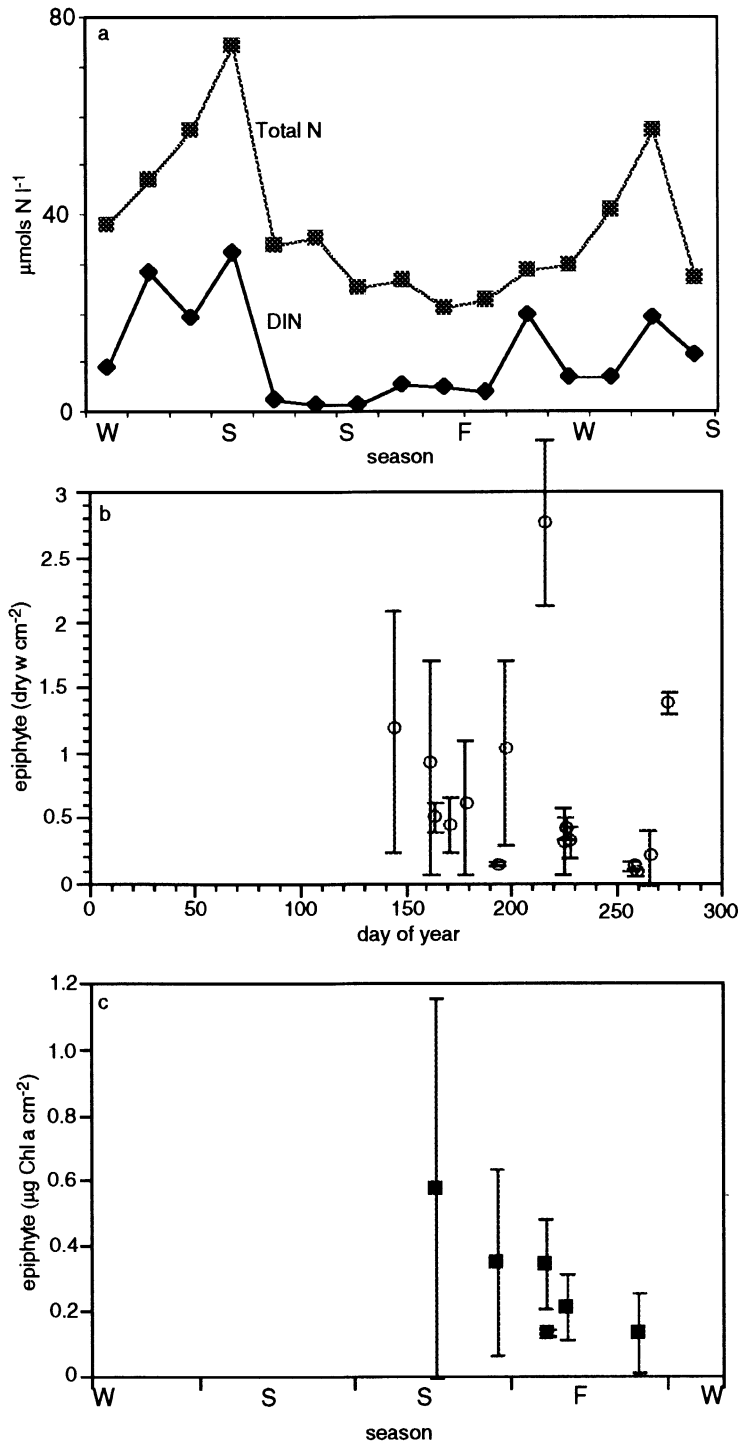
Figure 4.13. Contour plot of epiphyte biomass across bed at site TN1 in September 2001. Circles indicate sample locations. Rectangles on left are small *Ruppia* patches. Nearest shoreline is 200 m to the right of southern portion of the bed.
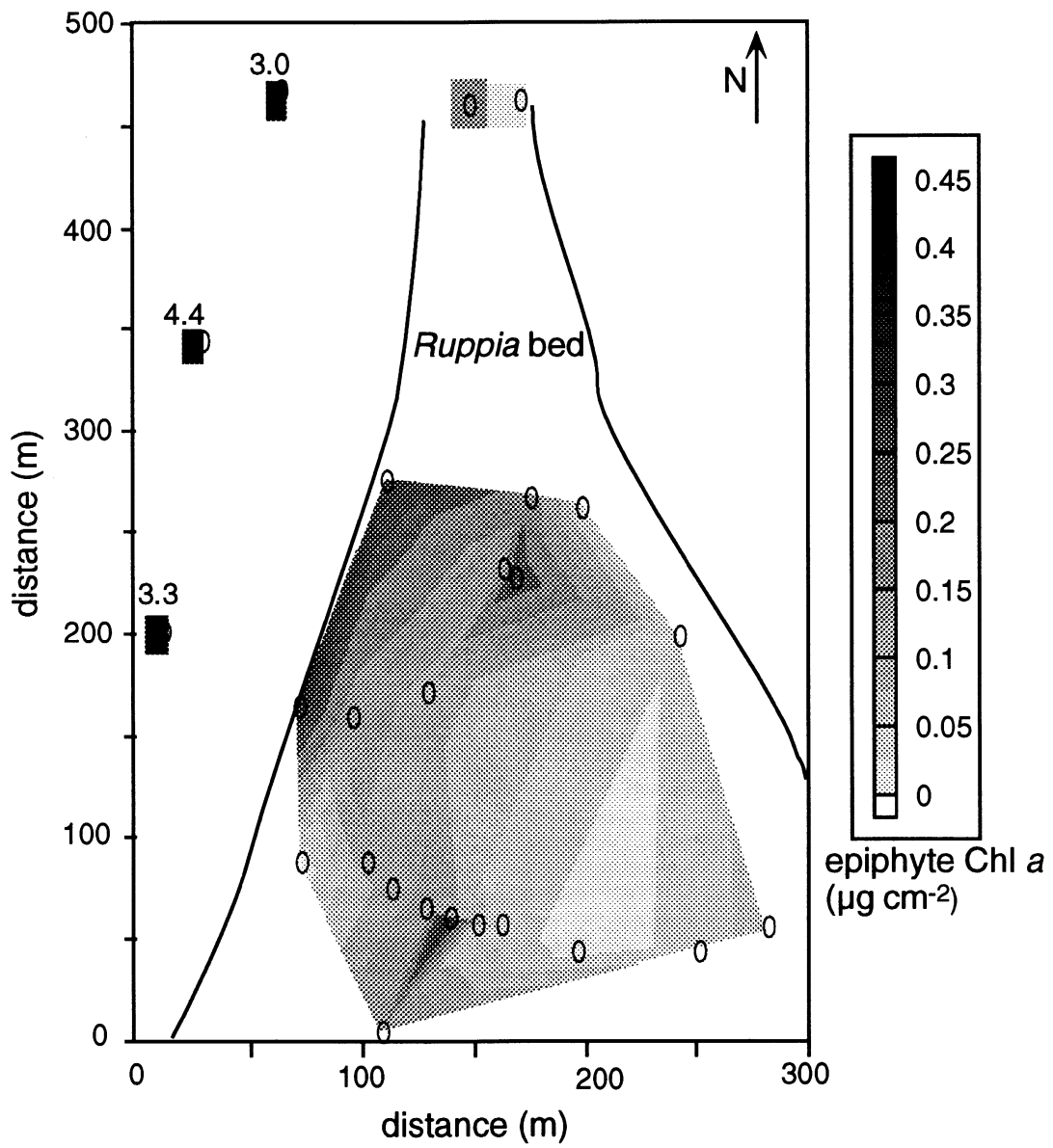
Rivers, and north in Eastern Bay and showed the same pattern of highest epiphyton

mass on bed edges (Figure 4.14). The fall 2001 median Chl a (μg cm^{-2} leaf) of the

inner sites was significantly lower than the outer edge sites ($P = 0.001$, Wilcoxon

matched-pairs signed-ranks test). The mean fall 2001 interior epiphytic algal Chl a

values were also significantly different than the summer values (0.098 vs. 0.521 μg

cm^{-2} leaf, Mann-Whitney U test, $p = 0.0006$). The average fall 2001 exterior epiphytic

algal Chl a was significantly higher than the summer average (0.926 vs. 0.521 μg cm^{-}

^{2} leaf, Mann-Whitney U test, $p = 0.033$).

Cross bed sediment characteristics

Sediment percent AFDW and grain size changed with distance into the beds

most dramatically at site TN1 in the fall of 2001 (Figure 4.15 and 4.16). Percent

silt/clay fraction (< 0.63 mm dia. grain size) was lowest outside the bed (offshore) at

site TN1 (2.5% vs. 6.8% inside). The inner station sediment was 72% very fine sand

(0.125 to 0.063 mm dia.) while the mid (100m into bed) and outer sites were

primarily (~70%) fine sand (0.25 to 0.125 mm dia). Cross bed differences in these

parameters were not as great at sites TC1 and CC1 (Figure 4.16). Sediment AFDW

was only slightly lower outside the beds ($M = 1.0$, $SD = 0.1$ % $n = 4$) than inside (M

$= 1.42$ %, $SD = 0.1$, n = 4, Mann-Whitney U test, $p = 0.014$). Grain size decreased

with distance into each bed, but since offshore sediment grain size was already small

at the more protected sites (CC1 and TC1), smaller differences were found there

(Figure 4.16b). In two fall 2001 measurements, sediment ammonium increased from

23 ($SD = 6$) μmol l^{-1} at the bed edge to 100 ($SD = 39$) μmol l^{-1} at the interior of site

Figure 4.14. Epiphyte Chl *a* inside and at the outer edge of grass beds in the Chesapeake Bay in fall 2001. Error bars represent 1 S.D.
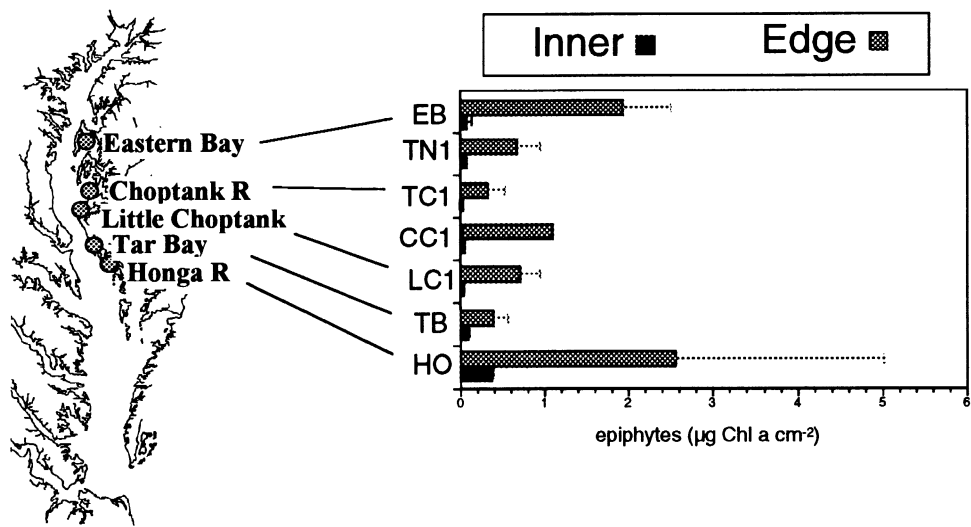
Figure 4.15. Sediment characteristics: ash free dry weight (a), grain size (b), and percent silt/clay (c) across *Ruppia* bed at Site TN1 on September 9, 2001. Bars represent 1 S.E.
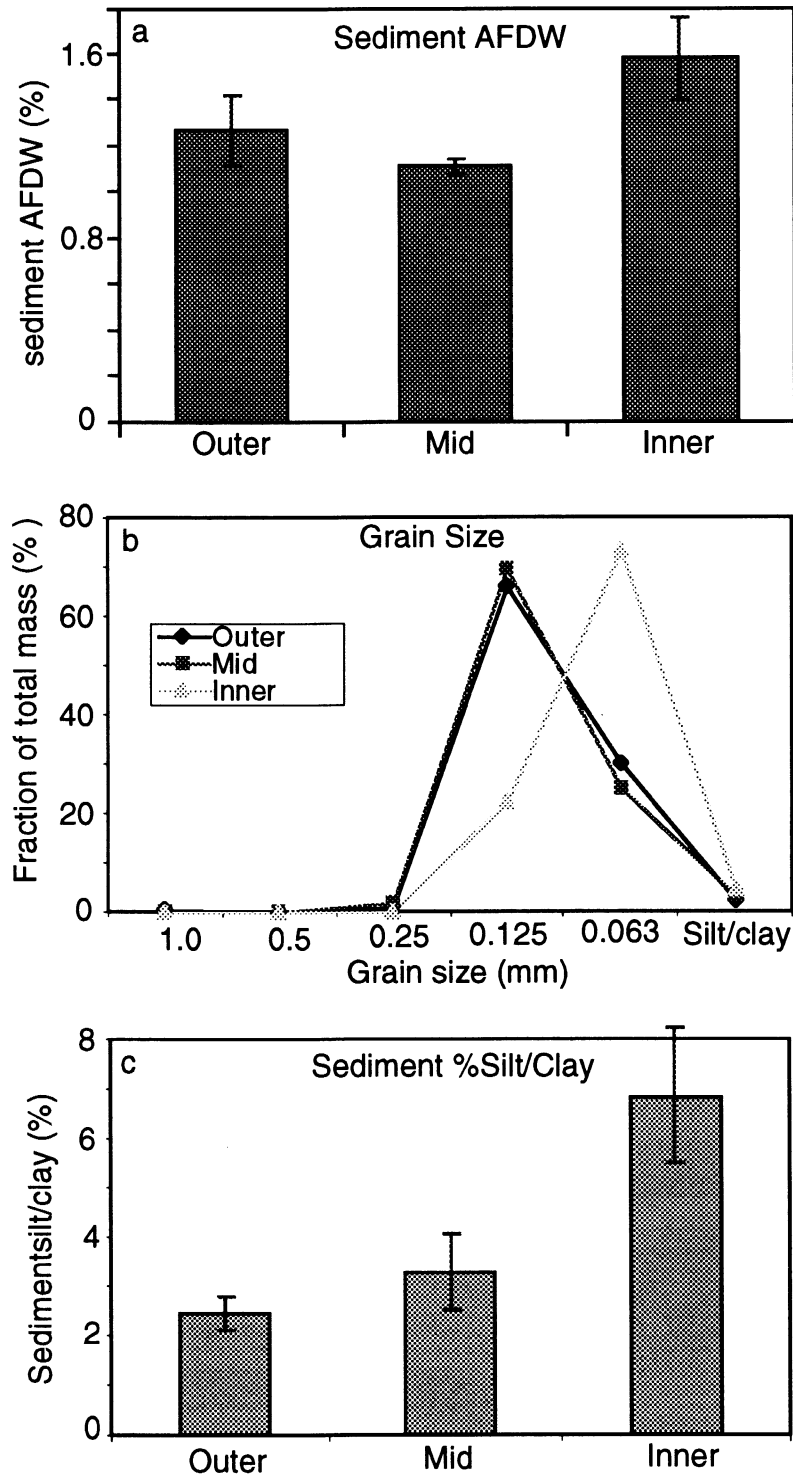
Figure 4.16. Comparison of sediment characteristics: ash free dry weight (AFDW, a) and fine sediment fraction (b), between sites in fall 2001. Distance between inside and up-current sites averaged 200 m. Error bars represent 1 S.E.
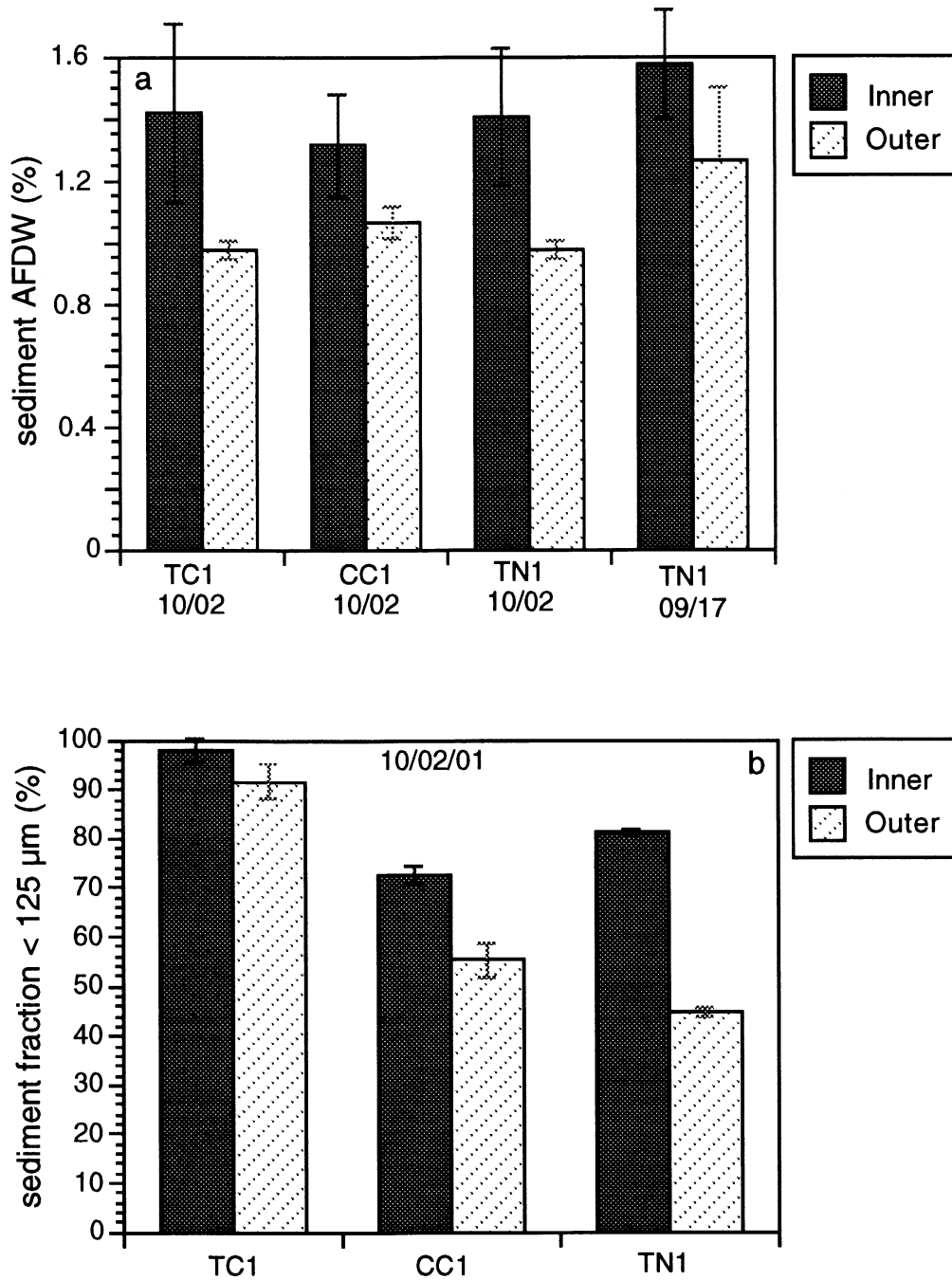
TN1. Sediment AFDW ranged from 0.9 to 1.6%. Sediment grain size in all samples was negatively skewed and leptokurtic (mainly fine to very fine sand).

On 08/29/00 at Site BB1, sediment oxygen flux in the light was significantly higher in cores from outside and bed edge samples, (M = 325, SD = 588 μmol l^{-1} hr^{-1}, n = 6) than in mid bed samples (M = -489, SD = 506 μmol l^{-1} hr^{-1}, n =3, Mann-Whitney U test, p = 0.048). Sediment Chl a was also higher in the outside and edge cores (M =116, SD = 35 mg m^{-2}, n = 6) than in mid-bed cores (M = 28, SD = 7 mg m^{-2}, n = 4, Mann-Whitney U test, p = 0.0095).

Discussion

In this study, I measured changes in water quality with distance into Widgeon Grass beds and evaluated whether these changes affected epiphytic algal accumulations. I also measured sediment characteristics within and outside the seagrass beds. I found that large, dense, seagrass beds consistently caused daytime gradients in water flow, pH, dissolved inorganic C, and DO across beds. At average current speeds, measurable increases in DO occur within 10 m of the edge of a bed, and increases of more than 50% were measured in large (> 400 m dia.), dense (> 60% cover) beds. Though oxygen production measurements indicated high N demand (~5 mmol m^{-2} hr^{-1} stoichiometrically), very small changes in water column NH_4^+ were recorded across beds. Hydrogen ion and DIC concentrations corresponded inversely to the DO concentrations. Changes in these parameters in the interior of large beds were sufficient to cause oxygen inhibition (e.g., Søndergaard 1979, Bowes 1985, Reiskind et al. 1989), C limitation (e.g.,Van Wijk 1989), and pH induced stresses (e.g., Heerkloss and Ring 1992). TSS concentrations were correlated with cownose

ray presence, and phytoplankton concentrations inside beds were not statistically

different than up-current. Epiphyton was correlated to TSS but not to location within

beds except in fall 2001, when significantly higher biomass was found at bed edges.

Bed size and biomass and water quality gradients

Water column DO changes found across beds corresponded with bed size as I

expected. The results support the idea that small beds will have little effect on water

quality, and that larger beds will have gradients of water quality due to the interaction

of the bed with the water column. Determining the percentage of the bed that has

elevated DO can give an idea of the size of bed needed to influence other water

quality parameters under the given hydrologic conditions. As the contour plots show

(Figure 4.5), much of a bed can be influenced by the altered water quality, and the

difference in DO within 100 m of the bed edge can be substantial. *Ruppia* beds larger

than 100 m in diameter can alter the DO concentration over a majority of the bed

(Figure 4.4b). Smaller beds would have to be in slow currents to have an effect on

water quality, since on average, I measured a 0.5 mg O_2 l^{-1} change across

approximately 50 m of seagrass bed. While small patches in moderate flows may not

have an effect on water quality individually, they could have a cumulative effect.

Water may flow around small patches, reducing interactions between the seagrass

community and the water column. At the highest velocities, the effect of macrophytes

on DO is minimized (Figure 4.4a). Dense beds will have the largest effects on water

flow and water quality.

Our sites were all characterized by relatively low flow and shallow depths. In

deep or fast moving water, there may be no water quality differences due to short

residence time, or minimal contact, greater degree of bending of shoots, and there will be less effect on water flow. The higher oxygen level near the bottom inside the bed (Figure A3) was due to the slower water motion essentially "trapping" water within the bed. The slopes of the lines are an indication of the rate of mixing of the bottom water with overlying water. Waves can enhance exchange between the canopy and the water column (Koch and Gust 1999).

The DIC and oxygen changes measured across the seagrass beds were not due to *Ruppia* production alone as epiphytic algal biomass at our sites occasionally exceeded leaf biomass. Epiphytic communities accounted for much of the production in other macrophyte beds (Penhale 1977, Cattaneo and Kallf 1980, Moncreiff et al. 1992, Pollard and Kogure 1993). Large daytime increases in DO have been noted in submersed macrophyte communities in fresh water (Carpenter and Gasith 1978, Kelly et al. 1983, Reddy 1981, Carter et al. 1988). Smaller changes have been noted in high salinities (Odum and Odum 1955, Nixon and Oviatt 1972, Leverone 1995, Moore 1996). Information on spatial differences in DO concentrations within beds or macrophyte biomass dependence of DO changes has not been well documented.

High DO concentrations combined with reduced DIC availability in bed interiors could combine to reduce net productivity of macrophytes (Søndergaard 1979, Bowes 1985) and algae (Reiskind et al. 1989) due to the affinity of both O_2 and CO_2 for Rubisco. Oxygen levels can also affect microbial processes such as nitrification (e.g., Kemp and Dodds 2002). The DO levels I measured within these beds were high enough to have the potential to inhibit photosynthesis of some algae (see Gordon and Sand-Jensen 1990), though some others (such as *Lomentaria*

articulata) are not affected (Kübler et al. 1999). There may be an indication of reduced net primary production (NPP) with distance into seagrass beds since DO concentrations level out, but respiration may increase with distance into beds, and of course, oxygen diffusion increases with DO concentrations above saturation, while CO_2 diffusion is much slower (e.g., Park et al. 1958).

Water column pH and DIC gradients

Water column pH varied across large *Ruppia* beds in agreement with our expectations. This supports the idea that centers of large seagrass beds may have more limiting conditions than bed edges or small beds. On most sampling trips, at the high pH values measured within dense beds during daylight (Figure 4.6), there was almost no free CO_2 (6.18×10^{-4} mmol l^{-1} at pH of 9.1). On 09/17/01 at site TN1, total DIC was reduced from 1.18 to 0.92 mmol l^{-1} and free HCO_3^- was reduced 45% to 0.51 mmol l^{-1}. These changes are large enough to significantly affect C availability to *Ruppia* plants and algae in bed interiors. Dissolved inorganic carbon (DIC) has been found to be limiting to algae and submersed rooted macrophytes (Allen and Spence 1981, Maberly and Spence 1983, Beer 1989, Madsen and Maberly 1991) in fresh and saline waters. DIC availability can also influence the growth of phytoplankton (e.g., Ibelings and Maberly 1998). Saturating concentrations of DIC vary (inversely) with pH (e.g., Millhouse and Strother 1986), but were as high as 5 mmol l^{-1} HCO_3^- for *Potamogeton pectinatus* (Van Wijk 1989) and *Zostera marina* (Beer and Rhenberg 1997). The total DIC concentration of saturated, full strength seawater (2.18 mmol l^{-1}) is not quite half this level. *Ruppia maritima* photosynthesis saturates at a lower level, however (Hellblom 2002) and DIC half saturation constants for macrophytes in

general range from 0.1 to 0.7 mmol l^{-1} compared to 0.04 to 0.1 for algae (see Maberly and Spence 1983 for review). Recent studies have shown that DIC saturation constants may have been artificially high (Hellblom et al. 2001). Another Chesapeake bay grass, *Potamogeton pectinatus* produced no biomass at 1 mmol l^{-1} bicarbonate (Van Wijk 1989).

The reduction of free CO_2 concentrations in the water column and further reduction within the diffusion boundary layer can lead to the uptake of carbon solely as HCO_3^- by seagrasses (Beer et al. 1977) with the catalyst of the enzyme carbonic anhydrase (e.g., Tsuzuki and Miyachi 1989, Beer and Israel 1990), or by direct transport (Beer and Rehnberg 1997). As free CO_2 is reduced with distance into a bed, algae may be less affected since they more readily take up HCO_3^- (Beer 1994). Thus, algal growth within a seagrass bed would be less affected than rooted macrophyte growth, which may slow due to the additional energy requirements for HCO_3^- uptake unless sufficient C can be obtained and stored at times when the supplies are greater. Some submersed macrophyte species have been show to be efficient at utilizing bicarbonate (see Hellblom et al. 2001, Beer et al. 2002), so algae may not always have a competitive advantage as a group.

This effect of dense vegetation on pH and DIC should be maximized in shallow, stagnant, soft water lakes. DIC concentrations dropped from 2.5 to < 0.75 mmol l^{-1} inside *Chara aspera* and *Potamogeton* spp. beds in one lake (Van den Berg et al. 2002). Large daytime increases in pH have also been noted in submersed macrophyte communities dominated by *Egeria densa* (Reddy 1981), and *Hydrilla verticillata* (Carter et al. 1988) in freshwater systems. The bicarbonate buffering

system and tidal resupply at brackish or saline sites should prevent DIC supplies from becoming as limiting as in freshwater systems (Stevenson 1988). For example, in Laguna Madre, Texas (Park et al. 1958, Ziegler and Benner 1998) and the Florida Keys (Odum 1957), smaller diel ranges of pH and DIC (0.6 mmol l^{-1}) than I found have been noted. The effect of salinity on the effect of photosynthesis on DIC is shown in Figue A5. But at the pH values I found in bed interiors (8.5 to 9.3), HCO_3^- is practically the sole source of C for seagrasses and algae. As carbon availability in estuaries increases from upstream to the ocean, cross-bed gradients of DIC will become less steep and DIC limitation will decrease (Figure A5).

One measure of the effect of high pH and reduced DIC on a submersed macrophyte's ability to fix carbon is the pH drift experiment (e.g., Allen and Spence 1981). *R. maritima* can fix bicarbonate (Hellblom 2002), and can continue to photosynthesize up to a pH of 9.4 and a DIC concentration of 0.8 mmol l^{-1} (Chapter 2). Other submersed angiosperms can also use bicarbonate (e.g., Beer and Rhenberg 1997). This ability is especially useful in stagnant waters and may be one reason that some species such as *R. maritima* are so widely distributed. Submersed macrophyte species that do not significantly increase water column pH may not be able to utilize bicarbonate and may have reduced productivity in large, dense beds. Since *R. maritima* can raise pH to 9.4, on average, it was not severely C limited at our sites. The DIC concentration did reach levels below 0.8 mmol l^{-1} on several trips, and the average DIC reduction of 11% could have a comparable effect on macrophyte production.

Some submersed macrophytes use other mechanisms that may reduce the limiting effect of C on production. Two submersed macrophytes in the Hydrocharitaceae family, *Hydrilla verticillata* and *Egeria densa*, can concentrate and store C (Holaday and Bowes 1980, Maberly and Madsen 1998, 2002) when it is more available (e.g., night), to supply C fixation when carbon is limiting. This ability has not been demonstrated in other species in the Hydrocharitaceae family or in other submersed monocot families. Some of the Charales (Lucas 1983) and some submersed monocots (van Ginkel and Prins 1998, Lara et al. 2002) have a leaf pH-polarity mechanism to facilitate C acquisition. Some species may reutilize C (Hough and Wetzel 1972), or obtain it from the sediments and store it in the lacunae (Wium-Andersen 1971, Søndergaard and Sand-Jensen 1979, Kimber et al. 1999). Canopy forming species may obtain carbon directly from the atmosphere (Stevenson 1988, Frost-Christensen and Sand-Jensen 1995) though this mechanism may only be useful between tides in estuaries. At velocities of 5 cm s^{-1}, the reproductive shoots of the Widgeon Grass beds at our sites were bent at an angle that prevented contact with the surface.

Due to the slow diffusion of DIC from air, in large, dense seagrass beds not in contact with the surface, the main mechanism for DIC supply is water exchange. The gradients in pH and DIC that form across beds may cause gradients in macrophyte growth or metabolic parameters. A spatial gradient in the δ^{13}C signature related to distance from exchange water sources was found in *Ruppia megacarpa* beds in Australia (Boyce et al. 2001). When pH is increased within seagrass beds,

micronutrients such as iron may turn into an insoluble form (Clark 1982) and alter sediment P and sulfide availability.

The average within-bed pH increase (0.42 units) was a substantial increase that would not occur in full-strength seawater. While bed edges are exposed to the pH range of the open water, bed interiors will fluctuate widely each day, as decomposition decreases the pH at night. pH affects phosphorus solubility, enzymes, microbial activity, toxicity of ammonia, and dissolution of exoskeletons (e.g., Bamber 1987). Fauna, flora, and microbes in seagrass beds have optimal pH ranges. The optimal pH range for nitrification is between 7.0 and 7.4, for example. At pH levels above 9, phytoplankton do not obtain maximum growth (see Hansen 2002) and survival of the copepod *Eurytemora affinis* is reduced (Heerkloss and Ring 1992). Growth rates of the clam *Mercenaria mercenaria* were lower at pH levels below 7.5 (Ringwood and Keppler 2002). The optimal pH range for many freshwater fish is between 6 and 9. Ammonia becomes increasingly toxic as pH increases. At pH levels above 9, total ammonium concentrations below 10 µmol become toxic (Chronic EC20) to a range of invertebrates and fish (USEPA 1998). Interiors of large seagrass beds thus may be less hospitable than edges to many species for these reasons. Other reasons for unequal faunal distributions in bed interiors are discussed by Irlandi (1996) and Bologna and Heck (2002). The pH effect on P solubility (e.g., Moore and Reddy 1994) could also result in large beds being a source of P to the estuary during the growing season.

Water column ammonium

Ammonium concentrations were lower within the beds as expected. The amount of change was small, however, due to the low nutrient conditions during the study. Though net nutrient uptake by macrophyte beds has been documented in the Chesapeake Bay (Stevenson et al. 1981) and elsewhere (Howard-Williams 1981) and nutrient concentration gradients across seagrass beds have been reported (Casey and Westlake 1974, Moore 1996), concentration gradients may depend on the bed location, net *Ruppia* growth rates, recent turbidity, and the sediment nutrient concentration. Protected beds in areas with high turbidity may trap much of the suspended organic matter that can serve as a nutrient source as it decomposes. Also, as water flow decreases with distance into a bed, more organic matter can settle, resulting in increased regeneration of nutrients. If the sediment nutrient concentration is lower near the bed edge due to water motion and lower organic content, the *Ruppia* leaves there may remove more nutrients from the water column. Decreases in nutrient concentrations across a bed may be more likely to occur while macrophyte biomass is accumulating. This occurred in a stream, where macrophyte accumulation accounted for the difference between up and downstream nutrient concentrations (Casey and Westlake 1974). As a bed matures and leaf density increases, sediment organic nutrients may accumulate due to increased deposition of dead leaves and allochthonous matter. Then, decomposition (recycling) may supply much of the community nutrient requirements (e.g., Landers 1982). Whether macrophyte beds are a source (e.g., Prentki et al. 1979, Carpenter 1980) or a sink (Mickle and Wetzel

1978) of dissolved nutrients over the long term may only be decided by measurements of nutrient burial rates in sediments.

In oligotrophic areas, as nutrients are removed from overlying water as it moves across a bed, eventually nutrients could become limiting for the macrophytes. This could limit bed size. A number of seagrass beds have been shown to be nutrient-limited (e.g., Short et al. 1985, Barko and Smart 1986, Terrados et al. 1999a). Water column ammonium concentrations within our beds may have been affected by regenerated nutrients. Thus, they were not a good indicator of the effect of the *Ruppia* beds on the water column and I may not expect reduced epiphyton mass due to seagrass community uptake of dissolved nutrients.

When NH_4^+ was inversely correlated with DO, the ratio of net NH_4^+ decrease to net O_2 increase was much smaller than Redfield's stoichiometric ratio (Redfield 1934). At an average measured DO increase of 13 µg l^{-1} m^{-1}, N demand would be ~ 5 µmols l^{-1} per 100 meters (120 O to 16 N). In this case, a 200 meter wide bed could absorb much of the DIN load from overlying water with a 10 µmol l^{-1} N concentration if sediment nutrient concentrations were relatively low. Since water column NH_4^+ concentrations were usually very low, and nutrient gradients indicated much lower uptake, this suggests that sediments play a larger role than the water column in supplying community N demand.

In the winter, the sediments, unprotected by seagrasses, are exposed to high wave energy during passing cold fronts. Sediment organic matter and sediment nutrients should be flushed out during this time. In addition, the low primary production during the winter results in low labile organic sedimentation rates. So in

early spring, sediment nutrients may be low, resulting in greater nutrient demand by leaf tissue. In spring, when water column nutrient concentrations were highest, I saw the largest decreases in NH_4^+ with distance into beds. In fall, when dissolved NH_4^+ concentrations were near the half-saturation coefficient of algae, algal community production could have been limited by mass transport, which is reduced by leaf drag-induced water flow reductions.

On sunny days when the water is clear, high dissolved oxygen is a good indicator of the water masses that have had the greatest interaction with the bed, and therefore, the highest potential nutrient and TSS change. As water moves through a productive bed, DO concentrations should increase due to oxygen release by the seagrass community. The rate of increase with distance will depend on the initial concentration, seagrass and algal biomass, current velocity, and factors affecting photosynthetic production, community respiration and oxygen saturation. Nutrients are taken up by macrophyte communities in stoichiometric proportion to C and to oxygen production. If the macrophytes only use water column nutrients, and regeneration rates are relatively low, elevated water column DO would correlate with reduced DIN concentrations. If sediment nutrients are used instead, or if sediment regeneration rates are relatively high, this will not be the case.

While DO gradients indicate the amount of photosynthesis that has occurred and the amount of influence a seagrass bed can have on the water column, they may not be a good indicator of net water column dissolved nutrient changes at our sites. Though submersed macrophytes can obtain all of their nutrients from the water column, high sediment nutrient concentrations can reduce water column nutrient

uptake (e.g., Thursby and Harlin 1984, Hensel 1992). Water column nutrient uptake by macrophytes will also be low at limiting nutrient levels. So if uptake occurs when water column nutrients are low, the epiphytic community may be primarily responsible.

TSS

TSS concentrations were controlled by factors other than seagrass beds contrary to our hypothesis that the *Ruppia* beds would cause decreases into beds. Cownose rays accounted for very significant changes in TSS concentrations, especially in June and July when they were most abundant. Gradients in phytoplankton biomass and TSS across seagrass beds may be influenced by water masses, hydrodynamic conditions, resuspension, and sinking rates. Particles and algae detaching from leaves within beds may be sources to the water column, and phytoplankton blooms may form in the warm, shallow water partially trapped within coves. A combination of these factors is responsible for the lack of consistent gradients of TSS at our sites (Table 4.2).

As water slows within a bed, suspended solids, including phytoplankton, can settle out. This process could result in reductions in concentrations with distance into beds. The more protected beds are more likely to trap small particles, which are easily resuspended. Site TN1, being farther from shore and exposed to the highest current and wave action may have small particles continually swept from the leaves (e.g., Koch 2002) and the sediment surface, leaving little for wind events to resuspend. It also had generally better water quality up-current the bed, which would also keep the

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bed "clean". The dense seagrass coverage there would also help keep trapped particles from being resuspended.

The effect of submersed macrophyte coverage (% of surface area) on Chl *a* and turbidity has been demonstrated for Florida lakes (Canfield et al. 1984). Though differences in TSS concentrations between the inside and outside of seagrass beds in estuaries have been documented (e.g., Ward et al. 1984), and seagrass biomass was correlated with TSS reductions at sites in the York River (Moore 1996), information about the size of bed necessary for suspended matter reductions to be seen has not been provided.

Epiphyton vs. water quality

Epiphyton mass was correlated with TSS and nutrients at our sites as expected. Many factors control epiphytic or periphytic development: light, season (Castenholz, 1960, Cattaneo 1987) depth (Cattaneo and Kalff 1980), waves (Strand and Weisner 1996, Pinckney and Micheli 1998), current velocity and nutrients (Horner and Welch 1981), trophic gradients (Cattaneo 1987), suspended sediment (Horner et al. 1990), macrophyte growth rate and leaf age (Borum 1987), grazers (Howard 1982), and allelopathic compounds (Hootsmans and Blindow 1994). The type of colonizing organism, such as: heterotroph, autotroph, colonial, or filamentous, and which is first to colonize, will also influence the epiphyton accumulation. Many of these same parameters varied or covaried with distance into the beds I sampled, so no one variable can be deemed responsible for variations in biomass. Some of these parameters are responsible for variability at a small scale. I noted another; that blades not surrounded by other blades may have much higher accumulations of loosely

attached epiphyton, probably from the lack of friction between leaves. Additional variability can be added when collecting leaves, since loosely attached material may be lost by moving the blades. Thus, finding statistical differences between sites, never mind determining their cause, is problematic.

During both summers, dissolved nutrient concentrations were near the half-saturation coefficient of microalgae (Table 4.1), and particulate organic nitrogen was a larger source of N, so a large percentage of the epiphytic biomass was heterotrophic. Colonial hydrozoans, bryozoans (mainly *Conopeum tenuissimum*) and stalked ciliates occasionally covered entire shoots and could have reduced colonization by algae. Colonies of bryozoans in seagrass beds filtering water at a rate of 8.8 ml zooid^{-1} day^{-1}, could filter 181 m^{-3} m^{-2} per day (Winston 1995). This could account for large reductions in plankton smaller than 45 µm in diameter. Particulate nitrogen, captured or settling within beds, increases nitrogen regeneration within beds and thus, reduces net uptake rates.

In the beginning of the 2000 sampling season, our epiphyton transects were close to shore. Proximity to shore can reduce current velocities, which decreases nutrient transport. But resuspension can increase total epiphytic mass and nutrient concentrations, and the lower energy near shore can allow a buildup of loosely attached algae. Turbidity generation due to resuspension as waves broke near shore, or due to cownose rays, increased epiphytic load and may have obscured an epiphytic accumulation gradient from outside to inside nearshore beds (Figure 4.7 and Table 4.3). Figure 4.8 and 4.9 also show the degree of influence TSS can have on epiphytic accumulations. Pond and microcosm studies found that TSS concentrations increased

epiphyton weight on submersed macrophytes under still-water conditions (Staver 1984, Guarraci 1999).

When TSS concentrations were high in offshore water, the calm conditions within beds or in protected areas may have allowed settling of large amounts of flocculent particles on the leaves (Figure 4.7 c) and the sediment surface. This flocculent material is easily resuspended, and when it is, TSS concentrations may be higher within beds than in the surrounding water. Beds that are exposed to higher average currents may have lower amounts of easily resuspended materials. It is more likely that TSS concentrations will decrease with distance into these beds. Trippe Bay site TN1 was the most energy-exposed site and so was least likely to be a source of TSS. There, current reduction across the seagrass bed is mainly due to bed drag.

Variability of epiphytic algae (Chl *a*) coverage may have obscured correlations with measured N or pH gradients at the sites near the bay (Figure 4.10). The lack of consistent gradients in algal biomass across seagrass beds may also have been due to oligotrophic conditions (0.62 ± 0.35 µmol NH_4^+ l^{-1} and < 28 µmol TN after July) or lack of consistent differences in water quality across beds. Generally low *Ruppia* biomass would have precluded water quality gradients across beds at upstream sites. Due to the low nutrient concentrations and the large heterotroph component of epiphytic growth, strong relationships between nutrient concentration and epiphyton mass should not be expected.

Though other factors besides water quality could be responsible for the epiphyton dry weight gradient from upriver to downriver in the Choptank, (Figure 4.11b) algal biomass was correlated with a larger scale nutrient gradient in Florida

Bay (e.g., Frankovich and Fourqurean 1997). The persistent downriver water quality gradient and the corresponding epiphyton gradient in July 2001, suggests that if a water quality gradient exists across a bed long enough that the epiphyton mass may correlate with it at this smaller scale.

Seasonality of epiphytic algae biomass has also been noted in other systems (e.g., Cattaneo 1983, Borum 1985, Cattaneo 1987). Colonization, macrophyte growth rate, grazer abundance, nutrient availability, and many other factors change over time. Thus, the decrease in epiphyton mass within beds in fall 2001 (Figure 4.12) may be due to factors besides water quality.

Most of our measurements of epiphytic algal Chl a were in the low range compared to levels found on other macrophytes at other locations. For example epiphytic algal Chl a was 500 µg mg dry weight^{-1} on submersed macrophytes in eutrophic Lake Okeechobee (Zimba 1995) while our values usually averaged less than 1 µg mg dry weight^{-1}. A study in a Rhode Island lagoon found no change in epiphytic algae on *R. maritima* or *Z. marina* with nutrient enrichment (Harlin and Thorne-Miller 1981). The morphology and growth rate of Widgeon Grass may make it less susceptible to epiphytic accumulations than some other species. Epiphytic algae accumulations increase with leaf age and are highest on the upper parts of other basal meristem seagrasses (e.g., Borum 1985, Borowitzka et al. 1990). The average vegetative shoot height of *R. maritima* at our sites was less than 15 cm, and it is thin-bladed and fast-growing. Even so, at an upstream Choptank River site (Horn Point), measured epiphyton mass was significantly higher than downstream. In a separate study at Horn Point (also summer 2001), the measured periphyton initial growth rate

on an artificial substrate (~1 mg dw cm^{-2} d^{-1}) could have kept up with leaf growth (see Brandt and Koch 2003).

Epiphyton vs. bed size, location

Contrary to our expectations, overall epiphyton mass did was not significantly different between inside and outside of beds except for fall 2001 samples. Gradients in conditions across beds may only exist for a short time, while epiphytic colonization and accumulation depend on conditions over several weeks (Borum 1987). Though gradients in water column nutrient concentrations and pH are found during the day, regeneration at night may allow algae in the interior to store enough nutrients to maintain similar growth rates to communities at the bed edge. Night time algal DIC uptake is mainly passive, and algae have lower ability to store C than rooted macrophytes, so they may have to take up the majority of their C during the day. The particulate nutrients that settle into bed interiors result in increased sediment nutrient concentrations with distance from bed edges, which may result in gradients of nutrient fluxes. Thus, there may be little reason to expect gradients in epiphytic biomass due to daytime water-column nutrient concentration gradients. Gradients in currents, wave induced turbulence and suspended solids are more consistent. The differences in epiphyton dry weight I found were mainly due to resuspension within the beds (Table 4.3), and there was no consistent difference in epiphytic algal Chl *a* on the bed outside edge vs. the interior (Table 4.4).

The fall 2001 gradient in epiphytic algal biomass (Figures 4.13 and 4.14) could have been due to reduced nutrient and DIC transport and increased boundary layers across beds, but many other factors could be responsible. *Ruppia* growth may

have been faster inside the beds due to higher sediment nutrient concentrations, and this could have reduced algal accumulations. Anti-algal and other allelopathic compounds could have been released (see Wium-Anderson et al. 1987) by the Widgeon Grass and possibly by benthic algae. Extracts of *R. maritima* (DellaGreca et al. 2000), other seagrasses (e.g., Harrison and Chan 1980) and many other macrophytes have anti-algal properties. The concentrations of these chemicals in the diffusive boundary layer (DBL) or in the trapped water within the beds may have been high enough to alter algal growth. Though phenolics and other defensive chemicals can be a large percentage of macrophyte weight, the concentration in the DBL or the trapped layer of water is not known. During fall, the bed interiors had trapped, decaying macrophytes and phenolic concentrations may have been higher in the leaves due to low DIN concentrations as was found in an eelgrass study (Ravn et al. 1994). This study concluded that the regulation of phenolic biosynthesis was not consistent with inhibition of epiphytic colonization. If low nutrient environments reduce leaf growth rate and turnover, anti-algal compounds may be more necessary though. I do not know why the epiphytic algal component during this fall was dominated by one species, but selective inhibition may have been a contributing factor. Inner bed (and shoreward) locations had siltier sediments and probably higher hydrogen sulfide concentrations, which could have reduced inner bed epiphytic algae accumulations at year-end.

Algal nutrient uptake and biomass increased with current velocity (Whitford and Schumacher 1961, 1964, McIntire 1968) up to a critical velocity, where dislodgement occurs (Horner and Welch 1981, Momo 1995). Higher algal biomass at

macrophyte bed edges was previously documented (Vermaat et al. 2000). Their finding was attributed to the bed acting as a sieve, filtering passing particles. Another study in eelgrass beds found no difference in epiphytic algae abundance with distance from bed edges (Saunders et al. 2003). Differences in epiphytic algae coverage were also found between exposed and protected locations in seagrass meadows in Australia (Kendrick and Burt 1997).

Epiphyton accumulations increased along a larger scale water-column N concentration gradient in a Danish Fjord (Borum 1985), and along available phosphorus gradients in Florida Bay (Frankovich and Fourqurean 1997) and in the Everglades (McCormick et al. 1996). Differences in epiphytic macroalgae assemblages at a large scale were attributed to environmental gradients in seagrass beds in Australia (Lavery and Vanderklift 2002). Large-scale water quality gradients were also evidenced by seagrass N and P content in Florida Bay (Fourqurean and Zieman 2002).

Artificial substrates may have been a better means of determining if differences in conditions across beds could influence epiphytic algae. They could eliminate the possible role of factors such as macrophyte growth rate and allelopathy on epiphytic algae accumulations. But though one study (Cattaneo and Kalff 1979) found little difference in algal communities in lakes between artificial and natural substrates, others have shown differences between the two (e.g., Pinckney and Micheli 1998). The surface texture and allelopathic properties of each species may play roles in epiphyton development. Beds of other macrophyte species could all be affected differently.

Autotrophs in shallow water can be viewed as competing for light or nutrients, depending on the nutrient concentration. Eutrophic systems favor epiphytic and planktonic algae (Duarte 1995), which shade macrophytes. So, if a bed is large enough to reduce dissolved nutrient and inorganic carbon concentrations to levels that limit algal growth, their survival may be enhanced. The role of epiphytic algae in the shading of *R. maritima* however, was generally low at our sites, with an average reduction of light to the leaves of <10% calculated using an attenuation coefficient (of 0.1 µg Chl *a* μg^{-1} cm^{-2}) from a study in Horn Point's ponds (Staver 1984). Even the highest epiphytic algal Chl *a* accumulations measured attenuated less than 33% of available light. Suspended solids contributed greatly to light extinction in deeper water and to total epiphytic mass in protected areas with rays present. The inorganic portion of epiphytic accumulations normally attenuated <15% of available light, using an attenuation coefficient of 0.25 mg dw^{-1} cm^{-2} (Staver 1984) and only caused substantial (>25%) shading when rays were in the beds in large numbers. Water column attenuation calculated from TSS contributed much more to leaf shading, reducing light at one meter by more than 82% on average. Since the settling of TSS in bed interiors could also affect sediment redox and sulfide levels, its negative effect on macrophyte growth could be substantial.

Cross bed sediment characteristics

Though I found gradients in sediment characteristics across beds as expected, they may have been due to wave exposure instead of seagrass bed effects. The well sorted sediments at our sites are indicative of low energy wave environments. The sandbars just offshore the beds at TN1 and CC1 indicate higher wave energy on the

bed edges. Since the gradient of sediment grain size and %AFDW decreased from offshore to onshore (Figures 4.15 and 4.16), part of the change was due to the decrease in wave energy with distance from the outer, wave-exposed edge. Due to the influence of the macrophytes on water velocity at the sediment surface, I know some of the effect is due to macrophyte influence. By sampling seasonally I may be able to determine the how much of the difference is due to macrophyte coverage. It is possible that submersed macrophytes were not totally responsible for altered sediment characteristics found within beds in other studies as well.

Increased sedimentation and reduced resuspension within submersed (Scoffin 1970, Wetzel 1979, Wanless 1981, Harlin and Thorne-Miller 1982, Koch 1999) and emergent (Stevenson et al. 1988, Wang et al. 1993) vegetation have been widely reported. Seasonal increases in sediment and phosphorus due to reduced water flow were noted within emergent stands of *Equisetum fluvitale* L. in an oligotrophic lake (Kairesalo and Matilainen 1994). The extent of alterations in sedimentation may be related to vegetation density (Gleason et al. 1979) and bed size. While sedimentation may increase with distance into a bed as water motion slows, at some distance into a large bed the sediment load may decrease enough to reduce sedimentation rates. This has not been noted, possibly because beds studied are not large enough (e.g., Vermaat et al. 2000), but partly because of limited spatial resolution of sampling (usually outer and inner) in most studies (e.g., Bartleson 1988, Gacia and Duarte 2001).

The depositional environment of seagrass beds is evidenced by smaller sediment grain size and increased organic content within the beds compared to outside. The sediment silt/clay percentage was twice as high in seagrass beds as

outside in the York River (13% vs. 6%, Moore 1996). Organic content, silt-clay content, ammonium and total N increased with distance into large seagrass beds in Back Sound, North Carolina (Kenworthy et al 1982). The exposure of seagrass beds to hydrodynamic energy was also negatively correlated to sediment silt/clay and organic percentage within beds in North Carolina sounds (Fonseca and Bell 1998). Besides influencing nutrient supply, gradients of sediment organic matter may affect sediment redox potential (e.g., Terrados et al. 1999b) and sulfides. Increases in sediment sulfide concentration and decreases in sediment oxygen during the growing season were noted in a *Ruppia cirrhosa* meadow in an Italian lagoon (Azzoni et al. 2001). These changes should also be correlated with distance from bed edges. Though density was found to influence sediment sulfate reduction rates, but not organic matter concentrations in an eelgrass bed in Foskilde Fjord, Denmark (Holmer and Nielsen 1997), the effects of macrophyte density on these processes are also not fully understood.

The increase in porewater dissolved ammonium inside vs. outside the bed at site TN1 could have been due to higher sediment porewater flushing in the higher flow edge, and higher sedimentation in the bed interior. Sediment nutrient concentrations and fluxes should also be related to differences in sediment grain size and organic matter across beds. These differences will be influenced by interior accumulations of fine particles and organic matter as the growing season progresses. Sediment oxygen demand at much deeper mid-bay sites indicated a seasonal pattern (Boynton and Kemp 1985), which may also occur at shallow water sites. As grain size decreases and organic matter increases, sediment oxidation near the roots may

decrease (Barko and Smart 1983, Barko and Smart 1986), macrophyte roots may

shrink or die (Bach et al. 1998, Halun et al. 2002, Bartleson unpublished data),

macrophyte production may be affected (Terrados et al. 1999b) and nutrient fluxes

from the sediment may increase. The sediment at more energy-exposed locations and

on the outside of beds, should be more oxidized, may be washed of nutrients due to

hydraulics (Koch and Gust 1999), and should have lower DIP fluxes (e.g., Boynton

and Kemp 1985). When bed edges coincide with wave energy gradients (sites TN1,

BB1 and CC1 here), the changes in hydrodynamics and sediment characteristics

across beds are due partly to the existing energy gradient and partly to macrophyte

effects.

The paradigm of the influence of seagrass beds on sedimentation and

sediment nutrients is supported by several studies (ibid). The effect of bed density on

sediment properties, the size of bed needed to cause differences, or how sediment

properties change with distance across a bed is still not known. The same factors

which influence how water quality changes with distance across seagrass beds should

similarly affect sediment properties. Decreases in water transport, turbulence, and

suspended load with distance should result in decreased sediment grain size and

increased sediment organics until the point at which supply is reduced. Stapel et al.

(2001) postulated that bed size should have an effect on N retention due to the effect

on particle trapping.

The sediment Chl a and O_2 flux measurements at site BB1 showed an

expected decrease in benthic algae and associated O_2 release within the bed. Shading

by macrophytes, and increased silt within the bed could both reduce algal biomass, while increased organic content would result in less O_2 release.

Relevance to other systems

The phenomenon of spatial gradients in water quality across benthic systems can be seen in other systems besides estuaries though the gradients will depend on the characteristics of the system. Small lakes or lagoons with little current velocity should have steep gradients in water quality at macrophyte bed edges (e.g., Goulder 1969), and could show differences in water quality over very small beds. Very dense vegetation can reduce water flow dramatically (Machata-Wenninger and Janauer 1991) and could cause sharp gradients in water quality even in strong currents. Conversely, deep systems and fast currents minimize affects of benthic communities on water quality. Coral reefs also influence the water flowing over them (e.g., Odum and Odum 1955, Bilger and Atkinson 1995) and shallow reefs should also experience feedbacks related to reef size and water exchange rates. Algae in marshes should be similarly affected by marsh size and distance from open water or creeks, and the density of the marsh macrophytes. Periphyton communities were more productive in a marsh with higher water flow (Cronk and Mitsch 1994). Exchange of nutrients will depend on the density and size of the marsh, as does water flow (Nepf 1999). Spatial measurements related to the effect of macrophytes on water flow and particle transport have been made in marshes. Reductions in suspended loads were measured with distance into a marsh in Louisiana (Wang et al. 1993) and gradients of total P were found in high flow marshes in Illinois (Mitsch et al. 1995). Reductions in

suspended loads should lead to reductions in sedimentation and accumulation with distance as has been shown in Chesapeake Bay marshes (Kearney et al. 1994).

Conclusions

Large, dense, Widgeon Grass beds consistently caused daytime gradients in water flow, pH, dissolved inorganic C, and DO across beds. These effects were correlated to bed size and should be influenced by macrophyte density and current speed. At average current velocities, measurable increases in DO occur within 10 m of the edge of a bed, and increases of more than 50% were measured in large (>100m dia), dense beds. DO concentrations within dense beds reached levels that could inhibit photosynthesis.

The large effect of seagrass beds on dissolved oxygen suggests the potential to reduce water column nutrients substantially under certain circumstances. Though oxygen production measurements indicated high N demand (~5 mmol $m^{-2} hr^{-1}$ stoichiometrically), I only measured very low rates of net water column NH_4^+ uptake. Thus, sediments were the likely N source for the seagrass community.

The calculated reductions in DIC and water flow in large, dense seagrass beds were similar to those found in freshwater systems. In the fall, when nutrient concentrations were already low, the combination of reduced flow and reduced DIN and DIC concentrations within beds could cause transport limitation of production and could result in a competitive advantage for certain species of algae in bed interiors. The high pH levels, and large daily swings in bed interiors could reduce growth rates of algae and resident fauna, and reduce occurrence of fish.

Epiphytic mass and Chl *a* did not consistently decrease with distance into large beds, but the epiphyton total dry weight in the interiors of beds was correlated with TSS supply, whether from offshore or from local resuspension. Though the effect of water quality on epiphytic Chl *a* and dry weight from up to downstream was apparent, the within-bed gradients in fall 2001 could have been due to a wide range of factors including, but not limited to, reduced water flow and DIC availability, and increased concentrations of sulfide and allelopathic substances. Sediment characteristics such as grain size distribution were related with distance from outside bed edges as well as distance from wave exposure. The decreased grain size and increased organic content within bed interiors could affect macrophyte root viability.

Chapter 5. Conclusions and Management Implications

This study has several implications for management of estuarine and other aquatic systems where eutrophication is an issue and submersed plant beds may be able to reduce water column nutrients. However, it was carried out during the day and largely under low to moderate wind and flow conditions; therefore, results may be different under high-flow or high-energy conditions. Under high flows, water residence times will be shortened and submersed plants will have less influence on nutrient concentrations. In addition, high wave energy often resuspends trapped sediments and reduces water clarity so that rates of photosynthesis and nutrient uptake are reduced. At night, nutrient and inorganic carbon demand is not as high, and increased concentrations can help replenish plant community deficits. Despite these limitations, several conclusions are warranted in my study and are outlined below:

- Field data indicate that epiphyton accumulations on *Ruppia maritima* leaves were mostly attributed to total suspended solids (TSS), suggesting that epiphytic algae were less of a factor than indicated by previous studies in Chesapeake Bay (Kemp et al. 1983, Ward et al. 1984).

- The MODFLOW/MT3D model adequately described transport of NH_4^+ in shallow *Ruppia* beds and is especially useful for visualization of effects of seagrass beds on flow and dissolved nutrients. The modeling package has

the advantage that of being freely available, running on personal computers with Microsoft operating systems. Field data were used in this study for calibration but more data are needed for validation of seagrass (or submersed aquatic macrophyte) community uptake of nutrients. To model nutrient transport in seagrass beds in deep water where water flows over the bed, as well as through it, other models (without visualization packages, e.g., Abdelrhman 2003) must be used.

- This study suggests that drag coefficients determined for submersed macrophytes in flumes (e.g. Sand-Jensen 2002) need to be adjusted downward for use in hydrodynamic models due to the effect of "group sheltering" (Thom 1971). Field measurements of flow and observations of *Ruppia* in this region of the Chesapeake Bay suggest that drag coefficients increase with distance into beds as shoots bent at the edges of the bed become more upright.

- Large submersed macrophyte beds with flow paths of 100 meters in freshwater tidal to mesohaline areas can reduce daytime dissolved inorganic carbon (DIC) concentrations in the bed interiors by about 5% and have the potential to reduce dissolved inorganic nitrogen (DIN) concentrations. In larger beds, greater DIC reductions (our measurements averaged 11%) and reductions in free HCO_3^- (up to 45% at Trippe Bay) would occur. Larger beds also have a greater capability for removing DIN.

- The ability of submersed macrophyte communities to provide ecosystem services such as nutrient reduction documented in this study, is becoming widely accepted and they are being used for nutrient removal in large restoration projects such as the Everglades stormwater treatment areas as well as a variety of other innovative wastewater treatment schemes.

- DIN or DIC limitation of photosynthesis within bed interiors could result from the combination of decreased nutrient transport, decreased nutrient concentrations and diffusion gradients, and increased thickness of diffusive boundary layers.

- This study suggests that total nutrient loading in relation to seagrass bed size is a more appropriate management framework than simple consideration of nutrient concentrations (i.e. 10 µM DIN), which are emphasized as goals in EPA's Technical Synthesis II Report (Batiuk et al. 2000). This value is about five or ten times the half-saturation coefficient for algae. At a typical current velocity of 10 cm s^{-1} in 1 meter of water, a 10 µM N concentration goal would result in a loading of 21.6 mols N m^{-2} per tidal excursion. This would be 100 times the possible sustained uptake rate of a dense 1 m^2 patch of *Ruppia*, while hectare - sized beds could possibly reduce nutrient concentrations to limiting levels.

- The optimal configuration of seagrass beds used for nutrient management will vary with specific goals, but larger is usually better. For example, if dissolved nutrient reduction within a confined area is a goal, a large continuous bed (1 hectare or more) would be best. If nutrient concentrations are generally well above the half saturation constant for plant uptake, large beds would be most suitable. Large grass beds will also maximize the depositional area for reduction of suspended solids.

- Clearly, the nutrient buffering at the downstream Choptank River sites was less than optimal due, in part, to low N concentrations in overlying waters. To optimize nutrient removal, beds should be established upstream in the estuary or close to point nutrient sources or farm runoff, where water column concentrations are highest. Downstream seagrass beds may rely more on regenerated nutrients or nitrogen fixation, so may remove less DIN from the water column. For optimal nutrient reduction, submersed plants should be established shallow enough to allow canopies to extend to the surface for maximization of flow reduction and contact time.

- In order to optimize nutrient buffering, barriers to flow around the perimeters of seagrass beds may be necessary to reduce exchange rates and the chance of overloading. These barriers could be biotic (reed beds) or artificial, using materials such as fencing and mesh, aquascape, or

artificial seagrass. Alternatively, beds could be planted in coves or surrounded by dredged sandbars to reduce exchange.

- For maximum dissolved nutrient reductions over large areas in oligotrophic waters, multiple small, dispersed beds may be better than one large, continuous bed because large beds could have reduced DIC and DIN concentrations in their centers, which limit rates of photosynthesis when concentrations fall below half saturation values.

- If nutrient and TSS reductions are desired, seagrass beds should be planted in such a way that they are parallel to the flow. This configuration will allow maximum contact time of the macrophytes and the water column and will increase the area of the bottom that is protected from resuspension by average current velocities.

- Since observations in this study reinforce another study (Orth 1975) that determined cownose rays can be very destructive to seagrass beds in the Chesapeake Bay and cause such high turbidities, some form of population control should be considered. This could perhaps be achieved by developing a commercial market for ray wing meat.

Appendicies:

Appendix A

Diffusion measurements

Diffusion coefficients were estimated by measuring changes in dye blob dimensions over time in the TC seagrass bed and adjacent to it, using the method described by Okubo 1971. Location markers (rafts or stakes) were installed, dye was injected at mid-depth, and photos were taken of the dye blobs using balloon aerial photography. Changes in dye blob dimensions were measured and the rate of change in the direction of the current and perpendicular to it were determined. The mixing coefficients in each direction were calculated as the slope of the regression of each variance as a function of time. Advection was calculated from the movement of the centers of the dye blobs. Rotational movement of the dyed patches was not considered in calculations.

The mixing coefficient in the direction of flow, K_a, averaged 0.022 was much greater than K_b which averaged 0.004. Thus, flow was anisotropic. Our within bed turbulent diffusion coefficients in the direction of flow were in the range of those found at other seagrass beds (Koehl et al. 1993, Worcester 1996) at similar length scales. Small differences could have been due to different wind conditions, localized non-uniformities, insufficient number of samples, or the increased velocities over the short vegetative shoots and the bending reproductive shoots and the resulting shear. Measurements are expected to have a large variance however, due to the range of eddy sizes encountered at this scale (see Stommel 1949). Turbulent diffusion rates in

shallow water are affected by wind, waves, velocity, and stratification. The lateral and within bed coefficients were lower and more like oceanic or other coastal values (Okubo 1971, Koehl et al. 1993). Though our values were measured at a much smaller scale than those of Okubo (1971) or Murthy (1975) they were similar to the prediction of Okubo's equation ($K = 2.6 \times 10^{-2} L^{1.1}$).

Drag and roughness coefficients

Flow through emergent and submersed macrophyte stands has been extensively studied in relation to managing water flow in canals (e.g., Pitlo and Dawson 1990). These studies usually determine the effect of an entire bed on bottom roughness and flow. The effect of small groups of macrophytes has been studied in flumes, where the drag coefficient of a group of macrophytes or cylinders (C_{Dg}) was determined to be less than the sum of the individual drag coefficients. C_{Dg} is then a function of the head difference, current speed, stem diameter and spacing,

$$C_{Dg} = \frac{2g\eta_y}{v^2 a_p}$$

This model formulation has been used for emergent communities (Burke and Stolzenbach 1983, Nepf 1999) that are similar to canopy-forming beds, except that submersed macrophytes are more flexible, so the surface area normal to flow changes with the angle of the macrophyte. The drag term is similar in concept to Manning's roughness coefficient, commonly used for calculations involving open channel flow in culverts and confined channels (Manning 1889)

$$n = \frac{k}{v} \, R_h^{\frac{2}{3}} \, S^{\frac{1}{2}}$$

where n is the dimensionless roughness coefficient, v is velocity in m s^{-1}, R_h is the hydraulic radius (depth in m), k is a unit converter (1 m$^{1/3}$ s^{-1}) and S is the slope. Manning's velocity equation is used for flows where the surface slope is the same as the bottom slope, which is reasonable for our tidal currents. The coefficient for R_h varies in the literature from $5/3$ to 1.62, which was found to better match data from a vegetated channel (Abdelsalam et al. 1992). For our depths (around 1 meter) the exponent is not very important. Substituting C_{Dg} for the group drag term in an equation derived by Petryk and Bosmajian (1975), and assuming the roughness coefficient is a function of macrophyte surface area normal to the flow, Manning's n can be related to vegetation induced drag,

$$n = n_b \sqrt{1 + \frac{C_{dg} \sum A_i}{2gAL} \left(\frac{1}{n_b}\right)^2 R^{4/3}}$$

where n_b is the unvegetated bottom roughness (0.025 for sand), A_i is the area of shoot surface area normal to flow, A is cross sectional area of the flow and L is the length of the reach being considered. This allows us to calculate group drag after measuring n.

Calculation of Manning's n and coefficient of drag for Widgeon Grass beds

Manning's equation (11) can be used to calculate water velocity in shallow water. A typical value of Manning's n for a sand bottom is 0.025. Using a typical velocity measured in the shallows of the Choptank, the surface slope over a flat, sandy bottom can be calculated,

$$S = (v / \frac{k}{n} R_h^{2/3})^2$$

$$S = (0.05 / \frac{1}{0.025})^2$$

$$S = 0.000001563$$

This is a head difference of 0.156 mm over 100 meters.

Vegetation increases the value depending on macrophyte density, distribution, morphology, surface area, and the ratio of shoot height to water depth. If the water velocity is decreased in macrophyte beds to 2.5 cm s^{-1} with this slope, the Manning's n due to the macrophytes and the bottom drag can be calculated,

$$n = \frac{1}{v} R_h^{2/3} S^{1/2}$$

$$n = \frac{1}{0.025} 1^{2/3} 0.000001563^{1/2}$$

n = 0.05

This value is on the low end of the range of values reported in the literature for submersed and emergent vegetation at this water velocity (e.g., Ree 1949, Abdelsalam et al. 1992). Explanations for the low value include the moderate macrophyte density, streamlined form of the macrophytes, shoot flexibility (Kouwen et al. 1981), angle (Koehl 1984) and low buoyancy, close spacing of stems (Thom 1971) and the uneven biomass distribution (biomass decreasing toward the surface and varying horizontally).The macrophyte density associated with this amount of flow reduction at one location was 97 g dry wt. m^{-2}. This corresponds to a surface area normal to the flow of 2.43 m^2 m^{-2} (The ratio of leaf surface area to weight of Widgeon Grass was measured as 0.5 cm^2 mg dry wt^{-1}). Using an equation derived by Petryk and Bosmajian (1975) we can calculate a drag coefficient for the seagrass bed using leaf surface area and the Manning's roughness coefficient. Since their drag term does not include a sheltering factor, and sheltering does occur, the use of C_{dg} is substituted for C_d.

$$n = n_b \sqrt{1 + \frac{C_{dg} * \sum A_i}{2gAL} \left(\frac{1}{n_b}\right)^2 R^{4/3}}$$

If there is 2.43 m^2 of leaf surface per meter square of bottom (ΣA_i), n is 0.05, n_b is 0.025
and assuming R and L are 1 m and A is 1 m^2, we can solve for C_{dg}.

C_{dg} = 0.0154

This is on the low end of values determined for *Vallisneria natans*, a similarly

streamlined species (Sand-Jensen 2003).

Vertical oxygen profiles

Dissolved oxygen was measured at intervals from the surface to the bottom across a *Ruppia* bed (BB1) on one occasion (8/25/00). Figure A3 shows how the vertical oxygen profile changed across the seagrass bed. Outside the bed, the constant DO with depth indicates complete vertical mixing, while the inside bed readings are highest at the bottom by as much as 1.5 mg l^{-1}. This illustrates the effect the macrophyte structure can have on reducing water motion in the vertical in addition to the horizontal direction.

Phytoplankton chlorophyll *a* inside vs. up-current from *Ruppia* beds

Phytoplankton chlorophyll *a* was sampled on some transects by using the filters used for nutrient samples. The filters were wrapped in aluminum foil and put on ice and returned to the lab for Chl *a* analysis as described above. In-situ fluorescence was measured at one site using a Wetlabs Wetstar (Model WS1S) fluorometer. The fluorescence reading was translated to units of µg chlorophyll l^{-1} after calibration with a Cuproporphyrin standard.

Figure A4 shows water column Chl *a* decreasing into the seagrass bed at site TN1. The average water column Chl *a* over four trips was not statistically lower within the seagrass bed at site TN1 (1.9 ± 0.40 vs. 2.9 ± 0.61 µg l^{-1}). Chl *a* values within and up-current from the seagrass bed at site TC1 in August 2001 were 4.38 ± 0.84 and 6.21± 0.13 µg l^{-1} respectively. The mean difference between inside and

outside bed phytoplankton Chl *a* measurements over all sites was not significant (Wilcoxon matched-pairs signed-ranks test, n = 14).

Of our seagrass beds, only site TN1 had a significant difference in phytoplankton between inside and up-current from the bed. The fluorometer measurements shown in Figure 4.7 give an idea of the *Ruppia* bed size needed to see phytoplankton changes at an average current velocity for our sites.

Net system primary production (NPP)

Net system primary production (NPP) was calculated by dividing the change in DO or DIC over horizontal distance by the water transport rate and water depth (Odum and Odum 1955). Diffusion to the atmosphere was ignored for simplicity. To extrapolate this value to a daily rate (for comparison with other studies), I multiplied this rate by 12 hours and subtracted the hourly dark bottle respiration rate multiplied by 12 hours.

Net system primary production calculated from DO averaged 38 mmol m^{-2} hr^{-1} and ranged from 13 - 71 mmol m^{-2} hr^{-1} (Table A3). By extrapolating to 24 hours and subtracting night-time respiration, the average NPP was about 5 g C m^{-2} d^{-1}. Site TN1 had the highest NPP (71 mmol m^{-2} hr^{-1} on 8/22/01) calculated using DO. A higher NPP (196 mmol m^{-2} hr^{-1}) was calculated from DIC for site CC1 on 9/13/01.

The NPP rates I determined (Table A3) were about equal to 10% of macrophyte biomass and comparable to values for *R. maritima* production (Williams and McRoy 1982) and NPP of other macrophyte beds (see Stevenson 1988 and Cebrian 2002 for reviews). The summer maximum net carbon fixation over a *Posidonia oceanica* bed in the saline Bay of Calvi was ~ 38 mmols C m^{-2} d^{-1}

(Frankignoulle and Bouquegneau 1991) compared with our average of 60 mmols C

m^{-2} d^{-1}. Their maximum daily CO_2 change was ~ 50 µmols l^{-1} compared to our cross-

bed average of 119 µmols l^{-1}. The physical characteristics of their bed were not

described in their reports.

Open-water production estimates have well-recognized caveats and should be

viewed as approximations of system NPP. A Lagrangian method of sampling water

quality changes with distance (e.g., Odum 1956) may be more suitable than the

synoptic approach (Odum and Odum 1955) that I used. Since dense beds may trap

part of a water mass, the cross-bed DO gradient may be steeper than it would be

without the water-trapping effect. Other errors of the open-water production method

(discussed in Odum and Odum 1955) include bubble loss (due to supersaturation) and

atmospheric diffusion, which depends on the concentration gradient and surface area

(wind speed), and can be in the same order of magnitude as net production. Also,

polarographic oxygen electrodes lose their accuracy at supersaturated concentrations,

so this method underestimates net production to an unknown extent. Production

estimates using DIC may be more accurate due to lower diffusion rates (Park et al.

1958).

Bubble production plus the difference in diffusion rates may account for the

low net photosynthetic quotients (PQ_N in Table A3) compared to the expected value

of 1 to 1.4 (Wetzel 1975). Low PQ_N values were also found in other seagrass beds

(Odum 1957, Park et al. 1958) and could also be due to microbial uptake of CO_2, and

H_2S reaction with O_2. These processes may also increase from spring to fall, from

energy-exposed to protected sites, from downstream to upstream, and from outside to inside beds.

The dependence of community productivity on water flow was noted in shallow water (Odum 1956) and marsh (Odum et al. 1983) ecosystems and termed a "tidal subsidy". As currents slow in large, shallow beds, the supply of nutrients, carbon and oxygen, and the removal of waste products such as hydrogen sulfide, is decreased.

Table A1. Process equations

Coeff.	Description	Formula

Potamogeton perfoliatus C

Coeff.	Description	Formula
Ps_{SL}	Carbon fixation	$SL \cdot K_{m1.1} \cdot e^{T \cdot K_{t1.2}} \cdot Lm_{SL}$
Lm_{SL}	Limitation	$lesser\_of\_\left(\dfrac{I_{SL}}{I_{SL}+I_{ks}}\right) \cdot e^{-SL \cdot K_{a9}} \_ or \_\left(\dfrac{SN}{SN+Ks}\right)$
I_{SL}	PAR at leaf surface	$I \cdot e^{-Eext}$
$Eext$	Epiphyte PAR extinction	$K_e \cdot \left(\dfrac{EA}{SL}\right)$
Mn_{SL}	Leaf loss	$SL \cdot K_{e1}$
Rs_{SL}	Leaf respiration	$SL \cdot K_{e2} \cdot e^{T \cdot K_{Tt4}} + (Ps_{SL} \cdot K_{e3})$
Tr_{SL}	Transport to roots	$Ps_{SL} \cdot K_{e5}$
In_{SL}	Grazing loss	$if\_\dfrac{In_{EA}}{AM} < AM \cdot K_{im}, \_then\_AM \cdot K_{ia} \cdot \left(\dfrac{SL-K_2}{SL-K_2+K_{g1}}\right)\_else\_0$
Ex_{SL}	Leaf exudation loss	$SL \cdot K_{ex}$
Mn_{SR}	Root loss	$SR \cdot K_{e6}$
Ex_{SR}	Root exudation	$SR \cdot K_{e7}$
Rs_{SR}	Root respiration	$Tr_{SL,SR} \cdot K_{e8} \cdot e^{T \cdot K_{t1.4}}$

Potamogeton perfoliatus non-structural N

Coeff.	Description	Formula
Up_{SL}	Leaf N uptake	$SL \cdot V_{m1} \cdot \left(\dfrac{NW}{NW+K_{sl}}\right) \cdot \left(1-\left(\dfrac{1}{1+(K_9 \cdot R_{NC}) \cdot K_{si}}\right)\right)$
Up_{SR}	Root N uptake	$SR \cdot V_m \cdot \left(\dfrac{NS}{NS+K_{sr}}\right) \cdot \left(1-\left(\dfrac{1}{1+(K_9 \cdot R_{NC}) \cdot K_{si}}\right)\right)$
Ls_{SL}	Leaf N loss	$\dfrac{SN}{SL+SR} \cdot (In_{SL}+Rs_{SL}+Ex_{SL}+Mn_{SL})$
Ls_{SR}	Root N loss	$\dfrac{SN}{SL+SR} \cdot (Rs_{SR}+Ex_{SR}+Mn_{SR})$
R_{NC}	Tissue N to C ratio	$\dfrac{SN}{SL+SR}$

Phytoplankton

Coeff.	Description	Formula
Ps_{PO}	Photosynthesis of PO	$K_{m1} \cdot PO \cdot \left(\dfrac{\ln\left(K_1+\left(I \cdot e^{-K_{d1} \cdot Z}\right)\right)}{K_{d1}} + \dfrac{\ln(K_1+I)}{K_{d1}}\right) \Big/ Z \cdot \left(\dfrac{NW}{NW+K_{sN}}\right) \cdot e^{T \cdot K_{t1}}$
Rs_{PO}	Respiration of PO	$K_{r1} \cdot PO \cdot e^{T \cdot K_{t2}} + K_{r1.2} \cdot Ps_{PO}$
Mn_{PO}	Mortality of PO	$K_3 \cdot PO^2$
Sk_{PO}	Sinking of PO	$K_5 \cdot PO$
Ex_{PO}	Exudation of PO	$K_6 \cdot Ps_{PO}$

Epiphytic algae

Coeff.	Description	Formula
Ps_{EA}	Carbon fixation	$K_{m1.2} \cdot Lm_{EA} \cdot Sa_{EA} \cdot EA \cdot e^{T \cdot K_{t1}}$
Lm_{EA}	Uptake limitation	$lesser\_of\_\left(\dfrac{I_{EP}}{I_{EP}+K_{1.1}}\right)\_or\_\left(\dfrac{NW}{NW+K_{sN}}\right)$

Table A1. (Continued)

Coeff.	Description	Formula
I_{EA}	PAR available to EA	$I \cdot e^{-K_u \cdot EA}$
Sa_{EA}	surface area effect	$1 - e^{-SG \cdot K_m / EA}$
Rs_{EA}	Respiration loss	$K_{r1} \cdot EA \cdot e^{T \cdot K_{r2}} + K_{r1.2} \cdot Ps_{EA}$
Mn_{EA}	Mortality loss	$K_3 \cdot EA^2 + \left(EA/SL \cdot SL \cdot K_{e1} \right) + In_{EA}$
Ex_{EA}	Exudation	$K_6 \cdot Ps_{EA}$

Macroalgae

Ps_{MA}	C fixation	$K_{m1.2} \cdot Lm_{MA} \cdot MA \cdot e^{T \cdot K_{t1}}$
Lm_{MA}	C uptake limitation	$lesser\_of\_\left(I_{MA}/I_{MA} + K_{1.1} \right) or \left(NW/NW + K_{sN} \right)$
I_{MA}	PAR available to MA	$I \cdot e^{-K_{41} \cdot (Z - 0.5)}$
Rs_{MA}	Respiration loss	$K_{r1} \cdot MA \cdot e^{T \cdot K_{r2}} + K_{r1.2} \cdot Ps_{MA}$
Mn_{MA}	Mortality loss	$K_3 \cdot MA^2$
Ex_{MA}	Exudation	$K_6 \cdot Ps_{MA}$

Benthic Algae

Ps_{AB}	C fixation	$K_{m1.2} \cdot Lm_{AB} \cdot AB \cdot e^{T \cdot K_{t1}}$
Lm_{AB}	C uptake limitation	$lesser\_of\_\left(I_{AB}/I_{AB} + K_{1.2} \right) or \left(N_H/N_H + K_{sN} \right)$
N_H	N source	$greater\_of\_NS\_or\_NW$
I_{AB}	PAR available to AB	$I \cdot e^{-K_{41} \cdot Z} + e^{-K_{431} \cdot AB}$
Rs_{AB}	Respiration of AB	$K_{r1} \cdot AB \cdot e^{T \cdot K_{r2}} + Ps_{AB} \cdot K_{r1.2}$
Mp_{AB}	Mortality of AB	$K_3 \cdot AB^2$
Ex_{AB}	Exudation of AB	$K_{62} \cdot Ps_{AB}$

Bacterioplankton

Up_{BP}	Bacterial uptake of CD	$K_{m2} \cdot BP \cdot \left(\dfrac{OW}{OW + K_{s4}} \right) \cdot e^{T \cdot K_{t5}} \cdot \left\{ \left[\left(\dfrac{(1 - A_{p1}) \cdot CD}{(1 - A_{p1}) \cdot CD + K_{s8}} \right) \cdot \left(1 - A_{p1} \right) \right] + \left[\left(\dfrac{A_{p1} \cdot CD}{A_{p1} \cdot CD + K_{s7}} \right) \cdot A_{p1} \right) \cdot \left(\dfrac{NW}{NW + K_{s5}} \right) \right] \right\}$
Rs_{BP}	Bacterial respiration	$K_{r2} \cdot BP \cdot e^{T \cdot K_{t6}} + K_{r3} \cdot In_{BP}$
Sd_{BP}	Sedimentation	$K_{12} \cdot BP$
Mn_{BP}	Mortality	$K_{14} \cdot BP$
A_{p1}	Percentage DOC	$Ex_{PP} / \sum Ip_{CD}$
$\sum Ip_{CD}$	Inputs to CD	$Ex_{SL} + Ex_{EA} + Ex_{MA} + Ex_{PO} + K \cdot Ex_{AM}$

Amphipods

In_{EA}	Ingestion of EA	$AM \cdot K_{i1} \cdot Pf_{AM} \cdot \left(1 - e^{K_7 (Iv_{EA} - EA)} \right) \cdot e^{T \cdot K_{t19}}$
In_{BA}	Ingestion of BA	$AM \cdot K_{i1} \cdot 1/Pf_{AM} \cdot \left(1 - e^{K_7 (Iv_{EA} - BA)} \right) \cdot e^{T \cdot K_{t19}}$
Pf_{AM}	Food preference	$\left(EA/BA \right) / \left(EA/BA \right) + K_{pf}$
Rs_{AM}	Respiration loss	$AM \cdot K_{r13} \cdot e^{T \cdot K_{t3}} + K_{r12} \cdot \sum In$

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Table A1. (Continued)

Coeff.	Description	Formula
Ex_{AM}	Excretion	$K_{51} \cdot \sum In$
Mn_{AM}	Mortality	$K_{53} \cdot AM^2$
In_{FI}	Fish ingestion	$K_{52} \cdot \left(1 - e^{K_4 \cdot (Kp_{11} - AM)}\right)$

Dissolved inorganic nitrogen

$\sum Rs$	Sum of respiration	$Rs_{OP} + Rs_{BP} + Rs_{AM} + Rs_{EA} + Rs_{SL} + Rs_{MA}$
$\sum Up_{NW}$	Nitrogen uptake	$K_{72} \cdot (Ps_{OP} + Ps_{EA} + Ps_{MA}) + Up_{SL}$

Water column dissolved oxygen

Df_{OW}	Atmospheric exchange	$\left(-3 \times A_{Csat} \times \dfrac{OW}{A_{Csat}} - 1.025\right) \Big/ K_{v2}$
A_{Csat}	O$_2$ saturation coeff.	$14.161 - (0.3943 \cdot T) + \left(7.714 \times 10^{-3} \cdot T^2\right) - \left(6.46 \times 10^{-5} \cdot T^3\right)$ $- \left(F_{sal} \cdot \left(0.00841 - (0.00256 \cdot T) + \left(3.74 \times 10^{-5} \cdot T^2\right)\right)\right)$

Sediment dissolved inorganic nitrogen

Ni_{NS}	Nitrification-denitrification	$K_{m19} \cdot \left(\dfrac{1}{1 + \left(K_{26} \cdot OS\right)^{K_{27}}}\right) \cdot \left(\dfrac{NS}{NS + K_{s26}}\right) \cdot e^{T \cdot K_{t24}}$
Df_{NS}	DIN flux rate	$K_{28} \cdot A_{bt} \cdot \left((NS \cdot K_{73}) - NW\right)$

Sediment dissolved oxygen

Df_{OS}	Sediment O$_2$ flux	$K_{vs} \times A_{sod}$
A_{sod}	Sediment oxygen demand	$K_{28} \cdot \left(OW - (OS \cdot K_{73})\right) + A_{bt} \cdot \left[K_{28} \cdot \left(OW - (OS \cdot K_{73})\right)\right]$
A_{bt}	Bioturbation effect	$\dfrac{Rs_{BD}}{Rs_{BD} + K_{s18}}$

Benthic Deposit Feeders

In_{BD}	Deposit feeder uptake	$BD \cdot \left(OS \Big/ OS + K_{s15}\right) \cdot e^{K_{t19} \cdot T} \cdot \left[K_{m16} \cdot \left(CL \Big/ CL + K_{s16}\right) + K_{m17} \cdot \left(CR \Big/ CR + K_{s17}\right)\right]$
Rs_{BD}	Deposit feeder resp.	$BD \cdot K_{r13} \cdot e^{T \cdot K_{t3}} + K_{r12} \cdot In_{BD}$
Eg_{BD}	Egestion of BD	$K_{51} \cdot In_{BD}$
Mn_{BD}	Mortality of BD	$K_{53} \cdot BD^2$

Labile sediment carbon

Sd_{CL}	CL sedimentation	$K_{vol} \cdot \left((K_{a13} \cdot Eg_{FI}) + K_{a11} \cdot (Sd_{OP} + \sum Mn_{SL,SR,EA,MA,AM})\right)$
Up_{CL}	CL mineralization	$K_{g1} \cdot \left(\dfrac{LC}{LC + K_{s24}}\right) \cdot e^{T \cdot K_{t22}} \cdot OS + K_{a14} \cdot \left[e^{K_{t21} \cdot T} \cdot \left(\dfrac{OS}{K_{76}}\right)^{K_{77}} \cdot K_{78} \cdot \left(\dfrac{LC}{LC + K_{s21}}\right)\right] + K_{a15} \cdot Ni_{NS}$

Table A1. (Continued)

Coeff.	Description	Formula
Eg_{FI}	Fish egestion	$K_{eg} \cdot In_{AM}$

Refractory sediment carbon

Coeff.	Description	Formula
Sd_{CR}	CR inputs	$K_{vol} \cdot \left((K_{a17} \cdot Eg_{FI}) + K_{a18} \cdot (Sd_{OP} + \sum Mn_{SL,SR,EA,MA,AM}) \right)$
Up_{CR}	CR mineralization	$K_{g2} \cdot \left(\dfrac{CR}{CR + Ks_{25}} \right) \cdot e^{T \cdot K_{123}} \cdot OS + K_{a20} \cdot \left[e^{K_{121} \cdot T} \cdot \left(\dfrac{OS}{K_{76}} \right)^{K_{77}} \cdot \left(K_{79} \cdot \dfrac{RC}{RC + K_{s22}} \right) \right]$
Bu_{CR}	Burial	$K_{10} \cdot CR$

Table A2. Model coefficients, values, units and sources

Coefficient	Description	Value	References
Potamogeton perfoliatus			
$K_{m1.1}$	Maximum C fixation rate	0.1 d^{-1}	Goldsborough and Kemp 1988
$K_{t1.2}$	Temp coeff. for uptake	0.69 °C^{-1}	Bulthuis 1987, Scheffer et al. 1993a
I_{s}	Light half-saturation coeff.	200 µE m^{-2} d^{-1}	Buesa 1975, Scheffer et al. 1993a, Harley and Findlay 1994
K_{a9}	Self shading coeff.	3 mg C^{-1} cm^{-2}	Staver 1984
K_{e}	Epiphyte shading coeff.	0.001 (unitless)	estimate
I	PAR	0-240 µE^{-2} d^{-1}	measured
K_{e1}	Leaf loss coeff.	0.025 d^{-1}	Sand-Jensen 1975
K_{e2}	Dark respiration coeff.	0.05 d^{-1}	McGahee and Davis 1971, Davis and McDonnell 1997
K_{e3}	Light respiration coeff.	0.1 g g C fixed^{-1}	estimate
$K_{t1.4}$	Temp coeff. for respiration	0.069 °C^{-1}	Scheffer et al. 1993
K_{e5}	Root transport coefficient	0.05 g C fixed^{-1}	Patriquin 1973
K_{g1}	Grazing half-saturation coeff.	1 g C m^{-2}	estimate
K_{2}	Grazing refuge biomass	200 mg C m^{-2}	estimate
K_{ia}	Maximum grazing rate	0.05 d^{-1}	Cattaneo and Mousseau 1995, Menéndez and Comín 1990
K_{im}	Minimum ingestion rate	0.02 d^{-1}	Menéndez and Comín 1990
K_{ex}	Leaf exudation rate	0.01 g C^{-1} d^{-1}	Patriquin 1973
K_{e6}	Root loss rate	0.01 d^{-1}	Sand-Jensen 1975
K_{e7}	Root exudation rate	0.05 g C fixed^{-1}	Bekku et al. 1997
K_{e8}	Active root respiration rate	0.1 g C transported^{-1}	Romero et al. 1999
V_{ml}	Leaf maximum N uptake rate	0.15 g g C^{-1} d^{-1}	Thursby and Harlin 1984
K_{sl}	Leaf N half-saturation coeff.	0.12 mg l^{-1}	Thursby and Harlin 1984
K_{NC}	Tissue N to C ratio	0.08 (unitless)	measured
K_{si}	Internal N uptake exponent	-1.1 (unitless)	estimate

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Table A2. (Continued)

Coefficient	Description	Value	References
K_9	Internal N uptake coeff.	0.01 (unitless)	estimate
V_{mr}	Root maximum uptake rate	0.03 g g C^{-1} d^{-1}	Thursby and Harlin 1984
K_{sr}	Root N half-saturation coeff.	0.04 mg l^{-1}	Thursby and Harlin 1984

Phytoplankton

K_{m1}	Maximum C fixation rate	0.575 d^{-1}	Talling 1957, Eppley et al. 1969
K_{d1}	Light attenuation by phytoplankton	0.5 µg C^{-1}	Tominaga and Ichimura 1966, Paasche 1973
K_1	Light half-saturation coeff.	15 % of ambient	Malone unpublished data
K_3	Mortality coeff.	10^{-6} mg^{-2} d^{-1}	see text
K_5	Sinking rate	0.2 d^{-1}	Boynton et al. 1988, Culver and Smith 1989
K_6	Exudation rate	0.1 - 0.15 g g fixed C^{-1}	Lancelot 1979
K_{t1}	Temperature coeff. for fixation	0.069 °C^{-1}	Eppley 1972
K_{t2}	Temperature coeff. for respiration	0.069 °C^{-1}	Somero and Hochachka 1976
K_{sN}	N half-saturation for OP uptake	10 mg N m^{-3}	Dugdale 1967, Eppley et al. 1969, Scavia 1980, Goldman and Gilbert 1983
Z	Water depth	0.2 m	measured
K_{r1}	Standard respiration rate	0.026 d^{-1}	Parsons et al. 1984
$K_{r1,2}$	Photosynthetic respiration rate	0.05 g g fixed C^{-1}	Geider 1992

Epiphytic algae

$K_{m1,2}$	Maximum C fixation rate	0.5 d^{-1}	Eppley et al. 1969
$K_{1,1}$	Light half-saturation coeff.	10 % of ambient	estimate
K_{se}	Self shading coeff.	0.00005 (unitless)	estimate
K_{sa}	Surface area effect coeff.	3 (unitless)	estimate

Table A2. (Continued)

Coefficient	Description	Value	References
Benthic Algae			
$K_{1.2}$	Light half-saturation coeff.	2 % of ambient	Cahoon et al. 1993
$K_{6.2}$	Exudation rate	0.1 g g fixed C $^{-1}$	Lignell 1990
$K_{aN.1}$	N half-saturation coeff.	30 mg N m^{-3}	Dugdale 1967
Macroalgae			
$K_{m1.3}$	Maximum C fixation rate	1.0 d^{-1}	Auer and Canale 1982
$K_{aN.1}$	N half-saturation coeff.	0.12 mg l^{-1}	Lapointe 1987, Pedersen and Borum 1996
$K_{t1.1}$	Temperature coeff. for fixation	0.069 °C^{-1}	Davison 1987
Bacterioplankton			
K_{m2}	Maximum uptake	0.25 d^{-1}	Ducklow 1982
K_{t5}	Temp coeff. for uptake	0.08° C^{-1}	Shiah 1993, Shiah and Ducklow 1994
K_{t6}	Temp coeff. for respiration	0.02- 0.10 (0.025) °C^{-1}	Pomeroy et al. 1991
K_{s4}	Oxygen half-saturation coeff.	0.5 mg l^{-1}	Shiah 1993
K_{s5}	N half-saturation coeff.	0-(2) mg m^{-3}	Shiah 1993, Fasham et al. 1990
K_{s7}	DOC half-saturation coeff.	(100)-100,000 mg m^{-3}	Semenov 1991
K_{r2}	Metabolic respiration coeff.	0.3 g g assimilated C^{-1}	Azam et al. 1983
K_{s3}	Subsistence respiration coeff.	0.05 d^{-1}	Novitsky and Morita 1978
K_{l4}	Mortality, DOC loss rate	0.01 d^{-1}	Azam et al. 1983
Amphipods			
K_{i1}	Maximum algal ingestion rate	0.3 d^{-1}	measured
K_7	Ivlev coeff for algal ingestion	0.3 g C^{-1}	estimate
Iv_{EA}	Refuge level for EA	200 mg C m^{-2}	estimate

Table A2. (Continued)

Coefficient	Description	Value	References
Iv_{BA}	Refuge level for BA	200 mg C m^{-2}	estimate
K_{52}	Maximum ingestion rate by fish	0.1 d^{-1}	estimate
K_{p11}	Refuge level for fish predation	200 mg C m^{-2}	estimate
K_4	Ivlev a coeff. for fish predation	0.2 g C^{-1}	estimate
Labile dissolved organic matter			
K_{81}	% from dead PO	0.8 (unitless)	Gieskes and Kraay 1984
K_{83}	% of BP lysis and excretion	0.9 (unitless)	estimate
Dissolved inorganic nitrogen			
K_{70}	Nitrogen to carbon ratio of respiration	0.176 gN gC^{-1}	Redfield 1934
K_{72}	Phytoplankton N/C uptake ratio	0.176 gN gC^{-1}	Redfield 1934
$K_{74,90}$	% of ingested C respired by predators	0.25 (unitless)	Vazquez 1989, Nemazie et al. 1993
K_{71}	Ratio of water to sediment volume	10 (unitless)	measured
K_{73}	Ratio of water volume to sediment surface area		0.2 m^3 m^{-2} measured
Water column dissolved oxygen			
K_{89}	Photosynthetic ratio	3.458 g O$_2$ g C fixed^{-1}	Ryther et al. 1971
K_{r14}	Respiratory O:C ratio for biota	3 g O$_2$ g C^{-1}	Valiela 1984
K_{v2}	Water depth	0.2 m	measured
K_{v8}	Ratio of sediment volume to surface area	100 l m^{-2}	measured
Sediment dissolved inorganic nitrogen			
K_{m19}	Maximum nitrification-denitrification rate	50 mg N m^{-2} d^{-1}	Henriksen and Kemp 1988

Table A2. (Continued)

Coefficient	Description	Value	References
K_{n26}	Oxygen effect coeff.	11 mg O_2^{-1}	Henriksen and Kemp 1988
K_{n27}	Oxygen effect coeff.	-4 (unitless)	Henriksen and Kemp 1988
K_{n26}	Nitrification–denitrification half-saturation coeff.	500 mg N m^{-2}	Henriksen and Kemp 1988

Sediment dissolved oxygen

Coefficient	Description	Value	References
K_{a18}	Infauna bioturbation half-saturation coeff.	50 mg C m^{-2}	estimate
K_{92}	O_2 to N ratio	4.57 g O_2 g N^{-1}	Christensen and Rowe 1984
K_{28}	Sediment / water mass flux coeff.	0.1 cm^2 d^{-1}	Berner 1980

Benthic Deposit Feeders

Coefficient	Description	Value	References
K_{m16}	Maximum uptake of labile sediment carbon	0.02–0.04 d^{-1}	Moloney and Field 1989
K_{m17}	Maximum uptake of refractory sediment carbon	0.002–0.004 d^{-1}	estimate
K_{m18}	Maximum predation rate	0.05 d^{-1}	Vimstein 1977
K_{p10}	Ivlev a coeff. for predation	-0.5 mg C^{-1} m^{-2}	estimate
K_{e10}	Refuge biomass	100 mg m^{-2}	Eggleston et al. 1992
K_{t19}	Temp coeff. for uptake	0.07 $°C^{-1}$	Oshida and Reish 1974
K_{o15}	Oxygen half-saturation coeff.	8 mg l^{-1}	Kristensen 1983
K_{a16}	Labile carbon half-saturation coeff.	7,000 mg C m^{-2}	estimate
K_{a17}	Refractory carbon half-saturation coeff.	30,000 mg C m^{-2}	estimate
K_{r12}	Standard respiration rate	0.02 d^{-1}	Taghon 1988
K_{r13}	Active respiration rate	0.1 g g ingested C^{-1}	Kristensen 1983, Taghon 1988
K_{t3}	Temp coeff. for respiration	0.07 $°C^{-1}$	estimate
K_{51}	Egestion	0.075 g g ingested C^{-1}	Grémare et al. 1989
K_{53}	Mortality	0.00004 g^{-2} d^{-1}	estimate

Table A2. (Continued)

Coefficient	Description	Value	References
Labile sediment carbon			
K_{a10}	% of sinking organic matter	0.45 (unitless)	Seiki et al. 1991
K_{a11}	% of sinking phytoplankton	0.6 (unitless)	Gieskes and Kraay 1984
K_{a12}	% of egestion and mortality of BD	0.6 (unitless)	Fabiano et al. 1994
K_{a15}	Carbon loss with nitrification	0.966 g g N denitrified^{-1}	Valiela 1984
K_{g1}	Maximum G1 aerobic decomposition. rate	10 mg d^{-1}	Westrich and Berner 1984
K_{a22}	Temperature effect on aerobic decomposition	0.09 °C^{-1}	Klump and Martens 1989
K_{a24}	Half-saturation coeff. for aerobic decomposition	5000 mg C m^{-2}	Westrich and Berner 1984
K_{g}	% of fish ingestion egested	0.5 (unitless)	estimate
K_{a13}	labile % of fish egestion sedimented	0.05 (unitless)	Seiki et al. 1991
Refractory sediment carbon			
K_{a16}	% of egestion and mortality of BD	0.4 (unitless)	Fabiano et al. 1994
K_{a18}	% of sinking phytoplankton	0.2 (unitless)	Gieskes and Kraay 1984
K_{g2}	Maximum G2 aerobic decomposition rate	0.7 mg d^{-1}	Westrich and Berner 1984
K_{a23}	Temperature effect on aerobic decomposition	0.09 °C^{-1}	Klump and Martens 1989
K_{a10}	Burial rate	0.001 d^{-1}	Krom and Bennett 1985
K_{a25}	Half-saturation coeff. for aerobic decomposition	5000 mg C m^{-2}	Westrich and Berner 1984
K_{a17}	refractory % of fish egestion	0.04 (unitless)	estimate

* Coefficients were estimated using cited literature values as a guide. Many of the values vary with conditions. Literature values were not always appropriate (different species or species vs. functional group) or in a format required for the model.

Table A3

Comparison of net primary production (NPP) based on pH (CO_2) and dissolved oxygen (O_2) measurements at selected sites at different times of the year and different biomass levels. The photosynthetic quotient, PQ_N, is calculated from net production. Dark respiration at TC1 ranged from 3 mmol m^{-2} hr^{-1} in spring to 5 to 7 mmol m^{-2} hr^{-1} in summer.

Site	Date	NPP (O_2) (mmol m^{-2} hr^{-1})	NPP (CO_2) (mmol m^{-2} hr^{-1})	PQ_N ($\delta O_2/\delta CO_2$)	min. DIC (mmol l^{-1})	max. O_2 (mg l^{-1})
2001						
TC1	05/31	49	97	0.47*	0.90	14.70
TC1	06/09	23	27	0.85	1.24	10.27
TC1	06/28	21	30	0.70	1.27	9.60
TC1	08/01	13	25	0.51	1.20	10.22
LC1	08/09	25				9.72
TN1	08/22	71	66	1.07*	1.14	12.22
TC1	09/08	19	37	0.53	0.88	10.35
CC1	09/13	50	196	0.25	0.86	10.20
TN1	09/17	29	66	0.48	0.92	12.10
TN1	09/18	13	27	0.46	0.62	12.77
CC1	09/18	16	36	0.43	0.69	11.18

* calm

Figure A1. Water surface elevation (left) and speed contours (right) across seagrass beds of various sizes. Bed widths are 320, 160 and 80 m. Flow is from the left at an initial velocity of 10 cm s⁻¹. Elevation units are meters. Model assumes a uniform plant distribution in 3 dimensions.

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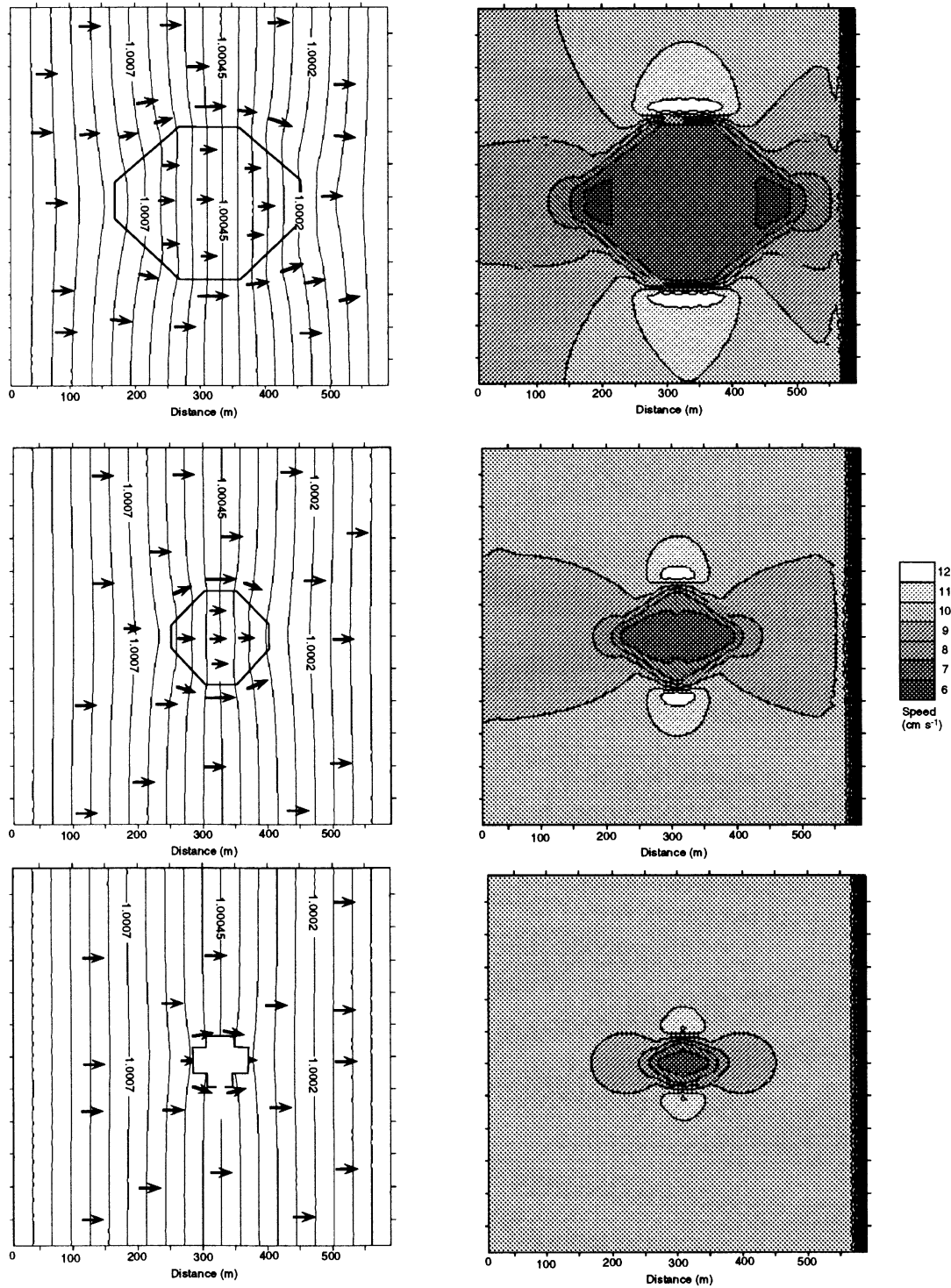
Figure A2. Half hour averages of 2001 wind speed at Horn Point weather station on the Choptank River plotted vs. direction of origin.

Wind speeds in miles per hour
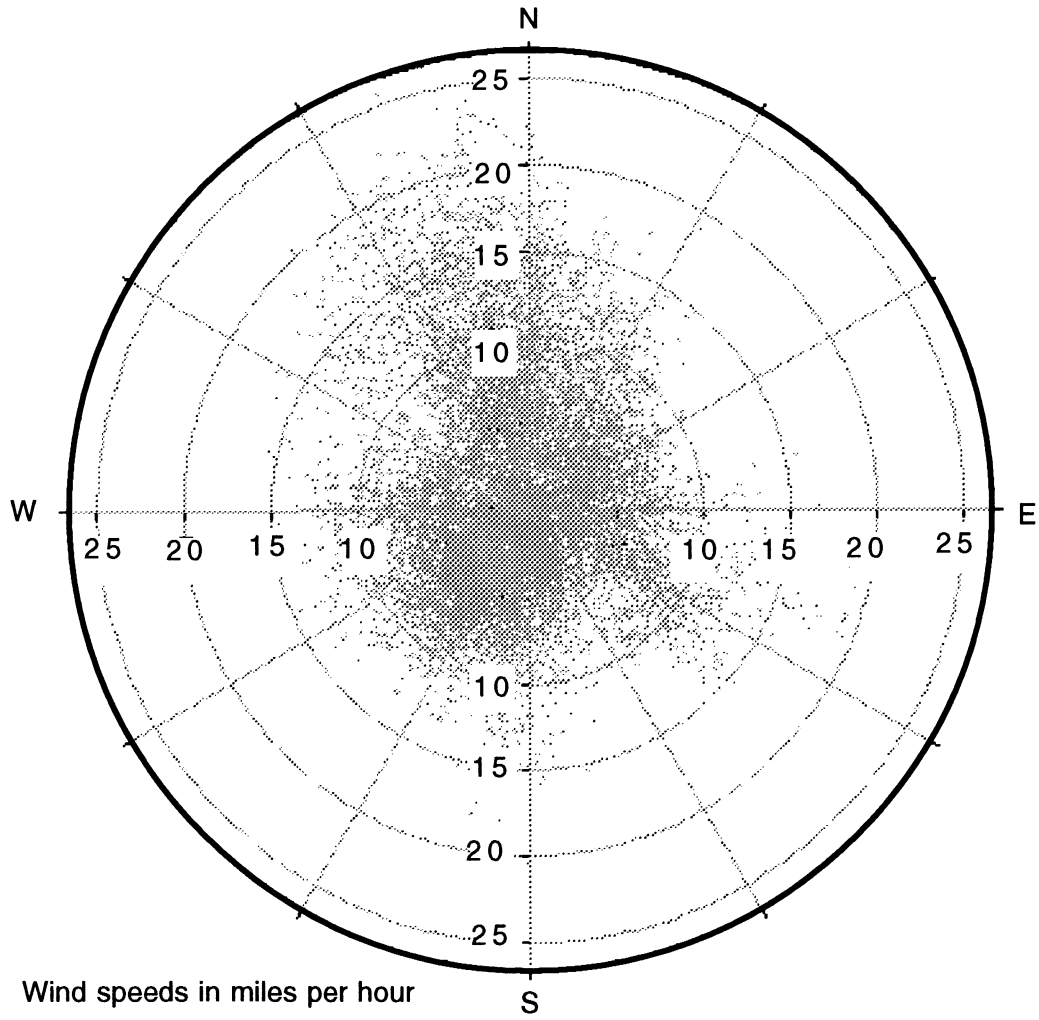
Figure A3. Dissolved oxygen (DO) profile transect across a grass bed showing incomplete mixing within the bed. The canopy extended to the surface, but was not continuous.
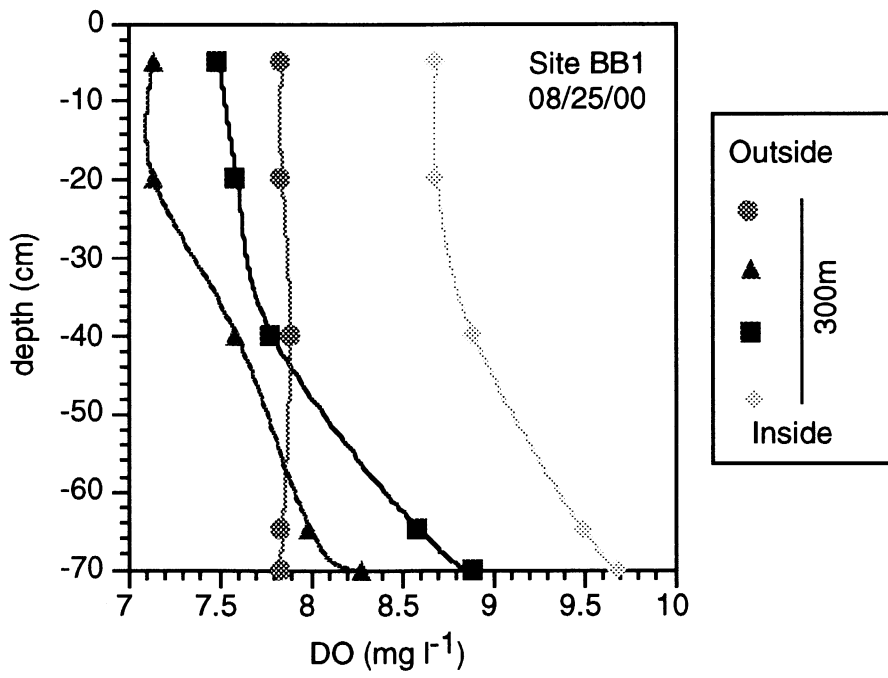
Figure A4. Gradient in water transport and phytoplankton concentration across
a short distance in a dense Widgeon grass bed (Site TN1) in September 2001. Square
symbols are measurements of in-vivo fluorescence. Circles are grab samples.
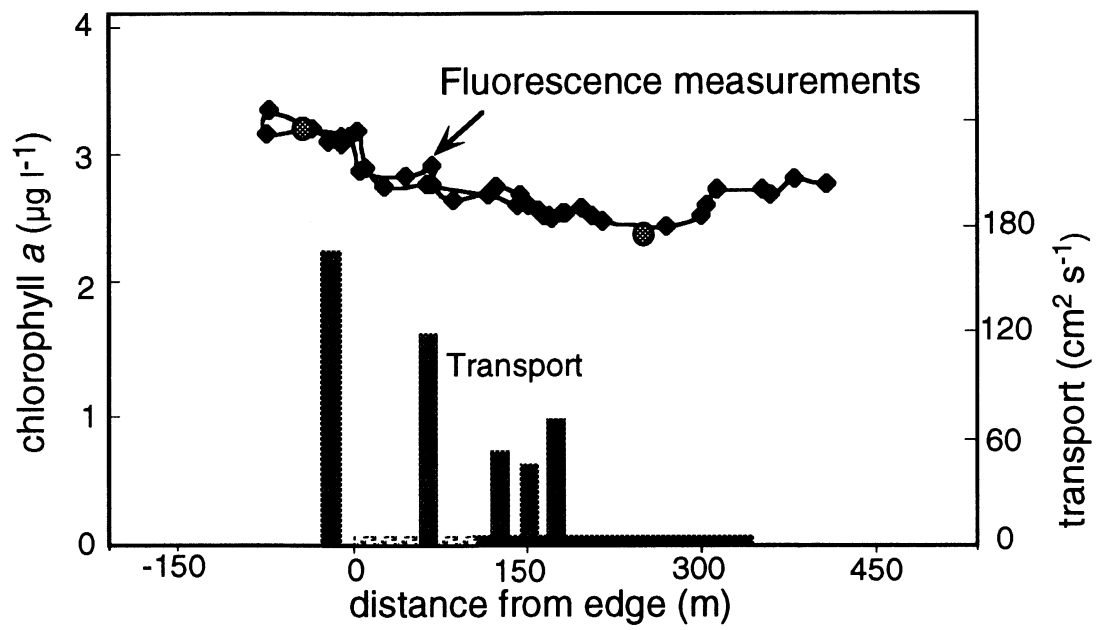
Figure A5. Effect of DIC change on pH along a salinity gradient. The DIC change of 0.15 mmol is approximately the amount caused by photosynthetic production of 2.5 g C m^{-2}.
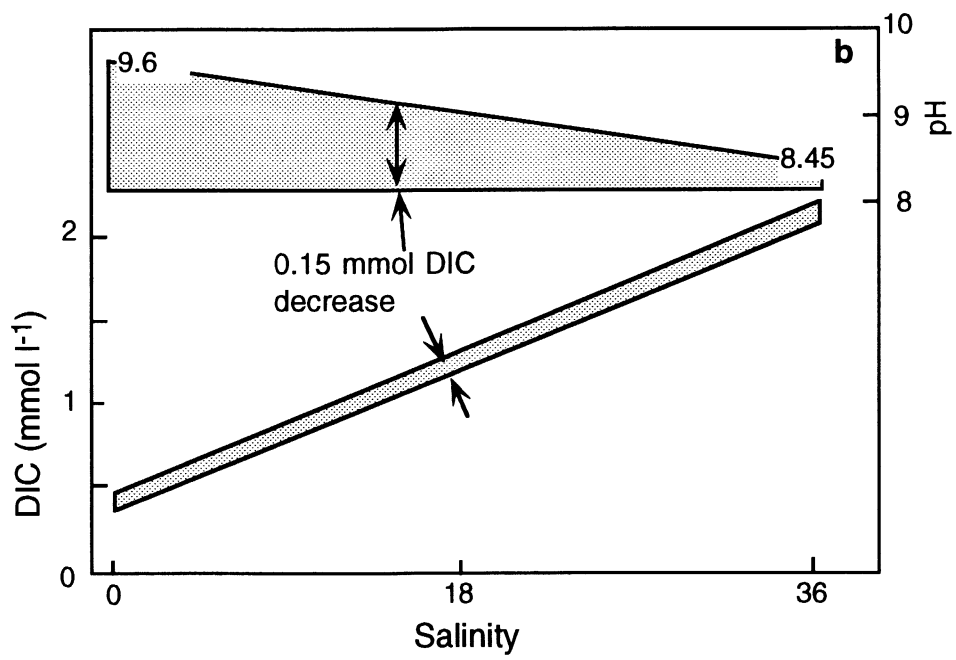
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