

Seagrasses and Protective Criteria: A Review and Assessment of Research Status

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This report is dedicated to the memory of Dr. Peter M. Eldridge, outstanding seagrass scientist, U.S. EPA colleague, and friend to many involved in this effort.

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Abstract

This report is a review and summary of the current status of scientific information relevant to the establishment of protective criteria for the most widely distributed seagrass species of the United States, eelgrass *Zostera marina*, and turtlegrass *Thalassia testudinum*. The report focuses on scientific information related to major limiting factors for seagrass survival, and assesses the degree to which environmental factors may need to be included in the development of adequately protective criteria. The review confirmed that there is a great deal of scientific information currently available concerning the responses of *Zostera marina* and *Thalassia testudinum* to a wide range of environmental factors. However, interactive effects among factors influencing seagrass survival remain relatively poorly known, especially across broader regional scales. This appears true even for such fundamental environmental characteristics as salinity and temperature and their interactions in the expression of nutrient or sediment impacts on SAV, although research is beginning to fill this gap. The question remains as to whether current modeling approaches, whether empirical or mechanistic, are adequate to predict the response of seagrasses to even single stressors. A key concern is that there is a high level of uncertainty in being able to predict the trophic pathway for expression of nutrient impacts on seagrasses. Thus, water quality criteria based on nutrient concentrations may not be adequately protective of seagrass resources. Alternate standards based on water clarity or water column chlorophyll *a* criteria may not be adequately protective if the principle expression of nutrient impacts occur through the epiphyte or macroalgal pathways. There are also important influences on seagrass survival through sediment associated mechanisms that may not be adequately captured by water quality criteria alone. There may be advantages to looking for integrative, plant based seagrass condition indicators, such as sucrose content, that relate to the ability of seagrasses to survive within a temporally varying environment. Such measures may be an appropriate method to integrate water column and sediment impacts into single protective criteria.

Table of Contents

Chapter 1 Conceptual Framework for a Review of Research Needs for Development of National Water Quality Criteria Protective of Seagrasses	1.1
<i>Walter G. Nelson</i>	
Chapter 2 The Role of Light and Sucrose as a Limitation to <i>Zostera marina</i> Growth and Distribution	2.1
<i>Robert J. Ozretich</i>	
Chapter 3 Water Column and Sediment Nutrients as Limits to Growth of <i>Zostera marina</i> and <i>Thalassia testudinum</i>	3.1
<i>James E. Kaldy III</i>	
Chapter 4 Salinity as a Limiting Factor for the Seagrasses <i>Zostera marina</i> and <i>Thalassia testudinum</i>	4.1
<i>Bruce L. Boese</i>	
Chapter 5 The Effects of Hydrodynamic Factors on Seagrasses	5.1
<i>Cheryl A. Brown</i>	
Chapter 6 Interactions of <i>Zostera marina</i> and <i>Thalassia testudinum</i> with Sediments	6.1
<i>Peter M. Eldridge, Mark G. Johnson, and David R. Young</i>	
Chapter 7 The Interaction of Epiphytes with Seagrasses under Nutrient Enrichment	7.1
<i>Walter G. Nelson</i>	
Chapter 8 Macroalgal Interactions with the Seagrasses <i>Zostera</i> spp. and <i>Thalassia testudinum</i>	8.1
<i>David R. Young</i>	
Chapter 9 The Effects of Temperature and Desiccation on the Seagrasses <i>Zostera marina</i> and <i>Thalassia testudinum</i>	9.1
<i>David T. Specht and Bruce L. Boese</i>	

Chapter 10

The Effects of Bioturbation and Bioirrigation on Seagrasses10.1

Theodore H. DeWitt

Chapter 11

Research Gaps in Relation to Setting Protective Criteria11.1

Walter G. Nelson

List of Figures

Figure 1.1. Example of pathway for establishing and implementing seagrass protection and restoration targets.	1.6
Figure 1.2. Diagram of the critical path from Goal Statement to Implementation by the States/Tribes of numeric standards for nutrients.	1.7
Figure 1.3. Diagram of the presumed relationship of effectiveness of a nutrient criterion in protecting resources at the site scale versus the scale at which the criterion is set.	1.8
Figure 2.1. Photosynthesis vs. Irradiance curve where alpha is the initial slope of the curve. ...	2.3
Figure 2.2. An idealized change in incident light intensity throughout a summer and winter day at 45 degrees N.	2.4
Figure 2.3. Gross maximum productivity, gross P_{\max} (■), I_k values (▲), and dark respiration rates.	2.13
Figure 2.4. Days to plant death in dark assuming the sole respiratory carbon source is leaf. ..	2.13
Figure 2.5. Photon flux necessary to replace carbon lost to respiration as a function of temperature (assuming equal daylight and nocturnal respiration rates).	2.18
Figure 3.1. Schematic diagram of the effects of increased nutrient loading.	3.8
Figure 5.1. Relationship between configuration of seagrass beds and shoot morphology and current regime.	5.8
Figure 5.2. Growth conditions of seagrass as a function of current speed.	5.10
Figure 6.1. Both the water column and sediment environments influence seagrasses.	6.3
Figure 7.1. Schematic diagram of seagrass plant illustrating typical patterns of distribution of epiphytes within and among blades.	7.3
Figure 7.2. Horizontal arrows indicate external factors influencing abundance of seagrass epiphytes.	7.4
Figure 8.1. Effects of experimental benthic green macroalgal (<i>Ulva</i> spp.) manipulations on shoot density of <i>Zostera marina</i>	8.2
Figure 10.1. Illustration of some of the adverse effects of bioturbation on seagrasses.	10.3

Figure 10.2. Effects of bioturbating burrowing shrimp (<i>Callianassa</i> spp.) on turtle grass (<i>Thalassia testudinum</i>) on subtidal sand flats on St. Croix island.	10.5
Figure 10.3. Results of two laboratory experiments showing decreased survivorship of seagrass.	10.13

List of Tables

Table 1.1. Sections of the Clean Water Act which pertain to the protection of seagrasses.	1.4
Table 1.2. List of factors potentially limiting seagrass growth and survival, and related chapter in this review.	1.10
Table 2.1. Observations of the death of <i>Zostera marina</i> plants in the field and laboratory. NR = not reported.	2.8
Table 2.2. P vs. I experimental results for <i>Zostera marina</i> L. from various locations and measurement conditions.	2.9
Table 2.3. Sucrose content of <i>Zostera marina</i> L. tissues. NR = not reported.	2.10
Table 2.4. Conversion factors from various sources.	2.12
Table 2.5. Statistics of variables used for calculations.	2.12
Table 3.1. Summary of nitrogen uptake rates for <i>Z. marina</i> . V_{\max} in units of $\mu\text{M gdw l}^{-1} \text{ h}^{-1}$ is the maximum uptake rate, K_s is the half saturation concentration (μM).	3.2
Table 3.2. C:N:P ratios for <i>Z. marina</i> from the literature.	3.3
Table 3.3. Selected list of literature examining the effect of eutrophication on <i>Z. marina</i> communities.	3.7
Table 3.4. Water column and sediment nutrient concentrations (μM) associated with selected studies of <i>Zostera</i> habitat.	3.10
Table 4.1. Reported salinity tolerance ranges for eelgrass (<i>Zostera marina</i>) populations.	4.2
Table 4.2. Reported salinity tolerance ranges for turtlegrass (<i>Thalassia testudinum</i>) populations.	4.2
Table 6.1. Distribution of <i>Zostera</i> species in relation to sediment texture or grain size.	6.4
Table 6.2. Literature values for dissolved sulfide toxicity to marine/estuarine plants.	6.6
Table 7.1. Studies of light attenuation by epiphytes in coastal marine systems, revised and expanded from Table 1, Brush and Nixon (2002).	7.6

Table 7.2. Summary of laboratory microcosm and mesocosm nitrogen and phosphorus enrichment assays using seagrasses.	7.12
Table 8.1. Summary of sources of significant bioturbation impacts for different seagrasses	8.2
Table 10.1. Summary of sources of significant bioturbation impacts for different seagrasses	10.3

1.0 Conceptual Framework for a Review of Research Needs for Development of National Water Quality Criteria Protective of Seagrasses

Walter G. Nelson

1.1 Background of EPA Submerged Aquatic Vegetation Research Program

U.S. coastal waters provide tremendous natural, economic, and public health benefits. Excess nutrients, together with excess carbon, cause cultural eutrophication. These nutrients, primarily nitrogen in marine systems, tend to stimulate excessive algal growth, which then causes a series of events leading to negative ecological effects such as loss of submerged aquatic vegetation (SAV), degradation of benthos, and areas of hypoxia/anoxia. Some of these changes affect use of the Nation's aquatic resources, and pose risks to human health and the environment (National Research Council 2000; U.S. EPA 2002). It has been estimated that 40% of U. S. estuarine surface area shows poor water quality conditions due to eutrophication (Bricker et al. 1999). Evidence suggests that nutrient inputs from point and nonpoint sources will continue to increase for the foreseeable future (Vitousek et al. 1997); therefore, it is important for the EPA to conduct research to diagnose, understand, quantify, and predict the risks that excessive nutrients pose to the coastal marine environment. While nutrients can be a stressor resulting from human activities, they can also have beneficial effects. Therefore, understanding the responses of estuarine and coastal water bodies to elevated nutrient loadings, and developing the ability to distinguish between positive and negative effects, is a priority of for EPA coastal research.

Within EPA, the National Health and Environmental Effects Research Laboratory (NHEERL) has undertaken an extensive research program to improve the scientific basis for setting ecologically based water quality standards. The research program is described in the NHEERL Aquatic Stressors Framework (U.S. EPA 2002). This document defined loss of SAV habitat as a major assessment endpoint for nutrient effects research. Seagrasses are one important component of the broad category of SAV within estuarine and some near coastal waters. Seagrasses typically inhabit mesohaline and polyhaline portions of estuaries, are critical to maintaining estuarine "health" and ecosystem function, and are widely regarded as a cornerstone of estuarine productivity. As such there is an increased awareness of their importance worldwide (Short & Wyllie-Echeverria 1996; Short & Neckles 1999).

Anthropogenic nutrient loading stress to seagrasses can be manifested in a variety of ways including a primary "toxicity type" stress (i.e., high nutrient loading kills plants directly), a secondary stress (i.e., light limitation from phytoplankton blooms) or a combination of primary and secondary stresses. Increased nutrient loading can result in an accumulation of epiphytic, macroalgal and phytoplankton biomass that shades seagrass and results in loss of areal coverage. Losses may result from direct impacts such as physical removal from the action of dense algal mats, or via indirect effects that result from sulfide toxicity and light reduction. Because estuaries are complex ecosystems, it is important to understand both the stressors (e.g., light,

temperature, plankton blooms, toxicity, algal mats, etc.) and end-point response variables (i.e. seagrass growth, biomass, C:N, carbohydrate reserves, etc.). The consequences of seagrass loss may be indirect but still have dramatic and far reaching consequences to the estuarine ecosystem (e.g. shifts in food web structure).

One aspect of the NHEERL nutrient effects research on SAV has focused on developing nutrient load-response relationships for seagrass habitats. This research effort is designed to provide a scientific basis for developing nutrient criteria that would help protect seagrass habitats from degradation or loss, and to provide management tools that will aid in SAV restoration efforts. A principal tool is the development of seagrass stress-response models focused on two dominant seagrass species of the U.S., eelgrass *Zostera marina* and turtlegrass *Thalassia testudinum*. These seagrass stress-response models are designed to deal with multiple stressors, such that the effects of nutrients, increased sediments in the water column, and effects on seagrasses due to alteration of the sediment biogeochemistry can be evaluated.

In the development of the SAV stress-response models, the ultimate goal is to develop and couple the stress-response models, which are plant scale and physiologically based, to population scale models. The Western Ecology Division (WED) has developed a seagrass stress-response model for *Z. marina* (Kaldy and Eldridge 2006), that has been parameterized with data from Yaquina Bay, Oregon, as representative of conditions in the Pacific Northwest. In parallel with this effort, Gulf Ecology Division (GED), Gulf Breeze, Florida, has validated a similar stress-response model previously developed for *Thalassia testudinum*, a common seagrass of the Gulf of Mexico region. Ultimately, the aim is that this suite of stress-response models can be applied to estimate seagrass response to nutrient stress over the range of distribution of the target seagrass species.

The specific objective of the eelgrass stress-response model development is to provide a tool for analysis of future scenarios that would indicate what changes might be expected to occur in response to nutrient enhancement in estuaries. The initial eelgrass stress-response model is one which predicts response at the individual seagrass plant level, and thus is applicable at the patch scale. Model components include seagrass responses to physical influences such as reduced light due to anthropogenic nutrient loading, and to anthropogenic influences on sediment geochemical cycling, in order to accurately predict seagrass nutrient responses.

While it would be desirable to link the patch scale models to population scale models, it is possible to use the patch scale model as a stand alone tool to assist in development of nutrient criteria protective of seagrasses (Brown et al. 2007). By collecting data on physical parameters (light availability, sediment conditions, water temperature) at stations located across the span of the estuarine system of interest, the model can be used to estimate seagrass plant responses to increased loads of nutrients and/or sediments at these measurement points. Under the assumption that stations are at least locally representative, model predictions at these multiple locations can be used to examine whether proposed nutrient standards are adequately protective across the entire estuarine system, or whether they may need to be varied across an estuarine gradient.

1.2 Regulatory Background

The U.S. Environmental Protection Agency is concerned with the protection of seagrasses under two sections of the Clean Water Act (33 U.S.C. 1252 et seq.), Section 304(a) and Section 404(c). Under section 304(a) (1) the agency is charged with development of water quality criteria reflecting the latest scientific knowledge on effects of pollutants on aquatic biota, including “plant life”. The agency is further charged (Section 304(a) (2)) with providing timely scientific information on factors necessary to maintain the chemical, physical and biological integrity of the nations waters. Under section 404 which regulates dredging and dredged material disposal under the lead of the Army Corps of Engineers, EPA is authorized to deny issuance of dredged material disposal permits where such activity will have “an unacceptable adverse effect on municipal water supplies, shellfish beds and fishery areas (including spawning and breeding areas), wildlife, or recreational areas.” While seagrasses are not specifically named, it is clear that the protection of seagrass habitat is encompassed within both sections of the Clean Water Act.

In response to the charge to develop water quality criteria for all of the nation’s waters, EPA (2001) has published the Nutrient Criteria Technical Guidance Manual: Estuarine and Coastal Waters. The document provides an extensive overview of the issues of nutrient over enrichment in marine waters. It provides guidance on steps for development of nutrient criteria (see section 1.4 below), and provides suggestions for key variables and measurement methods for assessing eutrophic condition. Finally it describes management approaches by which nutrient criteria can be used to protect water quality. Ultimately, it is the states and tribes that adopt water quality criteria and standards, and they would be responsible for adopting any criteria specifically protective of seagrasses.

1.3 Pathways to Water Quality Criteria Setting

Kenworthy (1992) provides a detailed history of the early evolution of water quality criteria relevant to submerged aquatic vegetation, tracing the original guidelines for developing state standards back to the Federal Water Quality Act of 1965. His review similarly addressed the history and development of the State of Florida water transparency and turbidity standards. His assessment at that time was that both the federal guidance and Florida state standard were inadequate and unlikely to sufficiently protect seagrass.

The Kenworthy review of the history and process of setting one state water quality standard, the Florida transparency standard, suggested that in the past, the process of setting water quality criteria might propagate uncertainties contained in guidance documents in such a way as to lead to flawed criteria. As a specific example, the state standard at the time included a numerical definition of a light compensation point derived from phytoplankton which was inappropriate for the survival of seagrasses.

Table 1.1. Sections of the Clean Water Act which pertain to the protection of seagrasses.

SEC. 304. (a)(1)	The Administrator, after consultation with appropriate Federal and State agencies and other interested persons, shall develop and publish, within one year after the date of enactment of this title (and from time to time thereafter revise) criteria for water quality accurately reflecting the latest scientific knowledge (A) on the kind and extent of all identifiable effects on health and welfare including, but not limited to, plankton, fish, shellfish, wildlife, plant life, shorelines, beaches, esthetics, and recreation which may be expected from the presence of pollutants in any body of water, including ground water; (B) on the concentration and dispersal of pollutants, or their byproducts, through biological, physical, and chemical processes; and (C) on the effects of pollutants on biological community diversity, productivity, and stability, including information on the factors affecting rates of eutrophication and rates of organic and inorganic sedimentation for varying types of receiving waters.
SEC. 304. (a)(2)	The Administrator, after consultation with appropriate Federal and State agencies and other interested persons, shall develop and publish, within one year after the date of enactment of this title (and from time to time thereafter revise) information (A) on the factors necessary to restore and maintain the chemical, physical, and biological integrity of all navigable waters, ground waters, waters of the contiguous zone, and the oceans; (B) on the factors necessary for the protection and propagation of shellfish, fish, and wildlife for classes and categories of receiving waters and to allow recreational activities in and on the water; and (C) on the measurement and classification of water quality; and (D) for the purpose of section 303, on and the identification of pollutants suitable for maximum daily load measurement correlated with the achievement of water quality objectives.
SEC. 404. (c)	The Administrator is authorized to prohibit the specification (including the withdrawal of specification) of any defined area as a disposal site, and he is authorized to deny or restrict the use of any defined area for specification (including the withdrawal of specification) as a disposal site, whenever he determines, after notice and opportunity for public hearings, that the discharge of such materials into such area will have an unacceptable adverse effect on municipal water supplies, shellfish beds and fishery areas (including spawning and breeding areas), wildlife, or recreational areas. Before making such determination, the Administrator shall consult with the Secretary. The Administrator shall set forth in writing and make public his findings and his reasons for making any determination under this subsection.

The development of water quality criteria is ultimately based on the concept of protection of a designated use for a particular body of water. For the example of Florida, there are five designated use categories for surface waters of which Class III - Recreation, Propagation and Maintenance of a Healthy, Well Balanced Populations of Fish and Wildlife is the Designated Use that applies to the protection of seagrasses (Kenworthy 1992). The language of the Florida Class III Designated Use is derived directly from the language of the Clean Water Act (e.g. Sec. 304. (a)(2), Table 1.1). While encompassing seagrasses, it does not specifically identify protection and propagation of seagrasses as a Designated Use.

The Seagrass Conservation Plan for Texas (1999) indicates that in order to achieve the stated objective to “Ensure water and sediment quality beneficial to the seagrass community” a series of steps were involved. A first and important strategy in the Texas plan was to propose that “Seagrass Habitat” be added to the list of Designated Uses for the state of Texas. With this

basis, water quality criteria specifically protective of seagrasses could be developed and added to the Texas Surface Water Quality Standards. Finally, the Texas Plan proposed the implementation of water-based Best Management Practices.

A second example of creating a specific designated use to address seagrass protection comes from Chesapeake Bay (EPA 2003). In order to reach the ambitious goal of correcting nutrient and sediment problems within the Bay and its tributaries by 2010, regional management organizations recognized the need to create new designated uses that would offer better protection of biotic resources and would be a better representation of desired water quality objectives. A very precisely defined “shallow-water bay grass designated use” was one such refined designated use proposed. The designated use applies to tidal waters, from the intertidal zone to segment specific depth zones from 0.5 to 2.0 m. Another interesting aspect is that the designated use includes a seasonal use component, such that it applies only during the bay grass growing season which varied among salinity zones within the Bay.

Development of water quality criteria protective of seagrasses may be principally driven by the desire to restore a severely degraded resource. One example of a critical path (Figure 1.1) for seagrass protection derived from seagrass restoration goals is provided by the plan developed by the Tampa Bay National Estuary Program (Johansson and Greening 2000). Within the framework of the general designated use, targets for extent of seagrass restoration are first set. Setting of quantitative seagrass restoration targets may be based on a variety of lines of evidence. Seagrass conservation targets developed for the Indian River Lagoon of Florida (Virnstein and Morris 2000, Steward et al. 2005) involves three approaches, development of a potential target based on distribution in the best available habitat (a reference condition approach), the use of a historically based distribution target, and a “critical minimum” approach which establishes the lowest threshold below which seagrass extent should not fall.

The site specific strategies developed by the Tampa Bay NEP (Johansson and Greening 2000), Texas Parks and Wildlife (1999), etc. can be generalized (Figure 1.2) to a critical process path (e.g. U.S. EPA 2001; Batelle 2008). Within the U.S. EPA Regional Offices, there are Nutrient Coordinators who establish Regional Technical Assistance Groups to assure that the best available current information is brought to the criterion development process, and inappropriate guidance is weeded out. As suggested by Figure 1.2, a critical early decision is the consideration of scale at which to set a water quality criterion. Considerations of estuarine system classification and the degree to which ecoregional classifications can be applied are required in order to reach beyond a water-body by water-body approach to criteria setting.

The challenge for U.S. EPA in developing guidance for water quality criteria protective of the seagrass resource on a national basis is presaged by Kenworthy (1992) in his consideration of development of a general state standard for Florida. He suggests that because of the broad variation in physical systems, and in the sources and causes of water quality impairments, “a general standard will fail to adequately protect seagrasses.” Instead, “site or region specific standards will be more effective”. The quandary of this trade off between site scale effectiveness and spatial scale at which a criterion is set is summarized in Figure 1.3. Variation in physical

systems becomes greatly magnified as one moves from state to national scales. The highly specific designated use boundary delineation defined for Chesapeake Bay (EPA 2003) is one example of the application of site-specific standards across an important regional resource.

However, at the national scale, factors limiting the ability to achieve broadly protective water quality criteria for seagrasses are the economic limitations and constraints imposed by the necessity to develop water-body specific criteria. In contrast to states such as Florida, or those bordering the Chesapeake Bay, many states have little or no technical capability for monitoring seagrass systems, and have far more limited resources for developing and implementing SAV criteria. The present report seeks to begin a process of considering how best to develop water quality criteria protective of seagrass by first evaluating current knowledge on seagrass ecology in the context of developing protective standards for seagrasses.

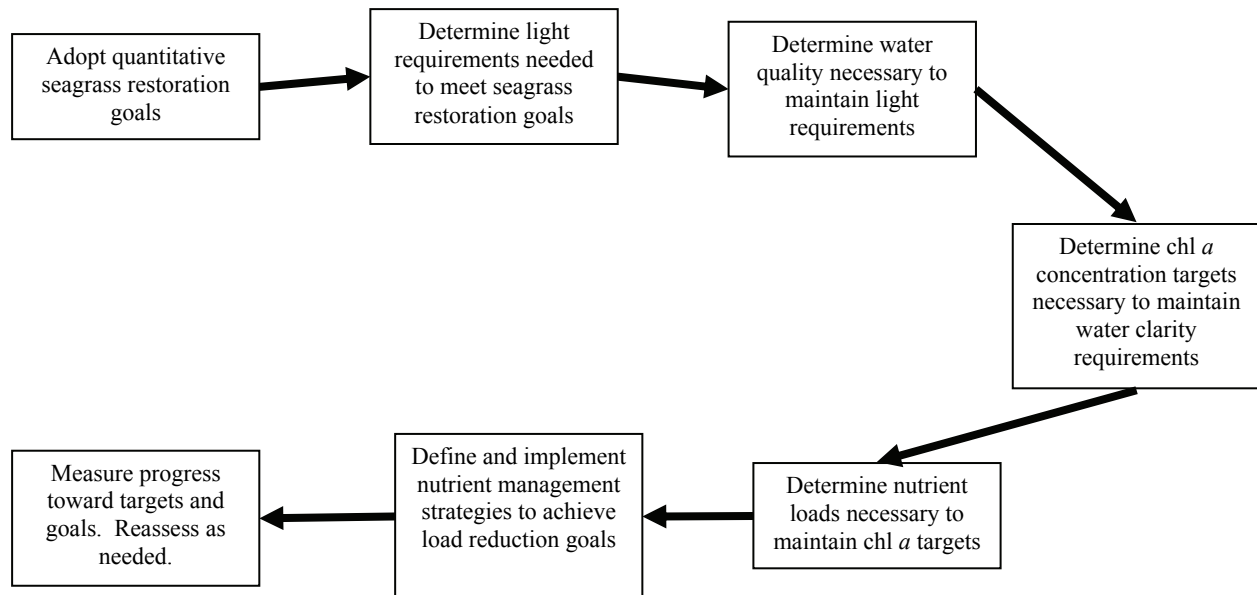


Figure 1.1. Example of pathway for establishing and implementing seagrass protection and restoration targets. The approach illustrated is for the Tampa Bay National Estuary Program (modified from Johansson and Greening 2000).

Numeric Nutrients Criteria Critical Development Path

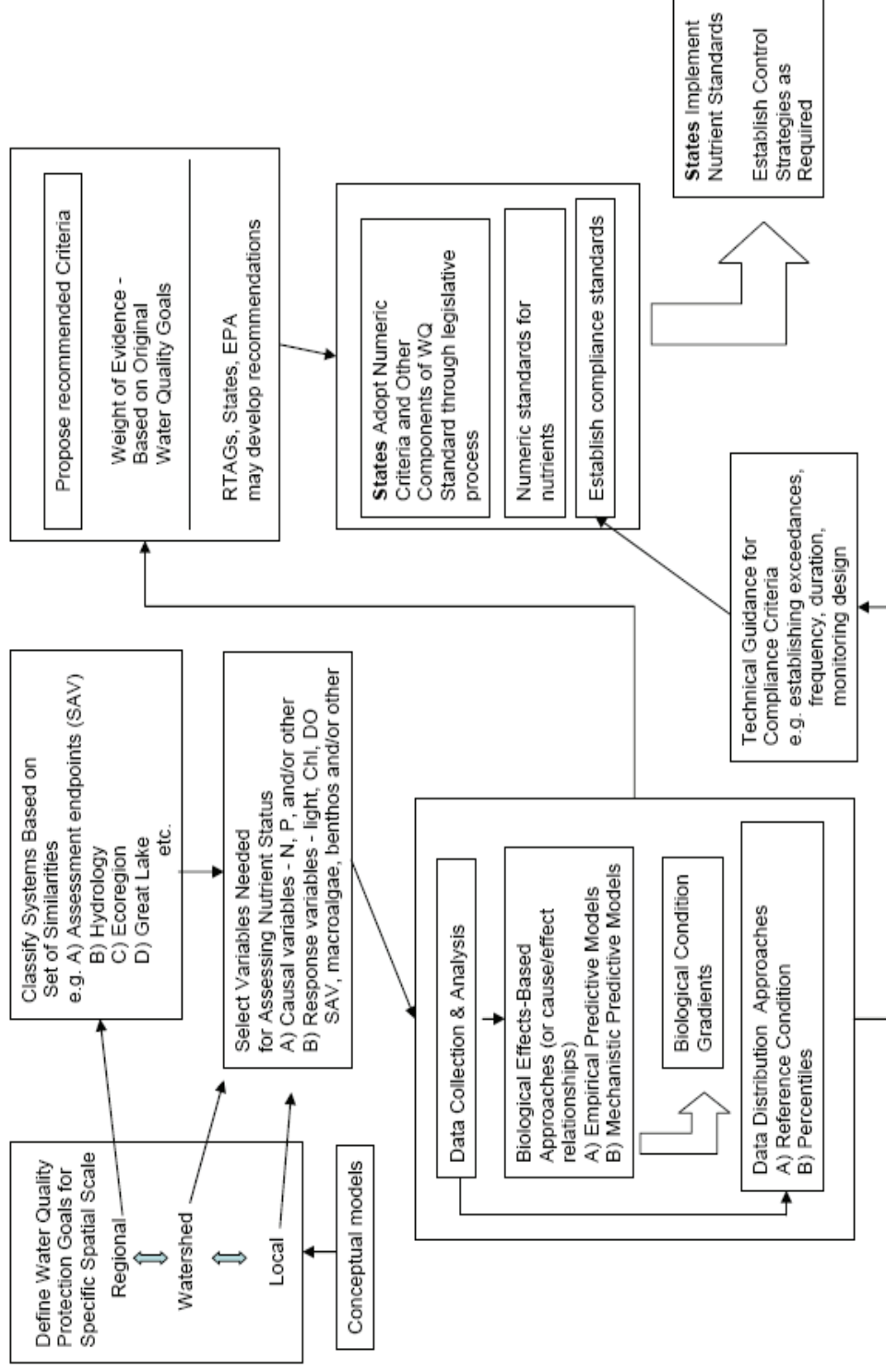


Figure 1.2. Diagram of the critical path from Goal Statement to Implementation by the States/Tribes of numeric standards for nutrients.

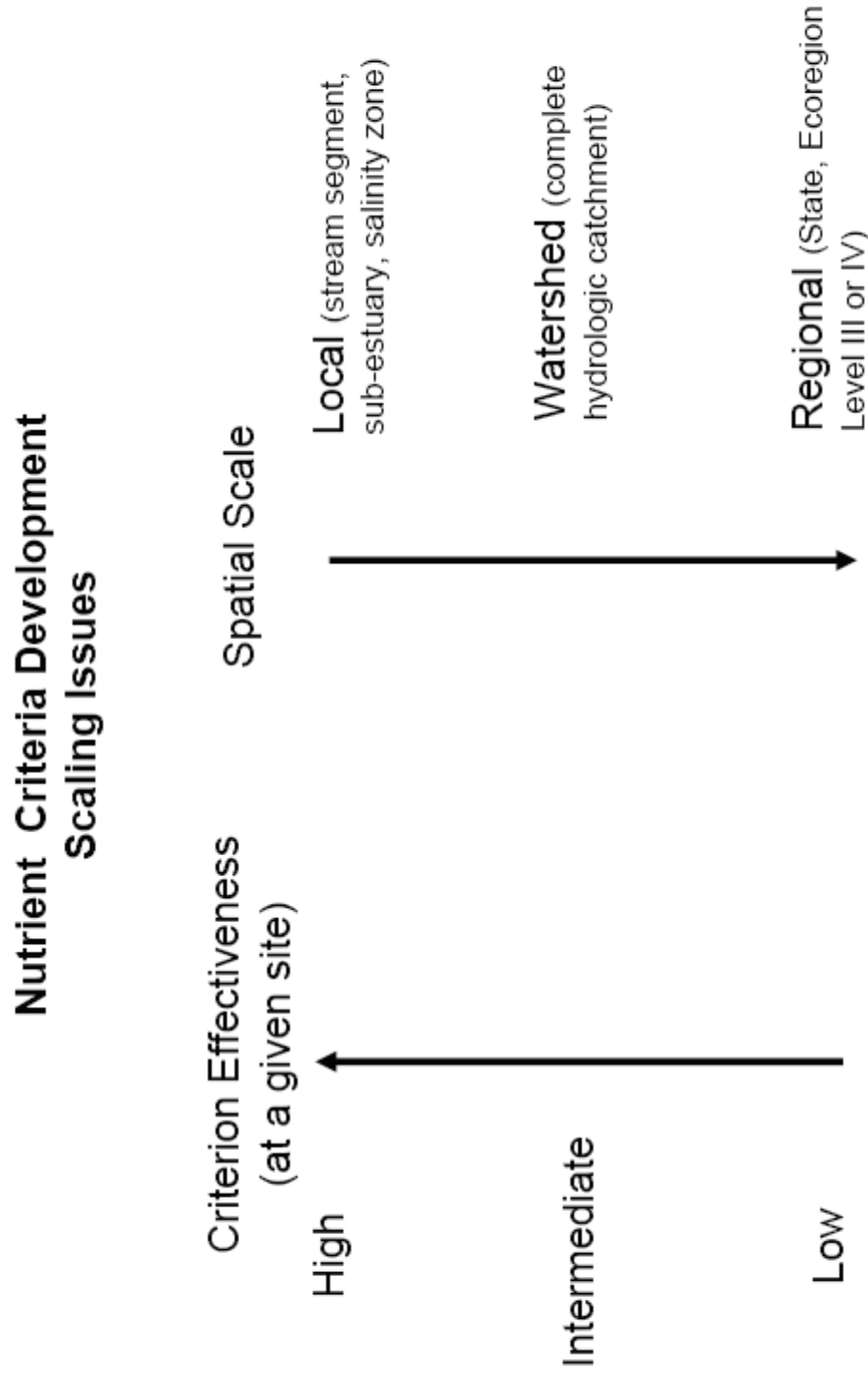


Figure 1.3. Diagram of the presumed relationship of effectiveness of a nutrient criterion in protecting resources at the site scale versus the scale at which the criterion is set.

1.4 Goals and Limitations: Reviewing the Environmental Requirements of Major U.S. Seagrass Species

During the 1980's, a series of summary documents on seagrass communities of the U.S. were produced by the U.S. Fish and Wildlife Service (Phillips 1984; Thayer et al. 1984; Zieman 1982; Zieman and Zieman 1989). These broad reviews encompassed aspects of seagrass ecology ranging from environmental tolerances to descriptions of the communities of plants and animals associated with seagrass habitats. Since that time there has been a tremendous increase in the research literature on seagrasses. In preparing for the present review, Western Ecology Division scientists established a Microsoft Access bibliographic database of greater than 10,000 entries related to seagrass biology.

The aim of the present report is not to duplicate the scope of earlier summaries, but instead to focus on providing an updated review of scientific knowledge of the most broadly distributed U.S. seagrass species that will be relevant to the process of developing protective criteria of major estuarine SAV resources of the continental U.S. As originally conceived, the review effort was to cover the three most widely distributed species of seagrasses in continental U.S. waters: *Z. marina* (eelgrass), *T. testudinum* (turtle grass), and *H. wrightii* (shoalgrass). The effort was to include authors from other EPA divisions who could provide regional knowledge on seagrass ecology, together with specialized knowledge on aspects of seagrass ecology. Unfortunately, this concept was not realized as divisional research priorities shifted and scientists were unable to fully participate in the project. Thus, individual chapter authors determined which seagrass species were included within the scope of coverage for a given topic area.

The principle focus of this review evolved to become the environmental requirements of *Z. marina*, while *T. testudinum* received more limited coverage depending on topic area, and other species are dealt with to a much lesser degree. A second limitation to the report is that publication has been repeatedly delayed, again due to shifting priorities, and therefore the most recent seagrass literature may not be included. Despite this, the report synthesizes a great deal of information that is highly relevant to the management and protection of seagrasses as a critical aquatic resource.

The principle goal of the review is to highlight any critical uncertainties that must be addressed by research in order to be able to develop protective criteria. Thus, our review examines what is known concerning the species-specific requirements for the range of principal factors potentially limiting seagrass growth and survival within the limits described above (Table 1.2). The review is structured in chapters which describe individual limiting factors. Each chapter provides the background for a particular factor or factors related to seagrass ecology, a review of relevant research, and an evaluation of whether or not there are significant research gaps in relation to providing guidance to the setting of effective protective criteria.

The background section describes the mechanisms by which the limiting factor (e.g. epiphytic load) may potentially influence the growth, survival, reproduction and distribution of seagrasses. The review of research has a narrow focus on work that is directly relevant to the

limiting factor and seagrass condition. For example, while a comprehensive evaluation of what is known about taxonomic composition of epiphytic cover may be of significant academic interest, it would not be a focus of the review unless it provides some essential insight into seagrass survival. The focus is instead on whether there is adequate evidence to indicate whether for example, epiphytes can limit seagrass growth, and under what conditions and by what mechanisms. The section on Research Gaps in Relation to Setting Protective Criteria assesses the state of the science for the limiting factor with regard to setting protective criteria for seagrasses. Questions addressed in this section are for example, “Should epiphyte loading be somehow integrated into a protective criterion?” or “Is there adequate research in place to suggest an approach, or even a potential target?”

Table 1.2. List of factors potentially limiting seagrass growth and survival, and related chapter in this review.

Limiting Factor	Subject to Anthropogenic Modification	Chapter
Light	Yes	2
Nutrients	Yes	3
Salinity	Yes	4
Current and Wave Exposure	Yes	5
Sediment Characteristics (Grain size, dissolved oxygen, sulfide)	Yes	6
Epiphytes	Yes, through indirect mechanisms	7
Macroalgae	Yes, through indirect mechanisms	8
Temperature (Freezing, Heat Stress, Desiccation)	Yes, through both direct and indirect mechanisms	9
Bioturbation	Yes, through indirect mechanisms	10
Diseases	Yes, through indirect mechanisms	10
Herbivory	Yes, through indirect mechanisms	7 for micrograzers

1.5 Literature Cited

- Batelle. 2008. Conceptual Plan for Nutrient Criteria Development in Maine Coastal Waters. Report prepared for EPA Region 1, Maine Dept. of Environmental Protection, and U.S. EPA Oceans and Coastal Protection Division. Batelle, Brunswick ME. EPA Contract No. 68-C-03-041. pp. 31.
http://www.maine.gov/dep/blwq/report/2008/nutrient_criteria_report_2008.pdf
- Bricker, S. B., C. G. Clement, D. E. Pirhalla, S. P. Orlando, and D. R. G. Farrow. 1999. National Estuarine Eutrophication Assessment: Effects of Nutrient Enrichment in the Nation's Estuaries. NOAA, National Ocean Service, Special Projects Office and the National Centers for Coastal Ocean Science. pp. 71.
- Brown, C.A., W.G. Nelson, B.L. Boese, T.H. DeWitt, P.M. Eldridge, J.E. Kaldy, H. Lee II, J.H. Power, and D.R. Young. 2007. An Approach to Developing Nutrient Criteria for Pacific Northwest Estuaries: A Case Study of Yaquina Estuary, Oregon. USEPA Office of Research and Development, National Health and Environmental Effects Laboratory, Western Ecology Division. EPA/600/R-07/046.
- Johansson, J. O. R. and H. S. Greening. 2000. Seagrass restoration in Tampa Bay: A resource-based approach to estuarine management. pp. 279-294. In: S. A. Bortone (ed.). Seagrasses: Monitoring, Ecology, Physiology, and Management. CRC Press. Boca Raton. pp. 318.
- Kaldy, J.E. and P.M. Eldridge (eds.). 2006. Development of mechanistic models to guide establishment of protective criteria for seagrasses. Report on the *Zostera marina* and *Thalassia testudinum* stress-response models. Office of Research and Development, National Health and Environmental Effects Research Laboratory, EPA Internal Report.
- Kenworthy, W. J. 1992. Do federal water quality criteria and Florida state water quality standards protect seagrasses? A feasibility evaluation of alternative criteria and standards to monitor, evaluate and regulate water transparency. Appendix II, pp. A-11 to A-29, In: A. Hart (ed.) Proceedings and Conclusions for the Submerged Aquatic Vegetation Initiative. Indian River Lagoon, National Estuary Program. Melbourne, Florida. (Also as pp. A-19 to A-48, In: Morris, L. J. and D. A. Tomasko (eds.), 1993. Proceedings and Conclusions of Workshops on: Submerged Aquatic Vegetation and Photosynthetically Active Radiation. Special Publication SJ93-SP13. St. Johns River Water Management District, Palatka, Florida.
- National Research Council. 2000. Clean coastal waters: understanding and reducing the effects of nutrient pollution. National Academy Press, Washington, DC. pp. 405.
- Phillips, R. C. 1984. The ecology of seagrass meadows in the Pacific Northwest: a community profile. US Fish and Wildlife Service. FWS/OBS-84/24. pp. 85.
- Short, F. T. and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrass. *Environmental Conservation* 23:17-27.
- Short, F. T. and H. A. Neckles. 1999. The effects of global climate change on seagrass. *Aquatic Botany* 63: 169-196.
- Steward, J., R.W. Virnstein, L. J. Morris, and E. F. Lowe. 2005. Setting seagrass depth, coverage, and light targets for the Indian River Lagoon system, Florida. *Estuaries* 28:923-935.

- Texas Parks and Wildlife. 1999. Seagrass conservation plan for Texas. Texas Parks and Wildlife Department, Resource Protection Division. Austin, Texas. pp. 79.
- Thayer, G. W., W. J. Kenworthy, and M. S. Fonseca. 1984. The ecology of eelgrass meadows of the Atlantic coast: a community profile. U.S. Fish and Wildlife Service FWS\OBS-84\02. pp. 147.
- U.S. EPA. 2001. Nutrient criteria technical guidance manual: Estuarine and coastal marine waters. U.S. EPA, Office of Water. EPA-822-B-01-003.
- U.S. EPA. 2002. Aquatic Stressors Framework and Implementation Plan for Effects Research. US EPA, Office of Research and Development, National Health and Environmental Effects Laboratory, pp. 179.
- U.S. EPA. 2003. Ambient water quality criteria for dissolved oxygen, water clarity and chlorophyll *a* for the Chesapeake Bay and its tidal tributaries. U.S. EPA, Office of Water and Office of Science and Technology. EPA 900-R-03-002.
- Vitousek P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7:737-750.
- Virnstein, R. W. and L. J. Morris. 2000. Setting seagrass targets for the Indian River Lagoon, Florida. pp. 211-218, In S. A. Bortone, ed. *Seagrasses: Monitoring, Ecology, Physiology, and Management*. CRC Press. Boca Raton.
- Zieman, J. C. 1982. The ecology of the seagrasses of south Florida: a community profile. U.S. Fish and Wildlife Service FWS\OBS-84\02. pp. 158.
- Zieman, J. C. and R. T. Zieman. 1989. The ecology of the seagrass meadows of the west coast of Florida: a community profile. U.S. Fish and Wildlife Service Biol. Rep. 85(7.25). pp. 155.

2.0 The Role of Light and Sucrose as a Limitation to *Zostera marina* Growth and Distribution

Robert J. Ozretich

2.1 Background

Light is a fundamental requirement for seagrasses. The energy derived from photons is used to reduce carbon dioxide and fuel the biosynthesis of carbohydrates that make up the bulk of these plants, amino acids and lipids. Without light consisting of a sufficient quantity of photons of wavelengths overlapping the absorption spectra of a seagrass' photosynthetic pigments, insufficient carbon dioxide will be fixed to fulfill the plant's respiratory needs resulting in the plant's death or failure to grow or reproduce.

Anthropogenic activities that affect the quality or quantity of light available to seagrasses can be direct and indirect. Uncontrolled construction sites within an estuary's watershed can lead to elevated loads of suspended sediments that increase light scattering in the water, thereby reducing the amount of light that can potentially reach seagrasses. Similarly, addition of nutrients to a watershed from excess run off of nutrients from agricultural and urban sources can promote blooms of phytoplankton and seagrass epiphytes that reduce both the quality and quantity of light available to seagrasses.

Determining the light requirements of seagrasses has been approached both by considering the needs of individual plants and from consideration of the maximum depth distributions of a given species. Individual plant requirements have focused on the plant's response to light through the experimental determination of P vs. I (photosynthesis versus irradiance) curves (Figure 2.1). By comparing rates of photosynthesis with respiration, the daily number of hours of light saturating irradiance (H_{sat} , Figure 2.2) necessary to balance respiratory demands has been estimated. Estimates of H_{sat} are often coupled with monitoring data to evaluate the suitability of locations for sustained *Zostera marina* growth. The maximum depth of occurrence of *Z. marina*, when compared to the local attenuation coefficient, has also been used to estimate the minimum light requirement as a percentage of water-incident light. This approach lets the plant's growth patterns account for the astronomically and meteorologically-induced variation in time and latitude of the incident light field (Figure 2.2) and the *in situ* changes in water composition to which it is exposed. In general, survival at a location over time requires that the plant's carbon balance is positive and that the periods of negative carbon balance are short enough that recovery is possible during more favorable conditions.

To reach the leaf surface of seagrasses, sunlight has to pass through the atmosphere, the air-water interface, through the water column and finally, through a film of epiphytes. Application of the current understanding of the spectral and intensity changes in light prior to reaching the leaf surface has resulted in bio-optical-physical models of varying complexities. Some models have progressed to the point where the spectral dynamics of light through a stand of seagrass has been coupled with primary production models to predict *in situ* growth and

distribution. Modeling of intensively and extensively studied systems has led to proposed habitat requirements for submerged aquatic vegetation.

2.2 Review of Relevant Research

2.2.1 Radiative Transfer Theory

Understanding the spectral and intensity changes in light as it travels from the sun into and through natural waters has led to several books and articles on radiative transfer theory and optical oceanography (Preisendorfer 1986; Jerlov 1976; Kirk 1994). This research has resulted in a thorough understanding of the interaction of light with dissolved and particulate material in water as well as the in-water consequences of meteorological and astronomical changes (Mobley 1994). This understanding is expressed through the publication of radiative transfer equations (RTEs) that, when combined in the numerical radiative transfer model, Hydrolight (Sequoia Scientific, Inc., Redmond, WA) represents a mathematically complete rendering of these processes that is available to the public. Other solutions of the RTEs have been published that produce comparable results in certain applications (Gallegos 1994; 2001).

The basic optical properties of natural waters that the RTEs deal with are the absorption and scattering of light as it passes through a volume of water; both of these processes are wavelength-dependent. This is because the scattering interaction of matter and light is a function of matter's dimensions compared to light's wavelengths, and because interactions with matter in which energy is absorbed are a quantum phenomena they are also a function of wavelength (Mobley 1994).

The absorption and scattering coefficients of light are considered to be a result of the summation of the contributions from each water component. This can be expressed in the following way for the spectral (by wavelength) absorption coefficient, $a(\lambda)$:

$$a(\lambda) = a_w(\lambda) + a_{\text{DOM}}(\lambda) + a_{\text{phto}}(\lambda) + a_{\text{TSS}}(\lambda) \quad \text{Equation 2.1}$$

where a_w , a_{DOM} , a_{phto} , and a_{TSS} are the contributions to absorption by water molecules, dissolved organic matter (DOM), phytoplankton, and total suspended solids, respectively. Each is wavelength-dependent and the last three are also concentration dependent.

Absorption and scattering are considered inherent optical properties (IOPs) of water and in combination contribute to the spectral, diffusive attenuation coefficient, K_D^λ which is considered an apparent optical property (AOP) because it varies with the in-air geometry and intensity of the light source.

The consequence of absorption and scattering of light in water is expressed through the following, familiar expression of "Beer's Law":

$$I_Z^\lambda = I_0^\lambda e^{(-K_D^\lambda * Z)} \quad \text{Equation 2.2}$$

where I_Z^λ is the irradiance of wavelength, λ , Z meters below the surface, and I_0^λ is the surface irradiance.

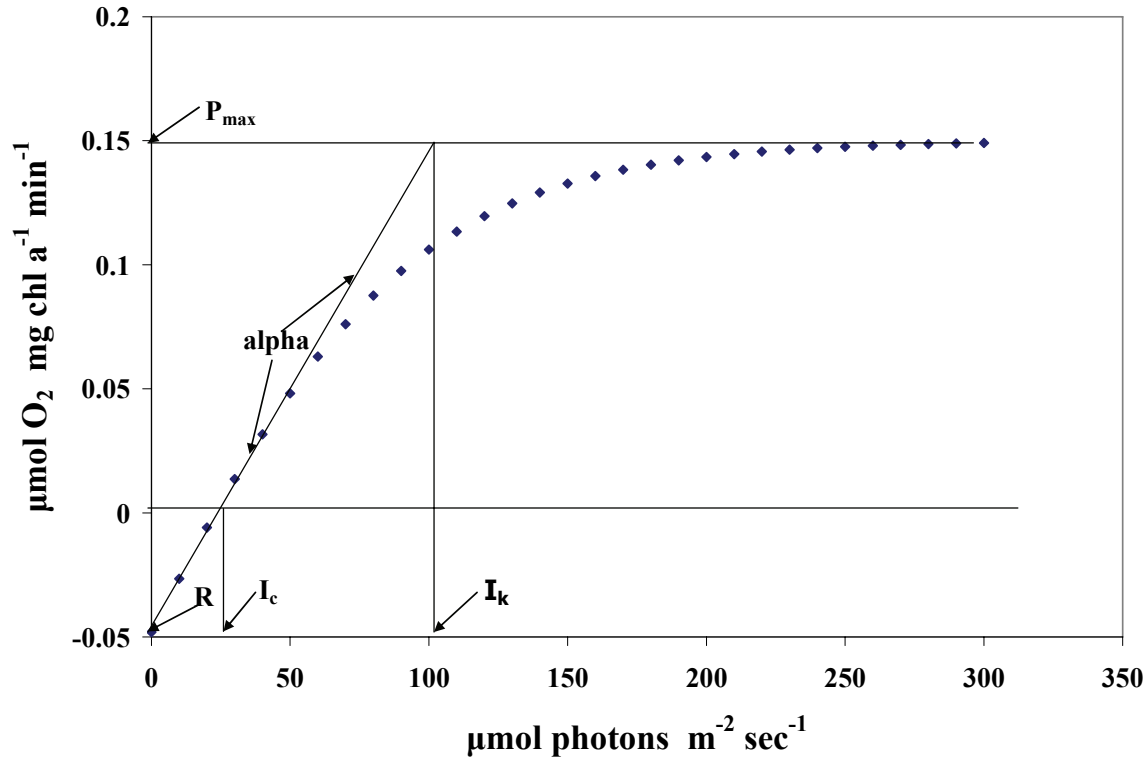


Figure 2.1. Photosynthesis vs. Irradiance curve where α is the initial slope of the curve, I_k is the light intensity at the onset of light-saturated photosynthesis, P_{max} ; I_c , the compensation light intensity, is the light intensity at which dark respiration, R , is equal to the rate of photosynthesis. The dark respiration determined graphically from P vs. I measurement represents dark respiration in the light but may not be representative of a lower nocturnal dark respiration because of the plant's response to the enhanced post-illumination respiration phenomenon (Heichel, 1979; Falkowski and Raven, 1997).

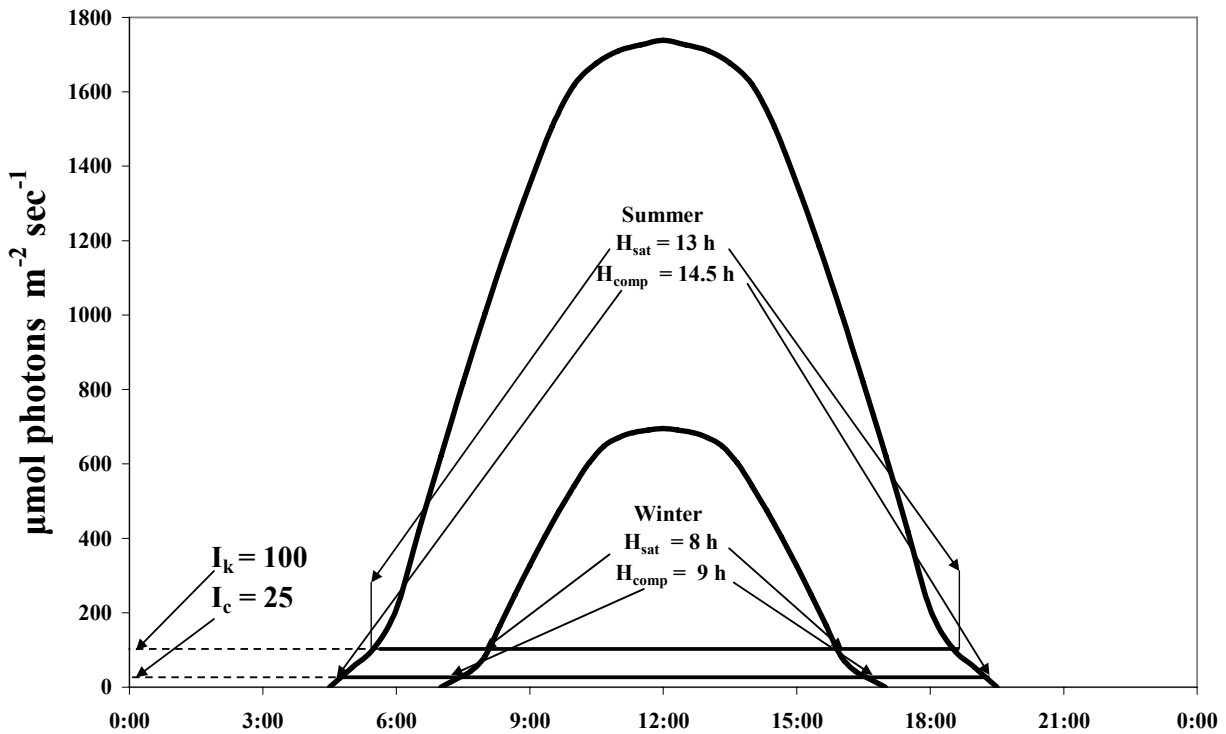


Figure 2.2. An idealized change in incident light intensity throughout a summer and winter day at 45 degrees N latitude where I_k and I_c are from the P vs. I curve in Figure 2.1. H_{sat} are the hours during which I_k is exceeded and H_{comp} are the hours during which production exceeds respiration and the light intensity exceeds I_c .

2.2.2 Application of Radiative Transfer Theory to Systems

Historically, Secchi depth measurements were the only estimates of water column optical properties that were available and conversion to K_D (PAR) for modern modeling applications has been found to be site-specific, especially for estuarine settings (Preisendorfer 1986; Giesen et al. 1990; Batiuk et al. 1992). These conversions have relied on direct comparisons to the results of the more recent, broad bandwidth, PAR sensors (LiCor Environmental, Lincoln, NE; Biospherical Instruments, San Diego, CA). The use of photoelectric instruments in permanent moorings or deployments from vessels have supplanted the Secchi depth measurement as their outputs are directly useful in calculating PAR attenuation coefficients under a wide range of *in situ* conditions. The spectrum of light that is useful for plants is that which overlaps the absorption spectra of the pigments involved with photosynthesis. This is light with wavelengths between 400 nm and 700 nm which is considered photosynthetically available radiation (PAR). Measured at the deepest sites where seagrasses are found, PAR has been used to assess long-term light requirements as a percentage of PAR incident on the water's surface (Duarte 1991;

Dennison et al. 1993). Multi-variant regression models using TSS (or turbidity), chlorophyll *a*, and DOM concentrations as combined predictors of K_D (PAR) were found to be insufficiently accurate in comparison to RTE-derived estimates of K_D (PAR) for the purposes of establishing management options for seagrasses in Chesapeake Bay (Gallegos 2001). The consequences of different mitigation strategies could be assessed in achieving water quality goals when the contributions of these water column components to light attenuation have been determined.

Using parameterized absorption and scattering for two different seagrass habitats (including *Zostera marina*), Zimmerman (2003) used the Hydrolight model in combination with his own model to investigate the light environment within the canopy of seagrass meadows as a function of leaf allometry, canopy structure and modeling boundary conditions. Combined model outputs compared favorably ($\pm 15\%$) with measured, spectral irradiances at various heights within the canopies.

If only the concentrations of the absorbing and scattering water components varied in time and space and not their spectral attributes, concentration-based models would be universally applicable. One such model parameterization, $K_D = 0.32 + 0.016 * \text{chl } a (\mu\text{g l}^{-1}) + 0.094 * \text{TSS (mg l}^{-1})$, has been done for Chesapeake Bay (Kemp et al. 2004) where, 0.32 is the contribution to attenuation by water molecules. Unfortunately, the spectral characteristics of the light absorbing and scattering components of natural waters appear to be at least system dependent, if not temporally dependent. For example, terrestrially derived material (abiotic particles and DOM) from different locales (Gallegos and Kenworthy 1996) can have different optical characteristics. Species succession and decomposition over time can affect the optical characteristics of a phytoplankton bloom as it reduces nutrient concentrations and is consumed. Determination of these characteristics of the optically important components of natural waters will therefore be required for each studied system (Gallegos 2001; Zimmerman 2003).

While solution of the RTEs computes PAR reaching the depth of a plant's leaves, it is not often the PAR that actually reaches the chlorophyll-containing surface of the leaves. This is because of the colonization of these surfaces by a variety of organisms and the settling of biotic and abiotic particles (Twilley et al. 1985; Losee and Wetzel 1983; Kemp et al. 2000; see Chapter 7). This epiphytic community, which tends to increase over time, absorbs and scatters light spectrally and reduces the amount of PAR reaching the leaf surface (Drake et al. 2003). This resulting light is the photosynthetically used radiation, or PUR. Kemp et al. (2000; 2004) developed algorithms to model K_D (PAR) through the epiphytic layer as a function of both growing season nitrogen or phosphorous concentrations and TSS. These algorithms were used to reduce the percentage of water-incident irradiance supporting seagrass populations that had been estimated from field measurements and RTE-modeled estimates of K_D (PAR).

2.2.3 Instrumentation Used in Support of RTE Parameterizations

Validation of modeling results requires *in situ* measurement of the light fields. Long-term and shipboard cast deployments of broad bandwidth, PAR sensors (LiCor Environmental, Lincoln, NE; Biospherical Instruments, San Diego, CA) have historically contributed greatly to understanding the temporal and spatial variability of this critical measurement. Field-deployable

full spectrum scanning radiometers have also been developed such as LiCor's LI-1800 and the much smaller HydroRad (HOBI Labs Inc., Tucson, AZ). In recent years, instruments have been developed that can simultaneously measure attenuation and absorption/scattering of multiple narrow bandwidths. Examples of these types of instruments are the ac-9 (WetLabs, Philomath, OR) and HOBI Lab's HydroScat. The ac-9 has been used extensively in estimating water column IOPs *in situ* (Zimmerman 2003; Gallegos and Jordan 2002). However, these field measurements require labor intensive complimentary laboratory determinations that involve filtering of samples to spectrally characterize the dissolved matter using standard scanning spectrophotometers and those with integrating sphere attachments (Drake et al. 2003) for particulate matter.

2.2.4 Failure to Survive in Optically Sufficient Systems

Although the correlations between the distribution of persistent seagrass meadows and seasonally-averaged K_D (PAR), optically important water column constituents, and the application of radiative transfer theory may be sufficient to describe general conditions that support seagrass growth (Dennison et al. 1993; Kemp et al. 2004) short-term events can also affect growth and survival of seagrasses. Such circumstances are not captured in annualized data. Loss of *Zostera marina* resulting from light limitation has been observed both during field observations (Dennison and Alberte 1985; Moore et al. 1996; 1997; Cabello-Pasini et al. 2002) and experimentation (Alcoverro et al. 1999; Cabello-Pasini et al. 2002; Thom et al. 2002; Biber et al. 2005). The field and experimental conditions, and observations of these losses of *Zostera marina* are found in Table 2.1.

Continuous monitoring of PAR during the time intervals over which these plants died provided researchers the opportunity to evaluate the light requirements of this species on a photon basis rather than on the statistically-based approach of percent of incident radiation requirement (Duarte 1991; Dennison et al. 1993). The observations of *Zostera* death (Table 2.1) all appear to share the same circumstances, over a similar, 3-5 week time frame they received either no light or severely diminished light exposure. For the plants in the dark (Cabello-Pasini et al. 2002; Biber et al. 2005, Table 2.1), respiration was the dominant process. While the aim of these studies differed, each invoked either, the concept of H_{sat} (the daily period of light-saturated photosynthesis, Figure 2.2), or H_{comp} (Dennison and Alberte 1982), the daily period of light above I_c , the compensation light intensity (Figure 2.1), in their attempts to interpret their observations. It has been hypothesized that *Zostera marina* needs to experience between 3 and 10 h of H_{sat} per day to meet the demands of growth and respiration (Dennison and Alberte 1982; Marsh et al. 1986; Zimmerman et al. 1989). Given the seasonality, frequency and duration of meteorological processes (night to day, clear to overcast and fog) that control the incoming light, and of episodic river discharges (freshets, localized flash floods, and hurricanes) delivering silts, clays, and nutrients to coastal waters, the recommended wide range in the number of hours of H_{sat} or H_{comp} is insufficiently proscriptive.

2.2.5 Laboratory Studies of *Zostera marina* Photosynthesis

Laboratory experiments to determine seagrass production in response to light have been performed with leaf segments (scraped of epiphytes), or whole plants. These tissues are

incubated in varying PAR intensity while monitoring the change of dissolved oxygen (Figure 2.1) or other constituents. The reported units of P in the P vs. I curve are varied (Table 2.2) and are often not easily converted to common units because of the lack of the necessary normalizing ratios, e.g., dry weight to wet weight, chlorophyll *a* (chl *a*) per g fresh weight (fw), dry weight (dw) or area (decimeter, dm²). In addition, the variability of the P vs. I components is usually not reported and is often high because of the few data points and the steep initial slope (alpha) of the relationship (Zimmerman et al. 1991). The effect of temperature on the P vs. I components have also been investigated (Drew 1979; Marsh et al. 1986; Bulthuis 1987; Zimmerman et al. 1989) (see Chapter 9). Instruments and techniques have been developed to monitor the fluorescence of various pigments involved in photosynthesis. These include the photosynthetic efficiency analyzer and pulse amplified modulated (PAM) fluorometry which have been used to assess various acute stresses (Major and Dunton 2002; Bjork et al. 1999) and light-limited chronic stress (Biber et al. 2005).

Section 2.2.6 The Role of Sucrose in the Biochemistry of *Zostera marina*

Sucrose has been identified as the dominant carbohydrate of *Zostera marina*'s tissues (Smith 1989) and is thought to be the primary carbon reserve during periods of light limitation (Smith et al. 1988; Smith 1989; Kraemer and Alberte 1995; Zimmerman et al. 1995; Zimmerman and Alberte 1996). Sucrose is the carbon source for dark respiration during respiratory or fermentative processes. During periods of light, sucrose and oxygen produced in the shoots are translocated to the roots and rhizomes. Upon the onset of darkness, the production of these products ceases and their translocation stops shortly afterwards (1h) (Zimmerman and Alberte 1996), at which time the roots become fully anoxic (Smith et al. 1984 and 1988). In the dark, roots continue to oxidize sucrose, but do so through a fermentative pathway and no metabolic products are transported to the shoots. Translocation of inorganic phosphate from the roots to shoots is strongly light dependent (Brix and Lingby 1985), whereas a sucrose gradient between rhizomes and shoots may offset the reduced downward translocation of sugars during prolonged periods of reduced light (Alcoverro et al. 1999). Under dark conditions, the sucrose content of *Zostera marina* leaves was nearly exhausted (~20 $\mu\text{mol sucrose gfw}^{-1}$) in 21 days (Cabello-Pasini et al. 2002) and the shoots did not survive. Under severely light-limited conditions leaves reaching similar concentrations also failed to survive (Alcoverro et al. 1999) while the rhizome sucrose content was much less reduced. Although the fresh weight concentration of sucrose in shoots, roots, and rhizomes is on average 166, 20, and 240 $\mu\text{mol sucrose gfw}^{-1}$, respectively (Table 2.3), the concentrations tends to vary with the age of the leaf and rhizome segment sampled (Kraemer and Alberte 1993; Kraemer et al. 1998). Each variable contributes to the range of published concentrations (Table 2.3).

Table 2.1. Observations of the death of *Zostera marina* plants in the field and laboratory. NR = not reported.

Location	Month/year	Study type	Temperature °C	Irradiance mol m ⁻² day ⁻¹	H _{sat} hour day ⁻¹	Time to death weeks	Reference
MA, Great Harbor	6/82	field experiment	15	~2	~6	~4	Dennison and Alberte 1985
MA, Great Harbor	8/82	field experiment	21	~2	~6	~4	Dennison and Alberte 1985
VA, York estuary	4-5/87	field monitoring	21	1.5-2.5	~0 (H _{comp})	3-4	Moore et al. 1997
Mexico, Baja California, Pacific coast	2-3/98	field monitoring	17	0-4	NR	~4	Cabello-Pasini et al. 2002
CA, Monterey Bay	11-12/93	lab experiment	12	~0.3	2	~4	Alcoverro et al. 1999
WA, Sequim Bay	11/95	lab experiment	9	1-2	NR	~4	Thom et al. 2002
Mexico, Baja California, Pacific coast	11/00	lab experiment	16	0	0	3-4	Cabello-Pasini et al. 2002
NC, North River	2-3/03	lab experiment	10 to 16	0	0	5-7	Biber et al. 2005

Table 2.2. P vs. I experimental results for *Zostera marina* L. from various locations and measurement conditions

Location	Temp °C	μmol photons m ⁻² sec ⁻¹		Parameters in published units			Published units	mg chl a [dm ⁻²] or gfw ⁻¹	Reference
		I _k	I _c	alpha x1000	P _{max}	Respiration			
AK					931		mg C h ⁻¹ gdw ⁻¹		McRoy 1974
NC					0.27-1.8		mg C h ⁻¹ gdw ⁻¹		Penhale 1977
CA	5-20	5 (15 °C)	1 (15 °C)		14.2 (15 °C)	1.4 (15 °C)	μg C h ⁻¹ cm ⁻²		Drew 1979
MA shall/deep	22				0.4	0.08 -0.13	μmol O ₂ min ⁻¹ mg chl a ⁻¹	[1.8]/[2.2]	Dennison and Alberte 1982
VA	1-28	80-385		4.4-8.9	1.13-2.8		mg C h ⁻¹ gdw ⁻¹		Wetzel and Penhale 1983
VA	15/25		37	11.4	0.42/0.62		μmol O ₂ min ⁻¹ mg chl a ⁻¹	1.5	Evans et al. 1986
MA	20		15-25	4.4	0.22	0.080	μmol O ₂ min ⁻¹ mg chl a ⁻¹	[2.5]	Dennison and Alberte 1985
MA shall/deep	20	67	18	2.7-3.7	0.09-0.21	0.06-0.09	μmol O ₂ min ⁻¹ mg chl a ⁻¹	[2.7]/[4]	Dennison and Alberte 1986
MA	0-35	7-90	1-17	4-9	0.055-0.45	0.0083- 0.13	μmol O ₂ min ⁻¹ mg chl a ⁻¹ and μmol O ₂ min ⁻¹ cm ⁻²	[2.2]	Marsh et al. 1986
MA shall/deep	20	78/71	13/14	4.2/2.4	0.33/0.17	0.053/0.034	μmol O ₂ min ⁻¹ mg chl a ⁻¹	[2.9]/[4]	Dennison et al. 1987
CA-Monterey	10/20					5/8	μmol O ₂ h ⁻¹ gfw ⁻¹	1.1/1.5	Zimmerman et al. 1989
CA-SF	15	35			0.74	0.06	μmol O ₂ min ⁻¹ mg chl a ⁻¹		Zimmerman et al. 1991
VA	25	210	12	3.8	0.84	0.06	μmol O ₂ min ⁻¹ mg chl a ⁻¹		Goodman et al. 1995
CA-Monterey	15				0.25	0.02	μmol O ₂ min ⁻¹ mg chl a ⁻¹	2.2	Zimmerman et al. 1996
CA-Monterey	15				0.2	0.085	μmol O ₂ min ⁻¹ gfw ⁻¹	1.5	Alcoverro et al. 1999
Mexico-Baja	16-22	1-350		10-60	0.6-2.45		μmol O ₂ min ⁻¹ gfw ⁻¹	2	Cabello-Pasini et al. 2002
Mexico-Baja	12-27	50-140		5-10	0.3-0.6	0.03-0.06	μmol O ₂ min ⁻¹ gfw ⁻¹		Cabello-Pasini, et al. 2003

Table 2.3. Sucrose content of *Zostera marina* L. tissues. NR = not reported

Sucrose content $\mu\text{mol sucrose gfw}^{-1}$ (leaves / roots / rhizomes)	Loss rate $\mu\text{mol sucrose gfw}^{-1} \text{ day}^{-1}$ (leaves / roots / rhizomes)	Reference
220 / 30 / 300		Zimmerman et al. 1989
NR/ 10 / 250		Kraemer and Alberte 1993
130 / 10 / NR	no significant loss (whole plants in dark over 12 hr at unknown temperature)	Zimmerman et al. 1995
40 / 15 / 250		Kraemer and Alberte 1995
100 / 30 / 200		Zimmerman et al. 1996
90 / 20 / 200	2.2 / NR / 3.4 (whole plants in $\sim 0.3 \text{ mol photons m}^{-2} \text{ day}^{-1}$ for 30 days at 12 °C)	Alcoverro et al. 1999
233 /NR /NR		Touchette and Burkholder 2001
350 / NR / NR	15 \pm 1 / NR/ NR (whole plants in dark at 16 °C over 21 days)	Cabello-Pasini et al. 2002

Section 2.2.7 Case for the Role of Sucrose in Establishing the Light Requirements of *Zostera marina*

The similar times-to-death found for *Zostera marina* (Table 2.1) suggests the existence of an initial reservoir of a relatively uniform concentration of respirable compounds. Sucrose is the likely compound that would sustain *Zostera marina* plants in the absence of light and would be replenished when irradiance exceeded I_{comp} for a long enough time. When its concentration was reduced to near zero, the plants could not recover and would, subsequently, die.

In the text that follows, a carbon budget is constructed from experiments where sucrose was monitored to support the following hypothesis that will be the basis for estimating the light requirements to sustain *Zostera marina* in an environment: *Zostera marina* survival depends upon the maintenance of a leaf sucrose content that is between a low of $\sim 15 \mu\text{mol sucrose gfw}^{-1}$ and an average, healthy plant, concentration of $166 \pm 40 \mu\text{mol sucrose gfw}^{-1}$ ($\pm 1\text{SE}$). The carbon equivalents of this range are ~ 180 and $1992 \pm 480 \mu\text{mol C gfw}^{-1}$.

Both P_{max} and respiration have been found to be linear functions of temperature (Drew 1979; Marsh et al. 1986) between 0 °C and 35 °C (Figure 2.3). For this carbon budget the temperature study results of Marsh et al. (1986) will be extensively used. Regression of gross P_{max} and respiration data of Marsh et al. (1986) yield the following relationships:

$$\text{gross } P_{\max} = (0.036 \pm 0.0053 * \text{deg C}) + 0.11 \pm 0.096 \quad (\text{to } 30^{\circ}\text{C}, n = 7) \quad \text{Equation 2.3}$$

$$\text{respiration} = (0.0085 \pm 0.00147 * \text{deg C}) - 0.02 \pm 0.031 \quad (\text{to } 35^{\circ}\text{C}, n = 8) \quad \text{Equation 2.4}$$

where the units are $\mu\text{mol O}_2 \text{ mg dm}^{-2} \text{ min}^{-1}$ and \pm is 1 SE of the regression coefficients and intercepts, respectively.

The similarities between P_{\max} values (on a leaf segment area basis) from photoacclimated plants with different chlorophyll contents (Dennison and Alberte 1982 and 1985) suggest that the temperature-dependent dark biochemical reactions control the optimum photosynthetic rate. It is for this reason that the area-normalized rather than chlorophyll-normalized rates of Marsh et al. have been computed.

The initial slope (alpha) of the P vs. I curve (Figure 2.1) represents the quantum yield of photosynthesis for this plant (Falkowski and Raven 1997). Mean alpha values from Table 2.2 were converted to quantum yields, $\mu\text{mol O}_2 \mu\text{mol photons}^{-1}$, using area normalizing relationships from within the references, e.g. mg chl a dm^{-2} , or using those of Andersen and Johnson (unpublished data) found in Table 2.4. The average quantum yield from the alphas in Table 2.2 is $0.029 \pm 0.0075 \mu\text{mol O}_2 \mu\text{mol photons}^{-1}$ ($n = 9$). Quantum yields are used to compute the photosynthesis-saturating irradiance, I_k , from gross P_{\max} (equation 2.12). Relatively invariant alphas, including some from likely photoacclimated plants, reflect the consequences of the tightly coupled, species dependent, chlorophyll *a* mediated light reactions (Falkowski and Raven 1997). A consequence of an invariant alpha, but temperature-dependent P_{\max} , is that I_k is also a function of temperature (Figure 2.3).

Sucrose constitutes approximately 90% of the soluble carbohydrate of *Zostera marina* (Drew 1983; Smith 1989; Alcoverro et al. 1999). Under optimal light conditions it appears to be maintained at seasonally-constant (Cabello-Pasini et al. 2002) but leaf and rhizome segment number-dependent, high concentrations (Table 2.3). Unlike the structural carbohydrates, it can be readily respired either aerobically or through fermentation (Smith et al. 1988; Zimmerman and Alberte 1996; Kraemer et al. 1998).

Direct evidence for sucrose as the key for *Zostera marina* survival can be found in the studies of Cabello-Pasini et al. (2002) and Alcoverro et al. (1999) where leaf sucrose was monitored under varying light conditions. Cabello-Pasini et al. monitored sucrose in leaves from a lagoon and offshore, and leaves that were experimentally exposed to no light. In the field, sucrose levels were reduced by ~85% following 3 weeks of limited light ($\sim 2 \text{ mol photons m}^{-2} \cdot \text{day}$) that continued to the next monthly sampling when the outer coast plants were found to have died. Sucrose was also monitored in plants transplanted to the laboratory with no light, which led to significantly reduced survival after 2 weeks, and death to all shoots at 4 weeks (Tables 2.1 and 2.3). This dark experiment, run at 16°C with aeration, would have a corresponding leaf

Table 2.4. Conversion factors from various sources.

	Andersen and Johnson¹			Evans et al. (1986)²	Nelson³	Chlorophyll <i>a</i> from Table 2.2	
Units	gfw dm ⁻²	gdw dm ⁻²	gfw gdw ⁻¹	gfw gdw ⁻¹	gdw dm ⁻²	mg dm ⁻²	mg gfw ⁻¹
Mean	2.168	0.350	6.26	4.4	0.25	2.79	1.6
SD	0.538	0.081	0.99	0.4	0.062	0.82	0.40
n	72			100	215	8	6

¹ unpublished 2005, mid leaf (#2, #3, #4) section data from Yaquina Bay, Oregon

² 2-3 cm leaf tip data (leaf number not specified)

³ unpublished 2004, whole #2 and #4 leaf data from Yaquina Bay, Oregon

Table 2.5. Statistics of variables used for calculations.

	Production		Respiration			Sucrose		
	$\mu\text{mol O}_2 \text{ dm}^{-2} \text{ min}^{-1}$				alpha	Content	Loss rate	
	5 °C	20 °C	5 °C	20 °C	$\mu\text{mol O}_2$ $\mu\text{mol photons}^{-1}$	$\mu\text{mol gfw}^{-1}$	$\mu\text{mol gfw}^{-1} \text{ day}^{-1}$	
mean	0.290	0.828	-0.027	-0.154	0.0285	166	-15.1 ¹	-2.2 ²
SD	0.199	0.157	0.070	0.049	0.0113	107	1.97	0.80
n	7	7	8	8	9	7	4	4

¹ Cabello-Pasini, et al. (2002)

² Alcoverro, et al. (1999)

respiration rate of $0.12 \mu\text{mol O}_2 \text{ dm}^{-2} \text{ min}^{-1}$ (from Equation 2.4). The following substitutions with the experimentally-determined fresh weight to leaf area conversions allow comparisons of the respiratory carbon and sucrose carbon losses:

$$\text{Respiration} = -79 \pm 8.0 \frac{\mu\text{mol C}}{\text{gfw day}} = \frac{-0.12 \mu\text{mol O}_2}{\text{dm}^2 \text{ min}} * \frac{\text{dm}^2}{2.17 \text{ gfw}} * \frac{1440 \text{ min}}{\text{day}} * \frac{1 \mu\text{mol C}}{1 \mu\text{mol O}_2} \quad \text{Eq. 2.5}$$

$$\text{Sucrose Loss} = -180 \pm 12 \frac{\mu\text{mol C}}{\text{gfw day}} = \frac{-15 \mu\text{mol sucrose}}{\text{gfw day}} * \frac{12 \mu\text{mol C}}{\mu\text{mol sucrose}} \quad \text{Equation 2.6}$$

where the rates and conversion factors are from Tables 2.3 to 2.5.

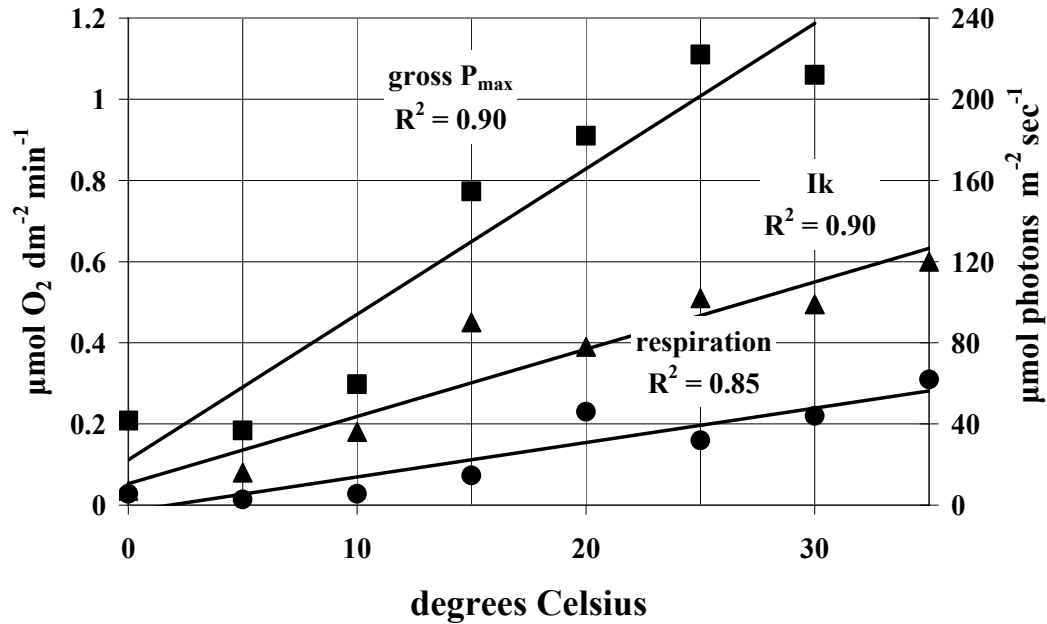


Figure 2.3. Gross maximum productivity, gross P_{\max} (■), I_k values (▲), and dark respiration rates (●) from Marsh et al. 1986.

While the dark respiration and the sucrose loss rates are significantly different (t_s 6.95, $t_{0.05[9]} = 2.262$), the higher sucrose loss rate appears to be sufficiently large to account for the respiratory losses in this experiment.

The uncertainties of these calculations were determined following the propagation of errors formulation for products and quotients (Beers 1957) and of sums and differences (Sokal and Rohlf 1981):

For the composite variable, v that is a multiplicative function of x , y and z , its fractional standard deviation S_v (the standard deviation (SD) of v divided by the computed value of v) is the square root of the sum of the squared fractional standard deviations of the variables of which it is a combination. For the composite variable that results from the sum or difference between variables, the SD is the square root of the sum of the squares of the variable SDs plus or minus any correlation between them (r_{xy} , below, is the correlation coefficient between x and y).

$$\text{for } v = x * y * z, \quad \frac{SD_v}{v} = S_v = \sqrt{\left(\frac{SD_x}{x}\right)^2 + \left(\frac{SD_y}{y}\right)^2 + \left(\frac{SD_z}{z}\right)^2} \quad \text{Equation 2.7a}$$

$$\text{for } v = x + y, \quad SD_v = \sqrt{SD_x^2 + SD_y^2 + 2r_{xy} * SD_x * SD_y} \quad \text{Equation 2.7b}$$

$$\text{for } v = x - y, \quad SD_v = \sqrt{SD_x^2 + SD_y^2 - 2r_{xy} * SD_x * SD_y} \quad \text{Equation 2.7c}$$

$$SD_v = SE_v * \sqrt{n} \quad \text{Equation 2.7d}$$

To conservatively compute the standard error of the calculated values from SD_v , n from the variable with the smallest sample size was used (Tables 2.4 and 2.5).

The lower sucrose loss rate (2.2 vs. 15 μmol sucrose $\text{gfw}^{-1} \text{day}^{-1}$) in the Alcoverro et al. (1999) experiments (Table 2.5) reflects the contributions of newly-fixed carbon during the two hours of saturating light the plants were exposed to when light was not completely excluded.

The carbon balance of this experiment at 12 °C is as follows:

Carbon equivalent of sucrose loss from leaves during the 30-day experiment:

$$-26 \pm 4.8 \frac{\mu\text{mol C}}{\text{gfw day}} = \frac{-2.2 \mu\text{mol sucrose}^\Delta}{\text{gfw day}} * \frac{12 \mu\text{mol C}}{\mu\text{mol sucrose}} \quad \text{Equation 2.8}$$

where Δ is the leaf sucrose loss rate from Tables 2.3 and 2.5.

Carbon balance from computed carbon fixation and respiration:

2 hours of saturating light at 12 °C from Equation 2.3 yields a gross production of:

$$24.9 \pm 2.6 \frac{\mu\text{mol C}}{\text{gfw day}} = \left(\frac{0.54 \mu\text{mol O}_2}{\text{dm}^2 \text{ min}} \right) * \frac{\text{dm}^2}{2.17 \text{ gfw}} * \frac{120 \text{ min}}{\text{day}} * \frac{1 \mu\text{mol C}}{1.2 \mu\text{mol O}_2} \quad \text{Equation 2.9}$$

where 1/1.2 is the molar carbon yield per oxygen evolved (Zimmerman et al.1996).

24 hours of respiration in leaf tissue at 12 °C from Equation 2.4 yields:

$$-57 \pm 6.6 \frac{\mu\text{mol C}}{\text{gfw day}} = \left(\frac{-0.086 \mu\text{mol O}_2}{\text{dm}^2 \text{ min}} \right) * \frac{\text{dm}^2}{2.17 \text{ gfw}} * \frac{1440 \text{ min}}{\text{day}} * \frac{1 \mu\text{mol C}}{1 \mu\text{mol O}_2} \quad \text{Equation 2.10}$$

The net production rate under this limited light exposure is $-32 \pm 9.3 \mu\text{mol C gfw}^{-1}\text{day}^{-1}$, where the SE was computed by propagating the uncertainty from the gross production and respiration using Equation 2.7a into their differences while accounting for the correlation of production and respiration (Equation 2.7b). They are strongly correlated ($r_{pr}=0.847$) because gross production includes respiration. The carbon loss as sucrose, $-26 \pm 4.7 \mu\text{mol C/gfw-day}$, is not significantly different than the net production rate ($t_s 0.88$, $t_{.05[9]} = 2.262$).

The accuracy of these budgets is completely dependent upon the accuracy of the rates and conversion factors that were used. It was assumed that while the P vs. I determined respiration rate was temperature dependent it was not light dependent. The efficacy of these respiration rates in long periods of darkness is questionable given that while these rates were determined in P vs. I experiments, the so-called “enhanced post-illumination effect” on respiration (Heichel 1970; Falkowski and Raven 1997) was likely occurring. The consequences of this effect in terrestrial plants and phytoplankton have been shown to be extended periods of decreasing respiration rates following the withdrawal of light that asymptotically approach a true, nocturnal rate. The author is not aware of a demonstration or quantification of this effect on *Zostera marina* respiration so the respiration rates from Equation 2.4 were used for all times.

Further inaccuracy may be introduced by the choice and source of conversion factors (Table 2.4). Factors for the same conversions may depend on the geographic source of plants and the methods used including age of leaves, leaf section measured (Table 2.4). The direct conversion of leaf area to fresh weight (2.17 gfw dm^{-2}) derived by Andersen and Johnson (unpublished 2005 data) was used to reduce the cumulative uncertainty of Equation 2.7a. The sequential conversion (4.4 gfw gdw^{-1} (Evans et al., 1986) and $0.25 \text{ gdryw dm}^{-2}$ from Nelson (unpublished 2004 data) results in a combined factor of 1.1 gfw dm^{-2} . Using this sequential conversion would increase the computed values in Equations 2.5, 2.9 and 2.10 by a factor of 2. With the sequential conversion, the totally dark respiration and sucrose utilization rates (Equations 2.5 and 2.6) become closer and not significantly different (157 and $180 \mu\text{mol C gfw}^{-1}\text{day}^{-1}$ while the net production with 2 hours of light (Equations 2.9 and 2.10) went up to $-64 \mu\text{mol C gfw}^{-1}\text{day}^{-1}$ which is significantly larger ($t_s 3.29$, $t_{.05[9]} = 2.26$) than the sucrose loss rate of $-26 \mu\text{mol C gfw}^{-1}\text{day}^{-1}$ (Equation 2.8). Given the uncertainty of the nocturnal respiration rate and the various conversion factors needed for these calculations, the net production losses attributed to sucrose losses are seen to be justified.

Section 2.2.8 A Strategy for Assessing the *In Situ* Health Status of *Zostera marina*

A consequence of the correspondence between negative net production and sucrose loss is that the leaf concentration of sucrose attained in optimal light conditions can be used as a benchmark for computing the “health” of this plant. Attaining and maintaining this maximum level is an indication of a healthy meadow. Concentrations much lower would be suggestive of plants under light stress.

Periodic sampling and analysis of leaf sucrose content could be used to evaluate the health status of an existing meadow. The suitability of a location and depth for *Zostera marina* transplantation, or the reason for the absence of *Zostera marina*, could be demonstrated by calculations from continuous monitoring of *in situ* irradiance and temperature. By combining these measurements with the P_{\max} and temperature relationships of Marsh et al. (1986) one can compute the *in situ* “sucrose status”.

In the laboratory experiments cited above, when carbon fixation was maximal or zero one only needed to compute the gross P_{\max} and respiration rates at the experimental temperatures to compute net production. In the field, production will not always be maximal (for the temperature) or zero (darkness), but will range from zero to gross P_{\max} because photons can contribute to carbon-fixation at fluxes down to $\sim 0.3 \mu\text{mol photons m}^{-2}\text{sec}^{-1}$ (Falkowski and Raven 1997). For those fluxes at or less than saturating irradiances, the gross production is proportional to the ratio of the measured irradiance to the temperature-dependent, photosynthesis-saturating irradiance, I_k . Therefore, net production computed from the *in situ* temperature and time-interval averaged irradiances is the following:

$${}_iP_{\text{net}} = \frac{{}_i\overline{I}}{I_k^t} * \text{gross } P_{\max}^t - R^t \quad \text{Equation 2.11}$$

Where, ${}_i\overline{I}$ is the average irradiance over time interval, i , and t is the *in situ* temperature.

I_k^t is calculated by dividing gross P_{\max} at temperature t by the quantum yield, alpha. This yields I_k^t with the following units:

$$\frac{\mu\text{mol photons}}{\text{m}^2 \text{ sec}} = \frac{\mu\text{mol } O_2}{\text{dm}^2 \text{ min}} * \frac{\mu\text{mol photons}}{0.029 \mu\text{mol } O_2} * \frac{100 \text{ dm}^2}{\text{m}^2} * \frac{\text{min}}{60 \text{ sec}} \quad \text{Equation 2.12}$$

The units for ${}_iP_{\text{net}}$ are:

$$\frac{\mu\text{mol C}}{\text{gfw } i} = \left(\left[\frac{1}{1} * \frac{\mu\text{mol } O_2}{\text{dm}^2 \text{ min}} * \frac{\mu\text{mol C}}{1.2 \mu\text{mol } O_2} \right] - \left(\frac{\mu\text{mol } O_2}{\text{dm}^2 \text{ min}} * \frac{\mu\text{mol C}}{\mu\text{mol } O_2} \right) \right) * \left[\frac{\text{dm}^2}{2.17 \text{ gfw}} * \frac{\text{min}}{i} \right] \quad \text{Eq.2.13}$$

To meet the expectations of the hypothesis, that sucrose maintained within a range of leaf concentrations is indicative of healthy *Zostera marina* plants, the following must occur when the optimal sucrose concentration (Sucrose_{\max}) is $166 \mu\text{mol sucrose gfw}^{-1}$ (Table 2.3) or $1992 \mu\text{mol C gfw}^{-1}$:

$$\text{Sucrose}_{\max} \geq {}_i\text{Sucrose} = ({}_i\text{Sucrose} + {}_iP_{\text{net}}/12) \leq 15 \quad \text{Equation 2.14}$$

where 12 is the number of carbon atoms per sucrose molecule. When iP_{net} is positive, carbon is added to the sucrose pool up to $Sucrose_{max}$.

For these computations, plant death occurs at $iSucrose \sim 15 \mu\text{mol sucrose gfw}^{-1}$, the levels found in dying plant leaves (Alcoverro et al. 1999; Cabello-Pasini et al. 2002) that may represent the physiological minimum for this tissue.

Computation of $iSucrose$ accounts for varying light and temperature conditions across time and would indicate when light and temperature conditions persisted long enough to sustain the growth of *Zostera marina*. A specific time under a given light flux, e.g. H_{sat} , and temperature can not be assigned *a priori* due to the dynamic nature of the sucrose pool these calculations are modeling. However, the time to draw down the sucrose pool in complete darkness from its maximum level can be estimated from the respiration rate alone as a function of temperature (Figure 2.4).

The minimum photon flux necessary to sustain a plant (no net production, $Sucrose_{max}$ maintained) was calculated in the following:

$$\frac{\text{mol photons}}{\text{m}^2 \text{ day}} = \frac{-\mu\text{mol C}}{\text{dm}^2 \text{ day}} * \frac{1.2 \mu\text{mol O}_2}{\mu\text{mol C}} * \frac{\mu\text{mol photons}}{0.029 \mu\text{mol O}_2} * \frac{100 \text{ dm}^2}{\text{m}^2} \quad \text{Equation 2.15}$$

where $\mu\text{molC dm}^{-2}\text{day}^{-1}$ is the temperature dependent daily respiration rate that is converted to photon flux through the quantum yield and normalizing relationships. The daily photon flux necessary to offset a plant's respiratory needs are found in Figure 2.5.

The values of Figure 2.5 result from the same logic as is invoked by the concept of a minimum number of H_{sat} , or H_{comp} hours. However, by themselves, neither is especially useful in regard to contributing to testable hypotheses about minimum light requirements because of the dynamic nature of *in situ* light fluxes.

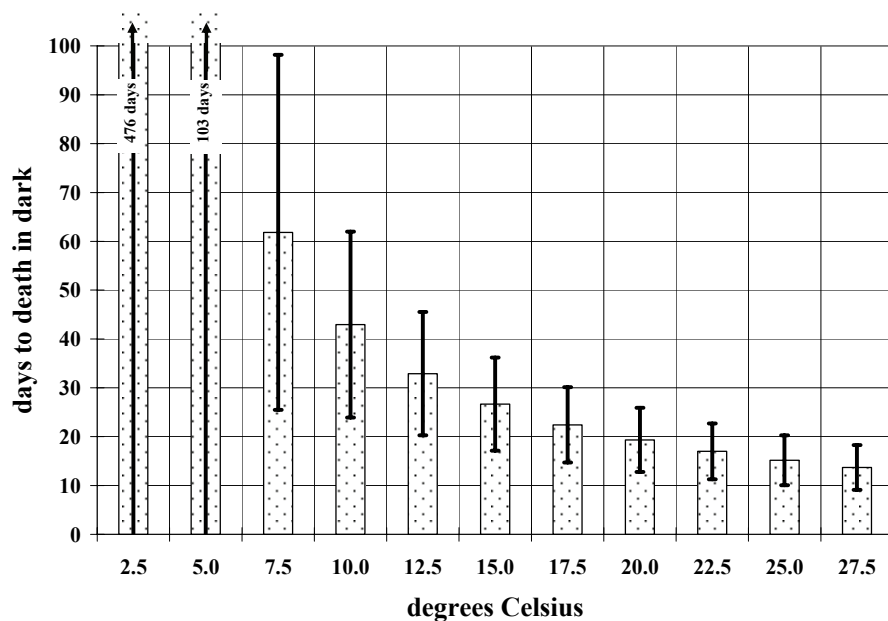


Figure 2.4. Days to plant death in dark assuming the sole respiratory carbon source is leaf sucrose. Error bars (± 1 SE) are from the computations incorporating the uncertainties of the underlying measurements (Tables 2.4 and 2.5).

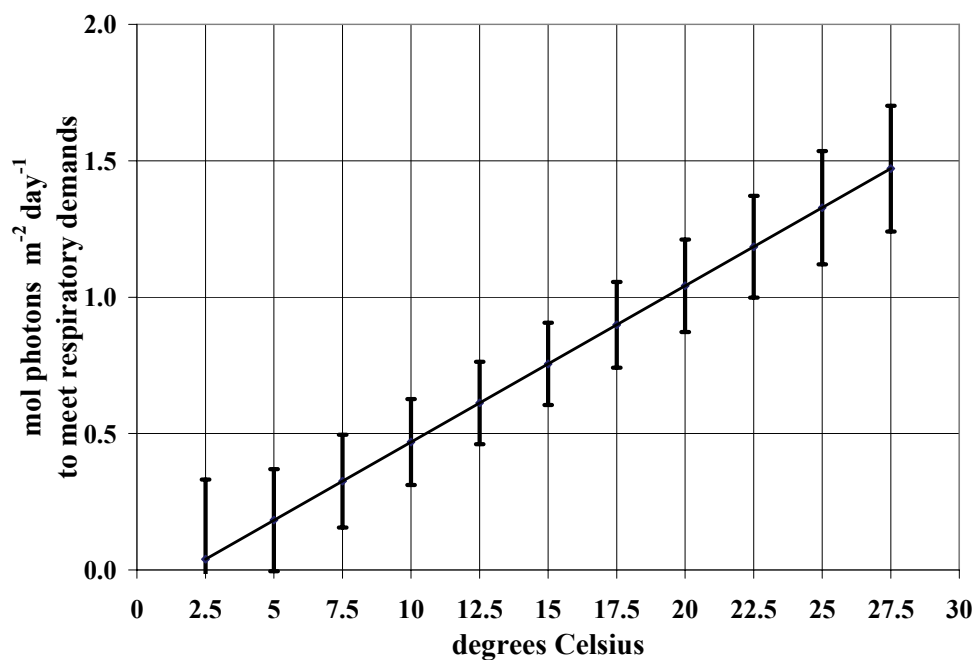


Figure 2.5. Photon flux necessary to replace carbon lost to respiration as a function of temperature (assuming equal daylight and nocturnal respiration rates). Error bars (± 1 SE) are from the computations incorporating the uncertainties of the underlying measurements.

2.3 Research Gaps in Relation to Setting Protective Criteria

The correlative approach utilizing growing season measurements for setting system habitat requirements is incapable of accounting for the varying periods of diminished irradiance that have led to loss of *Zostera marina* populations. The μ Sucrose model (above), utilizing irradiance and temperature values from continuous data sets collected from strategically placed locations within a system, would provide the means of assessing the system's ability to maintain the benchmark range of leaf sucrose over time and space. The growing season is not the only time that *Zostera marina* in a system can be vulnerable to sub-optimal light conditions.

The studies of Alcoverro et al. 1999 and Cabello-Pasini et al. 2002 were both done with intact roots and rhizomes but the leaf sucrose loss rate did not appear to be ameliorated by the mobilization of sucrose from the below-ground tissues as has been suggested in *Thalassia testudinum* (Lee and Dunton 1996). The inhibition of sucrose translocation during anaerobic periods of very reduced, or no photosynthesis (Zimmerman and Alberte 1996) may be responsible for the apparent isolation of the below-ground sucrose stores in *Zostera marina* during light stress. Because the utility of leaf sucrose concentrations in assessing the health of this plant depends on the isolation of its leaf sucrose pools from other tissues additional simultaneous studies of these sucrose pools under low light conditions are warranted. Such studies would assess the importance of this mechanism of mitigating low light conditions in this species.

The need to determine the properties of optically important components for each estuarine system should be broadly evaluated using the same laboratory techniques, same water samples, and to the extent possible, should incorporate the use of multi-spectral instruments, such as the WetLab ac-9. To reduce costs of such surveys, the resulting IOPs could be processed by the analytically robust, and freely-available RTE model of Gallegos (1994). This model is currently included as a Fortran module (C. Gallegos, personal communication, 3/12/07) of the Chesapeake Bay Water Quality Model (Cercio and Moore 2001). The goal would be to find regionally-similar absorption and scattering spectra (e.g., abiotic-mineral-derived turbidity, peat-derived DOM) and ranges of spectral responses for, say, mono-specific and mixed-species algal blooms. In addition, such surveys would demonstrate the advantages of uniform data sets for system comparisons across space and time.

The use of Secchi disk readings should be discontinued and replaced with measures of light intensity using PAR sensors as the conversion to K_D (PAR) from Secchi readings have introduced unnecessary uncertainty in this critical measurement.

Physiological studies of P vs. I, sucrose content etc., should always include a range of normalizing measures. The minimum, most critical measurements are chlorophyll per fresh weight and surface area per fresh weight of blades, and fresh weight for below ground components, if studied. Chlorophyll normalization has been shown to reduce the variability of several physiological parameters while normalization to fresh weight may minimize confounding photoacclimation issues resulting from varying chlorophyll content. The use of blade surface

area normalization is a means to directly couple *in situ* light fluxes and laboratory-determined photosynthetic rates.

2.4 Literature Cited

- Alcoverro, T., R. C. Zimmerman, D. G. Kohrs, and R. S. Alberte. 1999. Resource allocation and sucrose mobilization in light-limited eelgrass *Zostera marina*. Marine Ecology Progress Series 187:121-131.
- Batiuk, R. A., R. J. Orth, K. A. Moore, W. C. Dennison, J. C. Stevenson, L. W. Staver, V. Carter, N. B. Rybicki, R. E. Hickman, S. Kollar, S. Bieber, and P. Heasley 1992. Chesapeake Bay Submerged Aquatic Vegetation Habitat Requirements and Restoration Targets: A Technical Synthesis. CBP/TRS 83/92, Chesapeake Bay Program, Annapolis, MD.
- Beers, Y. 1957. Introduction to the Theory of Error, 2nd edition. Addison-Wesley Publishing Company, Reading, MA.
- Biber, P. D., H. W. Paerl, C. L. Gallegos, and W. J. Kenworthy. 2005. Evaluating indicators of seagrass stress to light limitation. pp. 167-176. Chapter 13. In: S.A. Bortone (ed.) Estuarine Indicators. CRC Press, Boca Raton, FL. pp. 318.
- Bjork, M., J. Uku, A. Weil, and S. Beer. 1999. Photosynthetic tolerances to desiccation of tropical intertidal seagrasses. Marine Ecology Progress Series 191:121-126.
- Brix, H. and J. W. Lingby. 1985. Uptake and translocation of phosphorous in eelgrass (*Zostera marina* L.). Marine Biology 90:111-116.
- Bulthuis, D. A. 1987. Effects of temperature on photosynthesis and growth of seagrasses. Aquatic Botany 27:27-40.
- Cabello-Pasini, A., R. Muñiz-Salazar, and D. H. Ward. 2003. Annual variations of biomass and photosynthesis in *Zostera marina* at its southern end of distribution in the North Pacific. Aquatic Botany 76:31-47.
- Cabello-Pasini, A., C. Lara-Turrent, and R. C. Zimmerman. 2002. Effects of storms on photosynthesis, carbohydrate content and survival of eelgrass populations from a coastal lagoon and the adjacent open ocean. Aquatic Botany 74:149-164.
- Cerco, C. F. and K. A. Moore. 2001. System-wide submerged aquatic vegetation model for Chesapeake Bay. Estuaries 24:522-534.
- Dennison, W. C. and R. S. Alberte. 1982. Photosynthetic responses of *Zostera marina* L. (eelgrass) to in situ manipulations of light intensity. Oecologia 55:137-144.
- Dennison, W. C. and R. S. Alberte. 1985. Role of daily light period in the depth distribution of *Zostera marina* (eelgrass). Marine Ecology Progress Series 25:51-61.
- Dennison, W. C. and R. S. Alberte. 1986. Photoadaptation and growth of *Zostera marina* L. (eelgrass) transplants along a depth gradient. Journal of Experimental Marine Biology and Ecology 98:265-282.
- Dennison, W. C., R. C. Aller, and R. S. Alberte. 1987. Sediment ammonium availability and eelgrass (*Zostera marina*) growth. Marine Biology 94:469-477.
- Dennison, W. C., R. J. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. W. Bergstrom, and R. A. Batiuk. 1993. Assessing water quality with submerged aquatic vegetation. BioScience 43:86-94.

- Drake, L. A., F. C. Dobbs, and R. C. Zimmerman. 2003. Effects of epiphyte load on optical properties and photosynthetic potential of the seagrasses *Thalassia testudinum* Banks ex König and *Zostera marina* L. *Limnology and Oceanography* 48:456-463.
- Drew, E. A. 1979. Physiological aspects of primary production in seagrasses. *Aquatic Botany* 7:139-150.
- Drew, E. A. 1983. Sugars, cyclitols and seagrass phylogeny. *Aquatic Botany* 15:387-408.
- Duarte, C. M. 1991. Seagrass depth limits. *Aquatic Botany* 40:363-377.
- Evans, A. S., K. L. Webb, and P. A. Penhale. 1986. Photosynthetic temperature acclimation in two coexisting seagrasses, *Zostera marina* L. and *Ruppia maritima* L. *Aquatic Botany* 24:185-197.
- Falkowski, P. G. and J. A. Raven. 1997. *Aquatic Photosynthesis*. Blackwell Science, Malden, MA.
- Gallegos, C. L. 1994. Refining habitat requirements of submersed aquatic vegetation: role of optical models. *Estuaries* 17:187-199.
- Gallegos, C. L. 2001. Calculating optical water quality targets to restore and protect submersed aquatic vegetation: overcoming problems in partitioning the diffuse attenuation coefficient for photosynthetically active radiation. *Estuaries* 24:381-397.
- Gallegos, C. L. and W. J. Kenworthy. 1996. Seagrass depth limits in the Indian River lagoon (Florida, U.S.A.): application of an optical quality model. *Estuarine, Coastal and Shelf Science* 42:267-288.
- Gallegos, C. L. and T. E. Jordan. 2002. Impact of the spring 2000 phytoplankton bloom in Chesapeake Bay on optical properties and light penetration in the Rhode River, Maryland. *Estuaries* 25:508-518.
- Giesen, W. B. J. T., M. M. van Katijk, and C. den Hartog. 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquatic Botany* 37:71-85.
- Goodman, J. L., K. A. Moore, and W. C. Dennison. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. *Aquatic Botany* 50:37-47.
- Heichel, G. H. 1970. Prior illumination and the respiration of maize leaves in the dark. *Plant Physiology* 46:359-362.
- Jerlov, N. G. 1976. *Marine Optics*. Elsevier, Amsterdam.
- Kemp, W. M., R. Bartleson, and L. Murray. 2000. Epiphyte contributions to light attenuation at the leaf surface, pp. 28-37. In R.A. Batiuk, et al. (eds.) *Chesapeake Bay Submerged Aquatic Vegetation Water Quality and Habitat-based Requirements and Restoration Targets: A Second Technical Synthesis*. U.S. Environmental Protection Agency, Chesapeake Bay Program, Annapolis, Maryland.
- Kemp, W. M., R. Batiuk, R. Bartleson, P. Bergstrom, V. Carter, C. L. Gallegos, W. Hunley, L. Karrh, E. W. Koch, J. M. Landwehr, K. A. Moore, L. Murray, M. Naylor, N. B. Rybicki, J. C. Stevenson, and D. J. Wilcox. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: water quality, light regime, and physical-chemical factors. *Estuaries* 27:363-377.
- Kirk, J. T. O. 1994. *Light and Photosynthesis in Aquatic Ecosystems*, 2nd edition. Cambridge University Press, Cambridge, U.K.

- Kraemer, G. B. and R. S. Alberte. 1993. Age-related patterns of metabolism and biomass in subterranean tissues of *Zostera marina* (eelgrass). *Marine Ecology Progress Series* 95:193-203.
- Kraemer, G. B. and R. S. Alberte. 1995. Impact of daily photosynthetic period on protein synthesis and carbohydrate stores in *Zostera marina* L. (eelgrass) roots: implications for survival in light-limited environments. *Journal of Experimental Marine Biology and Ecology* 185:191-202.
- Kraemer, G., P. D. Kohrs, and R. S. Alberte. 1998. Developmental changes of sucrose synthase activity and abundance in root and leaf tissues of *Zostera marina*. *Aquatic Botany* 62:189-198.
- Lee, K. S. and K. H. Dunton. 1996. Production and carbon reserve dynamics of the seagrass *Thalassia testudinum* in Corpus Christi Bay, Texas, USA. *Marine Ecology Progress Series* 146:201-210.
- Losee, R. J. and R. G. Wetzel. 1983. Selective light attenuation by the periphyton complex, pp. 89-96. In: R.G. Wetzel (ed.) *Periphyton of Freshwater Ecosystems*. Dr. W. Junk Publishers, The Hague, Netherlands.
- Major, K. M. and K. H. Dunton. 2002 Variations in light-harvesting characteristics of the seagrass *Thalassia testudinum*: evidence for photoacclimation. *Journal of Experimental Marine Biology and Ecology* 275:173-189.
- Marsh, J. A., W. C. Dennison, and R. S. Alberte. 1986. Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). *Journal of Experimental Marine Biology and Ecology* 101:257-267.
- McRoy, C. P. 1974. Seagrass productivity: carbon uptake experiments in eelgrass *Zostera marina* and its epiphytes. *Aquaculture* 4:131-137.
- Mobley, C. D. 1994. *Light and Water Radiative Transfer in Natural Waters*. Academic Press, New York.
- Moore, K. A., R. L. Wetzel, and R. J. Orth. 1997. Seasonal pulses of turbidity and their relations to eelgrass (*Zostera marina* L.) survival. *Journal of Experimental Marine Biology and Ecology* 215:115-134.
- Moore, K. A., H. Q. Neckles, and R. J. Orth. 1996. *Zostera marina* (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. *Marine Ecology Progress Series* 142:247-259.
- Penhale, P. A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. *Journal of Experimental Marine Biology and Ecology* 26:211-224.
- Preisendorfer, R. W. 1986. Secchi disk science: visual optics of natural waters. *Limnology and Oceanography* 31:909-926.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*, 2nd edition. Freeman and Company, New York.
- Smith, R. D., W. C. Dennison, and R. S. Alberte. 1984. Role of seagrass photosynthesis in root aerobic processes. *Plant Physiology* 74:1055-1058.
- Smith, R. D. 1989. Anaerobic metabolism in the roots of the seagrass *Zostera marina* L. PhD dissertation, The University of Chicago.

- Smith, R. D., A. M. Pregnall, and R. S. Alberte. 1988. Effects of anaerobiosis on root metabolism of *Zostera marina* (eelgrass): implications for survival in reducing sediments. *Marine Biology* 98:131-141.
- Thom, R., A. Borde, S. Rumrill, D. L. Woodruff, G. D. Williams, J. Southard, and S. L. Blanton. 2002. Factors influencing the spatial and annual variability in eelgrass (*Zostera marina* L.) meadows in Pacific Northwest, USA, Systems. Chapter 5, In: J.K Parrish and K. Litle, eds. Pacific Northwest Coastal Ecosystems Regional Study, 2001 Annual Report. K. Litle, Seattle, WA.
- Touchette, B.W. and J. Burkholder. 2001. Nitrate reductase activity in a submersed marine angiosperm: controlling influences of environmental and physiological factors. *Plant Physiology and Biochemistry* 39:583-593.
- Twilley, R. R., W. M. Kemp, K. W. Staver, J. C. Stevenson, and W. R. Boynton. 1985. Nutrient enrichment of estuarine submersed vascular plant communities: I. Algal growth and effects on production of plants and associated communities. *Marine Ecology Progress Series* 23:179-191.
- Wetzel, R. L. and P. A. Penhale. 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. *Marine Technology Society Journal* 17:22-31.
- Zimmerman, R. C. 2003. A biophysical model of irradiance distribution and photosynthesis in seagrass canopies. *Limnology and Oceanography* 48:568-585.
- Zimmerman, R. C., D. G. Kohrs, and R. S. Alberte. 1996. Top-down impact through a bottom-up mechanism: the effect of limpet grazing on growth, productivity and carbon allocation of *Zostera marina* L. (eelgrass). *Oecologia* 107:560-567.
- Zimmerman, R. C. and R. S. Alberte. 1996. Effect of light/dark transition on carbon translocation in eelgrass *Zostera marina* seedlings. *Marine Ecology Progress Series* 136:305-309.
- Zimmerman, R. C., D. G. Kohrs, D. L. Steller, and R. S. Alberte. 1995. Carbon partitioning in eelgrass. *Plant Physiology* 108:1665-1671.
- Zimmerman, R. C., J. L. Reguzzoni, S. Wyllie-Echeverria, M. Josselyn, and R. S. Alberte. 1991. Assessment of environmental suitability for growth of *Zostera marina* L. (eelgrass) in San Francisco Bay. *Aquatic Botany* 39:353-366.
- Zimmerman, R. C., R. S. Smith, and R. S. Alberte. 1989. Thermal acclimation and whole-plant carbon balance in *Zostera marina* L. (eelgrass). *Journal of Experimental Marine Biology and Ecology* 130:93-109.

3.0 Water Column and Sediment Nutrients as Limits to Growth of *Zostera marina* and *Thalassia testudinum*

James E. Kaldy

3.1 Background

Seagrasses are vascular plants that have returned to the aquatic habit. In contrast to the algae (e.g. seaweeds), seagrasses have highly differentiated tissues which form true roots, stems and leaves, and thus possess xylem and phloem for the transport of water and photosynthate respectively. The vascular system is much reduced but has been experimentally shown to exhibit bidirectional transport (Thursby and Harlin 1982; Brix and Lyngby 1985). Seagrasses can acquire nutrients through both the leaves and the root and thus access both water column and sediment nutrient sources to support growth and production. The relative importance of leaf vs root nutrient uptake appears to be dependent on the specific environmental conditions and nutrient concentrations. This review is intended to give the reader a current basic understanding of seagrass-nutrient interactions and dynamics. Additional comprehensive detail on seagrass-nutrient interactions are available (e.g., Butler and Jernakoff 1999; Hemminga and Duarte 2000; Short and Coles 2001; Larkum et al. 2006).

In general algae out-compete seagrasses for water column nutrients (WCN) than seagrasses, since they have a higher affinity for nitrogen they can take up WCN more quickly. *Z. marina* nitrogen uptake rates exhibit a wide range of values and are summarized in Table 3.1. Relatively few studies have addressed phosphorus uptake by *Zostera spp.* (McRoy and Barsdate 1970; McRoy et al. 1972; Penhale and Thayer 1980; Brix and Lyngby 1985; Perez-Llorens et al. 1993). Touchette and Burkholder (2000a,b) provide excellent reviews of carbon, nitrogen and phosphorus metabolism in seagrasses addressing many of the ecophysiological and biochemical aspects in detail. Unfortunately, there has been little attempt within the literature to report uptake rates with consistent units (Table 3.1). The units for phosphorus uptake are especially variable. Consequently, comparison of rates between systems is difficult without first making site specific conversions based on biomass or shoot density. The sediments of marine ecosystems typically have higher nutrient concentrations than the water column. Paradoxically, leaf uptake can account for up to 70% of the total plant N uptake (Hemminga et al. 1994). Access to both water column and sediment nutrients is an important adaptation that has permitted seagrasses to persist and to out-compete algae (seaweeds) under oligotrophic conditions. Additionally, recent work has shown that internal resorption of N and P from senescing leaves can meet part of the plant's nutrient requirements (Hemminga et al. 1999).

Table 3.1. Summary of nitrogen uptake rates for *Z. marina*. V_{\max} in units of $\mu\text{M gdw l}^{-1} \text{ h}^{-1}$ is the maximum uptake rate, K_s is the half saturation concentration (μM). Units for uptake rates are denoted by superscripted letter.

Location	Leaf uptake	V_{\max}	K_s	Root uptake	V_{\max}	K_s	Reference
<i>Zostera marina</i>							
Rhode Island		20.5	9.2		211	104	Thursby & Harlin 1982
Netherlands	0.03 – 0.19 ^a						Pedersen & Borum 1993
Netherlands	0.01 – 2.8 ^b			0.01 – 3.9 ^b			Hemminga et al. 1994
Netherlands	0.35 ^c			0.33 ^c			Pedersen & Borum 1992
Japan	0.001 ^d			0.011 ^d			Iizumi & Hattori 1982
Alaska	1.05 – 3.2 ^b			0.9 – 2.9 ^b			Short & McRoy 1984
<i>Thalassia hemprichii</i>							
Indonesia		32-37	21-60				Stapel et al. 1996.
<i>Thalassia testudinum</i>							
Texas (NH ₄ ⁺)		8-16.5	5-19		8-73	34-765	Lee & Dunton 1999b
Texas (NO ₃ ⁻)		3.4-6.5	2.2-38				Lee & Dunton 1999b

^a $\text{g N m}^{-2} \text{ d}^{-1}$

^b $\mu\text{M N gdw}^{-1} \text{ h}^{-1}$

^c $\text{mg N gdw}^{-1} \text{ d}^{-1}$

^d $\text{g N (g plant N)}^{-1} \text{ d}^{-1}$

Table 3.2. C:N:P ratios for *Z. marina* from the literature.

Seagrass	Location	%C	%N	%P	C:N	N:P	C:P	C:N:P	Reference
Multiple spp.	global	33.6	1.92	0.23	20	24	474	474:24:1	Duarte 1990
<i>Zostera marina</i>									
	various	36	2.5	0.39	17	15	246	255:15:1	Duarte 1990
	California	38.4	2.37	0.34	20	16	304		Fourqurean et al. 1997
	Oregon	34	2.7	0.4	15	17	255	255:17:1	² Kaldy 2006a
	Oregon	35	1.3	0.2	34	15	510	510:15:1	³ Kaldy 2006a
	Oregon	29	1.4	0.1	24	24	576	576:24:1	⁴ Kaldy 2006a
					18	27	481	481:27:1	¹ Pérez-Lloréns et al. 1991
					12	10	120	120:10:1	¹ Pérez-Lloréns et al. 1991
					13	6	79	79:6:1	¹ Pérez-Lloréns et al. 1991
					11	15	170	170:15:1	¹ Pérez-Lloréns et al. 1991
					19	3	57	57:3:1	¹ Pérez-Lloréns et al. 1991
	California	39			7	38	274	274:38:1	Atkinson and Smith 1983
	Rhode Island	34			18	27	481	481:27:1	Atkinson and Smith 1983
	Virginia	42			14	41	584	584:41:1	Atkinson and Smith 1983
	Virginia	35-39	2-3.8	0.2-0.3					² Moore and Wetzel 2000
	Virginia	27-35	1-2	0.06-0.15					³ Moore and Wetzel 2000
<i>Zostera capricorni</i>									
	Australia				20	17	349	349:17:1	² Atkinson and Smith 1983
	Australia				58	8	465	465:8:1	³ Atkinson and Smith 1983
	Australia				33	9	302	302:9:1	⁴ Atkinson and Smith 1983

<i>Zostera noltii</i>										
	Netherlands				12	9	104	104:9:1		² Pérez-Lloréns et al. 1991
					21	6	127	127:6:1		³ Pérez-Lloréns et al. 1991
					16	7	114	114:7:1		⁴ Pérez-Lloréns et al. 1991
<i>Thalassia testudinum</i>										
	Barbados							445:32:1		² Atkinson and Smith 1983
	Barbados							601:20:1		³ Atkinson and Smith 1983
	Texas	33-37	1.7-2.7		15-25					² Kaldy and Dunton 2000
	Texas	35-37	0.7-0.9		45-62					³ Kaldy and Dunton 2000
	Texas	34-36	1.7-2		21-24					² Lee and Dunton 1999a
	Texas	36-37	0.7-0.9		46-60					³ Lee and Dunton 199a
	Florida	34.6	2.2	0.095	18.5	40.2	1070			² Fourqurean et al. 1992
	Florida	36.9	1.82	0.113	24.6	40.2	937			² Fourqurean et al. 2002
<i>Thalassia hemprichii</i>										
	Indonesia		1.9	0.14		30				² Erftemeijer & Middelburg 1993
			0.48	0.07		15				³ Erftemeijer & Middelburg 1993
			0.98	0.06		36				⁴ Erftemeijer & Middelburg 1993

¹ Literature values from Table 1 for original citations see Pérez-Lloréns et al. 1991

² Ratios for leaf material

³ Ratios for rhizome material

⁴ Ratios for root material

In temperate systems with silastic mud sediments the general paradigm is that nitrogen is the limiting nutrient (Orth 1977; van Lent et al. 1995). However, there is some debate about the degree of nutrient limitation in temperate systems. Zimmerman et al. (1987) concluded from a modeling study that nitrogen limitation of *Z. marina* is probably very rare. In tropical systems with carbonate sediments, there is substantial evidence for phosphorus or iron limitation (Short et al. 1990; Fourqurean and Cai 2001; Fourqurean and Zieman 2002; Duarte et al. 1995).

However, recent work has shown that carbonate dissolution from seagrass organic acids may meet seagrass P requirements (Jensen et al. 1998; Burdige and Zimmerman 2002). In the Pacific Northwest (PNW) there appear to be few peer-reviewed publications on nutrient limitation with regard to seagrasses (Williams and Ruckelshaus 1993). However, it seems unlikely that nitrogen is limiting in these systems given that coastal upwelling occurs during summer bringing nutrient rich ocean water to the surface (10-25 μM nitrate; C. Brown unpubl. data). During winter, terrestrial run-off through anthropogenically impacted watersheds also results in large N loading. Terrestrial run-off through red alder (*Alnus rubra*) rich secondary growth forest can provide substantial N inputs because of the nitrogen fixing bacteria associated with the trees. Consequently, even forested watersheds can have high N loading rates (Compton et al. 2003).

The determination of nutrient limitation for many primary producers is often based on examination of nutrient ratios. Seawater typically has a relatively fixed ratio of elements. Deviations from these ratios provides preliminary evidence for specific processes controlling how much of an element is present but, it can be dangerous to use elemental ratios as the only evidence for limitation. When $\text{N:P} < 16$ the system may be nitrogen limited (excess phosphorus), $\text{N:P} > 16$ system may be phosphorus limited (excess nitrogen). The Redfield ratio may be reflective of unicellular organisms (phyto- and bacterioplankton); however because of the structural components associated with macrophytes (seaweeds and seagrasses) the classic oceanic Redfield ratio ($\text{C:N:P} = 106:16:1$) is not appropriate.

Elemental ratios can provide a general rule of thumb for nutrient limitation, but only experimental determinations truly indicate the rate limiting steps. Literature reviews indicate that the median leaf seagrass C:N:P is about 400:20:1 with considerable variability (Table 3.2). Thus, on a carbon basis, seagrasses require about 4 times more C and 4 times less N and P than phytoplankton cells (Hemminga and Duarte 2000). The C:N for rhizome tissue is often much higher than that for leaf material since the rhizomes store fixed carbon. Inference of nutrient limitation from C:N:P ratios is even more tenuous for seagrasses than for phytoplankton, since these plants have access to both water column and sediment nutrient pools as well as internal transport tissues (i.e. xylem and phloem). Consequently, nutrient ratios alone should not be used to infer limitation (Touchette and Burkholder 2000a). Manipulative experiments should be conducted to determine limiting factors. Additionally, other nutrients can play a role in controlling seagrass production, for example Herman et al (1996) present a case study where they suggest that decreases in dissolved silica may have been a factor in seagrass decline.

3.2 Nutrient Enrichment and Eutrophication

“Eutrophication” is frequently used to describe the increased input of nutrients, primarily nitrogen and phosphorus to receiving waters. Recent work has suggested that eutrophication be redefined as “an increase in the rate of supply of organic carbon to an ecosystem” (Nixon 1995). Sources of organic carbon supply are from either allochthonous or autochthonous primary production. Nixon (1995) goes on to suggest a trophic classification scheme based on organic carbon supply. Eutrophication is often incorrectly used to include not only the process of increased nutrient status but also the effects (e.g. hypoxia, algal blooms, etc.) of this enrichment (Richardson and Jorgensen 1996).

Eutrophication *sensu* Nixon is caused by both natural and anthropogenic alterations of nutrient supply (Jorgensen and Richardson 1996). Coastal upwelling, typically associated with western continental margins, is a wind-driven phenomenon that results in increased primary production and often leads to enhanced fisheries production (Thurman 1988). Anthropogenic or “cultural” eutrophication alters the availability of nutrient elements within receiving waters which has primary, secondary and tertiary level impacts on biogeochemistry, primary and secondary production (Jorgensen and Richardson 1996; Vollenweider et al. 1992; Howarth et al. 2000; Livingston 2001).

Numerous studies have investigated the effects of eutrophication on seagrass communities (Table 3.3). Additionally, the physiological response of *Z. marina* to light (Chapter 2) and nutrients (this chapter) have been intensively studied. Most eutrophication studies have examined the community level response in experimental systems ranging from aquaria to mesocosms to the natural environment (Table 3.3). For *Z. marina* much of this work has been conducted along the East Coast of North America and has resulted in a general theory of seagrass response. Specifically, that enhanced nutrient loading leads to a degradation of *Z. marina* habitat (Figure 3.1) by stimulating algal production (micro- and macroalgae) and shading seagrass (Short et al. 1991, 1995; McGlathery 2001; Havens et al. 2001). However, there does not appear to be a relationship between nutrient input and the algal type (epiphyte vs. macroalgae vs. phytoplankton) supplying primary production or between nutrient input and the amount of primary production (Nixon et al. 2001).

Table 3.3. Selected list of literature examining the effect of eutrophication on *Z. marina* communities. Abbreviations are as follows: Zm = *Zostera marina*, SAV = Submerged Aquatic Vegetation, Epi = Epiphytes, Phyto = Phytoplankton, Macro= Macroalgae, Algae = epiphytes + phytoplankton + macroalgae. Positive (+) or negative (-) response in biomass is denoted.

Organizational level	Experimental system	Response	Location	Reference
Community	aquaria	+Epi, -Zm	Virginia	Neckles et al. 1993
	aquaria	+Zm, -Zm ³	Netherlands	van Katwijk et al. 1999
	aquaria	+ Epi	Washington	Williams & Ruckleshaus 1993
	aquaria	+Epi, -Zm ²	Virginia	Moore & Wetzel 2000
	field	+Zm, +Macro	Rhode Island	Harlin & Thorne-Miller 1981
	field	+Zm	Netherlands	van Lent et al. 1995
	field	--	Maryland	Stevenson et al. 1993
	field	+Phyto, +Macro, -Zm	Mass.	Valiela et al. 1992
	field	- Epi, -Zm*	Washington	Williams & Ruckleshaus 1993
	field	+Macro, -Zm ⁴	Finland	Bostrom et al. 2002
	field	+Macro, -Zm	Mass.	Hauxwell et al. 2003
	mesocosm	+Epi, -SAV	Maryland	Twilley et al. 1985
	mesocosm	-Zm ¹	North Carolina	Burkholder et al. 1992, 1994
	mesocosm	+algae, -Zm	New Hampshire	Short et al. 1995
	mesocosm	+Phyto, -Zm, -Macro, -Epi	Rhode Island	Taylor et al. 1995
	Lit. review	--		Worm et al. 2000
	Lit. review	--		Nixon et al. 2001

*Suggested nutrient limitation of *Z. marina*

¹Suggested nitrate toxicity of *Z. marina*

²Concluded light dominant factor, only +Epi and -Zm at highest light level.

³ Positive and negative effects were dependent on source of seagrass and salinity.

⁴ Conclusion based on inference.

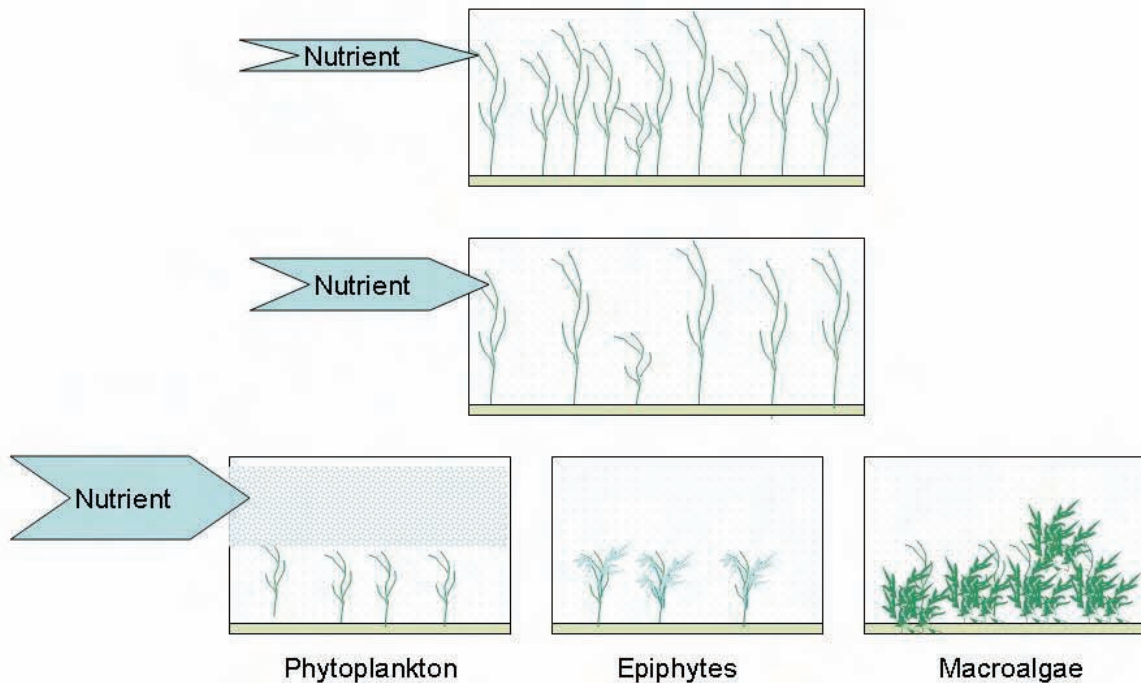


Figure 3.1. Schematic diagram of the effects of increased nutrient loading, which decreases seagrass density and biomass as well as promoting a shift toward phytoplankton, epiphyte or macroalgal community dominance. Adapted from Short et al. 1991.

This paradigm is based on several characteristics of East Coast systems and consequently may not be applicable to Pacific Northwest estuaries. Specifically, this paradigm applies to systems with relatively long residence times (months to years) and to places where nutrient inputs are dominated by atmosphere and freshwater. Most PNW estuaries exhibit very short residence times (1-30 days) as a result of large freshwater inputs and tidal exchange (Brown and Lee 2006). Nutrient inputs from the atmosphere are generally considered low in the PNW (Fenn et al. 2004; <http://nadp.sws.uiuc.edu/isopleths>) and dominant nutrient sources shift seasonally between river input during winter and ocean input during summer. The application of the nutrient loading/algal response paradigm to the PNW requires further scientific investigation.

The responses of lakes to nutrient loading and eutrophication abatement have been examined in a number of studies. Eutrophication abatement has also been an important research topic for the aquaculture industry (e.g. Kraufvelin et al. 2001; Porrello et al. 2003a, b) since effluent from mariculture activities is often high in nutrients. However, relatively few studies have examined the response of temperate estuaries to reduced nutrient loading. Although not directly linked to seagrass, O'Shea and Brosnan (2000) conclude that despite reductions in municipal and industrial waste water discharges to Long Island Sound, water quality, especially since bottom water hypoxia continues to be a problem. Thus nutrient loading and environmental problems may not exhibit linear responses, depending on the type of biological community dominating the system (Driscoll et al. 2003).

3.3 Relevant Research

Seagrass nitrogen metabolism and biochemistry has recently been reviewed in detail (Touchette & Burkholder 2000a). N acquisition occurs through the leaves and the roots and appears to be partially concentration dependent (Thursby and Harlin 1982). Nitrogen uptake rates from the literature are summarized in Table 3.1. Ammonium is the preferred N source, since it is the reduced form (Touchette and Burkholder 2000a). Leaf N acquisition can account for up to 70% of the total nitrogen required by the plant (Hemminga et al 1994; Pedersen and Borum 1992, 1993). Additionally, there is internal recycling of nitrogen from senescent tissues (Pedersen and Borum 1992; Stapel and Hemminga 1997; Hemminga et al. 1999). Nutrient uptake experiments are typically conducted in chambers with isolated root and leaf compartments. Changes in concentration through time, as well as radioactive (^{32}P , ^{14}C) and stable (^{15}N) isotopes have been used in these experimental systems. Ambient nutrient concentrations (Table 3.4) in temperate estuaries are typically sufficient to support seagrass production.

Seagrasses were initially believed to be a phosphorus pump, making sediment bound P available to water column organisms through translocation (McRoy and Barsdate 1970). However, more recent work suggest that excretion of phosphate is of minor importance (Brix and Lyngby 1985; Perez-Llorens et al. 1993). Ambient phosphorus concentrations in the environment are reported in Table 3.4.

Experimental manipulations of nutrient supply suggested that seagrasses can be nutrient limited. Some of the first field enrichment experiments added fertilizer to the sediments and showed increased leaf length, biomass and shoot density (Orth 1977). Additional field and mesocosm research also suggests that *Z. marina* can be nutrient limited in some situations, particularly in sediments with low organic content (Short 1983b, 1987). This implies that sediment and water column nutrient conditions need to be considered with regard to setting nutrient criteria protective of seagrass. While P is not considered a limiting nutrient in temperate systems, there is evidence for P and Fe limitation in tropical carbonate sediments.

Table 3.4. Water column and sediment nutrient concentrations (μM) associated with selected studies of *Zostera* habitat.

Seagrass	Location	Water NH_4^+	$\text{NO}_3^-/\text{NO}_2^-$	P	Sediment NH_4^+	$\text{NO}_3^-/\text{NO}_2^-$	P	Reference
<i>Zostera marina</i>								
	Alaska				20-147		4-28	Short 1983a
	Netherlands	3-15	1-18	5-17				Herman et al. 1996
	Rhode Island	0.1-1.5	0.1-0.8	0-1				Harlin & Thorne-Miller 1981
	Denmark	1-5.5	0.5-6		250-1100			Pedersen & Borum 1993
	Alaska				10-1500			Iizumi et al. 1982
	Mass.				270-1550			Dennison et al. 1987
	Alaska			2-7			5-75	Mc Roy et al. 1972
	North Sea	1-14	0-9		50-130	0-2		Hemminga et al. 1994
	Alaska					1-15		Iizumi et al. 1980
<i>Zostera japonica</i>								
	Oregon	2.2-2.9	7-35	0.6-1.1	60-170	0.8-2.0	3.3-5.6	Larned 2003
	Oregon	2-5	2-26	0.5-2	600-2400	0-30	7-40	Kaldy 2006b.

Research has clearly shown that seagrasses are affected by nutrients. Various processes, both natural and anthropogenic influence nutrient loading to estuaries. It is also apparent that nutrient loading processes are regionally variable and that this variability needs to be accounted for in the development of protective criteria. Driscoll et al. (2003) outlined many N sources in the northeastern US including atmospheric deposition, anthropogenic point and non-point sources (i.e. sewage treatment outfalls, septic system failure, ground-water inputs, etc.), and landscape practices (e.g. agriculture). However, this list ignores important N sources in the PNW that may influence seagrass including coastal ocean upwelling and forestry practices (Compton et al. 2003). The importance of the linkage between land use practices in watersheds and the resulting nutrient loads to estuaries is becoming more evident with continued research (Short and Burdick 1996; McClelland and Valiela 1998; Correll et al. 1992; Valiela and Bowen 2002; Hauxwell et al. 2003; Compton et al. 2003). Protective nutrient criteria may need to be tailored to account for regionally important processes (e.g. ocean currents).

Nitrogen supply is frequently described as either “new” or “old” nitrogen. New nitrogen is typically inorganic (e.g. N_2 , NO_3^- , NO_2^- , NO_x) and is generally made available through processes such as upwelling and nitrogen fixation. Old nitrogen is N made available through biological excretion and recycling and is typically composed of more reduced compounds such as amines, NH_4^+ , urea, etc. Seagrasses prefer NH_4^+ since it requires less energy for incorporation, although they can also utilize NO_3^- (Touchette and Burkholder 2000a). Anthropogenic inputs of N to estuarine ecosystems tend to be in the form of new nitrogen, which favors algal uptake and production.

As a result, the impact of enhanced nutrient supply to estuarine seagrass communities is typically observed through indirect effects. The shift in nutrient supply favors the development of algal communities which reduce underwater light and shade out seagrass. This general trend has been observed worldwide in both natural and experimental systems (Nixon et al. 2001). Thus, water quality criteria protective of seagrass will probably have a negative impact on algal production. Direct toxic effects from nutrients have been reported in the literature (Burkholder et al. 1992, 1994; van Katwijk et al. 1997). For example, Harlin and Thorne-Miller (1981) performed field nutrient addition experiments in Rhode Island, adding ammonium, nitrate, or phosphate to the water column rather than to the sediment. The nitrate supplements, while not causing a noticeable change in growth of the above-ground plant, did inhibit the root-rhizome fraction of the seagrass. They suggested that this might indicate toxicity of the nitrate addition to the test plants. Consistent with this hypothesis was the observation that the eelgrass plants sometimes disappeared within a half meter of the nitrate dispenser.

This observation was supported by the results of Burkholder et al. (1992), who reported from mesocosm experiments in North Carolina that nitrate enrichment of the water column caused declines of eelgrass, especially at higher temperatures, and that this was a direct physiological effect independent of shading by macroalgae. They attributed the effect to internal imbalances in nutrient ratios from sustained nitrate uptake through the leaf tissue. However, the evidence to support direct toxic effects is still considered somewhat tenuous and is a topic of debate in the literature (Moore and Wetzel, 2000). For example, *Zostera marina* thrives in at

least one Oregon estuary (Yaquina Bay) where both ambient water column and sediment nitrogen (nitrate and ammonium) concentrations are 3 to 10 times higher than the levels used in any of the experiments that exhibit toxic effects (Brown and Kaldy, US EPA, unpublished data). Touchette and Burkholder (2002) outline a physiological mechanism to support the nitrate toxicity hypothesis. However, it is important to note that temperature stress may be a confounding factor leading to seagrass decline. Bintz et al. (2003) observed that the negative effect of elevated water temperature on eelgrass was significantly increased when inorganic nutrient concentrations also were increased.

Experimental and observational evidence indicate that increased organic loading (i.e. eutrophication) in estuarine ecosystems results in a shift toward algal dominated production and degradation of seagrass habitat, thus altering the organization of trophic levels and the flow of energy through the system (See Chapter 8).

3.4 Gaps in Knowledge

While much of the physiology of nutrient uptake in *Z. marina* has been examined in a crude manner, the details of allocation within the plant and the dominant sources under given conditions remain somewhat ambiguous. The issue of direct nitrate or ammonium toxicity remains unresolved. This is of particular interest in the Pacific Northwest where water column and sediment nitrogen levels can be 3 to 10 times higher than reported toxic levels for long periods (days to months) as a result of coastal upwelling and riverine loading with no apparent negative impact to *Z. marina*. Relatively cold water temperatures (annual average 10 °C) may help to ameliorate stress. In comparison, areas that appear to show direct nutrient toxicity, e.g. Chesapeake Bay and Rhode Island coastal ponds, tend to have warmer summer water temperatures (up to 30 °C). As a result temperature and nutrient effects may be confounded and work synergistically. Detailed physiological work utilizing newly available technology (e.g. compound specific nitrogen isotope analyses, microelectrodes/optodes, mechanistic models, etc.) will provide valuable insight on how ramets respond to nutrient stress. Additionally, mesocosm and field experiments have shown that *Z. marina* communities are degraded in response to enhanced nutrient loading; however, few studies (if any) have addressed the recovery of these systems after abatement of loading. Furthermore, there appears to be little relationship between nutrient inputs and the rate and dominant primary producers (Nixon et al. 2001).

The absolute and relative contributions of different primary producers to net ecosystem primary production may provide an important metric for determining the degree of eutrophication and/or the potential for eutrophication related impairment of resources. In the PNW, the production ecology of benthic marine macrophytes (seagrasses and macroalgae) is poorly understood. The production ecology of microalgae is even less well known. It may be better to set water quality criteria protective of seagrass based on standards which minimize the response of algae to anthropogenic N inputs, since the primary response to nutrient loading is mediated through algal blooms which in turn smother seagrass (Nelson and Lee 2001). Additionally, whether nutrient criteria protective of seagrass will be equally protective of other

types of habitat (e.g. marshes), as well as economically and recreationally important fisheries, is poorly known.

3.5 Literature Cited

- Atkinson, M. J. and S. V. Smith. 1983. C:N:P ratios of benthic marine plants. *Limnology and Oceanography* 28:568-574.
- Bintz, J. C., S. W. Nixon, B. B. Buckley, and S. L. Granger. 2003. Impacts of temperature and nutrients on coastal lagoon plant communities. *Estuaries* 26:765-776.
- Bostrom, C., E. Bonsdorff, P. Kangas, and A. Norkko. 2002. Long-term changes of a brackish water eelgrass (*Zostera marina* L.) community indicate effects of coastal eutrophication. *Estuarine, Coastal Shelf Science* 55:795-804.
- Brix, H. and J. E. Lyngby. 1985. Uptake and translocation of phosphorus in eelgrass (*Zostera marina*). *Marine Biology* 90:111-116.
- Brown, C. A. and H. Lee II. 2006. Chapter 3: Environmental characteristics of the target estuaries. In: Lee, II., H., C. A. Brown, B. L. Boese and D. A. Young (eds.). Proposed classification scheme for coastal receiving waters based on SAV and food web sensitivity to nutrients. Volume 2. Nutrient drivers, seagrass distribution and regional classifications of Pacific Northwest estuaries. US Environmental Protection Agency. Internal Report. pp. 279.
- Brown, C. A. and J. E. Kaldy, US EPA, unpublished data.
- Burdige, D. J. and R. C. Zimmerman. 2002. Impact of seagrass density on carbonate dissolution in Bahamian sediments. *Limnology and Oceanography* 47:1751-1763.
- Burkholder, J. M., H. B. Glasgow, and J. E. Cooke. 1994. Comparative effects of water-column nitrate enrichment on eelgrass *Zostera marina*, shoal grass *Halodule wrightii* and widgeongrass *Ruppia maritima*. *Marine Ecology Progress Series* 105:121-138.
- Burkholder, J. M., K. M. Mason, and H. B. Glasgow. 1992. Water-column nitrate enrichment promotes decline of eelgrass *Zostera marina*: evidence from seasonal mesocosm experiments. *Marine Ecology Progress Series* 81:163-178.
- Butler, A. and P. Jernakoff. 1999. Seagrass in Australia: Strategic review and development of an R&D plan. CSIRO publishing, Collingwood, Australia. pp 210.
- Compton, J. E., M. R. Church, S. T. Larned, and W. E. Hogsett. 2003. Nitrogen export from forested watersheds in the Oregon Coast Range: The role of N₂-fixing red alder. *Ecosystems* 6:773-785.
- Correll, D. L., T. E. Jordan, and D. E. Weller. 1992. Nutrient flux in a landscape: effects of coastal land used and terrestrial community mosaic on nutrient transport to coastal waters. *Estuaries* 15:431-442.
- Dennison, W. C., R. C. Aller, and R. S. Alberte. 1987. Sediment ammonium availability and eelgrass (*Zostera marina*) growth. *Marine Biology* 94:469-477.
- Driscoll, C. T., D. Whitall, J. Aber, E. Boyer, M. Castro, C. Cronan, C. L. Goodale, P. Groffman, C. Hopkinson, K. Lambert, G. Lawrence, and S. Ollinger. 2003. Nitrogen pollution in the northeastern United States: Sources, effects and management options. *BioScience* 53:357-374.

- Duarte, C. M., M. Merino, and M. Gallegos. 1995. Evidence for iron deficiency in seagrasses growing above carbonate sediments. *Limnology and Oceanography* 40:1153-1158.
- Duarte, C. M. 1990. Seagrass Nutrient Content. *Marine Ecology Progress Series* 67:201-207
- Eftemeijer, P. L. A. and J. J. Middelburg. 1993. Sediment nutrient interactions in tropical seagrass beds: a comparison between a terrigenous and carbonate sedimentary environment in South Sulawesi (Indonesia). *Marine Ecology Progress Series* 102: 187-198.
- Fenn, M., L. Geiser, J. Peterson, E. Waddell, and E. Porter. 2004. Why federal land managers in the Northwest are concerned about Nitrogen emissions. <http://nature.nps.gov/air/Pubs/pdf/NOxPaper2004.pdf>
- Fourqurean, J. W., T. O. Moore, B. Fry, and J. T. Hollibaugh. 1997. Spatial and temporal variation in C:N:P ratios, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. *Marine Ecology Progress Series* 157:147-157.
- Fourqurean, J. W. and Y. Cai. 2001. Arsenic and phosphorus in seagrass leaves from the Gulf of Mexico. *Aquatic Botany* 71:247-258.
- Fourqurean, J. W., J. C. Zieman, and G. V. N. Powell. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* 37: 162-171.
- Fourqurean, J. W. and J. C. Zieman. 2002. Nutrient content of the seagrass *Thalassia testudinum* reveals regional patterns of relative availability of nitrogen and phosphorus in the Florida Keys, USA. *Biogeochemistry* 61:229-245.
- Harlin, M. M. and B. Thorne-Miller. 1981. Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. *Marine Biology* 65:221-229.
- Hauxwell, J., J. Cebrian, and I. Valiela. 2003. Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series* 247:59-73.
- Havens, K. E., J. Hauxwell, A. C. Tyler, S. Thomas, K. J. McGlathery, J. Cebrian, I. Valiela, A. D. Steinman, and S.-J. Hwang. 2001. Complex interactions between autotrophs in shallow marine and freshwater ecosystems: implications for community responses to nutrient stress. *Environmental Pollution* 113:95-107.
- Hemminga, M. A., B. P. Koutstaal, J. van Soelen, and A. G. A. Merks. 1994. The nitrogen supply to intertidal eelgrass (*Zostera marina*). *Marine Biology* 118:223-227.
- Hemminga, M. A., N. Marba, and J. Stapel. 1999. Leaf nutrient resorption, leaf lifespan and the retention of nutrients in seagrass systems. *Aquatic Botany* 65:141-158.
- Hemminga, M. A. and C. M. Duarte. 2000. *Seagrass Ecology*. Cambridge University Press, Cambridge, UK.
- Herman, P. M. J., M. A. Hemminga, P. H. Nienhuis, J. M. Verschuure, and E. G. J. Wessel. 1996. Wax and wane of eelgrass *Zostera marina* and water column silicon levels. *Marine Ecology Progress Series* 144:303-307.
- Howarth, R. W., D. M. Anderson, T. M. Chruch, H. Greening, C. S. Hopkinson, W. C. Huber, N. Marcus, R. J. Naiman, K. Segerson, A. N. Sharpley, and W. J. Wiseman. 2000. Clean coastal waters: understanding and reducing the effects of nutrient pollution. *Ocean*

- Studies Board and Water Science Technology Board, National Academy Press, Washington, DC.
- Iizumi, H., A. Hattori and C. P. McRoy. 1980. Nitrate and nitrite in interstitial waters of eelgrass beds in relation to the rhizosphere. *Journal Experimental Marine Biology and Ecology* 47:191-201.
- Iizumi, H., A. Hattori and C. P. McRoy. 1982. Ammonium regeneration and assimilation in eelgrass (*Zostera marina* L.) beds. *Marine Biology* 66:59-65.
- Iizumi, H. and A. Hattori. 1982. Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific coast of Japan III. Kinetics of Nitrogen uptake. *Aquatic Botany* 12:245-256.
- Jensen, H. S., K. J. McGlathery, R., Marino, and R. W. Howarth. 1998. Forms and availability of sediment phosphorus in carbonate sand of Bermuda seagrass beds. *Limnology and Oceanography* 43:799-810.
- Jorgensen, B. B. and K. Richardson (eds). 1996. Eutrophication in Coastal Marine Ecosystems. Coastal and Estuarine Studies Volume 52. American Geophysical Union, Washington, DC.
- Kaldy, J. E. and K. H. Dunton. 2000. Above- and below-ground production, biomass and reproductive ecology of *Thalassia testudinum* (turtle grass) in a subtropical coastal lagoon. *Marine Ecology Progress Series* 193: 271-283.
- Kaldy, J. E. 2006a. Carbon, nitrogen, phosphorus and heavy metal budgets: How large is the eelgrass (*Zostera marina* L.) sink in a temperate estuary? *Marine Pollution Bulletin* 52: 332-356.
- Kaldy, J. E. 2006b. Production ecology of the non-indigenous seagrass, dwarf eelgrass (*Zostera japonica* Ascher. & Graeb.), in a Pacific Northwest Estuary, USA. *Hydrobiologia* 553: 201-217.
- Kraufvelin P, B. Sinisalo, E. Leppakoski, J. Mattila, and E. Bonsdorff. 2001. Changes in zoobenthic community structure after pollution abatement from fish farms in the Archipelago Sea (N. Baltic Sea). *Marine Environmental Research* 51:229-245
- Larkum, A. W. D., R. J. Orth, and C. M. Duarte. 2006. Seagrasses: Biology, Ecology and Conservation. Springer, Netherlands. pp. 649.
- Larned, S. T. 2003. Effects of the invasive, nonindigenous seagrass *Zostera japonica* on nutrient fluxes between the water column and benthos in a NW Pacific estuary. *Marine Ecology Progress Series* 254:69-80.
- Lee, K. S. and K. H. Dunton. 1999a. Influence of sediment nitrogen availability on carbon and nitrogen dynamics in the seagrass *Thalassia testudinum*. *Marine Biology* 134: 217-226.
- Lee, K. S. and K. H. Dunton. 1999b. Inorganic nitrogen acquisition in the seagrass *Thalassia testudinum*: Development of a whole-plant nitrogen budget. *Limnology and Oceanography* 44: 1204-1215.
- Livingston, R. J. 2001. Eutrophication processes in coastal system. CRC Press, Boca Raton, Florida, USA.
- McClelland, J. W. and I. Valiela. 1998. Linking nitrogen in estuarine producers to land-derived sources. *Limnology and Oceanography* 43:577-585.
- McGlathery, K. J. 2001. Macroalgal blooms contribute to the decline of seagrass in nutrient enriched coastal waters. *Journal of Phycology* 37:453-456.

- McRoy, C. P. and R. J. Barsdate. 1970. Phosphate absorption in eelgrass. *Limnology and Oceanography* 15:6-13.
- McRoy, C. P., R. J. Barsdate, and M. Nebert. 1972. Phosphorus cycling in an eelgrass (*Zostera marina* L.) ecosystem. *Limnology and Oceanography* 17:58-67.
- Moore, K. A. and R. L. Wetzel. 2000. Seasonal variations in eelgrass (*Zostera marina* L.) responses to nutrient enrichment and reduced light availability in experimental ecosystems. *Journal Experimental Marine Biology Ecology* 244:1-28.
- Neckles, H. A., R. L. Wetzel, and R. J. Orth. 1993. Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina* L.) dynamics. *Oecologia* 93:285-295.
- Nelson, T.A., A. Lee. 2001. A manipulative experiment demonstrates that blooms of the macroalga *Ulvaria obscura* can reduce eelgrass shoot density. *Aquatic Botany* 79:149-154.
- Nixon, S. W. 1995. Coastal marine eutrophication: a definition, social causes and future concerns. *Ophelia* 41:199-220.
- Nixon, S., B. Buckley, S. Granger, and J. Bintz. 2001. Responses of very shallow marine ecosystems to nutrient enrichment. *Human and Ecological Risk Assessment* 7:1457-1481.
- O'Shea, M. L. and T. M. Brosnan. 2000. Trends in indicators of eutrophication in Western Long Island Sound and the Hudson-Raritan Estuary. *Estuaries* 23:877-901.
- Orth, R. J. 1977. Effect of nutrient enrichment on growth of the eelgrass, *Zostera marina* in the Chesapeake Bay, Virginia, USA. *Marine Biology* 44:187-194.
- Pedersen, M. F. and J. Borum. 1992. Nitrogen dynamics of eelgrass *Zostera marina* during a late summer period of high growth and low nutrient availability. *Marine Ecology Progress series* 80:65-73.
- Pedersen, M. F. and J. Borum. 1993. An annual nitrogen budget for a seagrass *Zostera marina* population. *Marine Ecology Progress Series* 101:169-177.
- Penhale, P. A. and G. W. Thayer 1980. Uptake and transfer of carbon and phosphorus by eelgrass (*Zostera marina* L.) and its epiphytes. *Journal Experimental Marine Biology and Ecology* 42:113-123.
- Perez-Llorens, J. L., P. de Visscher, P. H. Nienhuis, and F. X. Niell. 1993. Light dependent uptake, translocation and foliar release of phosphorus by the intertidal seagrass *Zostera noltii* Hornem. *Journal of Experimental Marine Biology Ecology* 166:165-174.
- Perez-Llorens, J. L., M. Muchtar, F. X. Niell, and P. H. Nienhuis. 1991. Particulate organic carbon, nitrogen and phosphorus content in roots, rhizomes and differently aged leaves of *Zostera noltii* Hornem. in Oosterschelde Estuary (Southwestern Netherlands). *Botanica Marina* 34:319-322.
- Porrello, S., M. Lenzi, E. Persia, P. Tomassetti, and M. G. Finoia. 2003a. Reduction of aquaculture wastewater eutrophication by phytotreatment ponds system I. Dissolved and particulate nitrogen and phosphorus. *Aquaculture* 219:515-529.
- Porrello, S., M. Lenzi, E. Persia, P. Tomassetti, M. G. Finoia, and I. Mercatali. 2003b. Reduction of aquaculture wastewater eutrophication by phytotreatment ponds system II. Nitrogen and phosphorus content in macroalgae and sediment. *Aquaculture* 219:531-544.

- Richardson, K. and B. B. Jorgensen. 1996. Eutrophication: Definition, History and Effects. In: BB Jorgensen and K Richardson (eds). Eutrophication in Coastal Marine Ecosystems. Coastal and Estuarine Studies Volume 52. American Geophysical Union, Washington, DC.
- Short, F. T. 1983a. The response of interstitial ammonium in eelgrass (*Zostera marina* L.) beds to environmental perturbations. *Journal of Experimental Marine Biology Ecology* 68:195-208.
- Short, F. T. 1983b. The seagrass *Zostera marina* L.: Plant morphology and bed structure in relation to sediment ammonium in Izembek Lagoon, Alaska. *Aquatic Botany* 16:149-161.
- Short, F. T. 1987. Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. *Aquatic Botany* 27:41-57.
- Short, F. T. and D. M. Burdick. 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. *Estuaries* 19:730-739.
- Short, F. T., D. M. Burdick, and J. E. Kaldy. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnology and Oceanography* 40:740-749.
- Short, F. T. and R. G. Coles. 2001. *Global Seagrass Research Methods*. Elsevier, Amsterdam.
- Short, F. T. and C. P. McRoy. 1984. Nitrogen uptake by leaves and roots of the seagrass *Zostera marina* L. *Botanica Marina* 27:547-555.
- Short, F. T., W. C. Dennison, and D. G. Capone. 1990. Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. *Marine Ecology Progress Series* 62:169-174.
- Short, F. T., G. E. Jones, and D. M. Burdick. 1991. Seagrass decline: Problems and solutions. Coastal Zone '91 Conference – ASCE. Long Beach, CA/July 1991. Pp 439-453.
- Stapel, J., T. L. Aarts, B. H. M. van Duynhoven, J. D. deGroot, H. H. W. van den Hoogen, and M. A. Hemminga. 1996. Nutrient uptake by leaves and roots of the seagrass *Thalassia hemprichii* in the Spermonde Archipelago, Indonesia. *Marine Ecology Progress Series* 134:195-206.
- Stapel, J. and M. A. Hemminga. 1997. Nutrient resorption from seagrass leaves. *Marine Biology* 128:197-206.
- Stevenson, J. C., L. W. Staver, and K. W. Staver. 1993. Water quality associated with survival of submersed aquatic vegetation along an estuarine gradient. *Estuaries* 16:346-361.
- Taylor, D. I., S. W. Nixon, S. L. Granger, B. A. Buckley, J. P. McMahon, and H.-J. Lin. 1995. Responses of coastal lagoon plant communities to different forms of nutrient enrichment—a mesocosm experiment. *Aquatic Botany* 52:19-34.
- Thurman, H. V. 1988. *Introductory Oceanography*. Merrill Publishing Company, Columbus, Ohio.
- Thursby, G. B. and M. M. Harlin. 1982. Leaf-Root interaction in the uptake of ammonium by *Zostera marina*. *Marine Biology* 72:109-112.
- Touchette, B. W. and J. M. Burkholder. 2000a. Review of nitrogen and phosphorus metabolism in seagrasses. *Journal Experimental Marine Biology Ecology* 250:133-167.

- Touchette, B. W. and J. M. Burkholder. 2000b. Overview of the physiological ecology of carbon metabolism in seagrasses. *Journal Experimental Marine Biology Ecology* 250: 169-205.
- Touchette, B. W. and J. M. Burkholder. 2002. Seasonal variations in carbon and nitrogen constituents in eelgrass (*Zostera marina* L.) as influenced by increased temperature and water-column nitrate. *Botanica Marina* 45:23-34.
- Twilley, R. R., W. M. Kemp, K. W. Staver, J. C. Stevenson, and W. R. Boynton. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects of production of plants and associated communities. *Marine Ecology Progress Series* 23:179-191.
- Valiela, I. and J. L. Bowen. 2002. Nitrogen sources to watersheds and estuaries: role of land cover mosaics and losses within watersheds. *Environmental Pollution* 118:239-248.
- Valiela, I., K. Foreman, M. LaMontagne, D. Hersh, J. Costa, P. Peckol, B. DeMeo-Anderson, C. D'Avanzo, M. Babione, C.-H. Sham, J. Brawley, and K. Lajtha. 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichments in Waquoit Bay, Massachusetts. *Estuaries* 15:443-457.
- van Katwijk, M. M., L. H. T. Vergeer, G. H. W. Schmitz, and J. G. M. Roelofs. 1997. Ammonium toxicity in eelgrass *Zostera marina*. *Marine Ecology Progress Series* 157:159-173.
- van Katwijk, M. M., G. H. W. Schmitz, A. P. Gasseling, and P. H. van Avesaath. 1999. Effects of salinity and nutrient load and their interaction on *Zostera marina*. *Marine Ecology Progress Series* 190:155-165.
- van Lent, F., J. M. Vershuure, and M. L. J. van Veghel. 1995. Comparative study on populations of *Zostera marina* L. (eelgrass): in situ nitrogen enrichment and light manipulation. *Journal Experimental Marine Biology Ecology* 185:55-76.
- Vollenweider, R. A., R. Marchetti, and R. Viviani. 1992. *Marine Coastal Eutrophication*. Elsevier, Amsterdam.
- Williams, S. L. and M. H. Ruckelshaus. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology* 74:904-918.
- Worm, B., T. B. H. Reusch, and H. K. Lotze. 2000. In situ nutrient enrichment: methods for marine benthic ecology. *International Review of Hydrobiologia* 85:359-375.
- Zimmerman, R. C., R. D. Smith, and R. S. Alberte. 1987. Is growth of eelgrass nitrogen limited? A numerical simulation of the effects of light and nitrogen on the growth dynamics of *Zostera marina*. *Marine Ecology Progress Series* 41:167-176.

4.0 Salinity as a Limiting Factor for the Seagrasses *Zostera marina* and *Thalassia testudinum*

Bruce L. Boese

4.1 Background

Eelgrass, *Zostera marina* is a euryhaline species (Phillips 1984) found world wide in coastal waters that vary from mildly hypersaline to nearly fresh (Table 4.1). However, it appears to grow best in estuarine waters with salinities in the range from approximately 5 to just below that of normal seawater. In contrast, subtropical turtle grass (*Thalassia testudinum*), which is the dominate seagrass species in Florida and the Caribbean (Phillips 1960) is more stenohaline (Table 4.2) and does not tolerate extreme salinity fluxes nor prolonged exposures to fresh water (Doering and Chamberlain 2000; Montague and Ley 1993).

Alterations in estuarine hydrology due to fresh water diversion, dredging and filling may result in alterations of estuarine salinity structure. Areas of high salinity and to a lesser extent variable salinities may displace brackish water areas further upstream where higher temperatures and more nutrients may be prevalent. Higher or less variable salinities may also encourage the growth of the slime mold, *Labyrinthula* sp. which has been implicated in the historic wasting disease die-offs that occurred in eastern and western Atlantic eelgrass populations in the early 1930's (den Hartog 1987; Giesen et al. 1990). Geographically isolated *Z. marina* populations may have genetically narrower salinity optima than is suggested by the euryhaline nature of the species taken as a whole. This makes it more difficult to predict the effect of local salinity alterations and may complicate restoration activities.

4.2 Salinity Ranges

The wide range of salinity tolerated in *Z. marina* (Table 4.1) appears to be related to the ability to adapt to changes in salinity by osmotic regulation of cellular solutes via salt excretion by epidermal cells (Jagels 1983) and the accumulation of the amino acid proline in hypersaline environments (van Diggelen et al. 1987). Although *Z. marina* is able to survive for a time in fresh water, net leaf photosynthesis decreases in waters below 5 and totally ceases in completely fresh water (Hellbom and Björk 1999; Biebl and McRoy 1971). Sand-Jensen and Borum (1983) noted that a die-off of *Z. marina* occurred in Danish coastal waters during the winter when plants were exposed to salinities below 2. In contrast turtlegrass, *T. testudinum* is found in a narrower salinity range (Table 4.2) with an optimal salinity ranges reported as 25 to 38.5 (Phillips 1960), and 17-36 Zimmermann and Livingston 1976).

Table 4.1. Reported salinity tolerance ranges for eelgrass (*Zostera marina*) populations.

Location	Salinity Range	Citation
World Wide	0-35	Thayer et al. 1984
World Wide	0-42	Phillips 1984
Northern Hemisphere	5-35	den Hartog 1970
Denmark	13-31	Pinnerup 1980
Denmark	12-31	Sand-Jensen and Borum 1983
Denmark (estuaries)	9-23	Wium-Anderson and Borum 1984
Baltic Sea	6-12	Hellblom and Björk 1999
Netherlands (marine environments)	~30	van Katwijk et al. 1999
Netherlands (estuaries)	15-25	van Katwijk et al. 1999
Netherlands (Lake Grevelingen)	22-32	Kamermans et al. 1999
France (Thau)	27-41	Rigollet et al. 1998
Italy (Venice)	25-33	Rigollet et al. 1998
Chesapeake Bay	14-22	Wetzel and Penhale 1983
Yaquina Bay, OR	25-33	Kentula and DeWitt 2003

Table 4.2. Reported salinity tolerance ranges for turtlegrass (*Thalassia testudinum*) populations.

Location	Salinity Range	Citation
Florida	28-36	Phillips 1960
Florida	17-36	Zimmermann and Livingston 1976*
Florida	24-35	Zieman and Zieman 1989* Zieman 1982*
Texas	30-40	Adair et al. 1994*
Florida	22-36	Doering and Chamberlain 2000
Dry Tortugas	35-38.5	Phillips 1960
Everglades National Park	28-48	Phillips 1960
Florida (west coast)	25-34	Phillips 1960

*As cited in Doering and Chamberlain 2000.

4.3 Growth/Shoot/Competition Effects

While *Z. marina* is tolerant of some exposure to fresh and hypersaline waters, optimal growth rates vary with populations. *Zostera marina* population increases and declines were correlated with relatively slight alteration in the salinity structure of Lake Grevelingen in The Netherlands, within the range of 22 to 32 (Kamermans et al. 1999). Laboratory experiments supported this interpretation showing optimal growth rates were higher at 22 than 32. However, *Z. marina* collected from an area of relatively greater salinity (Roscoff and Bay of Archchon, France) did not exhibit differences in growth rates when subjected to the same salinity regimes (Kamermans et al. 1999). Optimal salinities for Pacific Northwest (PNW) *Z. marina* populations have not been determined, but *Z. marina* appears to grow best at 20-32 in Puget Sound (Philips 1984). Laboratory experiments on PNW *Z. marina* suggested that higher growth rates occurred at 30 than 10 and that the highest densities of *Z. marina* in the field were in areas of high salinities and lowest temperature (Thom et al. 2001, 2003). This apparent relationship between plant densities (as estimated from percent cover) and high salinities combined with low temperature was also evident in the Yaquina estuary, Newport, OR (Kentula and DeWitt 2003).

Similar studies have been conducted on *T. testudinum*. In six week laboratory mesocosm experiments (Doering and Chamberlain 2000), *T. testudinum* was exposed to a range of salinities from 6 to 35, with a variety of simple plant metrics (blades per shoot, growth, biomass, tissue nitrogen) determined. The results of this experiment suggested that *T. testudinum* was adversely affected by prolonged exposures to salinities less than 12 (Doering and Chamberlain 2000). The results of that study were similar to that of a study (Lirman and Cropper Jr. 2003) in which *T. testudinum* was exposed to short-term (14 day) exposure to salinities which ranged from 5 to 45. In that study the maximum growth rate for *T. testudinum* was observed between 30 and 40 with reduced rates at 5 and 45.

Field populations of *T. testudinum* appear to occupy a narrower range of salinities than those they have been shown to tolerate in the laboratory. This is likely due to competition from other seagrass species (*Halodule wrightii*, *Syringodium filiforme*) which often co-occur with *T. testudinum* and appear to replace it in hyper- and hyposaline conditions. Greenawalt-Boswell et al. (2006) found that in hydrologic regions of Charlotte Harbor (southwest Florida) characterized by highly variable salinity regimes, overall seagrass biomass was reduced and that *H. wrightii* was likely to replace *T. testudinum* as the dominant species. In contrast, the construction of the Gulf Intracoastal Waterway tended to reduce and moderate hypersalinity events in Laguna Madre (southeast Texas). This resulted in a decrease in *H. wrightii* with its replacement by *S. filiforme* and *T. testudinum* (Quammen and Onuf 1993).

Hypersaline conditions have been observed to occur in Florida Bay and have been suggested as a contributing cause to a die off of *T. testudinum* which began in 1987 (Zieman et al. 1999). However, more recent laboratory studies suggest that *T. testudinum* is highly tolerant of salinities as great as 60 (Koch et al. 2007) and field studies which examined the responses of a *T. testudinum* meadow to brine discharges from a desalination plant show no apparent adverse effects (Tomasko et al. 2000). The most likely cause of this die off was an interaction between

high salinities, high temperatures (Florida Bay Science Plan 1994). High temperatures and salinities also may affect photosynthetic oxygen production, resulting in an increase in sediment sulfides which in combination with high temperatures has been implicated in seagrass die-offs (Koch and Erskin 2001). Hypersalinity was also implicated in seagrass losses in a Yucatan (Mexico) coastal lagoon (Herrera-Silveira et al. 2000). In that study mean salinity of 42 resulted in an overall reduction in seagrass coverage which was remediated by increasing freshwater inputs to the lagoon which reduced mean to 35 resulting in an increase in seagrass coverage and a change in dominate seagrass species which included the appearance of some patches of *T. testudinum* (Herrera-Silveira et al. 2000).

However, diverting of fresh water into estuaries has been implicated in several long-term seagrass declines (Estevez 2000). For example, *Zostera hornemanniana* meadows in the Etang de Berre, a French Mediterranean lagoon, began to degrade after the completion of a hydroelectric dam in 1996 which erratically diverts fresh water into the lagoon (Stora and Arnoux 1983). Within a few years most of the *Zostera* meadows had disappeared with a concurrent change in the benthos to a degraded euryhaline community (Stora and Arnoux 1983). Montegue and Ley (1993) noted that overall seagrass biomass in Florida Bay decreased with increasing variation in salinity, and that these decreases were greatest where salinity was lowest. Their work suggests that even when mean salinity changes of water diversion projects are small, a small increase in salinity variance may have drastic effects on seagrass populations. Similarly fresh water diversions which reduce salinities below the optimal range may adversely affect *T. testudinum* populations, especially recruitment from seedlings. In mesocosm experiments, Kahn and Durako (2006) found that while turtle grass seedlings tolerated a reduction in salinity of ~10 below their optimal range (30-40), they were less adaptable than mature shoots. In addition ammonium toxicity tended to increase at these lowered salinities which imply that fresh water inputs with high nutrients may be detrimental to recruit survival (Kahn and Duranko 2006).

In *Z. marina* there appears to be a significant interaction between tolerance to higher salinity and nutrients. Laboratory experiments in which both salinity and nutrients were manipulated suggest that *Z. marina* subjected to high salinities (30) responded adversely to nutrient additions (van Katwijk et al. 1999). Van Katwijk et al. (1999) went on to speculate that the world wide decline in *Z. marina* may be related to nutrient increases in high salinity coastal environments. In a more recent paper describing a conceptual model for habitat suitability for *Z. marina* transplants (van Katwijk et al. 2000), this idea was further refined by the suggestion that stress resulting from high salinity would adversely affect the plants ability to cope with any additional stressor. However, the responses of *Z. marina* populations to changes in salinity also appear to be related to the ambient salinities from which these populations originated, suggesting genotypic differences in salinity tolerances (Kamermans et al. 1999; van Katwijk et al. 1999, 2000). Genotypic differences in eelgrass populations have also been implicated in the apparent geographic differences in leaf widths (McMillan 1978).

4.4 Wasting Disease

The slime mold (*Labyrinthula* sp.) is a secondary decomposer of seagrasses and algae, and may have been the cause of the “wasting disease” decline in *Z. marina* that occurred in Eastern North American Atlantic waters in 1932 (den Hartog 1987) and in the Wadden Sea during the same time period (van Katwijk et al. 2000). The co-occurrence of drought and associated high salinity waters with this die off has led to speculation that high salinity with high temperatures favored this infective agent (Martin 1954). Further support for this idea is that *Labyrinthula*, appears not to be pathogenic below 12-15 (Giesen et al. 1990) and that *Z. marina* populations found in brackish water appeared not be affected by the disease (den Hartog, 1987; Vergeer et al. 1995). Whether *Labyrinthula* was the underlying cause or merely acted as a decomposer of eelgrass stressed by some other agent is debatable (den Hartog 1987; Vergeer et al. 1995).

Wasting disease has also been implicated in the die off of *T. testudinum* in Florida Bay (Blakesly et al. 2002). As with *Labyrinthula* infestations in eelgrass, it primarily has affects high density turtle grass meadows when salinities are high (Blakesly et al. 2002). However, it is likely not the major cause of the seagrass die-off noted in Florida Bay (Boesch et al. 1993; Zieman et al. 1999; Blakesly et al. 2002). However, as *Labyrinthula* prefers more saline waters, fresh water diversions and possible droughts resulting from global climate change will have a positive influence on its growth thus making it more likely to adversely affect seagrasses.

4.5 Summary/Research Gaps

Generally both turtle and eelgrass have wide salinity tolerances with turtle grass being the more stenohaline species. In areas of suboptimal or highly variable salinities both species are often precluded by complex interactions with other stressors such as high temperatures, suboptimal lighting conditions, wasting disease, and competition with species more tolerant of hypo- and hypersaline conditions.

With the exception of van Katwijk et al. (1999) studies have not addressed the interrelationship between nutrients and salinity. Based on that study it is at least possible that nutrient additions may have greater impact on eelgrass populations in high salinity areas, possibly requiring greater regulatory controls. By the same logic, water diversion projects which increase salinity may result in greater potential stress from nutrients and wasting disease. Erratic fresh water discharges into bays and estuaries have been shown to have deleterious effects on tropical and subtropical seagrasses beyond which would have been predicted by the mean change in salinity. However experimental work on the effect of increasing the variance in salinity on *Z. marina* and *T. testudinum* appears to be lacking. Studies that address these research gaps should be conducted on a variety of seagrass genets to assess effects on localized populations.

4.6 Literature Cited

- Adair, S. E., J. L. Moore, and C. P. Onuf. 1994. Distribution and status of submerged vegetation in estuaries of the Upper Texas Coast. *Wetlands* 14:110-121.
- Biebl, R. and C. P. McRoy. 1971. Plasmatic resistance and rate of respiration and photosynthesis in the seagrass *Zostera marina* at different salinities and temperatures. *Marine Biology* 8:48-56.
- Blakesley, B. A., D. M. Berns, M. F. Merello, M. O. Hall, and J. Hynirva. 2002. The dynamics and distribution of the slime mold *Labyrinthula* sp. and its potential impacts on *Thalassia testudinum* populations in Florida. pp. 199-207. In: H.S. Greening (ed). *Seagrass Management: Its Not Just Nutrients!* Aug 22-24, 2000. St. Petersburg, FL. Tampa Bay Estuary Program.
- Boesch, D. F., N. E. Armstrong, C. F. D'Elia, N. B. Maynard, H. W. Paerl, and S. L. Williams. 1993. Deterioration of the Florida Bay Ecosystem: An evaluation of the scientific evidence. Report to the Interagency Working Group on Florida Bay. Sept. 15, 1993. pp.30.
- denHartog, C. 1970. *The Seagrasses of the World*. North-Holland Publication Amsterdam. pp. 275.
- denHartog, C. 1987. 'Wasting disease' and other dynamic phenomena in *Zostera* beds. *Aquatic Botany* 27:3-14.
- Doering P. H. and R. H. Chamberlain. 2000. Experimental studies on the salinity tolerance of turtle grass, *Thalassia testudinum*. pp. 81-98 In: S. A. Bortone (ed)., *Seagrasses: Monitoring, Ecology, Physiology and Management*. CRC Press, Boca Raton. pp. 318.
- Estevez, E. D. 2000. Matching Salinity Metrics to Estuarine Seagrasses for Freshwater Inflow Management. pp. 295-307. In: S. A. Bortone (ed)., *Seagrasses: Monitoring, Ecology, Physiology and Management*. CRC Press, Boca Raton. pp. 318.
- Florida Bay Science Plan. 1994. Florida Bay Interagency Working Group.
- Giesen, W. B. J. T., M. M. van Katwijk, and C. den Hartog. 1990. Temperature, salinity, insolation and wasting disease of eelgrass (*Zostera marina* L.) in the Dutch Wadden Sea in the 1930's. *Netherlands Journal of Sea Research* 25:395-404.
- Greenawalt-Boswell, J. M., J. A. Hale, K. S. Fuhr, and J. A. Ott. 2006. Seagrass species composition and distribution trends in relation to salinity fluctuations in Charlotte Harbor, Florida. *Florida Scientist* 69: 24-35.
- Hellblom, F. and M. Björk. 1999. Photosynthetic responses in *Zostera marina* to decreasing salinity, inorganic carbon content and osmolality. *Aquatic Botany* 65:97-104.
- Herrera-Silveira J. A., J. Ramírez-Ramírez, N. Gómez, and A. Zaldivar-Jimenez. 2000. Seagrass bed recovery after hydrological restoration in a coastal lagoon with groundwater discharges in the north of Yucatan (southeastern Mexico). pp 219-229. In: S. A. Bortone (ed)., *Seagrasses: Monitoring, Ecology, Physiology and Management*. CRC Press, Boca Raton. pp. 318
- Jagels, R. 1983. Further evidence for osmoregulation in epidermal leaf cells of seagrasses. *American Journal of Botany* 70:327-333.

- Kahn, A. E. and M. J. Durako. 2006. *Thalassia testudinum* seedling response to changes in salinity and nitrogen levels. *Journal of Experimental Marine Biology and Ecology* 335: 1-12.
- Kamermans, P., M. A. Hemminga, and D. J. de Jong. 1999. Significance of salinity and silicon levels for growth of a formerly estuarine eelgrass (*Zostera marina*) population (Lake Grevelingen, The Netherlands). *Marine Biology* 133:527-539.
- Kentula, M. E and T. H. DeWitt. 2003. Abundance of seagrass (*Zostera marina* L.) and macroalgae in relation to the salinity-temperature gradient in Yaquina Bay, Oregon, USA. *Estuaries* 48:1130-1141.
- Koch, M. S. and J. M. Erskine. 2001. Sulfide as a phytotoxin in the tropical seagrass *Thalassia testudinum*: interactions with light, salinity and temperature. *Journal of Experimental Marine Biology and Ecology* 266:81-95.
- Koch, M. S., S. A. Schopmeyer, C. Kyhn-Hansen, C. J. Madden, and J.S. Peters. 2007. Tropical seagrass species tolerance to hypersalinity stress. *Aquatic Botany* 86:14-24..
- Lirman, D. and W. P. Cropper Jr. 2003. The influence of salinity on seagrass growth, survivorship, and distribution within Biscayne Bay, Florida: Field, experimental, and modeling studies. *Estuaries* 26:131-141.
- Martin, A. C. 1954. A clue to the eelgrass mystery. *Transactions of the 19th North American Wildlife Conference, Washington, D.C* 441-449.
- McMillan, C. 1978. Morphogeographic variation under controlled conditions in five seagrasses, *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*, *Halophila engelmannii*, and *Zostera marina*. *Aquatic Botany* 4:169-189.
- Montague, C. L. and J. A. Ley. 1993. A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in northeastern Florida Bay. *Estuaries* 16:703-717.
- Phillips R. C. 1960. Observations on the ecology and distribution of the Florida seagrasses. Professional papers series, No 2, Contribution No. 44, Florida Sate Board of Conservation Marine Laboratory, St. Petersburg. FL, 72pp.
- Phillips, R. C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: A community profile. U.S. Fish and Wildlife Service 85 pp.
- Pinnerup, S. P. 1980. Leaf production of *Zostera marina* L. at different salinities. *Ophelia* (Supplement) 1:219-224.
- Quammen, M. L. and C. P. Onuf. 1993. Laguan Madre: Seagrass changes continue decades after salinity reduction. *Estuaries* 2:302-310.
- Rigollet, V., T. Laugier, M. L. De Casabianca, A. Sfriso, and A. Marcomini. 1998. Seasonal biomass and nutrient dynamics of *Zostera marina* L. in two Mediterranean lagoons: Thau (France) and Venice (Italy). *Botanica Marina* 41:167-179.
- Sand-Jensen, K. and J. Borum. 1983. Regulation of growth of eelgrass (*Zostera marina* L.) in Danish coastal waters. *Marine Technology Society Journal* 17:15-21.
- Stora, G. and A. Arnoux, 1983. Effects of large freshwater diversions on benthos of a Mediterranean lagoon. *Estuaries* 6:115-125.
- Thayer, G. W., W. J. Kenworthy, and M. S. Fonseca. 1984. The ecology of eelgrass meadows of the Atlantic coast: A community profile. U.S. Fish and Wildlife Service. FWS/OBS-84/02. 147 pp

- Thom R. M., A. B. Borde, S. Rumrill, D. L. Woodruff, G. D. Williams, J. Southard, and S. L. Blanton. 2001. Factors influencing the spatial and annual variability in eelgrass (*Zostera marina* L.) in Pacific Northwest, USA, System (Chapter 5). PINCERS 2001 Annual Report.
- Thom R. M., A. B. Borde, S. Rumrill, D. L. Woodruff, G. D. Williams, J. A. Southard, and S. L. Sargeant. 2003. Factors influencing spatial and annual variability in eelgrass (*Zostera marina* L.) meadows in Willapa Bay, Washington, and Coos Bay, Oregon. *Estuaries* 26: 1117-1129.
- Tomasko, D. A., N. J. Blake, C. W. Dye, and M. A. Hammond. 2000. Effects of the disposal of reverse osmosis seawater desalination discharges on a seagrass meadow (*Thalassia testudinum*) offshore of Antigua West Indies. pp. 99-112. In: S. A. Bortone (ed.), *Seagrasses: Monitoring, Ecology, Physiology and Management*. CRC Press, Boca Raton. pp. 318.
- van Diggelen, J., J. Rozema, and R. Broekman. 1987. Mineral composition of and proline accumulation by *Zostera marina* L. in response to environmental salinity. *Aquatic Botany* 27:169-176.
- van Katwijk, M. M., G. H. W. Schmitz, A. P. Gasseling, and P. H. van Avesaath. 1999. Effects of salinity and nutrient load and their interaction on *Zostera marina*. *Marine Ecology Progress Series* 193:155-165.
- van Katwijk, M. M., D. C. R. Hermus, D. J. de Jong, R. M. Asmus, and V. N. de Jonge. 2000. Habitat suitability of the Wadden Sea for restoration of *Zostera marina* beds. *Helgoland Marine Research* 54:117-128.
- Vergeer L. H. T., T. L. Aarts, and J. D. de Groot. 1995. The 'wasting disease' and the effect of abiotic factors (light intensity, temperature, salinity) and infection with *Labyrinthula zosterae* on the phenolic content of *Zostera marina* shoots. *Aquatic Botany* 52: 35-44.
- Wetzel, R. L. and P. A. Penhale. 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. *Marine Technology Society Journal* 17:22-31.
- Wium-Andersen, S. and J. Borum. 1984. Biomass variations and autotrophic production of an epiphyte-macrophyte community in a coastal Danish area: I. Eelgrass (*Zostera marina* L.) biomass and net production. *Ophelia* 23:33-46.
- Zieman, J. C. 1982. The ecology of the seagrasses of South Florida: a community profile. U.S. Fish and Wildlife Services, Office of Biological Services, Washington, D.C., FWS/OBS-82/25, pp. 158.
- Zieman, J. C., J. W. Fourqurean, and T. A. Frankovich. 1999. Seagrass die-off in Florida Bay: Long-term trends in abundance and growth of turtle grass, *Thalassia testudinum*. *Estuaries* 22:460-470.
- Zieman, J. C. and R. T. Zieman. 1989. The ecology of the seagrass meadows of the west coast of Florida: a community profile, U.S. Fish and Wildlife Service Biological Report 85(7.25), 155 pp.
- Zimmerman, M. S. and R. J. Livingston. 1976. Seasonality and physico-chemical ranges of benthic macrophytes from a North Florida estuary (Apalachee Bay). *Contributions in Marine Science* 20:33-45.

5.0 The Effects of Hydrodynamic Factors on Seagrasses

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5.1 Background

Most biological, geological, and chemical processes in seagrass beds are influenced by water motions (Koch 2001). In addition, the presence of seagrasses influences the motions of the water. Seagrasses reduce water flow (Worcester 1995; Fonseca et al. 1982; Peterson et al. 2004), attenuate waves (Fonseca and Cahalan 1992), modify turbulent mixing (Worcester 1995), generate vertical secondary flows (Nepf and Koch 1999), induce coherent, canopy-scale eddies (Ackerman and Okubo 1993), and retain water during low tides (Powell and Schaffner 1991). Water motions have the potential to affect the growth, survival, and distribution of seagrasses through both direct and indirect mechanisms.

This chapter reviews the effect of hydrodynamic stressors on seagrass growth, survival, and distribution, including the effects of current motions, waves and turbulence. Currents are relatively steady uni-directional flows, while wave-induced flows are oscillatory. Turbulence is temporally and spatially irregular water motions that are superimposed over the larger flow pattern, such as unidirectional current or oscillatory wave action (Koch and Verduin 2001). The reader is referred to Koch et al. (2006a) for a review of the fundamentals of fluid flow, particularly as it relates to seagrass. Hydrodynamic stressors can influence seagrass through numerous mechanisms, including direct damage or uprooting of plants due to the hydrodynamic forces, erosion of sediment surrounding the plant, and by limiting productivity through either shading or diffusional boundary layer limitation. In addition, water motions influence seagrass populations through dispersal of pollen (Ackerman 2002), seeds (Orth et al. 1994), and reproductive shoots (Harwell and Orth 2002).

Anthropogenic activities have the potential to modify the current and wave exposure of seagrass communities, which may, in turn, affect their growth and distribution. Hydraulic and hydrodynamic modifications of coastal ecosystems, such as freshwater diversions, channelization, and damming, have been identified as one of the major environmental issues of coastal regions (National Research Council 1994). Hydrological and hydrodynamic alterations influence salinity patterns, tidal dynamics, circulation patterns, as well as the supply of nutrients, toxics, and sediments to coastal ecosystems, all of which can impact seagrass. There has also been an increase in boat and ship traffic in coastal regions, which produces currents and waves that can potentially influence seagrass. In addition to anthropogenic factors, natural extreme hydrodynamic events such as storms and hurricanes have influenced seagrass distribution and survival.

Most of the research on the interaction of hydrodynamics and seagrass focuses on the effect of seagrass on the hydrodynamics with relatively few studies of the impact of the

hydrodynamics on seagrass productivity and distribution. In addition, most of the studies on the effects on hydrodynamic stressors on seagrass are correlative rather than causative.

5.2 Effect of Seagrass on Currents, Waves, and Turbulence

The effect of seagrass on currents, waves and turbulence is complicated and depends on the hydrodynamic regime as well as specifics of the seagrass habitat (e.g., seagrass type and morphology, orientation of leaves and canopy, location within the seagrass bed and depth, shoot density, presence of epiphytes and macroalgae). There have been field, laboratory, and modeling studies on the interaction of seagrasses and currents, waves and turbulent mixing. Koch et al. (2002, 2006a, 2006b) present an excellent review on this topic.

Hydrodynamics influence the architecture of seagrass meadows. Seagrass blades are easily bent by currents (Fonseca et al. 1982). When bent over, the blades form a dense layer that redirects the water flow over and under it. As the current increases, the canopy becomes more compressed with maximum canopy bending occurring at water speeds of about 40-50 cm s⁻¹ (Fonseca et al. 1982). Seagrass blades also flap or flutter when subjected to water flow. The range of movement of the seagrass blades may depend upon the amount of epiphyte cover on the seagrass blades and heavy epiphyte cover may result in the formation of a closed canopy with strong flows above the canopy and little flow within the canopy (Koch 1996). Canopy bending and flapping has implications for light availability for seagrass photosynthesis (Zimmerman 2003) as well as the transport of particulate and dissolved materials between the water column and the canopy.

The water flow inside seagrass beds is often reduced by a factor of 2 to 10 compared to adjacent bare areas (e.g., Scoffin 1970; Worcester 1995; Komatsu 1996; Koch 1996; Koch et al. 2002; Peterson et al. 2004). Numerous field and laboratory studies have found a reduction of flow inside the seagrass canopies resulting from drag associated with the seagrass blades (Fonseca et al. 1982; Fonseca et al. 1983; Fonseca and Fisher 1986; Gambi et al. 1990; Ackerman and Okubo 1993; Komatsu 1996; Nepf and Vivoni 2000; van Keulen and Borowitzka 2000; Peterson et al. 2004); however, the degree of reduction is variable. Studies have found that the degree of flow reduction is dependent upon the vertical distribution of plant material (Ackerman and Okubo 1993; van Keulen and Borowitzka 2000), the vegetation density (Fonseca et al. 1982; Peterson et al. 2004), the seagrass morphology (van Keulen and Borowitzka 2000; Fonseca and Fisher 1986), the water depth relative to canopy height (Fonseca and Fisher 1986), the degree of bending of the seagrass blades (Thomas et al. 2000), the magnitude of the water velocity (Fonseca et al. 1982; Gambi et al. 1990), and the distance from the leading edge of the seagrass bed (Fonseca et al. 1983; Gambi et al. 1990; Peterson et al. 2004). Friction associated with the seagrass canopy may also act to retain water in seagrass beds. Dense seagrass beds in shallow regions have been shown to retain a thin layer (< 20 cm) of water during falling tides and this water trapping ability appears to be related to the morphology of the seagrass and seagrass density (Powell and Schaffner 1991). This water trapping ability may be important in

preventing desiccation (see Chapter 10) of the seagrass and other organisms that live in the habitat.

Generally, water flow is reduced with increasing seagrass density and a recent study found that the vertically integrated flow varied inversely with the square root of vegetation density (Peterson et al. 2004); however, some studies have found that the degree of flow reduction is independent of vegetation density (Fonseca et al. 1983; Fonseca and Fisher 1986). Current speeds decrease with increasing distance from the leading edge of seagrass meadow with maximum reduction occurring within 25 to 50 cm into the bed (Gambi et al. 1990). The width of this region of decelerating flow is dependent upon the seagrass density (Peterson et al. 2004) and within this region the transport of material is dominated by advection from the leading edge of the canopy (Nepf and Vivoni 2000). The flow reducing capability of seagrass is negatively correlated with the degree of bending of the seagrass canopy (Thomas et al. 2000). When the seagrass blades are upright the friction is at a maximum and as the blades bend over when subjected to faster current speeds the friction coefficient decreases. There is often accelerated flow above the seagrass canopy (Gambi et al. 1990; Worcester 1995) which, when combined with the reduced flow within the canopy, results in a high shear stress layer at the canopy-water interface (Gambi et al. 1990; Nepf and Vivoni 2000). The presence of flow acceleration over the canopy may depend upon whether the seagrass occurs in patches or as a continuous meadow (Worcester 1995). In addition, some studies have found that there is a local velocity maximum near the bed within the canopy due to a decrease in vegetation density in the sheath region of the canopy (Fonseca and Kenworthy 1987; Ackerman and Okubo 1993; Koch 1996, Nepf and Vivoni 2000). This near bottom increase in flow speed may result in elevated sediment resuspension (Koch 1999b). Some have suggested that there is acceleration around seagrass beds due to flow being deflected above and around the seagrass bed (Gambi et al. 1990). Granata et al. (2001) found that the interaction of hydrodynamics and seagrass distribution (i.e., spatial variation in seagrass density, and presence of edges and gaps) results in three-dimensional circulation patterns, including increase in current above meadows, upward flow at the edge of the canopy, and recirculation patterns at gaps.

The interaction of current flow and the eelgrass blades can result in large-amplitude synchronous waving of the blades (Fonseca and Kenworthy 1987; Ackerman and Okubo 1993; Grizzle et al. 1996), which has been termed “monami” by Ackerman and Okubo (1993). At low current speeds, eelgrass blades gently undulate with low-amplitude motions and gentle flapping. When the above-canopy water velocity exceeds 10 cm s^{-1} monami occurs, with maximum amplitude motions occurring at current velocities of about 30 cm s^{-1} (Grizzle et al. 1996). The turbulent vertical transfer of momentum is enhanced during monami resulting in more vertical exchange between overlying water column and interior of the canopy (Ghisalberti and Nepf 2002). These coherent eddies have implications for scalar fluxes that govern gas and nutrient exchange, seed dispersal, sediment deposition, and chemical reactions in submerged plant canopies (Ackerman and Okubo 1993; Grizzle et al. 1996; Ghisalberti and Nepf 2002). Nepf and Koch (1999) demonstrated that submerged plant-like arrays exposed to gradients in longitudinal velocity in the laboratory produced vertical pressure gradients that drove vertical

secondary flows. These vertical secondary flows can reach up to 15% of local longitudinal velocity and may affect the exchange of nutrients between the sediment and water column. However, these vertical velocities are not expected under conditions of extreme bending (skimming flow) where the mean current is almost entirely deflected over the top of the canopy.

Numerous studies have documented a reduction of wave energy (which is proportional to wave height squared) in seagrass habitat (Fonseca and Cahalan 1992; Koch 1996; Granata et al. 2001; Newell and Koch 2004; Koch et al. 2006b). Oscillatory orbital wave motion is reduced with depth inside the seagrass canopies (Koch and Gust 1999). Generally, near bed orbital wave velocities are lower in seagrass beds and decrease with increasing plant density (Granata et al. 2001). Fonseca and Cahalan (1992) used a wave tank to examine the effect of *H. wrightii*, *S. filiforme*, *T. testudinum*, and *Z. marina* on wave energy under various combinations of shoot density and water depth to leaf length ratio. When the length of the seagrass blades was similar to the water depth, the wave energy reduction per meter of seagrass bed was about 40%. Despite differences in morphologies, the four species of seagrass had a similar effect on wave energy reduction. As the water depths increased (relative to blade length), wave attenuation was reduced. Negligible wave energy reduction occurred at water depths greater than 2 times the mean leaf length. For *S. filiforme*, there was a significant increase in wave energy reduction with increasing shoot density, though this effect was not seen in the other three species. Oscillatory flow generated by waves results in the seagrass blades' flapping back and forth at the frequency of the waves (Koch and Gust 1999), resulting in an opening and closing of the seagrass canopy enhancing exchange between the water column and seagrass canopy. Field measurements of waves in *Ruppia maritima* beds showed that the degree of wave attenuation was dependent upon water depth and characteristics of the seagrass bed (Newell and Koch 2004, Koch et al. 2006b). The degree of wave attenuation varied with tidal stage with maximum observed attenuations of 50% observed during low tides. Wave attenuation was only observed at shoot density > 1000 shoots m^{-2} , and highest wave attenuation was observed when the plants were reproductive, occupying the entire water column.

The interaction of seagrass with hydrodynamics can have various effects on turbulence and turbulent mixing between the water column and the seagrass canopy. The reduction of water flow caused by drag associated with the seagrass blades and canopies results in the conversion of kinetic energy of the mean flow into turbulent kinetic energy (Gambi et al. 1990). Typically, there is a maximum of turbulent intensity near the top of the seagrass canopy (Gambi et al. 1990; Nepf and Vivoni 2000), which is generated in part by the large shear stress in this region. There is a vertical reduction in turbulence with depth inside the canopy (Koch and Gust 1999). Some studies have documented a reduction of turbulence (Koch 1996; Granata et al. 2001) and turbulent mixing within seagrass canopies (Ackerman and Okubo 1993; Ackerman 2002), while others have found that there is an increase in turbulence inside the canopy relative to adjacent upstream bare regions (Gambi et al. 1990). Some studies have shown that the presence of seagrass blades results in the production of turbulent flow with mean turbulent intensity and amount of the water column influenced by the presence of the canopy increasing with distance from the leading edge of the grass bed (Gambi et al. 1990). The conflicting effect of seagrass on turbulence may be related to the flow dynamics and the configuration of the seagrass bed (e.g.,

continuous versus patchy distribution, location within the meadow and canopy, presence of epiphytes, vegetation density). Worcester (1995) found that at low seagrass density and low current flow, the presence of eelgrass had no effect on turbulent mixing compared to adjacent bare areas, while at sites with continuous eelgrass cover there was an increase in turbulent mixing above the seagrass canopy relative to adjacent bare areas. Granata et al. (2001) found an increase in turbulence at the edge of seagrass meadows. The seagrass blades and canopies may also rescale turbulent energy by attenuating low frequency energy and generating high frequency energy (Koch 1996). Presence of epiphytes has been found to result in elevated turbulence within seagrass canopies (Koch 1996).

Koch and Gust (1999) found that the effect of seagrass on hydrodynamics, including the effect on mean flow, turbulence and mixing, may depend upon the hydrodynamic conditions at the site. At tide-dominated sites, the current bends the seagrass blades producing a skimming flow over the seagrass canopy. This closure of the canopy results in reduction of turbulence inside the canopy and reduced mixing between the overlying water column and the seagrass blades. In contrast, at wave-dominated sites oscillatory wave action causes seagrass blades to flap back and forth, and the canopy is repeatedly opened and closed increasing the water exchange between the water column and canopy. Using a model combined with observations, Abdelrhman (2003) found that the vertical distribution of a constituent in the water column determines whether the canopy will enhance or reduce the transport of the constituent. For example, a constituent with a vertical profile with maximum concentrations at the surface would have transport enhanced by 20%, whereas a constituent with maximum concentrations at the bottom would have transport reduced by 30%.

5.3 Effects of Water Velocity on Seagrass Growth and Distribution

The reduction of current velocities by seagrasses has positive and negative effects on their growth. Advantages of reduced flow include reduced self-shading, reduced sediment resuspension, increased settlement of organic and inorganic particles, and high water residence time increasing potential for nutrient uptake (Koch 2001). Detrimental effects of reduced water velocity include increased phytotoxin concentrations in the sediment and an increase in the thickness of the diffusional boundary layer, which may limit photosynthesis (Koch 2001; Koch et al. 2002).

5.3.1. Direct Damage to Seagrass resulting from Currents

Scoffin (1970) conducted flume experiments to examine the effect of unidirectional currents on erosion of *T. testudinum*. At current velocities of about 70 cm s⁻¹ flapping of seagrass blades occurred, dislodging attached epiphytes and sometimes causing breakage of the blades. Sediment removal around the base of the shoots was dependent upon current speed and density of the seagrass bed. Extensive sediment removal around the rhizomes and roots occurred at current speed of 50 cm s⁻¹ in a sparse grass bed, 100 cm s⁻¹ in a medium density bed, and at 150 cm s⁻¹ in a dense grass bed (current velocity measured just above the blades). Fonseca et al. (1983) proposed that the maximum current velocity that *Z. marina* can tolerate is 120 to 150 cm s⁻¹.

To determine the susceptibility of seagrasses to hydrodynamic stressors, one can measure the biomechanical properties of seagrass, such as the breaking stress, breaking strain, elastic modulus, and toughness. Comparison of these properties to the hydrodynamic forces encountered in different environments allows prediction of the probability of damage (Patterson et al. 2001). There have been three studies that characterized the biomechanical properties of eelgrass (Kopp 1999; Patterson et al. 2001; Fonseca et al. 2007). Patterson et al. (2001) found that in natural populations of *Z. marina* there are always a few strong reproductive shoots that would be resistant to extreme hydrodynamic events (such as hurricanes and tropical storms), which may ensure the survival of the population. Fonseca et al. (2007) measured the force on *Z. marina* blades in a flume under unidirectional and oscillatory flow and these forces were compared to blade tensile strength. Fonseca et al. (2007) conclude that these seagrass blades may be damaged or broken under frequently observed storm conditions, and that damage was more likely when the seagrass blades were subjected to oscillatory versus unidirectional flow.

Previous studies have demonstrated that the morphology of eelgrass leaves is dependent upon the nutrient availability (e.g., Short 1983) and there is some evidence that structural components of plant tissues (e.g., C:N ratio and cellulose content) may be influenced by the nutrient conditions. Kopp (1999) proposed that these changes in morphology and structural composition of the leaves may affect the tensile strength of the leaves and the ability of the shoots to withstand current and wave energy. Kopp (1999) conducted a set of mesocosm experiments to examine the effect of nutrient enrichment on the biomechanical properties of *Z. marina*. This study found that there was a reduction in tensile forces that leaves could withstand when subjected to nitrate enrichment for nine weeks. In addition, field measurements of the tensile strength of *Z. marina* leaves revealed that leaves at low nutrient locations could withstand 26% more force than leaves from high nutrient sites.

5.3.2 Effect of Currents on Plant Morphology and Configuration of Seagrass Beds

Fonseca et al. (1983) found that the physical configuration of *Z. marina* meadow (the ratio of the height to length) was positively correlated with current velocity and that the continuity of seagrass cover is inversely related to current speeds (Figure 5.1). There was increased mounding of the substratum with increasing current velocity. In regions of unidirectional flow, seagrass is often observed growing in rows perpendicular to the axis of the flow (Fonseca et al., 2007; Figure 5.1). Schanz and Asmus (2003) found that hydrodynamics influenced the morphology of *Z. noltii* in the Wadden Sea. Their study included field surveys of morphology of *Z. noltii* in exposed and sheltered locations, cross transplantation experiments, and flume experiments to manipulate the current environment. These studies revealed that under higher flow conditions the density of the seagrass beds declined, and the seagrass leaf and shoot lengths became shorter. A significant decline in shoot morphology and density was observed at current velocities $> 8 \text{ cm s}^{-1}$. Flume experiments conducted by Peralta et al. (2006) demonstrated the growth rates and morphometry of *Z. noltii* was dependent upon flow conditions. At high current velocities (35 cm s^{-1}), the root system enlarged, the cross-sections of the rhizomes and leaves increased, and the ratio of above to below ground biomass decreased. Similar changes in morphometry (decreased leaf width and length) were observed in natural populations of *Z. noltii*

exposed to more energetic environment associated with the opening of a new tidal inlet (Peralta et al., 2005).

5.3.3 Effects of Current on Photosynthesis and Growth

Some studies have found that seagrass photosynthesis and growth is related to current speed. Conover (1964 and 1968) found that oxygen evolution from individual shoots of *Z. marina* increased as current velocity increased for current speeds of up to 40 cm s^{-1} . Conover (1968) reported that the standing stock of *Z. marina* decreased dramatically in currents greater than 50 cm s^{-1} . Nixon and Oviatt (1972) found maximum oxygen evolution of an eelgrass meadow at about 16 cm s^{-1} . Using a flume with *Z. marina* plants, Fonseca and Kenworthy (1987) found increased leaf production with increasing current velocity (up to 34 cm s^{-1}). Peralta et al. (2006) found a similar increase in growth rates for *Z. noltii* plants in flume for current velocities ranging from $1 - 35 \text{ cm s}^{-1}$. Koch (1994) found that the rate of *T. testudinum* photosynthesis increased with increasing flow only at low current speeds with saturation occurring at about 0.25 cm s^{-1} (expressed as blade friction velocities, u_*) and photosynthesis was inhibited under stagnant conditions. The presence of epiphytes resulted in temporal and spatial variability in the boundary layer thickness, thereby reducing the potential for boundary layer limitation. Field measurements of blade friction velocities revealed that boundary layer limitation should only occur during extremely calm conditions and for very short time periods (i.e., fractions of second). Even during relatively quiescent conditions, the boundary layer thickness oscillates between non-limiting and limiting at high frequency, suggesting that diffusional boundary layer limitation is a transient phenomenon in seagrass environments. Koch (1994) suggested that there may be a threshold effect for epiphyte cover. It was hypothesized that if the epiphyte cover exceeds a certain thickness, then water will flow over the epiphyte cover rather than through it, increasing the thickness of the boundary layer and result in further limiting conditions (Koch 1994). Enríquez and Rodríguez-Román (2006) found that the photosynthetic electron transport rates of *T. testudinum* was reduced under low flow conditions ($< 5.4 \text{ cm s}^{-1}$); however, this seagrass also appears to be able acclimate to flow conditions reducing their sensitivity to low flow by about 64%.

Zimmerman (2003) developed a bio-optical model of irradiance distribution and photosynthesis in *Z. marina* and *T. testudinum* canopies. This model incorporated the effects of canopy architecture on light availability for photosynthesis. The biomass-specific photosynthesis of the seagrass canopy responded non-linearly to leaf bending angle. When seagrass blades are erect with bending angles less than 10° , photosynthesis is limited by the leaf orientation. Bending angles greater than 20° limit photosynthesis because a larger fraction of light is absorbed by the upper layers of the seagrass canopy where photosynthesis is already light saturated. As discussed previously, bending angle is a function of current velocity therefore self-shading increases with increasing current. Zimmerman (2003) proposed that the production-enhancing aspects of flow (e.g., reduction in diffusive boundary layer thickness) may be offset by increased self-shading as leaves bend in response to the flow.

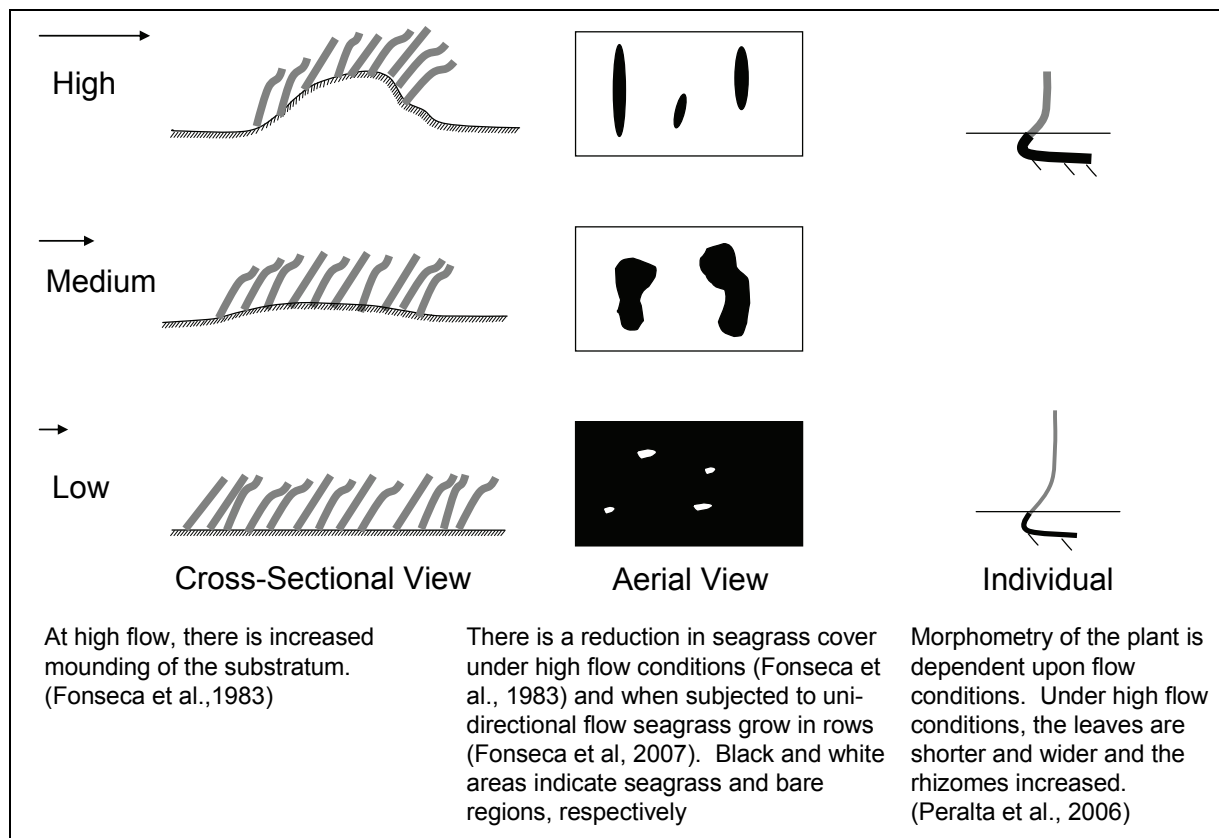


Figure 5.1. Relationship between configuration of seagrass beds and shoot morphology and current regime. At higher current velocities, there is increased mounding of the beds and reduction in seagrass cover (Fonseca et al., 1983). Under high flow conditions, the shoots become shorter and wider and the rhizomes increase (Peralta et al., 2006).

5.3.4 Effect of Currents on Nutrient Uptake

Thomas et al. (2000) conducted flume experiments in natural communities of *Halodule wrightii* and *T. testudinum* over a range of uni-directional current speeds. They found that ammonium uptake by the seagrass community was dependent upon water velocity and was influenced by canopy morphology. Thomas et al. (2000) found that there was a decline in efficiency ammonium uptake at higher flow velocities when the seagrass bend. Cornelisen and Thomas (2002) used flume experiments combined with isotopically-labeled ammonium to isolate the effect of water flow on an individual component of a seagrass community. Ammonium uptake of both epiphytes and seagrass leaves were positively correlated with current velocity. There was a stronger relationship between the epiphytes and flow than with seagrass leaves and flow. Seagrass leaves contributed less than epiphytes to the total uptake of the seagrass community.

5.3.5 Effect of Currents on Sediment Geochemistry and Seedling Survival

Koch (1999a) found that the interaction of currents and porewater chemistry may influence the growth and development of *T. testudinum* seedlings. In this study, seedling mortality was higher for stagnant conditions compared to medium and high current velocities.

Seedling morphology was influenced by current velocity with those seedlings exposed to stagnant conditions having reduced biomass with shorter blades and roots, while those exposed to medium velocities had the longest blades, largest blade area, and greatest biomass and number of roots. In addition, nitrogen, phosphorous and sulfide concentrations in the porewater were the highest under stagnant conditions. This study suggests that an intermediate level of porewater flux may be beneficial to seagrass growth, while stagnant and high flow conditions may contribute to lower biomass through increased phytotoxin and reduced porewater nutrient concentrations, respectively.

The presence of seagrass shoots in current flow can influence the flux of materials between the water column and sediments in permeable sediments. In flume experiments, Koch and Huettel (2000) found that the presence of *T. testudinum* shoots enhanced advective porewater exchange. At current velocities of 10 cm s^{-1} there was enhanced flux of porewater upstream and downstream of the shoots. The region of sediment influenced by the shoot-flow interaction was dependent upon salinity and orientation of the seagrass shoots.

5.3.6 Effects of Current on Deposition on Leaves

Currents can affect the amount of suspended solids deposited on leaves, thus influencing photosynthesis (Tamaki et al. 2002). Tamaki et al. (2002) performed experiments to determine the effect of deposition of suspended solids on *Z. marina* leaves on light availability and the role of current velocity in removing deposited sediments from leaves. They found that the presence of deposited suspended solids on eelgrass leaves (at 3 mg cm^{-2}) reduced the light availability by as much as 36%. Based on flume experiments, suspended solids were removed from leaves at current velocities greater than 8 cm s^{-1} . Field experiments indicated that suspended solids were deposited on transplanted eelgrass in the field at levels that would be sufficient to inhibit photosynthesis.

5.3.7 Effects of Currents on Dispersal and Expansion of Population

Hydrodynamics have the potential to influence the expansion of seagrasses to unvegetated regions through dispersal of seeds and reproductive shoots. Orth et al. (1994) conducted field and flume experiments to examine the role of currents in the dispersal of *Z. marina* seeds. They found that there was limited seed dispersion with 80-93% of the seeds that germinated remaining inside the 5-m plot. The maximum dispersion distance ranged from 4 to 14 m. Based on flume experiments, the authors suggest that the limited dispersal of the seeds resulted from small-scale topographic features on the bottom (such as burrows, pits, mounds, and ripples) that shield the seeds from the flow. Although there is limited seed dispersal, Harwell and Orth (2002) found that reproductive shoots with mature seeds were positively buoyant for up to 2 weeks during which they can be transported relatively large distances by currents. Based on field observations, they found that currents can transport reproductive shoots up to 34 km from natural beds.

5.3.8 Effects of Currents on Epiphyte Coverage

Schanz et al. (2003) found that epiphyte biomass on *Z. noltii* was highest at seagrass sites exposed to water movement (average current speed of 26 cm s^{-1}), while at sheltered (average

current speed of 10 cm s^{-1}) sites epiphyte coverage was negligible. Results of cross-transplantation and enclosure experiments showed that the epiphyte grazer, *Hydrobia ulvae*, was washed off the seagrass blades at exposed sites. Flume studies revealed that grazer density was negatively correlated with current speed and epiphyte biomass was positively correlated with current speed.

5.3.9 Summary

In summary, seagrass can be limited by both low and high current velocities (Koch 2001). The minimum and maximum current velocity for *Z. marina* growth and occurrence based on physiological and mechanical limits are a minimum flow of 3 cm s^{-1} and a maximum current of $50\text{-}180 \text{ cm s}^{-1}$ (Koch 2001). The growth conditions of seagrass as a function of current speed reviewed in this chapter are summarized in Figure 5.2.

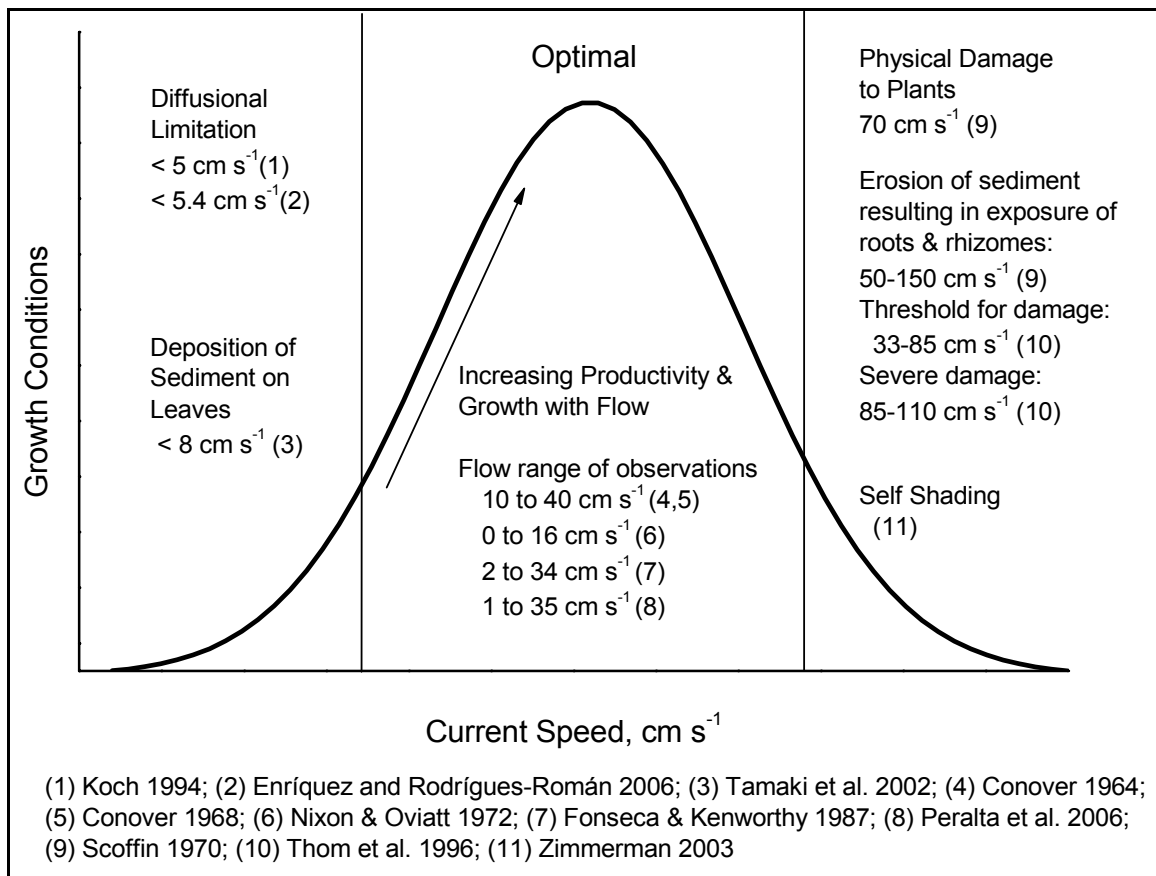


Figure 5.2. Growth conditions of seagrass as a function of current speed.

5.4 Effects of Wave Exposure on Seagrass Growth and Distribution

Wave exposure can influence seagrass growth and distribution in several ways, including plant breakage, erosion of edges of seagrass beds, influencing plant morphology, modifying water exchange between canopy and overlying water column, increasing flux between porewater and the overlying water column, and causing sediment resuspension which can result in reduced light availability. In a recent review, Koch (2001) suggested that seagrass distribution and growth appear to be limited by high but not low wave energy. Koch et al. (2002) proposed that the upper limit of seagrass beds can be shifted into deeper waters due to wave energy. In high wave energy regions, the shallow region is unvegetated due to continuous sand movement (Koch et al. 2006a). In the deeper regions, seagrass typically establish below the maximum wave penetration depth.

Waves can impact seagrasses by influencing the concentration of suspended particulates, which may alter the light environment and availability of nutrients. Suspended particulate concentrations are usually higher in unvegetated areas compared to adjacent seagrass beds (Ward et al. 1984; Koch 1999b; Granata et al. 2001). The amount of suspended particulates is usually reduced in seagrass beds due to reduced resuspension and enhanced settling resulting from reduced current velocities in the canopy, reduced turbulence energy within the canopy and at the sediment surface, attenuation of wave-induced currents, as well as binding of sediments by the roots and rhizomes. Sediment resuspension has the ability to influence not only the light environment, but the water column nutrient concentration as well. Nutrients associated with the sediments may be released to the water column when sediment is resuspended (Morin and Morse 1999).

Fonseca and Bell (1998) examined the effect of physical setting on the distribution and abundance of *Z. marina* and *H. wrightii* in North Carolina. Their correlative analysis revealed that tidal current speeds, exposure to waves and relative water depths influenced landscape-scale features of the seagrass beds. Wave exposure was estimated using a relative exposure index (REI), which is based on the maximum wind speeds, percent frequency of wind direction, and the effective fetch of the site. Percent cover of seagrass, seagrass perimeter to area ratio, sediment organic content, and percent silt-clay declined with increasing REI and current speed. There were species-specific differences in the effect of physical setting on seagrass distribution and abundance. Along a wave exposure gradient, *Z. marina* was more likely to be found in sheltered rather than exposed areas, while the opposite was true for *H. wrightii*. There was increased flowering and belowground biomass of *Z. marina* in areas with higher wave exposure. Fonseca and Bell (1998) also found that a 50% cover corresponded to a transition level for loss: Beds with >50% cover survived in chronic and acute storm events; while beds below this threshold did not.

Using a multiple logistic regression analysis, Krause-Jensen et al. (2003) found that light, salinity, and relative wave exposure (REI) were the main factors influencing eelgrass cover in Danish coastal waters. Eelgrass cover was inversely related to REI in water depths of 0 to 4 m. However, there was a high occurrence (~50% of observations) of absence of eelgrass in areas

that the regression model predicted as suitable habitat. Krause-Jensen et al. (2003) suggested that these discrepancies may be associated with stochastic phenomena, such as extreme storms, that are not adequately described by average conditions. Recovery of seagrass populations after extreme events may take several years.

Frederiksen et al. (2004) found that *Z. marina* distribution in Danish estuaries was related to the amount of exposure to wave dynamics. Eelgrass beds at the sheltered sites were continuous, while at exposed sites they formed elongated patches. Patches were more complex in wave-dominated regions and the large fluctuations in spatial coverage over interannual time scales occurred at exposed sites. Shallow eelgrass populations form characteristic landscapes with configuration that is related to degree of physical exposure. Aggregated populations may be more resistant to physical disturbances than patchy populations, due to the stabilizing effect of the root/rhizome matrix and the reduced patch edge exposed to damage from waves or tidal currents. Numerous studies have found that the variability of eelgrass populations (i.e., variability in shoot density and biomass) is highest in shallow regions where they are subjected to frequent disturbance, due to hydrodynamics and other environmental factors (Middleboe et al. 2003; Krause-Jensen et al. 2000; Krause-Jensen et al. 2003). In addition, the wave environment may influence the plant morphology. Krause-Jensen et al. (2000) found that the shoot to rhizome ratio increases with depth (more allocation to photosynthetic tissue) as light and wave exposure decrease.

High wave energy may prevent seagrass from becoming established and reduce survival of seagrass transplants (van Keulen et al. 2003; Paling et al. 2003). Most North American seagrasses occur in low energy environments, while along the Australia coast there is more exposure to wind and swell waves. In Australia, the limited success of seagrass transplantation has been attributed to high wave energy conditions. In the North Sea, van Katwijk and Hermus (2000) found a negative relationship between *Z. marina* transplant success and tidal depths, and they hypothesized that this was due to water dynamics (waves) and sediment resuspension and movement. At a high energy transplant site, where maximum orbital velocity at the sediment surface frequently exceeded 60 cm s^{-1} , none of the transplanted plants survived. While at two lower energy transplant sites, with mean orbital velocity of 40 cm s^{-1} , survival was related to water depth. They proposed that wave action is too severe at water depths deeper than -0.20 m mean sea level (MSL) to support establishment of *Z. marina*. To re-establish *Z. marina* beds the authors recommend providing shelter from wave action (e.g., use of biodegradable dam-like structures).

Several recent studies have found that the presence of waves substantially influences the porewater flux between the sediment and overlying water column (Precht and Huettel 2003; Precht and Huettel 2004), which has the potential to influence seagrass productivity. In laboratory flume experiments, Precht and Huettel (2003) found that shallow water waves can increase the fluid exchange between sandy sediments (no vegetation) and the overlying water column as much as 50-fold relative to molecular diffusion rates. They identified two mechanisms which increase the flux of porewater, hydrostatic pressure induced wave pumping and topography-related filtering. Oldham and Lavery (1999) found an increase in water column

ammonium that they attributed to increased porewater fluxes associated with interactions between hydrodynamics (increased currents, waves and turbulence) and the sediment surface.

Thomas and Cornelisen (2003) conducted flume experiments in the field in *T. testudinum* habitat to examine the effect of unidirectional and oscillatory flow on ammonium uptake rates. The uptake of ammonium from the water column by the seagrass community was 1.5 times higher in oscillatory flow than in unidirectional flow. Uptake rates were positively dependent on water velocity and turbulent energy in the water column.

5.5 Effects of Turbulence on Seagrass Growth and Distribution

Increased turbulence can be both beneficial and detrimental to seagrass growth. Benefits associated with enhanced turbulence include faster removal of undesirable substances, and enhanced transport of nutrients and carbon through the blade boundary layers (Koch 1996). On the negative side, increased turbulence can also lead to more sediment resuspension, resulting in reduced light availability (Koch 1996). Seagrasses can benefit from increased turbulence through enhanced supply of carbon and nutrients across the blade boundary layer and enhanced removal of undesirable substances. There have been no studies that show direct linkage of turbulence on seagrass growth and distribution.

5.6 Anthropogenic Modification of Hydrodynamic Stressors

There is the potential for anthropogenic activities to influence the hydrodynamic environment, which may influence seagrass distribution and productivity. There has been an increase in recreational and commercial boat traffic in coastal waters. Most of the research on the impact of boat activities has focused on direct impacts, including propeller scarring and vessel groundings. However, seagrasses may also be impacted by hydrodynamic stressors associated with boating activity. Boating activities can modify the hydrodynamics through the generation of wakes and currents. Potential impacts associated with boat wakes include increased sediment resuspension, release of sediment nutrients into the water column, and reduced light. Koch (2002) examined the effect of small-boat wakes on environmental conditions in a low wave energy region inside *Ruppia maritima* habitat and found that the potential negative impacts were small compared to natural fluctuations in seagrass habitat. There was an increase in water column ammonium associated with increased porewater pumping associated with increased wave height. A potential benefit of increased wave activity was the dislodgement of epiphytes and particulate matter on leaves.

Thom et al. (1996) conducted flume experiments to assess the impact of propeller washes on *Z. marina*. Flume experiments were conducted on intact patches of eelgrass subjected to current velocities ranging from 0 to 3.25 m s⁻¹. The lower threshold for plant damage, including loss of plants and exposure of rhizome and roots, occurred at current velocities between 33 and 85 cm s⁻¹. Severe damage occurred when the current speeds were between 85 and 110 cm s⁻¹.

Eleuterius (1987) proposed that seagrass damaged by motor vessel impacts, such as propeller scars and vessel landings, are more susceptible to further erosion and scour due to hydrodynamic stressors. Whitfield et al. (2002) found that regions of seagrass that had been damaged by vessel landings are more vulnerable to storm events. They found that regions of seagrass damage increased in size after the passage of a class 2 hurricane, thereby hindering the recovery process. In contrast, healthy intact seagrass beds were undamaged by the passage of the hurricane. In addition, it has been proposed that climate change may result in increases in the impact of hydrodynamic stressors on seagrass communities, due to increased tidal range, currents, and storm activity (Short and Neckles 1999).

5.7 Large-Scale Alterations in Estuarine Hydrodynamics

Large-scale engineering projects that alter estuarine hydrodynamics have the potential to affect salinity patterns which in turn can influence the distribution of seagrasses. Nienhuis et al. (1996) suggested that alterations in salinity patterns associated with the emplacement of dikes may be responsible for some of the observed changes in *Z. marina* distribution in the Netherlands. Eleuterius (1987) proposed that the alteration of freshwater discharges associated with the Mississippi River caused the decline of *S. filiforme* and elimination of *H. engelmannii* in Mississippi Sound. Quammen and Onuf (1993) proposed that a species shift of the seagrasses in Laguna Madre, Texas resulted from moderation of the salinity associated with dredging of the Gulf Intracoastal Waterway. For a review of salinity effects on seagrasses, see Chapter 4. It has been postulated that one of the reasons why *Z. marina* has not re-established in the Dutch Wadden Sea after its decimation by the wasting disease has been due to hydrodynamic stressors (De Jonge and De Jong 1992). Hydrologic modifications in the region resulted in an increase in tidal range of 15 to 30 cm and increased current velocities by as much as a factor of 3 in some regions. Analysis by De Jonge and De Jong (1992) demonstrated that the reduction in light associated with increased tidal range (i.e., increased water depth) is not responsible for the changes in the underwater light regime. More recently, hydrodynamics has been proposed as a contributing factor to the widespread die off of *T. testudinum* in Florida Bay, Florida that began in 1987. It has been postulated that chronic hypersalinity resulting from freshwater diversions and alterations in exchange between the bay and the Atlantic and infilling of the bay due to a lack of severe storms may be contributing factors to this decline (Fourqurean and Robblee 1999).

The natural variability of seagrass populations is large in shallow water where the populations are disturbed by wave action and other physical parameters (Krause-Jensen et al. 2000; Middleboe et al. 2003; Krause-Jensen et al. 2003). The high frequency of perturbation in shallow water is expected to cause a wide range of developmental stages (Krause-Jensen et al. 2000). Because eutrophication has caused a shift in seagrass distributions to shallower environments due to light limitation, there may be an increase in the occurrence of hydrodynamic stressors influencing the distribution of seagrass since hydrodynamic stressors are elevated in shallow environments (Patterson et al. 2001; Middleboe et al. 2003).

5.8 Natural Hydrodynamic Stressor Events

Extreme events, such as storms, hurricanes, and floods, have been reported to damage seagrass beds (e.g., Eleuterius and Miller 1976; Preen et al. 1995; Aioi and Komatsu 1996). The effects of hurricanes on seagrasses vary widely from increased growth (Oppenheimer 1963), no visible effect (Tilmant et al. 1994), removal of shoots (van Tussenbroek 1994), massive loss of leaf material (Thomas et al. 1961), to complete destruction of the beds (Preen et al. 1995). During extreme events, seagrass beds may be damaged by physical destruction of above ground biomass, removal of plants by wave action or sand abrasion, and by smothering due to burial by sediment deposits. If storm-related seagrass loss occurs, it is usually rapid and localized; however, Preen et al. (1995) documented that 1000 km² of seagrass was lost from Hervey Bay, Australia, following two major floods and a cyclone within a three week interval. The effect of hurricanes on seagrass can be localized with some regions showing no effect, while other regions are damaged (Van Tussenbroek 1994). In addition to the physical stresses associated with storms, there is also usually modification to the environment including reduced salinity and elevated suspended particulate concentrations. The occurrence of Tropical Storm Agnes has been postulated as a contributing factor to the decline of seagrass in Chesapeake Bay due to reduced salinities and increased suspended sediments (Orth and Moore 1983). After a major storm disturbance, eelgrass populations may exhibit extensive growth and increased survival of new shoots (Krause-Jensen et al. 2000; Aioi and Komatsu 1996). Fonseca et al. (2000) proposed that wave-exposed seagrass habitat may be particularly vulnerable to the effects of extreme storm events.

5.9 Research Gaps in Relation to Setting Protective Criteria

In a recent review of the physical, chemical and geological factors influencing seagrasses, Koch (2001) concluded that more data are needed to define current velocity and wave criteria for setting protective criteria. In addition, Koch (2001) suggested that the life stage of the plant needs to be taken into account when setting protective criteria. Seagrasses may be more susceptible to hydrodynamic stressors when they are seedlings versus when they are in mature intact beds. It may be difficult to separate out the effect of the hydrodynamics stressors from other environmental stressors due to their interactions. Alterations to the hydrodynamics often results in changes in the environment (e.g., salinity, turbidity, nutrients, and sedimentation), which may in turn control the distribution of the seagrass. Hydrodynamic stressors may be a contributing factor to seagrass decline rather than a limiting factor.

In order to develop effective protective criteria, we need more research on the effects of hydrodynamics on the productivity, survival and distribution of seagrass. One difficulty in setting protective criteria for hydrodynamic stressors is that many factors influence the interaction between hydrodynamics and the seagrass. Much of the research reviewed in this chapter has demonstrated that the presence of seagrass can have conflicting effects on the hydrodynamics (particularly on turbulence). In order to further our understanding of the effect of hydrodynamic stressors, we need to be sure to collect sufficient ancillary data for interpretation of study results. When collecting hydrodynamic data in seagrass habitat,

information also needs to be collected on water depth, location of measurements (both within the bed and elevation), canopy height, percentage of water column occupied by seagrass canopy, seagrass density, size and patchiness of seagrass bed, wind intensity and direction, tides, obstructions to flow (such as macroalgae, gorgonians, clams, and epiphytes), and observations on interaction of flow and seagrass (e.g., occurrence of monami, skimming flow, and blade flapping) (Koch and Verduin 2001).

Koch et al. (2006b) suggested that numerical models of the interaction of waves and seagrasses are useful for developing testable hypotheses, explaining observations, designing observational studies or restoration efforts, and interpolating sparse data in space and time. Hydrodynamic and sediment resuspension and transport models have been developed for estuarine systems (e.g., Teeter et al. 2001); however, they often require extensive site-specific information for model formulation and calibration. Teeter et al. (2001) reviewed that status of hydrodynamic and sediment transport modeling in shallow, vegetated regions and recommended that more quantitative information was needed on the effect of atmospheric friction and shear stress in shallow seagrass regions and more detailed laboratory and field measurements are needed to improve model formulations for sediment resuspension within seagrass beds.

Although more research is needed on the effect of hydrodynamic stressors on seagrasses, several studies include the effect of hydrodynamic stressors in models/indices to predict the success of seagrass restoration projects and provide guidance for which areas are suitable for restoration. De Jonge et al. (2000) presented a restoration strategy for *Z. marina* in the Dutch Wadden Sea, which included a GIS-based site selection tool for transplantation sites that included hydrodynamic stressors in the selection procedure. Selection of suitable transplant sites were based on sediment composition, emersion time, current velocity and wave action. Kelly et al. (2001) take into account hydrodynamics, in determining which regions you would expect to have high probability of restoration success. Short et al. (2002) presented a site-selection tool for transplantation of *Z. marina* which included wave exposure.

5.10 Literature Cited

- Abdelrhman, M. A. 2003. Effect of eelgrass *Zostera marina* canopies on flow and transport. Marine Ecology Progress Series 248:67-83.
- Ackerman, J. D. 2002. Diffusivity in a marine macrophyte canopy: Implications for submarine pollination and dispersal. American Journal of Botany 89:1119-1127.
- Ackerman, J. D. and A. Okubo. 1993. Reduced mixing in a marine macrophyte canopy. Functional Ecology 7:305-309.
- Aioi, K. and T. Komatsu. 1996. A preliminary report on the recovery process of *Zostera marina* in Otsuchi Bay, Northern Japan after disturbance by large atmospheric depressions. pp. 319-322. In: Kuo, J., Phillips, R.C., Walker, D.I., and Kirkman H. (eds.) Seagrass Biology: Proceedings of an International Workshop. Faculty of Sciences, The University of Western Australia, Nedlands, Western Australia.
- Conover, J. T. 1964. The importance of natural diffusion gradients and transport of substances related to benthic marine plant metabolism. Environmental relationships of benthos in salt ponds (Plant Relationships), vol 1, Technical Report 3, Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island.
- Conover, J. T. 1968. The importance of natural diffusion gradients and transport of substances related to benthic marine plant metabolism. Botanica Marina 11:1-9.
- Cornelisen, C. D. and F. I. M. Thomas. 2002. Ammonium uptake by seagrass epiphytes: isolation of the effects of water velocity using an isotope label. Limnology and Oceanography 47:1223-1229.
- De Jonge, V. N., D. J. de Jong, and M. M. van Katwijk. 2000. Policy plans and management measures to restore eelgrass (*Zostera marina* L.) in the Dutch Wadden Sea. Helgoland Marine Research 54:151-158.
- De Jonge, V. N. and D. J. de Jong. 1992. Role of tide, light and fisheries in the decline of *Zostera marina* L. in the Dutch Wadden Sea. Netherlands Institute for Sea Research 20:161-176.
- Eleuterius, L. N. 1987. Seagrass ecology along the coasts of Alabama, Louisiana, and Mississippi. pp. 11-24. In: Durako, M. J., Phillips, R.C., Lewis, R.R. (eds). Proceedings of the symposium on subtropical-tropical seagrasses of the southeastern United States. Florida Marine Research Publication No. 42, Florida Department of Natural Resources, St. Petersburg, FL.
- Eleuterius, L. N. and G. J. Miller. 1976. Observations on seagrasses and seaweeds in Mississippi Sound since Hurricane Camille. Journal of the Mississippi Academy of Science 21:58-63.
- Enríquez, S. and A. Rodríguez-Román. 2006. Effect of water flow on the photosynthesis of three marine macrophytes from a fringing-reef lagoon. Marine Ecology Progress Series 323:119-132.
- Fonseca, M.S., M. A. R. Koehl, and B. S. Kopp. 2007. Biomechanical factors contributing to self-organization in seagrass landscapes. Journal of Experimental Marine Biology and Ecology. 340:227-246.
- Fonseca, M. S., W. J. Kenworthy, and P. E. Whitfield. 2000. Temporal dynamics of seagrass landscapes: a preliminary comparison of chronic and extreme disturbance events. p. 373-

376. In: Pergent G, Pergent-Martini C, Buia MC, Gambi MC (eds). Proceedings 4th Int. Seagrass Biology Workshop, Sept 25-Oct 2, 2000, Corsica, France.
- Fonseca, M. S. and S. S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Ecology Progress Series* 171:109-121.
- Fonseca, M. S. and J. A. Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuarine and Coastal Shelf Science* 35:565-576.
- Fonseca M. S. and J. S. Fisher. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series* 29:15-22.
- Fonseca, M. S., J. S. Fisher, J. C. Zieman, and G. W. Thayer. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuarine and Coastal Shelf Science* 15:351-364.
- Fonseca, M. S. and W. J. Kenworthy. 1987. Effects of current on photosynthesis and distribution of seagrasses. *Aquatic Botany* 27:59-78.
- Fonseca, M. S., J. C. Zieman, G. W. Thayer, and J. S. Fisher. 1983. The role of current velocity in structuring eelgrass (*Zostera marina*) meadows. *Estuarine and Coastal Shelf Science* 17:367-380.
- Fourqurean, J. W. and M. B. Robblee. 1999. Florida Bay: a history of recent ecological changes. *Estuaries* 22(2B):345-357
- Frederiksen M., D. Krause-Jensen, M. Holmer, and J. S. Laursen. 2004. Spatial and temporal variation in eelgrass (*Zostera marina*) landscapes: influence of physical setting. *Aquatic Botany* 78:147-165.
- Gambi, M. C., A. R. M. Nowell, and P. A. Jumars. 1990. Flume observations of flow dynamics in *Zostera marina* (eelgrass) beds. *Marine Ecology Progress Series* 61:159-169.
- Ghisalberti M. and H. M. Nepf. 2002. Mixing layers and coherent structures in vegetated aquatic flows. *Journal of Geophysical Research* 107(C2):1-11.
- Granata, T. C., T. Serra, J. Colomer, X. Casamitjana, C. M. Duarte, and E. Gacia. 2001. Flow and particle distributions in a nearshore seagrass meadow before and after a storm. *Marine Ecology Progress Series* 218:95-106.
- Grizzle, R. E., F. T. Short, C. R. Newell, H. Hoven, and L. Kindblom. 1996. Hydrodynamically induced synchronous waving of seagrasses: 'monami' and its possible effects on larval mussel settlement. *Journal of Experimental Marine Biology and Ecology* 206:165-177.
- Harwell, M. C. and R. J. Orth. 2002. Long-distance dispersal potential in a marine macrophyte. *Ecology* 83:3319-3330.
- Kelly, N. M., M. Fonseca, and P. Whitfield. 2001. Predictive mapping for management and conservation of seagrass beds in North Carolina. *Aquatic Conservation: Marine Freshwater Ecosystems* 11:437-451.
- Koch, E. W. 2002. Impact of boat-generated waves on a seagrass habitat. *Journal of Coastal Research* 37:66-74.
- Koch, E. W. 2001. Beyond light: Physical, geological and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24:1-17.
- Koch, E. W. 1999a. Preliminary evidence on the interdependent effect of currents and porewater geochemistry on *Thalassia testudinum* Banks ex König seedlings. *Aquatic Botany* 63:95-102.

- Koch, E. W. 1999b. Sediment resuspension in a shallow *Thalassia testudinum* Banks ex König bed. Aquatic Botany 65:269-280.
- Koch, E. W. 1996. Hydrodynamics of a shallow *Thalassia testudinum* bed in Florida, USA. In: Seagrass Biology: Proceedings of an international workshop, 105-110.
- Koch, E.W., J. D. Ackerman, J. Verduin, and M. van Keulen. 2006a. Fluid dynamics in seagrass ecology-from molecules to ecosystems. pp. 193-225. In: A.W.D. Larkum, R.J. Orth and C. M. Duarte (eds.), Seagrasses: Biology, Ecology and Conservation, Springer, Netherlands.
- Koch, E. W., S. Ailstock, and J. C. Stevenson. 2002. Chapter VI, Beyond Light: Physical, geological and chemical habitat requirements. pp. 71-94. In: Chesapeake Bay Submerged Aquatic Vegetation Water Quality and Habitat-Based Requirements and Restoration Targets: A Second Technical Synthesis. U.S. Environmental Protection Agency.
- Koch, E. W. and G. Gust. 1999. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. Marine Ecology Progress Series 184:63-72.
- Koch, E. W. 1994. Hydrodynamics, diffusion-boundary layers and photosynthesis of the seagrasses *Thalassia testudinum* and *Cymodocea nodosa*. Marine Biology 118:767-776.
- Koch, E. W. and M. Huettel. 2000. The impact of single seagrass shoots on solute fluxes between the water column and permeable sediments. Biologia Marina Mediterranea 7:235-239.
- Koch, E.W., L. P. Sanford, S.-N. Chen, D. J. Shafer, and J. McKee Smith. 2006b. Waves in seagrass systems: Review and technical recommendations. Report ERDC-TR-06-15, Engineer Research and Development Center, U.S. Army Corps of Engineers, Washington, DC.
- Koch, E. W. and J. J. Verduin. 2001. Measurements of physical parameters in seagrass habitats. pp. 325-344. In: F. T. Short and R. G. Coles (eds.). Global Seagrass Research Methods. Elsevier, Amsterdam.
- Komatsu, T. 1996. Influence of a *Zostera* bed on the spatial distribution of water flow over a broad geographic area. pp. 111-116. In: Kuo, J., Phillips, R.C., Walker, D.I., and Kirkman H. (eds.) Seagrass Biology: Proceedings of an international workshop.
- Kopp, B. S. 1999. Effects of nitrate fertilization and shading on physiological and biomechanical properties of eelgrass (*Zostera marina* L.) Ph.D. dissertation, University of Rhode Island. pp. 187.
- Krause-Jensen, D., A. L. Middleboe, K. Sand-Jensen, and P. B. Christensen. 2000. Eelgrass *Zostera marina*, growth along depth gradients: upper boundaries of the variation as a powerful predictive tool. Oikos 91:233-244.
- Krause-Jensen, D., M. F. Pedersen, and C. Jensen. 2003. Regulation of eelgrass (*Zostera marina*) cover along depth gradients in Danish coastal waters. Estuaries 26:866-877.
- Middleboe, A. L., K. Sand-Jensen, and D. Krause-Jensen. 2003. Spatial and interannual variations with depth in eelgrass populations. Journal of Experimental Marine Biology and Ecology 291:1-15.
- Morin, J. and J. W. Morse. 1999. Ammonium release from resuspended sediments in the Laguna Madre estuary. Marine Chemistry 65: 97-110.

- National Research Council. 1994. Priorities for coastal ecosystem science. National Academy Press, Washington, D.C.
- Nepf, H. M. and E. W. Koch. 1999. Vertical secondary flows in submersed plant-like arrays. *Limnology and Oceanography* 44:1072-1080.
- Nepf, H. M. and E. R. Vivoni. 2000. Flow structure in depth-limited, vegetated flow. *Journal of Geophysical Research* 105:28547-28557.
- Newell, R. I. E. and E. W. Koch. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27:793-806.
- Nienhuis, P.H., B. H. H. De Bree, P. M. J. Herman, A. M. B. Holland, J. M. Verschuure, and E. G. J. Wessel. 1996. Twenty five years of changes in the distribution and biomass of eelgrass, *Zostera Marina*, in Greverlingen Lagoon, the Netherlands. *Netherlands Journal of Aquatic Ecology* 20:107-117.
- Nixon, S. W. and C. A. Oviatt. 1972. Preliminary measurements of midsummer metabolism in beds of eelgrass, *Zostera marina*. *Ecology* 53:150-153.
- Oldham, C. E. and P. S. Lavery. 1999. Porewater nutrient fluxes in a shallow fetch-limited estuary. *Marine Ecology Progress Series* 183:39-47.
- Oppenheimer, C. H. 1963. Effects of hurricane Carla on the ecology of Redfish Bay, Texas. *Bulletin of Marine Science of the Gulf and the Caribbean* 13:59-72.
- Orth, R. J., M. Luckenbach, and K. A. Moore. 1994. Seed dispersal in a marine macrophyte: implications for colonization and restoration. *Ecology* 75:1927-1939.
- Orth, R. J. and K. A. Moore. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* 222:51-53.
- Paling, E. I., M. van Keulen, K. D. Wheeler, J. Phillips, and R. Dyhrberg. 2003. Influence of spacing on mechanically transplanted seagrass survival in a high wave energy regime. *Restoration Ecology* 11:56-61.
- Patterson, M. R., M. C. Harwell, L. M. Orth, and R. J. Orth. 2001. Biomechanical properties of the reproductive shoots of eelgrass. *Aquatic Botany* 69:27-40.
- Peralta, G., F. G. Brun, J. L. Pérez-Lloréns, and T. J. Bouma. 2006. Direct effects of current velocity on the growth, morphometry, and architecture of seagrasses: a case study on *Zostera noltii*. *Marine Ecology Progress Series* 327:135-142.
- Peralta, G., F. G. Brun, I. Hernández, J. J. Vergara, and J. L. Pérez-Lloréns. 2005. Morphometric variations as acclimation mechanisms in *Zostera noltii* bed. *Estuarine, Coastal and Shelf Science* 64:347-356.
- Peterson, C. H., R. A. Luettich, Jr., F. Micheli, and G. A. Skilleter. 2004. Attenuation of water flow inside seagrass canopies of differing structure. *Marine Ecology Progress Series* 268:81-92.
- Powell, G. V. N. and F. C. Schaffner. 1991. Water trapping by seagrasses occupying bank habitats in Florida Bay. *Estuarine and Coastal Shelf Science* 32:43-60.
- Precht, E. and M. Huettel. 2003. Advective porewater exchange driven by surface gravity waves and its ecological implications. *Limnology and Oceanography* 48:1674-1684.
- Precht, E. and M. Huettel. 2004. Rapid wave-driven advective pore water exchange in a permeable coastal sediment. *Journal of Sea Research* 51:93-107.

- Preen, A. R., W. J. Lee Long, and R. G. Coles. 1995. Flood and cyclone related loss, and partial recovery, of more than 1000 km² of seagrass in Hervey Bay, Queensland, Australia. *Aquatic Botany* 52:3-17.
- Quammen, M. L. and C. P. Onuf. 1993. Laguna Madre: Seagrass changes continue decades after salinity reduction. *Estuaries* 16:302-310.
- Schanz, A. and H. Asmus. 2003. Impact of hydrodynamics on development and morphology of intertidal seagrasses in the Wadden Sea. *Marine Ecology Progress Series* 261:123-134.
- Scoffin, T. P. 1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *Journal of Sedimentary Petrology* 40:249-273.
- Short, F. T. 1983. The seagrass, *Zostera marina* L.: Plant morphology and bed structure in relation to sediment ammonium in Izembek Lagoon, Alaska. *Aquatic Botany* 16:149-161.
- Short, F. T., R. C. Davis, B. S. Kopp, C. A. Short, and D. M. Burdick. 2002. Site-selection model for optimal transplantation of eelgrass *Zostera marina* in the northeastern US. *Marine Ecology Progress Series* 227:253-267.
- Short, F. T. and H. A. Neckles. 1999. The effects of global climate change on seagrasses. *Aquatic Botany* 63:169-196.
- Tamaki, H., M. Tokuoka, W. Nishijima, T. Terawaki, and M. Okada. 2002. Deterioration of eelgrass, *Zostera marina* L., meadows by water pollution in Seto Inland Sea, Japan. *Marine Pollution Bulletin* 44:1253-1258.
- Teeter, A. M., B. H. Johnson, C. Berger, G. Stelling, N. W. Scheffner, M. H. Garcia, and T. M. Parchure. 2001. Hydrodynamic and sediment transport modeling with emphasis on shallow-water, vegetated areas (lakes, reservoirs, estuaries, and lagoons). *Hydrobiologia* 444:1-23.
- Thom, R. M., A. B. Borde, P. J. Farley, M. C. Horn, and A. Ogston. 1996. Passenger-only ferry propellor wash study: Threshold velocity determinations and field study, Vashon Terminal. Battelle Marine Sciences Laboratory, Sequim, WA.
- Thomas, F. I. M. and C. D. Cornelisen. 2003. Ammonium uptake by seagrass communities: effects of oscillatory versus unidirectional flow. *Marine Ecology Progress Series* 247:51-57.
- Thomas, F. I. M., C. D. Cornelisen, and J. M. Zande. 2000. Effects of water velocity and canopy morphology on ammonium uptake by seagrass communities. *Ecology* 81:2704-2713.
- Thomas, L. P., D. R. Moore, and R. C. Work. 1961. Effects of hurricane Donna on the Turtle Grass beds of Biscayne Bay, Florida. *Bulletin of Marine Science of the Gulf and Caribbean* 11:191-197.
- Tilmant, J. T., R. W. Curry, R. Jones, A. Szmant, J. C. Zieman, M. Flora, M. B. Robblee, D. Smith, R. W. Snow, and H. Wanless. 1994. Hurricane Andrew's effects on marine resources. *Bioscience* 44:230-237.
- van Katwijk, M. M. and D. C. R. Hermus. 2000. Effects of water dynamics on *Zostera marina*: Transplantation experiments in the intertidal Dutch Wadden Sea. *Marine Ecology Progress Series* 208:107-118.
- van Keulen, M. and M. A. Borowitzka. 2000. Comparison of water velocity profiles through morphologically dissimilar seagrasses. *Biologia Marina Mediterranea* 7:143-146.

- van Keulen, M., E. I. Paling, and C. J. Walker. 2003. Effect of planting unit size and sediment stabilization on seagrass transplants in Western Australia. *Restoration Ecology* 11:50-55.
- van Tussenbroek, B. I. 1994. The impact of Hurricane Gilbert on the vegetative development of *Thalassia testudinum* in Puerto Morelos coral reef lagoon, Mexico: a retrospective study. *Botanica Marina* 37:421-428.
- Ward, L. G. W., M. Kemp, and W. R. Boynton. 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Marine Geology* 59:85-103.
- Whitfield, P. E., W. J. Kenworthy, K. K. Hammerstrom, and M.S. Fonseca. 2002. The role of storms in the expansion of disturbances initiated by motor vessels on subtropical seagrass –coral banks. *Journal of Coastal Research* 37:86-99.
- Worcester, S. E. 1995. Effects of eelgrass beds on advection and turbulent mixing in low current and low shoot density environments. *Marine Ecology Progress Series* 126:223-232.
- Zimmerman, R. C. 2003. A biooptical model of irradiance distribution and photosynthesis in seagrass canopies. *Limnology and Oceanography* 48:568-585.

6.0 Interactions of *Zostera marina* and *Thalassia testudinum* with Sediments

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6.1 Background

As rooted aquatic plants, seagrasses are influenced by the sedimentary environment in which they grow. Sediment characteristics such as grain size, mineral composition and organic matter content may influence the overall biogeochemical environment of the root zone. Human actions can also alter sediment grain size distribution (i.e., dredging activities, soil erosion, production of excessive fine sediments through jetty and dike construction, prop wash and wakes from boats) which in turn may affect the sedimentary geochemical environment and the rooting environment. Further, human actions can affect sediment organic matter content through water-column nutrient elevations and the subsequent development of phytoplankton, epiphytes and macroalgal blooms. The resulting sedimentation of organic matter (OM) to the benthos leads to changes in sediment mineralization rates and redox conditions. Of particular concern are generation of phytotoxic substances in anaerobic sediments (e.g., elevated sediment ammonia, sulfide, metal ions, and other reduced chemical species) (Figure 6.1). Here we review and consider the effects of sediment characteristics on the establishment, survival or growth of *Zostera marina* and *Thalassia testudinum*.

Seagrasses interact physically, biologically and geochemically with both the water column and the sediment in which they are rooted. These interactions are often complex and depend on local conditions (Thayer et al. 1984; Koch 2001). Probably the most important physical process affecting seagrass is light. Low-light stress is manifested in a cascade of effects that are intimately related to the sediment geochemistry, especially that of sulfide production. A key component controlling sediment geochemistry is the input of organic matter that can become available for mineralization. Complex hydrodynamic interactions (see Chapter 2) can cause seagrass beds to be either sources or sinks for particulate matter (Nepf and Koch 1999) (Figure 6.1). Because of mineralization of organic matter input to the root zone through burial, DOM release from seagrass (Kaldy et al. 2006) and particle retention of irrigating infauna (Eldridge et al. 2004), the seagrass roots and rhizomes are nearly always surrounded by anaerobic sediments (Eldridge and Morse 2000; Hebert and Morse 2003; Eldridge et al. 2004). However, if anaerobic metabolites are not transformed by secondary redox processes to non-toxic forms, phytotoxic substances can concentrate around the roots and rhizomes at levels sufficient to kill the seagrass (Carlson et al. 1994; Koch 2001).

6.2 Review of Research

6.2.1 Interactions of Sediment Grain Size and *Zostera*

The majority of information on the relationship of *Zostera* to sediment grain size results is from field surveys (Table 6.1), and thus is correlative in nature. *Zostera* spp. are typically

found growing in substrata of fine or muddy sand, although this genus is also found growing over a wide range of sediment size classes. In the Pacific Northwest, Boese and Young (unpublished data) found *Z. marina* growing in a range of sediment texture classes in Yaquina Bay, OR. Although a majority of the *Z. marina* habitat was in the lower estuary associated with sediments characterized by 75-100% sand (up to 25% silt/clay), *Z. marina* meadows also occurred up estuary in sediments containing up to 75% silt/clay. Unfortunately, it is not possible to determine if there is an optimum grain size composition for *Zostera* growth and survival with these data. In an experimental study of eelgrass using mesocosms, Short (1987) showed that leaf biomass, weight, and shoot height were significantly greater in plants growing on fine grained mud than on coarse grained sand although the differences between treatments in this case may have been due to nutrient limitation. Thom et al. (2001) cultivated *Z. marina* for 13 weeks in sediment types typically occupied by this species in the Pacific Northwest, as well as coarse, organic-poor sand and gravel, which typically are not inhabited by *Z. marina* (Phillips 1984). The greatest growth was observed in the finer grained sediments containing organic matter, and lowest growth was measured in the gravel substratum. Coarse-grained sand and a sand/gravel mixture produced intermediate growth rates. These experimental results are consistent with the *Z. marina* distribution data summarized in Table 6.1, but as in previous experiments, may be confounded by differences in nutrient availability or mineralogy.

6.2.2 Interactions of Sediment Grain Size and *Thalassia*

Sediments found in *Thalassia* beds typically fall in the “medium sand” size class, and range from fine to coarse sand (Table 6.1). As is the case for *Zostera*, grain size distributions have been observed to shift toward finer grain sizes in *Thalassia* beds (Orth 1977). However, values for silt and clay typically are low, ranging from 1 to 34%, and the overall median value (taking the mid-point of the range for a given study) is 10% (Table 6.1). Terrados et al. (1998), reporting from a study of seagrasses in southeastern Asia (including *T. hemprichii*), observed that seagrass species richness and community leaf biomass declined sharply when the silt and clay content of the sediment exceeded 15%. Thus, *Thalassia* would appear to be more vulnerable to damage from siltation than is *Zostera*.

6.2.3 Interactions of Sediment with Seeds

Zostera seed germination is surprisingly robust with efficiencies often between 80 to > 90% under a wide range of oxygen and salinity conditions (Brenchley and Probert 1998; Moore et al. 1993). Moore et al. (1993) reported that *Z. marina* seed germination was often triggered by anoxic conditions (in either sediment or water). Such conditions typically occur seasonally in finer, organic-rich sediments where the exchange between overlying oxygenated water and the sediment is restricted (Koch 2001). Seeds buried to 5 mm in the sediments showed lower germination success in the autumn than seed buried at 15 to 25 mm, but in the winter there was no apparent effect of burial depth in the sediment. In general, germination of buried *Z. marina* seeds began when water temperature dropped below 15 degrees C. Moore et al. (1993) also pointed out that there was only about a 1-2 week delay between germination in the sediments and the emergence of sprouting seedlings. Furthermore, they found no ungerminated viable seeds in any of their test treatments after March. That is, seed germination was >90% with about 80% of these forming seedlings. This high success rate might be partially due to the fact that only seeds

characterized by an intact, hard seed coat of dark color, and a fully developed embryo were used in the Moore et al. (1993) experiment. Harwell and Orth (1999) found high (41-56%) seedling survival in burlap bag treatments but only 5-15% in bare sediment treatment due to predation, burial, or lateral transport.

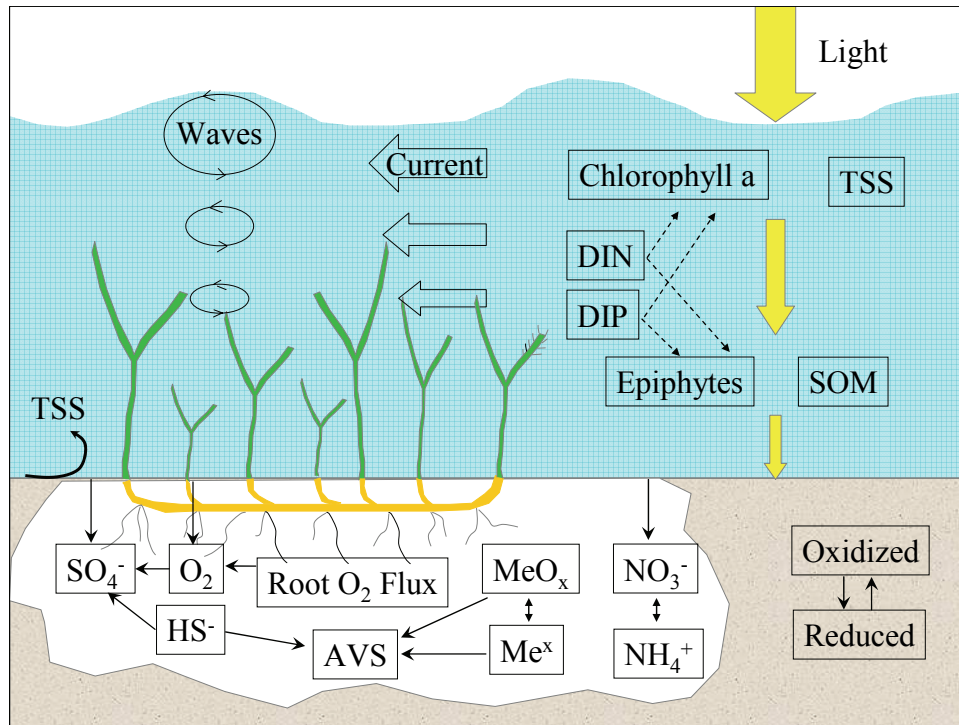


Figure 6.1. Both the water column and sediment environments influence seagrasses. While the physical and light attenuating water-column stressor may be the most important to the survival of the plant, the sediment geochemical processes, stimulated by sedimentation of reactive organic material from the water column, can affect seagrass health. Highly reduced sulfidic environments (HS⁻) can reduce seagrass production and at times can become lethal to seagrass due to root death. HS⁻ and metals (Me^x) combine to produce non-toxic acid volatile sulfides (AVS). Thus the combination of high metal (Fe and Mn) in the sediments and diffusion of oxygen from the seagrass roots can reduce the toxic effects of sulfide in the near root environment (i.e., the rhizosphere) even under conditions of relatively high organic matter input to the sediments. (DIN – dissolved inorganic nitrogen, DIP – dissolved inorganic phosphorus, SOM – settling organic matter)

The typical range of salinity (~15-30) generally found in estuaries also has minimal effects on seed germination (Brenchley and Probert 1998), although under aerobic conditions and at salinities > 30 there was a small reduction in germination success (60% versus 80%) for lower salinities under aerobic conditions. Anaerobic conditions seem to promote greater germination success and shorter germination periods (Brenchley and Probert 1998).

Table 6.1. Distribution of *Zostera* species in relation to sediment texture or grain size. Texture was available in some publications while grain size was reported in others.

Seagrass	Organic Matter (%)	Size Class	Median Grain Size (mm)	Silt+Clay (%)	Source
<i>Zostera marina</i>	1.2			14	Marshall and Lucas (1970)
	1.2	very fine - fine sand ²	0.100 - 0.146 ¹		Orth (1977)
		medium - muddy sand	0.12 - 0.50		Nienhuis and DeBree (1977)
	2.2 - 2.7			11 - 13	Kenworthy et al. (1982)
	1.7			6 - 24	Peterson et al. (1984)
	0.4 - 1.0	medium-fine sand ²	0.17 - 0.34		Kenworthy and Fonseca (1992)
	6.4 - 16				Short et al. (1983)
		fine sand - silty clay			Lalumiere et al. (1994)
	0.4 - 3.5			5 - 35	Townsend and Fonseca (1998)
	0.4 - 1.4				Dan et al. (1998)
		medium - fine sand ²	0.14 - 0.27 ¹	8 - 13	Webster et al. (1998)
		fine sand ²	0.17 - 0.20 ¹	4 - 6	Frost et al. (1999)
	0.4 - 12			2 - 56	Koch (2001)
		medium sand - fine sand/silt			Thom et al. (2001)
		medium - very fine sand ²	0.06 - 0.35 ³		Lee et al. (2002)
<i>Zostera japonica</i>	1.7 - 3.8	fine sand ²	0.13 - 0.23 ^{1,3}		Posey (1988)
<i>Zostera noltii</i>		fine sand ²	0.13 - 0.23	40 - 70	van Lent et al. (1991)
		very fine sand ²	0.07		Sprung (1994)
<i>Zostera muelleri</i>	0.8 - 7.3			1 - 72	Edgar and Shaw (1995)
<i>Zostera novelandica</i>		fine sand	0.19 ³		Heiss et al. (2000)
<i>Thalassia testudinum</i>	3.5 - 4.9			5	Wood et al. (1969)

				15	Scoffin (1970)
				1 – 34	Burrell and Schubel (1977)
		medium sand ²	0.35 - 0.36 ¹		Orth (1977)
	0.8	medium sand ²	0.24 ^{1,3}	3	Grady (1981)
		fine sand ²	0.15 - 0.20		Wanless (1981)
				12 – 34	Hoskin (1983)
				22	Lee and Dunton (1996)
	0.5 - 0.6				McGlathery et al. (1994)
		medium - coarse sand ²	0.24 - 0.59 ³		Kuenen and Debrot (1995)
		fine - coarse sand ²	0.19 - 0.50 ¹		Kalbfleisch and Jones (1998)
				2 - 9	Livingston et al. (1998)
	0.5 – 2.3			2 - 17	Koch (2001)
				5 - 12	Terrados et al. (1998)
				23 - 35	Kaldy and Dunton (2000)
<i>Thalassia hemprichii</i>	3.5 - 10	medium sand ²	0.24 - 0.37 ^{1,3}		Paula et al. (2001)

1. Calculated from phi (ϕ) values: (ϕ) = $-\log_2(\text{mm})$ (Krumbein and Pettijohn 1938)

2. Wentworth size class obtained from grain size (Wentworth 1922; Percival and Lindsay 1997)

3. Median grain size

6.2.4 Seagrasses and sediment sulfides

Sulfate reduction is quantitatively the most important diagenetic process in anoxic marine waters (Blaabjerg et al. 1998). The metabolites from sulfate reduction (H_2S and HS^-) may inhibit seagrass photosynthesis, growth, and survival through sulfide toxicity (Goodman et al. 1995; Terrados et al. 1999). The high concentration of sulfate (2700 ppm) in the seawater and within the sediment profile insures that sulfate is nearly always available for reduction in seagrass roots and rhizomes. Other oxidants (e.g., nitrate and oxy-hydroxy-metals) although more chemically energetic than sulfate are often reduced within the first few centimeters below the sediment surface (Berner 1980). Because sulfate is abundant deep within the sediments, sulfide metabolites may persist in the sediments for several months to years after mineralization. Hence the sediment sulfide can provide a chemical record from phytoplankton blooms, dredging or other natural or anthropogenic sedimentation (Eldridge et al. 2004).

To counteract sulfide accumulation in the rhizosphere, seagrasses transport photosynthetically produced O_2 through lacunae to the roots (Smith et al. 1988; Caffrey and Kemp 1991; Kraemer and Alberte 1993). This transport mechanism is probably an adaptation to support aerobic root respiration, but excess O_2 diffusing from the roots into the rhizosphere has the added benefit of oxidizing sulfide to non-toxic sulfate (Caffrey and Kemp 1991). In addition to the photosynthetically produced O_2 , dissolved O_2 in the water column can diffuse through *Z. marina* and *T. testudinum* lacunal systems, thereby reducing the exposure of seagrass to sulfides at night when photosynthetic processes are not active (Koch and Erskine 2001). Binzer et al.

(2005) showed that in the dark the degree of O₂ saturation in water, and flow velocity were the primary determinates of internal oxygen conditions in *Cymodocea nodosa*. *Zostera marina* may also exhibit some anatomical plasticity in the development of lacunae and shoot size that allows the plant to adapt to low light conditions (Penhale and Wetzel 1983; Abal et al. 1994)

Table 6.2. Literature values for dissolved sulfide toxicity to marine/estuarine plants.

Pore Water (PW) or Water (W) Exposure	Marine/Estuarine Plant	Effect Conc. (μM)	Duration	Response Variable	Citation
PW	<i>Zostera marina</i>	2300	24 hr	root respiration not reduced	Penhale and Wetzel (1983)
PW	<i>Zostera marina</i>	400 - 800	21 day	decreased photosynthesis	Goodman et al. (1995)
PW	<i>Zostera marina</i>	70	2 mo	decreased leaf elongation rate; shoot density unaffected	Terrados et al. (1999)
W	<i>Zostera marina</i>	100-1000	1-3 weeks in water	photosynthesis stopped leaf elongation rate stopped leaves/shoot decreased 37% root non-structural carbohydrate decreased 81% above-ground biomass (shoot/root) decreased 55%	Holmer and Bondgaard (2001)
PW	<i>Thalassia testudinum</i>	~ 1,500	4-6 weeks	sulfide suggested as synergistic secondary stressor	Carlson et al. (1994)
PW	<i>Thalassia testudinum</i>	80	6 mo	seedling mortality 100%	Koch (1999)
PW	<i>Thalassia testudinum</i>	2000-6000	48 hr	leaf elongation rate decreased 43% root energy charge decreased 22% root ATP production decreased no visual signs of acute toxicity	Erskine and Koch (2000)
PW	<i>Thalassia testudinum</i>	6000	14 day	high salinity (S), 50% mortality high temperature (T), 33% mortality high S and T, 100% mortality	Koch and Erskine (2001)
PW	<i>Thalassia testudinum</i>	5500	38 day	net shoot loss 65% at 34-35°C no new leaf emergence at 34-35°C	Koch et al. (2007)

In marine environments, there is a constant composition of major ions relative to salinity so that in high salinity waters there is, as discussed above, an abundance of sulfate to support anaerobic diagenesis (Stumm and Morgan 1981). Owing to the potential for sulfide formation, plants in euryhaline and mesohaline waters may require sediments which are more oxygenated (i.e., coarser sediments) and have higher rates of pore water exchange (Koch 2001) than is needed in brackish waters to reduce the effect of sulfide toxicity.

Although sulfate competes poorly as an oxidant, its abundance in seawater ensures that sulfate reduction is a dominant geochemical process in near shore sediments (Berner 1980). However, the extrapolation of the general trends in near shore sediment diagenesis to seagrass sediments is not direct. While Holmer and Bongaard (2001) found that the depth distribution of sulfate reduction in a tropical seagrass (*Cymodocea rotundata*) was positively correlated with below-ground biomass, they also found that sulfate reduction was not the major diagenetic process leading to nutrient re-mineralization, possibly because of the ability of seagrasses to inject O₂ and other oxidants into the root zone.

The ability of seagrasses to promote mineralization of organic material to release NH₄⁺ while regulating sulfate reduction in the root zone may be an important mechanism to insure seagrass survival (Eldridge et al. 2004). The regulation of sulfate reducing bacteria by seagrasses may have other benefits. Sulfate reducing bacteria often fix nitrogen (Welsh et al. 2001), which may lead to increased nitrogen availability and which can also be beneficial to the growth of seagrasses. By regulating sulfate reduction the plant can maximize the benefit of sulfate reduction while minimizing its toxic effects. Other complicating factors that may mitigate the effects of sulfide concentration include the presence of iron (Fe(II)) and manganese (Mn²⁺) in the rhizosphere which may also reduce sulfide toxicity by the formation of insoluble metal sulfides (Erskine and Koch 2000). This might support the hypothesis that accumulation of sulfides could be mitigated by fertilization of seagrass habitats with Fe(III) compounds. An advantage of this proposition would be competitive anaerobic mineralization of organic matter by Fe(III) instead of sulfate. The products of iron reduction are not thought to be toxic to *Z. marina*.

In terrestrial systems, root exudates (i.e., plant-derived organic compounds added to the rhizosphere) can bind with toxic metal ions or other compounds to provide protection under chemically adverse soil conditions (Höberg and Jensen 1994). It is possible that seagrasses have similar mechanisms to protect against toxic chemicals in sediments; however, little is known about root exudation, root growth, and root longevity and mortality in seagrasses.

Several studies report on the tolerance of seagrass to soluble sulfides (Table 6.2). While there is some evidence that 1 to 2 mmol H₂S in the water-column may inhibit seagrass growth or cause death of *Z. marina* (Goodman et al. 1995; Smith et al. 1988), there are few definitive studies that show the dose-response of seagrass in long-term controlled-environment studies of exposure to sulfides. Holmer and Bondgaard (2001) showed that photosynthesis stopped after 6 days at water column sulfide concentrations between 100 and 1000 µmol. This study was done at saturating irradiance (400-500 µmol photon m⁻² s⁻¹). Koch and Erskine (2001) determined the response of *Thalassia testudinum* to sulfides under varying conditions of light, salinity, and temperature. *T. testudinum* showed no response to sulfides until the dose reached 6 mM concentration, and a response occurred only in the high temperature treatment (35°C). In contrast, longer-term studies by Carlson et al. (1994) showed *T. testudinum* died after being exposed to ~1.5 mM sulfide concentrations. However, Carlson et al. (1994) note that the high sulfides at their research sites are probably just one of several factors that contribute to die-off episodes rather than the primary cause of death. Other factors such as hyperthermia,

hypersalinity and microbial pathogens may act in synergy with high sulfides to induce mortality in seagrass (Carlson et al. 1994).

There are several internal plant mechanisms through which sulfides can affect seagrass survival. Sulfides bind to metal ion cofactors of proteins, inhibiting their activities. Sulfides bind the Fe(III) in the heme moiety of the mitochondrial enzyme cytochrome a_3 oxidase, blocking the terminal step in the electron transport system. Sulfides can also bind Zn(II) in carbonic anhydrase replacing the bound hydroxyl necessary for the inter-conversion of CO_2 and water to bicarbonate (Beauchamp et al. 1984). Currently, there is little information on how various plant organelles individually respond to sulfides. In particular, more information is needed to determine the effect of sulfides on seagrass plant meristems since this is the site of most anabolic processes. Further we have found no studies that address pH effects on sulfide toxicity. The pH effect may be important since it affects the speciation of the sulfide. HS^- has been shown to be more toxic to some faunal species than the other sulfide species (Stumm and Morgan 1981). New microelectrode methods are now available to measure sulfide concentration in the roots, rhizomes, and meristem (Pedersen et al. 2004) making possible toxicological studies of seagrass response to sulfides in the meristem and other tissues.

6.2.5 The Role of the Infaunal Irrigators

The benefit of seagrass as a source of nutrition and refuge for infaunal communities has been demonstrated in numerous studies (e.g., Bostrom et al. 2002; Mattila et al. 1999; Webster et al. 1998). Fewer studies, however, have demonstrated the benefits that seagrasses derive from the presence and activity of infaunal organisms. Peterson and Heck (2001) found a positive relationship between infaunal nutrient cycling and seagrass productivity. Based on modeling studies of *Thalassia testudinum*, Eldridge et al. (2004) suggest that seagrasses derive additional benefits from irrigating infauna through the introduction of oxidants from the water column into the root zone. The additional oxidants in the rhizosphere help maintain low levels of sulfides and other reduced toxicants. A more detailed discussion of the interactions of infaunal irrigators and seagrasses is found in Chapter 11.

6.2.6 Trapping of Particles by Seagrasses

Seagrasses produce more organic matter than can be consumed by water-column, epifaunal, and infaunal organisms (Kaldy et al. 2006; Jones et al. 2003). Much of this organic matter becomes sequestered in the sediments (Eldridge and Morse 2000). Particulate deposition is further enhanced by the capacity of seagrass to directly retain sestonic particles. The three dimensional structure of the seagrass canopy buffers the effects of current velocity and turbulence within the canopy (Koch 2001) (Figure 6.1) thereby reducing sediment resuspension, total suspended solids concentrations and increasing water clarity. In addition to the settling of particles due to decreased turbulence and water flow (Koch 2001), particles physically adhere to seagrass leaf surfaces or are trapped by protozoa and possibly other epiphytes that reside on leaves. These trapping mechanisms may be the dominant particle sequestration mechanism in seagrass canopies, and add significantly to the high rates of organic carbon input into seagrass sediments (Agawin and Duarte 2002).

Field studies have shown that surficial sediments within seagrass meadows tend to have a higher percentage of “fine” material (silt/clay), and a higher organic carbon content, than the surrounding non-vegetated (or lightly vegetated) sediments. For example, Marshall and Lukas (1970) found that surficial (0-1 cm) sediments from an eelgrass bed in Rhode Island averaged $14 \pm 6\%$ silt/clay, compared to $5 \pm 3\%$ in unvegetated sediments. Corresponding values for organic carbon in eelgrass and unvegetated sediments were $1.89 \pm 0.34\%$ and $0.88 \pm 0.17\%$. Orth (1977) reported that the median sediment diameter for sediment cores collected within a Chesapeake Bay eelgrass bed was about 0.10 mm (3.3 phi units), compared to about 0.17 mm (2.6 phi units) at the edges of the bed. Corresponding values for percent total organic matter were 1.4 and 0.5%. In another study, Peterson et al. (1984) reported that silt/clay comprised 14-18% of sediments from a *Z. marina* meadow in North Carolina versus 2-3% from the adjacent control sand flat. Variations in sediment texture generally reflect differences in physical processes related to waves and currents (Burrell and Schubel 1977). Seagrasses often impede currents, reduce the flow velocity (Ginsburg and Lowenstam 1958), and increase the accumulation of silt/clay fraction affecting the sorting and skewness of the grain size distribution (Wood et al. 1969; Burrell and Schubel 1977; Fonseca 1981; Kenworthy et al. 1982; Peterson et al. 1984; Gambi et al. 1990; Ackerman and Okubo 1993).

Fonseca et al. (1983) found no predictable distribution of silt/clay in low surface current regimes (up to 53 cm/sec) in *Z. marina* meadows in North Carolina, while in high currents (up to 94 cm/sec) there was an inverse relationship between fine sediment content and shear velocity. Expanding on this work, Fonseca and Bell (1998) found that sediment composition in seagrass habitats was highly variable below a current velocity of about 25 cm/sec, while this variance was much reduced at higher current speeds. They suggested that the initiation of motion of sediment for the fine sand, characteristic of the North Carolina site, occurs at unidirectional current speeds of about 25 cm/sec, and that this speed constitutes a disturbance threshold for silt/clay and organic content there. Further, they suggested that at velocities greater than 25 cm/sec there was a decreased accumulation of fine sediment that could reduce vegetative spreading and inhibit seedling colonization of eelgrass.

Seasonality in temperate regions may be important to both the flushing of organic matter out of the seagrass beds (Hemminga and Duarte 2000) during winter and the accumulation of seagrass or macroalgal biomass in the autumn (Carlson et al. 1994). These disturbances may be important for the long term survival of seagrass by preventing the deterioration of sediment condition (Hemminga and Duarte 2000) or by providing organic material which, upon mineralization, provides sufficient NH_4^+ to avoid a nitrogen limitation (Zimmerman et al. 1987).

6.2.7 Sediment Nutrient Effects

Seagrasses assimilate nutrients from both the water column and sediments. There is some debate as to which nutrient source is more important. Active nutrient uptake from sediments occurs during daylight hours when the rhizosphere is aerobic. However, during the dark period when roots and rhizomes are often subject to fermentation, active below-ground uptake is reduced and shoot uptake may become more important. The ability of seagrasses to regulate uptake processes depends on a number of factors including the rate of photosynthesis

and utilization of stored carbohydrates, the availability of NH_4^+ and NO_3^- in the water-column, and the rate of organic sediments mineralization. (Pedersen et al. 1997; Koch 2001; Eldridge et al. 2004; Kaldy et al. 2006).

Mineralization is an important source of nitrogen and phosphorous to plants (Short 1987; Perez et al. 1991; Perez et al. 1994; Pederson et al. 1997). Mineralization rates may be regulated to some degree by the seagrass plant. In sediments with low organic matter content (less than about 2.5%), seagrasses receiving high irradiance at the canopy can regulate the sediment redox environment with lacunal O_2 diffusion from the roots and rhizomes. Maintaining healthy redox conditions in the sediments allows the plant to maintain normal physiological nutrient uptake and photosynthetic capacity (Koch 2001 and references within; Eldridge et al. 2004). Sulfide concentrations (Hebert and Morse 2003) and sulfate reduction rates (Blaabjerg et al. 1998) showed diel cycles with greater H_2S concentrations during the night and, surprisingly, higher sulfide production rates during the day. High sulfate reduction rates during periods of maximum photosynthesis suggests that excess carbon produced by primary production is released as DOM from the roots and stimulates sulfate reduction. Simultaneously, lacunal O_2 oxidizes this released sulfide. Radioactive and stable isotope data from several studies suggests that there is a strong linkage between seagrass production and DOM release (Holmer and Laursen 2002; Kaldy et al. 2006). Using tracer experiments, Kaldy et al. (2006) showed a direct link from seagrass to DOM, and then to sediment bacteria, and Holmer and Laursen (2002) showed a positive relationship between seagrass photosynthesis and sulfate reduction. A conclusion we reach from these result, is that diel variations in seagrass photosynthesis produce pulses of DOM exudates from the seagrass roots and rhizomes that simulate daily cycles in sediment sulfate reduction.

The interaction between seagrass production and organic matter in the sediment is highly variable, and there are studies showing that healthy seagrass can occur in highly enriched organic sediments (Koch 2001) (Table 6.1). We assume that either the organic matter in these sediments is relatively unreactive or that infaunal irrigation (as discussed earlier) and lacunal O_2 release aerates the sediments in the vicinity of the seagrass. We note, however, that both infaunal irrigation and lacunal O_2 release also involves excretion of labile DOC. The literature is unclear as to how these metabolites alter the sediment geochemistry (Holmer and Laursen 2002; Kaldy et al. 2006).

Ammonium, the preferred form of nitrogen for eelgrass, is taken up from pore water through the roots (Short 1987). Dennison et al. (1987) established an upper limit for this uptake and utilization, finding in mesocosm experiments that interstitial water concentrations of NH_4^+ above $100\ \mu\text{M}$ saturate the growth response of *Z. marina*. In contrast, Van Katwijk et al. (1997) reported that an NH_4^+ concentration of $125\ \mu\text{M}$ was toxic to eelgrass, and suggested that the toxicity threshold was as low as $25\ \mu\text{M}$. However, Hebert et al. (2007) reported up to $2500\ \mu\text{M}$ concentration of NH_4^+ in the root zone of healthy *Z. marina* in Yaquina Bay, OR.

Maier and Pregnall (1990) showed that *Z. marina* also utilizes nitrate-rich groundwater flowing through a permeable sand layer sandwiched between fine-grained sediments into the near shore waters from sandy beaches in Massachusetts. The nitrate-rich groundwater induced

nitrate reductase activity in eelgrass plants. This finding suggests the importance of high-porosity sandy sediments as a conduit for nutrient-rich ground water to near shore aquatic vegetation, including seagrass and macroalgae. The interlayering of permeable sandy sediments with fine-grained sediments in a Georgia estuary provided conduits for advective transport of pore water constituents out of the sediments (Jahnke et al. 2003). They concluded that such fluxes are concentrated into small layers, and as such may constitute a significant input of nutrients to the estuary even if permeable, sandy layers comprise a very small proportion of the total bottom area. Again, these findings indicate a relationship between sediment grain size and the rate at which nutrient-rich ground water can seep into near shore waters, stimulating the growth of seagrass and algae. The relationship between aqueous concentrations of nutrients and the abundance and health of *Zostera* is discussed in detail in Chapter 3.

Reduction in surficial sediment grain size can decrease the rate of exchange of pore water nutrients with overlying water. For example, Short (1983) investigated the accumulation of NH_4^+ in interstitial water and onto sediment particles. He found that in highly-reduced eelgrass sediments, NH_4^+ is lost from the interstitial pool by diffusion into the thin, oxidized sediment surface layer, by adsorption onto sediment particles, and by uptake into bacterial cells and eelgrass roots. However, part of this pore water NH_4^+ is termed “exchangeable” because it is easily released from the particle surfaces by ion exchange. Short noted that the amount of exchangeable NH_4^+ is dependent upon texture, mineralogy, and organic content of the sediment.

6.3 Research Gaps in Relation to Setting Protective Criteria

Both field and laboratory results indicate that *Zostera marina* and other seagrass species are most abundant or productive in fine or muddy sand containing substantial organic matter. This type of sediment can contain elevated pore water concentrations of substances such as NH_4^+ or dissolved sulfides. Whether or not these constituents act as nutrients or toxins to eelgrass plants may depend upon the pore water concentrations, other characteristics of the sediment, and the physiology of the exposed plants. Thus, although grain size of the substratum does appear to influence the distribution and health of *Zostera marina*, relatively little is known of the specific processes involved in such effects. The percent organic matter in sediments is related to the sulfate reduction potential, and hence to the sulfide concentrations in the sediment. The ability of seagrass to protect itself from high levels of sulfide in the root zone will be directly dependent on availability of light to drive photosynthesis, and may be indirectly dependent on irrigating infaunal associates or to the presence of Fe or Mn minerals that detoxify the sulfides in seagrass sediments. Quantifying bioirrigation effects and better definition of the relationship between available light levels and sulfide concentrations would be helpful in insuring that protective criteria based on light levels will be adequate. Additionally, the presence of metal minerals (as detoxifying agents) could be used as an evaluation factor in seagrass protective criteria. The reported sediment pore water concentrations of NH_4^+ tolerated by *Z. marina* range over two orders of magnitude. Again a better understanding of the relationship between dissolved inorganic nutrients and *Z. marina* physiology is needed.

6.4 Literature Cited

- Abal, E. G., N. R. Loneragan, P. Bowen, C. J. Perry, J. W. Udy, and W. C. Dennison. 1994. Physiological and morphological responses of the seagrass *Zostera capricorni* Ashers. to light intensity. *Journal of Experimental Marine Biology and Ecology* 178: 113-129.
- Ackerman, J. D. and A. Okubo. 1993. Reduced mixing in a marine macrophyte canopy. *Functional Ecology* 7:305-309.
- Agawin, N. S. R. and C. M. Duarte. 2002. Evidence of direct particle trapping by a tropical seagrass meadow. *Estuaries* 25:1205-1209.
- Beauchamp, R. O., Jr., J. S. Bus, J. A. Popp, C. J. Boveiko, and D. A. Andjelkovich. 1984. A critical review of the literature on hydrogen sulfide toxicity. *CRC Critical Reviews in Toxicology* 13:25-97.
- Berner, R. A. 1980. *Early Diagenesis: A Theoretical Approach*. Princeton University Press. Princeton, N.J.
- Binzer, T., J. Borum, and O. Pedersen. 2005. Flow velocity affects internal oxygen conditions in the seagrass *Cymodocea nodosa*. *Aquatic Botany*, 83: 239-247.
- Blaabjerg, V., K. N. Mouritsen, and K. Finster. 1998. Diel cycles of sulphate reduction rates in sediments of a *Zostera marina* bed (Denmark). *Aquatic Microbial Ecology* 15: 97-102.
- Bostrom C., E. Bonsdorff, P. Kangas, and A. Norkko. 2002. Long-term changes of a brackish-water eelgrass (*Zostera marina* L.) community indicate effects of coastal eutrophication. *Estuarine Coastal and Shelf Science* 55:795-804.
- Brenchley, J. L. and R. J. Probert. 1998. Seed germination responses to some environmental factors in the seagrass *Zostera capricorni* from eastern Australia. *Aquatic Botany* 63:177-188.
- Burrell, D. C. and J. R. Schubel. 1977. Seagrass ecosystem oceanography. Pp. 195-232. In: C. P. McRoy and C. Helfferich (eds.), *Seagrass Ecosystems*. Marcel Dekker, New York, NY.
- Caffrey, J. M. and W. M. Kemp. 1991. Seasonal and spatial patterns of oxygen production, respiration and root-rhizome release in *Potamogeton perfoliatus* L. and *Zostera marina* L. *Aquatic Botany* 40:109-128.
- Carlson, P. R., Jr., L. A. Yarbro, and T. R. Barber. 1994. Relationship of sediment sulfide to mortality of *Thalassia testudinum* in Florida Bay. *Bulletin of Marine Science* 54:733-746.
- Dan, A., A. Moriguchi, K. Mitsuhashi, and T. Terawaki. 1998. Relationship between *Zostera marina* and bottom sediments, wave action offshore in Naruto, Southern Japan. *Fisheries Engineering* 34: 229-204.
- Dennison, W. C., R. C. Aller, and R. S. Alberte. 1987. Sediment ammonium availability and eelgrass (*Zostera marina*) growth. *Marine Biology* 94:469-477.
- Edgar, G. J. and C. Shaw. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology* 194:107-131.

- Eldridge, P. M., J. E. Kaldy, and A. Burd. 2004. Stress response model for the tropical seagrass *Thalassia testudinum*: The interactions of light, temperature, sedimentation, and geochemistry. *Estuaries*, 6: 923-937.
- Eldridge, P. M. and J. W. Morse. 2000. A diagenetic model for sediment-seagrass interactions, *Marine Chemistry* 70:89-103.
- Erskine, J. M. and M. S. Koch. 2000. Sulfide effects on *Thalassia testudinum* carbon balance and adenylate energy charge. *Aquatic Botany* 67:275-285.
- Fonseca, M. S. and S. S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Ecology Progress Series* 171:109-121.
- Fonseca, M. S., J. C. Zieman, G. W. Thayer, and J. S. Fisher. 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. *Estuarine, Coastal and Shelf Science* 17:367-380.
- Fonseca, M. S. 1981. The interaction of a seagrass, *Zostera marina* L. with current flow. M.Sc. Thesis, University of Virginia, Charlottesville, VA, pp. 35.
- Frost, M. T., A. A. Rowden, and M. J. Attrill. 1999. Effect of habitat fragmentation on the macroinvertebrate infaunal communities associated with the seagrass *Zostera marina* L. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9:255-263.
- Gambi, M. C., A. R. M. Nowell, and P. A. Jumars. 1990. Flume observations on flow dynamics in *Zostera marina* (eelgrass) beds. *Marine Ecology Progress Series* 61:159-169.
- Ginsburg, R. N. and H. A. Lowenstam. 1958. The influence of marine bottom communities on the depositional environment of sediments. *Journal of Geology* 66:310-318.
- Goodman, J. L., K. A. Moore, and W. C. Dennison. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon, *Aquatic Botany* 50:37-47.
- Grady, J. R. 1981. Properties of sea grass and sand flat sediments from the intertidal zone of St. Andrew Bay, Florida. *Estuaries* 4:335-344.
- Harwell, M. C. and R. J. Orth. 1999. Eelgrass (*Zostera marina* L.) seed protection for field experiments and implications for large-scale restoration. *Aquatic Botany*, 64:51-61.
- Hebert, A. B., and J. W. Morse. 2003. Microscale effects of light on H₂S and Fe²⁺ in vegetated (*Zostera marina*) sediments. *Marine Chemistry* 81:1-9.
- Hebert, A. B., J. W. Morse, and P. M. Eldridge. 2007. Small-scale heterogeneity in the geochemistry of seagrass vegetated and non-vegetated estuarine sediments: causes and consequences. *Aquatic Geochemistry*, 13:19-39.
- Heiss, W. M., A. M. Smith, and P. K. Probert. 2000. Influence of the small intertidal seagrass *Zostera novazelandica* on linear water flow and sediment texture. *New Zealand Journal of Marine and Freshwater Research* 34:689-694.
- Hemminga, M. A. and C. M. Duarte. 2000. *Seagrass Ecology*. Cambridge University Press, Cambridge, UK. pp. 298.
- Höberg, P. and P. Jensen. 1994. Aluminum and uptake of base cations by tree roots: a critique of the model proposed by Sverdrup et al. *Water Air and Soil Pollution* 75:121-125.
- Holmer, M. and L. Laursen. 2002. Effect of shading of *Zostera marina* (eelgrass) on sulfur cycling in sediments with contrasting organic matter and sulfide pools. *Journal of Experimental Marine Biology and Ecology* 270:25-37.

- Holmer, M. and E. J. Bondgaard. 2001. Photosynthetic and growth response of eelgrass to low oxygen and high sulfide concentrations during hypoxic events. *Aquatic Botany* 70:29-38.
- Hoskin, C.M. 1983. Sediment in seagrasses near Link Port, Indian River, Florida. *Florida Scientist*. 46:153-161.
- Jahnke, R. A., C. R. Alexander, and J. E. Kostka. 2003. Advective pore water input of nutrients to the Satilla River estuary, Georgia, USA. *Estuarine, Coastal and Shelf Science* 56:641-653.
- Jones, W.B., L. A. Cifuentes, and J. E. Kaldy, 2003. Stable carbon isotope evidence for coupling between sedimentary bacteria and seagrasses in a sub-tropical lagoon. *Marine Ecology Progress Series* 255:15-25.
- Kalbfleisch, W. B. C. and B. Jones. 1998. Sedimentology of shallow, hurricane-affected lagoons: Grand Cayman, British West Indies. *Journal of Coastal Research* 14:140-160.
- Kaldy, J. E., P. M. Eldridge, L. A. Cifuentes, and W. B. Jones. 2006. Utilization of DOC from Seagrass Rhizomes by Sediment Bacteria: ¹³C Tracer Experiments and Modeling. *Marine Ecology Progress Series* 317:41-55.
- Kaldy, J. E. and K. H. Dunston. 2000. Above- and below-ground production, biomass and reproductive ecology of *Thalassia testudinum* (turtle grass) in a subtropical coastal lagoon. *Marine Ecology Progress Series* 193:271-283.
- Kenworthy, W. J. and M. S. Fonseca. 1992. The use of fertilizer to enhance growth of transplanted seagrasses *Zostera marina* L. and *Halodule wrightii* Aschers. *Journal of Experimental Biology and Ecology* 163:141-161.
- Kenworthy, W. J., J. C. Zieman, and G. W. Thayer. 1982. Evidence for the influence of seagrasses on the benthic nitrogen cycle in a coastal plain estuary near Beaufort, North Carolina (USA). *Oecologia* 54:152-158.
- Koch, E. W. 2001. Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24:1-17.
- Koch, E. W. 1999. Preliminary evidence on the interdependent effect of currents and porewater geochemistry on *Thalassia testudinum* Banks ex König seedlings. *Aquatic Botany* 63: 95-102.
- Koch, M. S. and J. M. Erskine. 2001. Sulfide as a phytotoxin to the tropical seagrass *Thalassia testudinum*: interactions with light, salinity and temperature. *Journal of Experimental Marine Biology and Ecology* 266:81-95.
- Koch, M. S., S. Schopmeyer, C. Kyhn-Hansen, and C. J. Madden. 2007. Synergistic effects of high temperature and sulfide on tropical seagrass. *Journal of Experimental Marine Biology and Ecology* 241: 91-101.
- Kraemer, G. P. and R. S. Alberte. 1993. Age related patterns of metabolism and biomass in subterranean tissues of *Zostera marina*. *Marine Ecology Progress Series* 95:193-203.
- Krumbein, W. C. and F. J. Pettijohn. 1938. Principles and methods of size analysis, in *Manual of Sedimentary Petrography*, K.F. Mather Ed., Appleton-Century-Crofts, New York. pp. 91.
- Kuenen, M. M. C. E. and A. O. Debrot. 1995. A quantitative study of the seagrass and algal meadows of the Spaanse Water, Curaçao, The Netherlands Antilles. *Aquatic Botany* 51:291-310.

- Lalumière, R., D. Messier, J.-J. Fournier, and C. P. McRoy. 1994. Eelgrass meadows in a low arctic environment, the northeast coast of James Bay, Québec. *Aquatic Botany* 47:303-315.
- Lee, K. S. and K. H. Dunton. 1996. Production and carbon reserve dynamics of the seagrass *Thalassia testudinum* in Corpus Christi Bay, Texas, USA. *Marine Ecology Progress Series* 143:201-210.
- Lee, S. Y., C. J. Kwon, K. S. Lee, and C. Choi. 2002. Distribution of eelgrass, *Zostera marina* L. on coasts of the Korean Peninsula: Preliminary study for eelgrass restoration. *Ocean and Polar Research* 24:55-61.
- Livingston, R. L., S. E. McGlynn, and X. Niu. 1998. Factors controlling seagrass growth in a gulf coastal system: Water and sediment quality and light. *Aquatic Botany* 60:135-159.
- Maier, C. M. and A. M. Pregnall. 1990. Increased macrophyte nitrate reductase activity as a consequence of groundwater input of nitrate through sandy beaches. *Marine Biology* 107:263-271.
- Marshall, N. and K. Lukas. 1970. Preliminary observations on the properties of bottom sediments with and without eelgrass, *Zostera marina*, cover. *Proceedings of the National Shellfish Association*. 60:107-111.
- Mattila, J., G. Chaplin, M. R. Eilers, K. L. Heck, J. P. O'Neal, and J. F. Valentine. 1999. Spatial and diurnal distribution of invertebrate and fish fauna of a *Zostera marina* bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). *Journal of Sea Research* 41:321-332.
- McGlathery, K. J., R. Marino, and R. W. Howarth. 1994. Variable rates of phosphate uptake by shallow marine carbonate sediments: Mechanisms and ecological significance. *Biogeochemistry* 25:127-146.
- Moore, K. A., R. J. Orth, and J. F. Norwak. 1993. Environmental regulation of seed germination in *Zostera marina* L. (eelgrass) in Chesapeake Bay: effects of light, oxygen and sediment burial. *Aquatic Botany* 45:79-91.
- Nepf, H. M. and E. W. Koch. 1999. Vertical secondary flows in submersed plant-like arrays. *Limnology and Oceanography* 44:1072-1080.
- Nienhuis, H. and B. H. H. DeBree. 1977. Production and ecology of eelgrass (*Zostera marina* L.) in the Grevelingen estuary, The Netherlands, before and after the closure. 1977. *Hydrobiologia* 52:55-66.
- Orth, R. J. 1977. The importance of sediment stability in seagrass communities. pp. 281-300. In: B. C. Coull (ed.), *Ecology of Marine Benthos*. University of South Carolina Press, Columbia, SC.
- Paula, J., P. Fidalgo e Costa, A. Martins, and D. Gove. 2001. Patterns of abundance of seagrasses and associated infaunal communities at Inhaca Island, Mozambique. *Estuarine Coastal and Shelf Science* 53:307-318.
- Penhale, P. A. and R. G. Wetzel. 1983. Structural and functional adaptations of eelgrass (*Zostera marina* L.) to the anaerobic sediment environment. *Canadian Journal of Botany* 61:1421-1428.
- Pedersen, M. F., C. M. Duarte, and J. Cebrian. 1997. Rates of changes in organic matter and nutrient stocks during seagrass colonization and stand development. *Marine Ecology Progress Series* 159:29-36.

- Pedersen, O., T. Binzer, and J. Borum. 2004. Sulphide intrusion in eelgrass (*Zostera marina* L.). *Plant, Cell and Environment* 27:595-602.
- Percival, J. B. and P. J. Lindsay. 1997. Measurement of physical properties of sediments. Pp. 7-44. In: A. Mudroch, J.M. Azcue, and P. Mudroch Eds. *Manual of Physical-Chemical Analysis of Aquatic Sediments*. Lewis Publishers. New York.
- Perez, M., J. Romero, C. M. Duarte, and K. Sand-Jensen. 1991. Phosphorus limitation of *Cymodocea nodosa* growth. *Marine Biology* 109:129-133.
- Perez, M., C. M. Duarte, J. Romero, K. Sand-Jensen, and T. Alcoverro. 1994. Growth plasticity in *Cymodocea nodosa* stands: The importance of nutrient supply. *Aquatic Botany* 47: 249-264.
- Peterson, C. H., H. C. Summerson, and P. B. Duncan. 1984. The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria mercenaria*. *Journal of Marine Research* 42:123-138.
- Peterson, B. J. and K. L. Heck, Jr. 2001. Positive interactions between suspension-feeding bivalves and seagrass - a facultative mutualism. *Marine Ecology Progress Series*. 213:143-155.
- Phillips, R. C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: a community profile. U.S. Fish and Wildlife Service, FWS/OBS-84/24 (repr.). pp. 8585.
- Posey, M. H. 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. *Ecology* 69:974-983.
- Scoffin, T. P. 1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *Journal of Sedimentary Petrology* 40:249-273.
- Short, F. T. 1983. The response of interstitial ammonium in eelgrass (*Zostera marina* L.) beds to environmental perturbations. *Journal of Experimental Marine Biology and Ecology* 68:195-208.
- Short, F. T. 1987. Effects of sediment nutrients on seagrasses: Literature review and mesocosm experiment. *Aquatic Botany* 27:41-57.
- Smith, R. D., A. M. Pregall, and R. S. Alberte. 1988. Effects of anaerobiosis on root metabolism of *Zostera marina* (eelgrass); implications for survival in reducing sediments. *Marine Biology* 98:131-141.
- Sprung, M. 1994. Macrobenthic secondary production in the intertidal zone of the Ria Formosa – a lagoon in Southern Portugal. 1994. *Estuarine Coastal and Shelf Science* 38:539-558.
- Stumm, W. and J. J. Morgan. 1981. *Aquatic Chemistry: an introduction emphasizing chemical equilibria in natural waters*, 2nd Edition, John Wiley & Sons, New York.
- Terrados, J., C. M. Duarte, M. D. Fortes, J. Borum, N. S. R. Agawin, S. Bach, U. Thampanya, L. Kamp-Nielsen, W. J. Kenworthy, O. Geertz-Hansen, and J. Vermaar. 1998. Changes in community structure and biomass of seagrass communities along gradients of siltation in SE Asia. *Estuarine Coastal and Shelf Science* 46:757-768.
- Terrados, J., C. M. Duarte, L. Kamp-Nielsen, N. S. R. Agawin, E. Gacia, D. Lacap, M. D. Fortes, J. Borum, M. Lubanski, and T. Greve. 1999. Are seagrass growth and survival constrained by the reducing conditions of the sediment? *Aquatic Botany* 65:175-197.
- Thayer, G. W., W. J. Kenworthy, and M. S. Fonseca. 1984. The ecology of eelgrass meadows of the Atlantic coast: A community profile. US Fish and Wildlife Service, FWS/OBS-84/02. pp. 147.

- Thom, R., A. Borde, S. Rumrill, D. L. Woodruff, G. D. Williams, J. Southard, and S. L. Blanton. 2001. Factors influencing the spatial and annual variability in eelgrass (*Zostera marina* L.) meadows in Pacific Northwest, USA, Systems. pp. 38-51. In: J. K. Parrish and K. Litle (eds.), PNCERS 2001 Annual Report. Coastal Oceans Program, National Oceanographic and Atmospheric Administration.
- Townsend, E. C. and M. S. Fonseca. 1998. Bioturbation as a potential mechanism influencing spatial heterogeneity of North Carolina seagrass beds. *Marine Ecology Progress Series* 169:123-132.
- van Katwijk, M. M., L. H. T. Vergeer, G. H. W. Schmitz, and J. G. M. Roelofis. 1997. Ammonium toxicity in eelgrass *Zostera marina*. *Marine Ecology Progress Series* 157:159-173.
- van Lent, F., P. H. Neinhuis, and J. M. Verschuure. 1991. Production and biomass of the seagrasses *Zostera noltii* Hornem, and *Cymodocea nodosa* (Ucria) Aschers. at the Banc d'Arguin (Mauritania, NW Africa): a preliminary approach. *Aquatic Botany* 41:353-367.
- Wanless, H. R. 1981. Fining-upwards sedimentary sequences generated in seagrass beds. *Journal of Sedimentary Petrology* 51:445-454.
- Webster, P. J., A. A. Rowden, and M. J. Attrill. 1998. Effect of shoot density on the infaunal macro-invertebrate community within a *Zostera marina* seagrass bed. *Estuarine, Coastal and Shelf Science* 47:351-357.
- Welsh, D. T., G. Castadelli, M. Bartoli, D. Poli, M. Careri, R. de Wit, and P. Viaroli. 2001. Denitrification in an intertidal seagrass meadow, a comparison of ¹⁵N-isotope and acetylene-block techniques: dissimilatory nitrate reduction to ammonia as a source of N₂O? *Marine Biology* 139:1029-1036.
- Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology*, 30: 277.
- Wood, E. J. F., W. E. Odum, and J. C. Zieman. 1969. Influence of seagrasses on the productivity of coastal lagoons. pp. 495-502. In: Ayala Castanares, A. and F.B. Phelger (eds.). *Coastal lagoons*. Universidad Nacional Autonoma de Mexico, Ciudad Universitaria, Mexico, D.F.
- Zimmerman, R. C., R. D. Smith, and R. S. Alberte. 1987. Is growth of eelgrass nitrogen limited? A numerical simulation of the effects of light and nitrogen on the growth dynamics of *Zostera marina*. *Marine Ecology Progress Series* 41:167-176.

Sources of Unpublished Data

- Boese, B. and D. Young. in prep. Pacific Coastal Ecology Branch, Western Ecology Division, U.S. EPA.

7.0 The Interaction of Epiphytes with Seagrasses under Nutrient Enrichment

Walter G. Nelson

7.1 Background

The surfaces of seagrass blades are often covered by a variable layer of epiphytes, which may respond in complex ways to variation in environmental nutrient concentrations and light availability. This chapter reviews the observational and experimental literature through approximately 2004 on the effects of nutrient enrichment on seagrass epiphytes. The goal was to determine whether there is an adequate understanding of the effects of epiphytes on seagrass growth and survival to allow incorporation of this factor in criteria protective of seagrasses.

Seagrass epiphytes are a diverse, mixed assemblage (Harlin 1980) of macroalgae (Phillips 1960; Humm 1964; Ballantine and Humm 1975; Hall and Eiseman 1981; Hall 1988), microalgae (e.g. Sand-Jensen 1977; Sand-Jensen and Borum 1984), and a variety of sessile animal groups including polychaetes, bryozoans, hydroids and tunicates (Kita and Harada 1962; Nagle 1968; Lewis and Hollingworth 1982). The term "epiphytes" will be used to refer to the combined microalgal, macroalgal, animal and inorganic components covering seagrass blades. Major reviews of seagrass epiphytes include Harlin (1980) and Borowitzka and Lethbridge (1989), while van Montfrans et al. (1984), Orth and van Montfrans (1984) and Jernakoff et al. (1996) summarized knowledge on epiphyte-seagrass interactions with a particular emphasis on micrograzing interactions.

While epiphytic algae may have some beneficial effects on seagrasses (Orth and van Montfrans 1984; Brandt and Koch 2003), negative impacts appear to predominate (Borowitzka and Lethbridge 1989). These effects include: 1) reduction in light available for photosynthesis, 2) a reduction in the rate of diffusion of materials such as CO₂ across the seagrass blade surface, and 3) an increase in physical drag, resulting in increased loss of leaves or plants. It has been suggested that seagrass leaves with heavy epiphyte cover may become more brittle and break off (Borowitzka and Lethbridge 1989), although quantitative data supporting this effect are limited (e.g. Heijs 1985). Harlin (1975) suggested that epiphytes may compete with seagrass for water column nutrients, but the magnitude of any effect should be minor relative the main effects listed above. Suggested benefits of epiphytes include serving as a UV-B filter, which might be most important in tropical, oligotrophic waters (Trocine et al. 1981; Brandt and Koch 2003), and as a factor potentially limiting desiccation damage for plants in the upper intertidal zone (Penhale and Smith 1977, and see Chapter 11).

Epiphytes are patchily distributed on seagrass blades (Figure 7.1), and are typically more abundant on the distal portions of all blades (Figure 7.2), and most abundant on the oldest blades within a plant. The mean life span of leaves will influence the degree to which epiphyte biomass can build up on seagrass blades. Typical life spans are *Z. marina* (27 - 63 d), *H. wrightii* (34 d), and *T. testudinum* (24 - 50 d) (Borowitzka and Lethbridge 1989). Rates of blade turnover for

seagrass can vary widely across seasons, and for *Z. marina* may range from 50-70 days in summer to a maximum leaf age of 200 days in winter (Borum et al. 1984). In some cases, low blade turnover rates can result in higher epiphytic biomass accumulation, and hence in increased light attenuation. Dixon and Kirkpatrick (1995) observed that light attenuation by epiphytes was highest during winter months in Sarasota Bay when leaf turnover rates were reduced. However, at higher latitudes where winter light may be limiting, winter may be a period of low epiphytic biomass in spite of lower blade turnover rate (Williams and Ruckelshaus 1993; Nelson and Waaland 1997).

Although there have been suggestions that seagrasses such as *Z. marina* contain compounds in the leaf tissue that may inhibit settlement by epiphytes, Borowitzka and Lethbridge (1989) concluded that there is little evidence that seagrasses have any means of inhibiting epiphyte colonization and growth.

Borowitzka and Lethbridge (1989) reviewed the evidence that translocation of nutrients from seagrass to epiphytes may occur. They suggested that the work by Brix and Lyngby (1985) showed that earlier reports of high rates of nutrient release from seagrass leaves was probably the result of methodological problems. Rates of nutrient release reported from seagrasses are too low to support levels of epiphyte growth generally observed, so the major source of nitrogen and phosphorus appears to be from the water column (Borowitzka and Lethbridge 1989). Thus seagrasses function primarily as a substratum supporting the growth of epiphytes, not as a primary source of nutrients.

7.2 Review of Relevant Research

7.2.1 Epiphyte Loads and Limitation of Seagrass Growth and Distribution

The dominant effect of heavy epiphytic cover appears to be decreased seagrass growth and a reduced potential for survival caused by reduced light availability (Sand-Jensen 1977; Borum and Wium-Anderson 1980, Bulthuis and Woelkerling 1983; Cambridge et al. 1986; Silberstein et al. 1986; Sand-Jensen and Revsbach 1987). Epiphytic shading has been suggested to be particularly important at lower ambient light levels (Morgan and Kitting 1984; Twilley et al. 1985; Wetzel and Neckles 1986).

Cambridge et al. (1986), working with seagrasses from Cockburn Sound, Australia, provided one of the first suggestions that high epiphytic loads resulting from eutrophic conditions directly causes loss of seagrasses. Transplantation experiments with *Posidonia sinuosa* seedlings resulted in leaf area ~60% lower for plants growing in Cockburn Sound after 48 d. Seedlings were heavily covered with macroepiphytes. Differences in leaf area may have been partly due to senescence and breakage of leaf tissue during a storm rather than strictly an effect of growth reduction, however. The study noted but did not quantify the presence of macroalgal blankets up to 1 m thick in Cockburn Sound, and the relative role of these macroalgae versus epiphytes in seagrass loss is unclear.

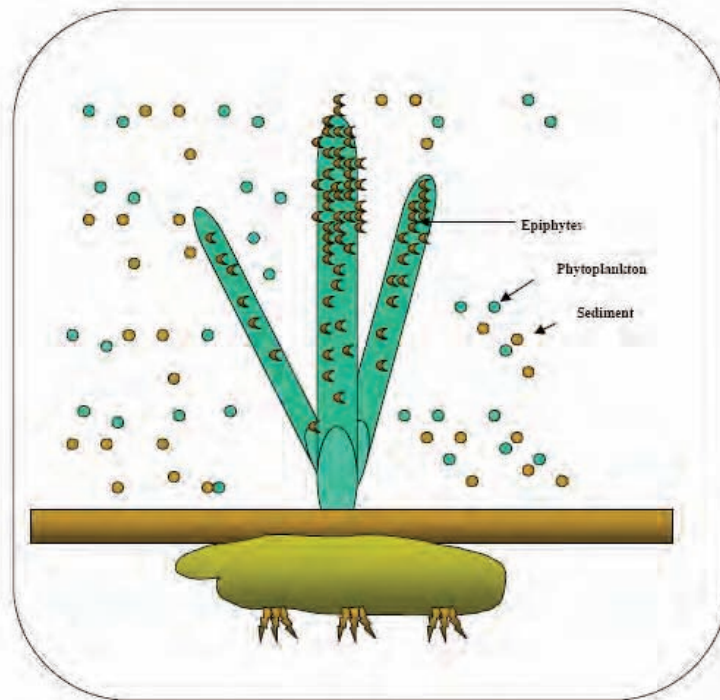


Figure 7.1. Schematic diagram of seagrass plant illustrating typical patterns of distribution of epiphytes within and among blades. Epiphyte cover increases from base to tip and from youngest to oldest blades.

For the freshwater macrophyte (*Littorella uniflora*) in Danish lakes, Sand-Jensen (1990) found a relation of epiphytic load, nutrient load, and depth distribution. Maximum depth of macrophyte distribution was inversely related to epiphytic load, and was 0.2 m in the eutrophic lake, versus 2.2 m in the most oligotrophic lake. Mean light attenuation due to epiphytes was 82% (range 64-100%) in the eutrophic lake, and this factor accounted for 62% of the total (water column + epiphyte) light attenuation at the leaf surface, versus only 5% at the most oligotrophic lake.

Studies of light attenuation by epiphytes accumulating on seagrasses or on seagrass mimics (glass slides or plastic strips) indicate that the presence of epiphytes can lead to nearly 100% attenuation of incident light to the surface of individual seagrass blades (Table 1). When averaged over entire plants to account for heterogeneity of epiphyte distribution on blades of different ages, average light reduction to a seagrass plant is more typically 50-60% (Harden 1994). Annual averages of light reduction, resulting from seasonal variation in epiphytic load,

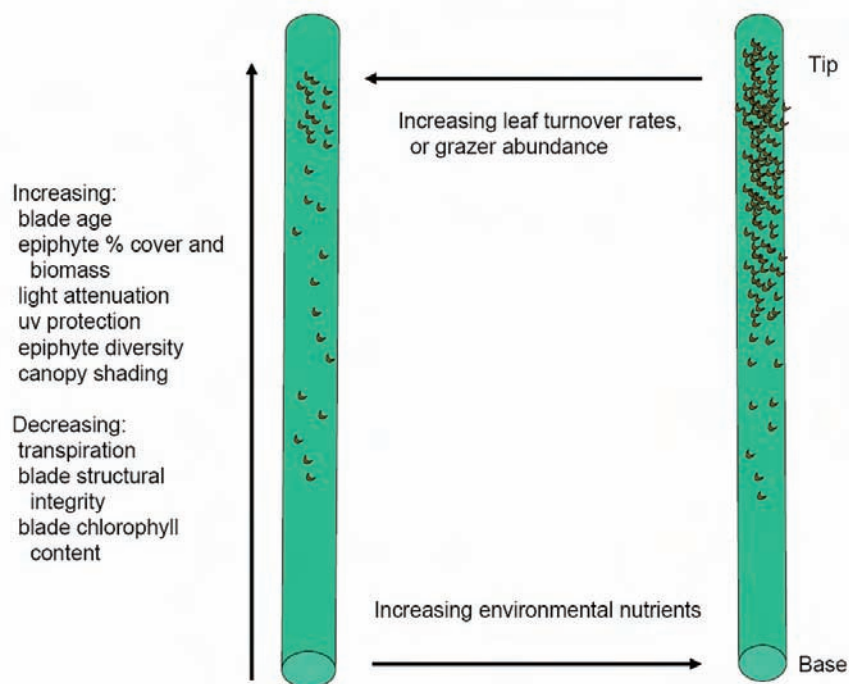


Figure 7.2. Horizontal arrows indicate external factors influencing abundance of seagrass epiphytes. The vertical arrow indicates the variation in important factors associated with epiphytes along the transition from the basal to distal portions of seagrass blades.

were in the range of 32-36% for *Thalassia testudinum* at the deep edge of its distribution in Tampa Bay, Florida (Dixon and Kirkpatrick 1995; Dixon 2000). Monthly averages of light reduction ranged from 17-59%, while shallower sites where light was not limiting tended to have greater light attenuation by epiphytes (Dixon 2000).

A review of seagrass light attenuation studies (Brush and Nixon 2002), suggests that studies which have estimated light attenuation using epiphyte suspensions (see Table 7.1) may overestimate the attenuation of light for high epiphytic loads. They observed that highest epiphytic biomass tended to be generated by larger arborescent algae which tended to float away from the seagrass blade when submersed, thus allowing more light to reach the blade than would be predicted by the suspension approach.

There are few direct measurements of the effect of epiphytes on photosynthesis rates. Sand-Jensen (1977) demonstrated that diatom epiphytes reduced the photosynthetic rate of *Z. marina* both by acting as a barrier to carbon uptake and by reducing light intensity. At constant illumination, reduction of leaf photosynthesis was a function of bicarbonate concentration, with a maximum reduction of 45% at low concentrations, and no reduction at higher concentrations. Results indicated that epiphytes are a barrier to carbon uptake because they change the initial slope of the photosynthesis (P/I) curve. The inhibition of photosynthesis was proportionally

greater (58% vs. 31%) at lower light intensities, again suggesting the impact of epiphytes may be most severe when ambient light is low.

Using in situ incubations of clipped blades of *Halodule wrightii*, Morgan and Kitting (1984) examined the relative productivity of the seagrass and its epiphytes over a range of light intensities. At light levels $\geq 50\%$ of surface illumination, the epiphytic loads did not appear to have a shading effect. This assessment was based on what was deemed a “limited” increase of *Halodule* productivity with higher light levels, although the magnitude of the production increase was nearly 50%. In the absence of direct measurements of production with and without epiphytes, the conclusion of no shading effect at high light levels appears tenuous.

Extrapolation of results from productivity measurements on clipped blades to prediction of impacts on rooted plants under field conditions are difficult. Because epiphytes are also affected by ambient light levels, the net effect of epiphyte shading on seagrass survival is likely to be determined by complex interactions. For example, Neverauskas (1988) experimentally reduced light to *Posidonia* spp. (*P. sinuosa* and *P. angustifolia*) by 50% using shade cloth over small experimental quadrats (0.0625 m^2) with rhizome connections severed. Epiphyte biomass decreased from an initial value of approximately 30 g m^{-2} to near 0 after nine months of shading. The shoot density of *Posidonia* did not show a decrease until after 9 months, although leaf density began to decline after 3 months. Rhizome reserves were sufficient to sustain the plants beyond the point in time where low light levels had greatly reduced epiphytic loads.

In spite of multiple uncertainties, the guidance document for management of seagrasses for Chesapeake Bay (U.S. EPA 2003) incorporates the concept of a percent of surface illumination available at the leaf surface to account for the additional attenuation of light resulting from the presence of epiphytes. The percent light-at-the-leaf (PLL) can be used to establish a minimum light level required for persistence of seagrass in the face of combined light attenuation in the water column, and that due to epiphytes. PLL values are calculated by the formula:

$$\text{PLL} = 100 [e^{-(K_d)(Z)}][e^{-(K_e)(B_e)}]$$

where K_d is the light extinction coefficient in the water column, Z is the depth, K_e is the epiphyte biomass specific PAR attenuation coefficient, and B_e is the epiphyte biomass per unit seagrass biomass. Specific equations for determination of K_e and B_e are given in U.S. EPA (2003, Table VII-1). Data for the tidal-fresh, oligohaline, mesohaline, and polyhaline salinity zones of Chesapeake Bay (Appendix J, U.S. EPA 2003), indicated that the additional reduction in light intensity at the leaf surface due to epiphytes was 20-60 % in the lower salinity regions, and 10-50% in the mesohaline and polyhaline regions. Using an average of 30% additional light attenuation due to epiphytes leads to the calculation that the PLL requirement to sustain seagrasses is 9% of surface illumination for tidal fresh and oligohaline areas, and 15% for mesohaline and polyhaline areas.

Table 7.1. Studies of light attenuation by epiphytes in coastal marine systems, revised and expanded from Table 1, Brush and Nixon (2002). Maximum epiphyte density reported here is the highest measured in the study, and not necessarily the highest recorded in light absorbance measurements, and may differ from that reported by Brush and Nixon (2002). A: artificial light; N: natural light.

Macrophyte Study area (Reference)	Method	Light source	Max epiphyte density (mg cm ⁻² leaf)	Max % light absorbance (mean)	Comments, Reference
<i>Zostera marina</i>					
Øresund, Denmark	Suspension	A	1.9 (DW)	99.7	Borum & Wiium-Andersen 1980
Øresund, Denmark	Suspension	A	9.5 (DW)	99.7	Same absorbance data as 1980; Borum et al. 1984
Roskilde, Denmark	Suspension	A	.0039 (chl a)	76	May underestimate total absorption, Borum 1987
Mesocosms, VA	Suspension	A	20(DW)		Measured spectral absorption, Neckles (1993 and unpubl. data), cited in Brush & Nixon 2002
Mesocosms, RI	Scraped and unscraped leaves	N	99 (DW)	90	Effect varied with type of epiphyte, Brush & Nixon 2002
Elkhorn Slough, CA	Scraped and unscraped leaves	A		60	Measured spectral absorption, underestimated epiphyte biomass by use of phospholipid measure only; Drake et al. 2003
<i>Thalassia testudinum</i>					
Terminos Lagoon, Mexico	Suspension	N	17 (DW)		Kemp et al. (1988), cited in Brush & Nixon 2002
Tampa Bay, FL	Suspension	A		81(51)	Excluded necrotic blade tips, underestimates total absorbance; Dixon & Kirkpatrick 1995
Indian River Lagoon, FL	Scraped and unscraped leaves	A	18 (DW)	85 (61)	Harden 1994
Bahamas	Scraped and unscraped leaves	A		36	Measured spectral absorption, underestimated epiphyte biomass by use of phospholipid measure only; Drake et al. 2003
<i>Halodule wrightii</i>					
Tampa Bay, FL	Suspension	A		99(48)	Excluded necrotic blade tips, underestimates total absorbance; Dixon & Kirkpatrick 1995
Indian River Lagoon, FL	Scraped and unscraped leaves	A	30 (DW)	90 (60)	Harden 1994

<i>Syringodium fliforme</i>						
Indian River Lagoon, FL	Scraped and unscraped leaves	A	22 (DW)	97 (61)	Harden 1994	
<i>Posidonia oceanica</i>						
Mediterranean Sea, Spain	Collection on GF/F filters	A	71 (DW)	95(~70)	Measured only pigment effect, underestimated total light absorbance, Cebrián et al. 1999	
<i>Heterozostera tasmanica</i>						
Victoria, Australia	Scraped and unscraped leaves	A	3.3 (DW)	75	Bulthuis & Woelkerling 1983	
Artificial substrates						
Cockburn Sound, Australia	Growth on glass slides	A	0.004 (chl a)	96(63)	Silberstein et al. 1986	
Success Bank, Australia	Growth on plastic slides	A	4.2 (AFDW)		Burt et al. (1995), cited in Brush & Nixon 2002	
Banc d'Arguin, Mauritania	Growth on glass slides	N	3 (DW)		Hootsmans et al. (1993), cited in Brush & Nixon 2002	
Delaware Inland Bays	Scraped and unscraped mylar strips	N	17 (DW)		Glazer (1999), cited in Brush & Nixon 2002	
Virginia, Maryland Bays	Scraped and unscraped plastic strips	A	4 (DW)	96	Measured spectral absorption, Brandt & Koch 2003	

7.3 Role of Nutrient Loads in Determining Epiphytic Load

7.3.1. Field Observations

There are a number of correlative studies of field distribution of epiphyte load versus nutrient concentrations which suggest nutrient enrichment increases epiphyte loading. Orth and Van Montfrans (1984) reviewed a number of studies from freshwater systems that indicated a relation between nutrient enrichment, epiphyte increases, and decrease or loss of macrophytes. Borum (1985) observed that the biomass of epiphytes on *Zostera marina* increased exponentially with increasing total N concentration in the water column along a transect in Roskilde Fjord, Denmark. The relative increase of epiphytes was 10 times greater than the phytoplankton response.

Neverauskas (1987) studied the impact of sewage sludge outfalls on the seagrasses *Posidonia* and *Amphibolis* near Adelaide, Australia. Near the outfall, total loss of seagrass was observed within 4 years after discharge was initiated, while partially affected areas at greater distances from the outfalls showed high epiphytic loads. Experiments placing artificial substrata along a distance gradient from the outfall showed highest epiphytic recruitment at sites closest to outfall.

Examination of accumulation rates of epiphytes on *Heterozostera tasmanica* in Victoria, Australia showed that highest epiphyte levels were found at the site with the highest nutrient input (Bulthius and Woelkerling 1983). During conditions of peak epiphytic growth, biomass accumulated at rates that were estimated to diminish light below the compensation point within 36 days, about half the mean life span of the seagrass leaves. However, the expression of impacts on the seagrass tended to be site specific.

Silberstein et al. (1986) compared characteristics of the seagrass *Posidonia australis* and its epiphytes between two sites, one of which was near a sewage dispersal line. Epiphytic loads, measured as chlorophyll per unit leaf area, were higher at the sewage site which also had lower seagrass standing stock, shoot density, flowers, leaf production, and growth. However, the study did not sample prior to the introduction of sewage, and it is possible some differences were present before the sampling. Also, grazer densities were not compared at the sites.

In a comparison of epiphyte and seagrass (*Thalassia*, *Syringodium*, *Halodule*) production rates from three sites in Florida and the Bahamas, Jensen and Gibson (1986) found that the highest epiphytic biomass were at sites with the highest concentrations of phosphorus and silicate. Both Tomasko and Lapointe (1991) and Lapointe et al. (1994) also found relationships between total nitrogen concentrations and seagrass and epiphyte response patterns in the Florida Keys and Caribbean for *Thalassia testudinum* and *Halodule wrightii*. Sites with highest nutrients were found offshore both from a populated island with septic tanks and a bird rookery island, and were associated with higher epiphytic loads, and low shoot density and biomass (Tomasko and Lapointe 1991). In a further comparative study, nutrient concentration zones at sites in the Florida Keys were defined as hypereutrophic, eutrophic, mesotrophic, or oligotrophic

corresponding to total N concentrations in winter of 38.8, 30.3, 21.6, and 12.8 μM , respectively. Seagrasses from the oligotrophic zone typically had lowest epiphyte levels, while those in the hypereutrophic and eutrophic zones had high levels of epiphytes and mat-forming macroalgae, and low shoot densities and productivity.

Epiphyte loads on *Thalassia testudinum* were also measured along nutrient gradients of differing scales in Florida Bay by Frankovich and Fourqurean (1997). At a fine scale, they found significantly higher epiphyte loads nearest a bird rookery island, with the enhancement effect decreasing at between 15 and 30 m from the island. Across Florida Bay as a whole, they found that epiphyte load was weakly correlated with total phosphorus, and concluded that epiphyte levels are not very sensitive to moderate nutrient enrichment. They suggested that epiphytes played no role in generating the Florida Bay seagrass die off, but were instead stimulated by nutrients released by dying seagrass. They concluded that epiphyte load may be only a late response to nutrient enrichment, and thus not a sensitive nutrient condition indicator.

Emphasizing the spatial variability in the expression of epiphyte standing stock in response to nutrients loads, Tomasko et al. (1996) found that although the greatest epiphyte biomass at sites within Sarasota Bay, Florida was found on one date at the site with highest total nitrogen loading, the general pattern of epiphyte biomass showed little relation to the pattern of nitrogen loadings. Relative grazer densities, which might have affected the results, were not reported, however.

Results of an intensive data collection effort in multispecies seagrass beds of the Indian River Lagoon, Florida both confirm the importance of spatial variability and also emphasize the complexity of interpretations possible from field data (Hanisak 2001). In spite of spatial differences in nutrient concentrations at study sites, there were no consistent spatial patterns in epiphyte load. Seasonality was a much stronger effect on epiphyte levels than location. However, when all data were combined to a single mean per site, above-ground seagrass biomass at a site decreased as a function of increased epiphyte biomass. Mean epiphyte load in turn decreased as grazer abundance increased. Mean grazer abundance showed a positive relationship to above-ground seagrass biomass. As Hanisak (2001) points out, these results may be interpreted in two ways: 1) that decreased grazing rates allow increased epiphytes, which reduce seagrass biomass, or 2) that increased seagrass biomass increases the amount of grazers which leads to reduced epiphytes.

The number of in situ experimental nutrient additions in seagrass beds was relatively limited until recently. Harlin and Thorne-Miller (1981) performed single nutrient addition experiments to *Z. marina* beds in Rhode Island over a 2-3 month period. While responses of seagrass and macroalgae were noted, epiphyte biomass was not quantified, and the nutrient additions did not alter the species composition of epiphytic algae. Williams and Ruckelshaus (1993) conducted in situ, short term (15 d) ammonium enrichment experiments of both water and sediments in *Z. marina* beds in Puget Sound, WA. There was no significant increase in epiphyte

biomass, and in fact epiphyte biomass was significantly reduced by water column ammonium enrichment.

7.3.2 Mesocosm nutrient addition experiments

Conditions of various mesocosm experiments conducted to examine the effects of nutrient additions on seagrasses are summarized in Table 7.2. Unfortunately, as noted by Murray et al. (2000), the extreme variation in mesocosm size, flow rates, type of nutrient addition (pulse versus continuous addition), and presence or absence of grazers within experimental systems make generalizations difficult.

Large mesocosm ponds were used by Twilley et al. (1985) to expose *Potamogeton perfoliatus* and *Ruppia maritima* to pulse additions of nitrogen and phosphorus (Table 7.2). Concentrations of N greater than 60 μ M caused declines in the vascular plants in the ponds in 6-10 weeks. At the highest nutrient addition levels, phytoplankton blooms in the ponds were evident. Dense epiphytes developed on plants in all nutrient addition treatments. Epiphytic cover was estimated to decrease >80 % of light at the leaf surface at highest nutrient concentrations. Epiphytic cover was shown to decrease macrophyte photosynthesis, but the authors concluded that the negative effect of epiphytes was insufficient to eliminate macrophytes without the additional effect of light attenuation by water column phytoplankton.

The effect of elevated ammonium levels in the water column on *Z. marina* were examined by Williams and Ruckelshaus (1993) who used experimental nutrient diffuser systems in small laboratory aquaria (Table 7.2). Epiphyte biomass was positively correlated with ammonium concentration, and eelgrass growth also decreased significantly with increased epiphyte biomass. Epiphyte loads on the order of 75mg/shoot decreased eelgrass growth rates, and at loads above 100 mg/shoot, growth rates were reduced by 50%.

Using mesocosm tanks of 800 l capacity with high water turnover rates (200 % per day), Short et al. (1995) applied bags of slow release fertilizer to achieve a continuous release of nutrients. Tanks included mud snails which may have done some grazing on seagrass. Nutrient additions decreased eelgrass shoot densities by >50%. There were no interaction effects between nutrient addition and light reduction treatments, suggesting that the mechanism causing plant decrease in nutrient treatments was light limitation. With full light levels, large increases of phytoplankton, macroalgae and epiphytes occurred relative to controls. These results also show that under nutrient addition, the magnitude of response of epiphytes can be limited if water column light levels are reduced. Kopp (1999) also used continuous nitrate additions in combination with a 45% light reduction treatment. There was no statistically significant effect of nitrate treatment, while the reduced light treatment significantly reduced epiphytic load. However, while not significantly different, the highest epiphytic loads observed were under high light and high nutrient conditions.

Several studies with large mesocosms have used pulse additions of nutrients to examine responses of *Zostera marina*. The experiment reported by Lin et al. (1996) had limited water

turnover (5% per day), while all tanks included a variety of fish and invertebrates, but without significant numbers of grazers. There was no increase in epiphyte biomass on eelgrass leaves in any treatment. The lack of epiphyte response was attributed to the fact that the mesocosm contained multiple trophic pathways, with the primary nutrient response having occurred in the form of phytoplankton blooms. These results led the authors to suggest that epiphyte biomass may be strongly regulated by light limitation, which is consistent with other mesocosm study results (Short et al., 1995; Moore and Wetzel, 2000). The authors concluded that elevated nutrient levels are not necessarily predictive of an epiphyte increase.

Taylor et al. (1999) used the same experimental systems and similar conditions to those used by Lin et al. (1996), but applied a wider range of nutrient treatments. No significant effects of nutrient treatments were observed on epiphytes, *Z. marina*, or drift algae in the mesocosms. In these experiments, a brown tide bloom occurred in the control tanks which may have made differences with nutrient enrichment treatments more difficult to detect. Using the same experimental systems, but switching to a continuous addition of nutrients, Bintz et al. (2003) examined the interactive effects of water temperature and nutrient addition. Epiphytic levels were shown to significantly increase in warm, nutrient addition treatments as compared to unenriched warm or mean temperature treatments, or cool temperature treatments, either ambient or nutrient enriched.

Experiments by Burkholder et al. (1992) using mesocosms of 1570 l with pulse additions of nutrients and limited water turnover showed no effect of nutrient additions on epiphytic loads on *Z. marina*, measured as cell counts rather than biomass. Grazer densities in both nutrient additions and controls tended to be quite high in these experiments, and may explain the lack of epiphyte response.

Moore and Wetzel (2000) used replicated 110 l aquaria to test effects of elevated nutrients and reduced light on *Zostera marina*. The experiment used 16 turnovers per day with continuous flow nutrient additions, and tanks included moderate densities of gastropod grazers. Epiphyte responses were highly dependent on treatment, with only the spring experiment at high light levels showing a major (10 times) elevation in epiphyte biomass, principally due to macroepiphytes rather than microepiphytes. Both above-ground and below-ground biomass showed reductions in apparent response to an epiphyte load of $\sim 16 \text{ g g}^{-1}$ of eelgrass. The experimental design did not examine the response of seagrass and epiphytes under the combination of low light, high nutrients, and low grazers.

Mesocosm studies of nutrient impacts are more limited for *Thalassia testudinum* and *Halodule wrightii*. Tomasko and Lapointe (1991) and Lapointe et al. (1994) conducted a series of mesocosm experiments (Table 7.2) examining effects of added nutrients alone or in combination with light reduction. Using daily pulsed addition of nutrients, both N and P additions resulted in increases in epiphyte biomass (as a percent of seagrass biomass versus controls). There was also a decrease in rhizome growth rates with nutrient additions in both

Table 7.2. Summary of laboratory microcosm and mesocosm nitrogen and phosphorus enrichment assays using seagrasses. Treatment Abbreviations: C = control (ambient conditions), +N = NO₃ addition, +P = PO₄ addition, +NP = NO₃ and PO₄ addition, +A = NH₄ addition, +AN = NH₄ and NO₃ addition, +AP = NH₄ and PO₄ addition, +NAP = NO₃ and NH₄ and PO₄ addition, +G = grazer addition, D = depleted NH₄, ? = unable to determine from information in reference. All ratios presented in Treatment Variables are relative nutrient concentrations.

Species: Location	Treatment Variables	Nutrient Addition Method	Mesocosm Volume: Turnover rate	Shoots per meso- cosm: m ⁻²	Algae	Grazers	Experimental Results and Comments
<i>Zostera marina</i>							
Netherlands: van Katwijk et al.1997	Temperature: 15, 20 °C Sediment: Mud, Sand Nutrients: +AN (9.3;25;25;25;50;25;12 5;75;75;125;25 µM)	Continuous feed from stock solutions	19.4 l : 1.2 d ⁻¹	40	Epiphytes not apparently measured	No	+A - toxic at 125 µM, probably toxic as low as 25 µM +N - no effect Toxicity ↑ with ↑ temperature.
Washington: Williams & Ruckelshaus 1993	Sediment: C, D, +A (5, 20 µM) Water: C, +A (10, 33 µM)	Continuous feed from stock solutions	75 l: 61 d ⁻¹	26-62	Epiphyte biomass measured	Amphipods possibly present	Epiphyte biomass ↑ with ↑ water column NH ₄ . Eelgrass leaf growth ↓ with ↑ epiphyte biomass.
Rhode Island: Lin et al. 1996	Nutrients: C, +P(.7µM), +N(7.6µ M), +NP(7.6,.7µM), +A(7.6,.7µM)	Once per day, dissolved	4554 l: .05 d ⁻¹	518: 250 m ⁻²	Epiphyte biomass measured	Added inverts & fish, no epiphyte grazers	No ↑ in epiphytes in nutrient additions. Phytoplankton blooms may have limited epiphyte response.

Rhode Island: Taylor et al. 1999	Nutrients: C, +AP (.9,1;1.8,2.3.6,3;7.3,. 6 μ M)	Once per day, dissolved	4554 l: .05 d ⁻¹	518: 250 m ⁻²	Epiphyte biomass measured: added 4 macroalgae	Added inverts & fish, bottom grazing snails @100	No significant treatment effects on seagrass, epiphytes or drift algae.
Rhode Island: Kopp 1999	Nutrients: C, +N (50, 75, 100, 150 μ M) Light: C, 55%	Continuous feed from stock header tanks	150 l: 1 d ⁻¹	50: 200 m ⁻²	Epiphyte biomass measured after 1 month	No	No sig. effect of nitrate treatment on epiphytes (although trend for ↑ for high light, high nutrient), low light level ↓ epiphyte load significantly.
Rhode Island: Bintz et al. 2003	Nutrients: C, +NP (6.5,.5 μ M) Temperature: 3 levels (9 yr mean, 4 ° above, 4 ° below)	Continuous feed from drip bags	4554 l: .1 d ⁻¹	580: 365 m ⁻²	Epiphyte biomass measured: added 2 macroalgal species	Grass shrimp @ 8 per tank	Epiphytes ↑ in warm, nutrient enriched versus cool treatments.
Virginia: Neckles et al. 1993	Nutrients: C, +AN (16.4-37.8 μ M) P (1.8- 3.3 μ M) Grazers: C, +G	Continuous feed from stock solutions	110 l: 16 d ⁻¹	92 (15/pot): 1500 m ⁻²	Epiphyte biomass measured	Snails, isopods, amphipods 9- 11.4 x10 ³ m ⁻²	Seasonally varied grazer densities and nutrients. Epiphyte biomass ↑ with ↑ nutrients.
Virginia: Moore & Wetzel 2000	Light: C, 9,28,42% Nutrients: C, +ANP (7-16.3; 6.6-7.7; 1.4- 1.8 μ M)	Continuous feed from stock solutions	110 l: 16 d ⁻¹	92 (15/pot): 1500 m ⁻²	Epiphyte biomass measured	Snails; 5,200 m ⁻¹	Shading inhibited epiphytes and eelgrass. Epiphytes ↑ only with high light and nutrients in Spring.
North Carolina: Burkholder et al. 1992	Nutrients: C,+N (3.5,7, 35 μ M)	Pulse, daily	1570 l: 0.5-0.1 d ⁻¹ over a 2 hr period only	~2000: 700 m ⁻²	Epiphytes assessed as cell counts only	Amphipods + isopods @ 25-58 x10 ³ m ⁻²	No significant treatment effects on epiphytes. Variable macroalgal response. Grazer density was high in spring experiment.

North Carolina: Burkholder et al. 1994	Nutrients: Spring C,+N (5 μ M) Fall C, +N (10 μ M)	Pulse, daily	1570 l: 0.5-0.1 d ⁻¹ over a 2 hr period only	~2500: 800 m ⁻²	Epiphytes assessed as cell counts only	Amphipods @ ~7-80 x10 ³ m ⁻²	Epiphyte biomass was “negligible”. Grazer densities very high in both spring and fall experiments
New Hampshire: Short et al. 1995	A)Light: 11,21,41,61, 94% of ambient B) Nutrients: C,+AP @ 6x C) Light: 1,41,94% x Nutrients: C,+AP (7- 13 μ M) (1.4-2.4 μ M)	Continuous, from bags of slow release fertilizer	800 l, 2 d ⁻¹	200: 133 m ⁻²	Macroalgae and epiphyte biomass assessed	Added amphipod predators and mud snails	Epiphytes \uparrow compared to control in high light treatment. Variable responses to nutrients at lower light levels.
<i>Thalassia testudinum</i>							
Florida: Tomasko and Lapointe 1991	Light: C, -33% Nutrients: C, +ANP (10,1,10 μ M)	Pulse daily, from solutions	120 l: (?50 d ⁻¹) static for 14 hr d ⁻¹	? 9	Epiphyte biomass measured	Added mixed grazers, density?	+ANP \uparrow epiphytes and \downarrow rhizome growth. Shading \downarrow epiphyte effect.
Florida: LaPointe et. al 1994	Nutrients: C, +A (10 μ M), +P (1 μ M)), +AP (10,1 μ M)	Pulse daily, from solutions	120 l: 50 d ⁻¹ static for 14 hr d ⁻¹	?	Epiphyte biomass measured	Added mixed grazers, density ?	Both +A and +P \uparrow epiphytes and \downarrow rhizome growth.
<i>Halodule wrightii</i>							
Florida: LaPointe et. al 1994	Nutrients: C, +A, +P, +AP	Pulse daily, from solutions	120 l: 50 d ⁻¹ static for 14 hr d ⁻¹	?	Epiphytes assessed	Added mixed grazers, density?	Both +A and +P \uparrow epiphytes; only +P \downarrow rhizome growth.
North Carolina: Burkholder et al. 1994	Nutrients: Fall C, +N (10 μ M)	Pulse, daily	1570 l: 0.5-0.1 d ⁻¹ over a 2 hr period only	~3768: 1200 m ⁻²	Epiphytes assessed as cell counts only	Amphipods @ ~7-80 x10 ³ m ⁻²	Epiphyte biomass was “negligible”. Grazer densities very high in both spring and fall experiments

<i>Ruppia maritima</i>							
Maryland: Twilley et al. 1985	Nutrients: C, +NAP @ 3 levels	Pulse, 6 @10 d intervals, fertilizer	340,000 l: pulse turnover @8-9 d	? 50-80% cover	Epiphytes measured	? not specified but likely	+N at >60 μM caused seagrass ↓. Epiphytes ↑.
North Carolina: Burkholder et al. 1994	Nutrients: Fall C, +N (10 μM)	Pulse, daily	1570 l: 0.5-0.1 d ⁻¹ over a 2 hr period only	~3768: 1200 m ⁻²	Epiphytes assessed as cell counts only	Amphipods @ ~7-80 x10 ³ m ⁻²	Epiphyte biomass was “negligible”. Grazer densities very high in both spring and fall experiments
<i>Potamogeton perfoliatus</i>							
Maryland: Murray et al. 2000	A) C, +NP as Pulse, +NP as Continuous (both 38 μM N, 3.8 μM P) B) Nutrients: D(2-4 μM), +N (20-24 μM) Water exchange: 1,3,6,12 d ⁻¹ C) Nutrients: +N (<10 μmol l ⁻¹ N, >30 μmol l ⁻¹ N) Grazers: C, +G	A) Pulse and continuous B, C) Continuous	A) 10 l B) 100 l: see Treatment Variables C) 100 l: 1 d ⁻¹	?	Epiphyte biomass measured	A) No B) No C) 0.25 gm ⁻² , amphipods, density ?	B, C) Used sequential runs for different treatments, therefore interpretation of results is difficult because of uncontrolled time effect. See text for effects.

Halodule and *Thalassia*. When light reduction was combined with nutrient addition, the shading reduced the relative increase in epiphyte biomass.

7.4 Role of Grazers in Control of Epiphyte Loads

There is a variety of evidence emerging that complex interactions among trophic components in seagrass systems may determine the ultimate extent of the effect of epiphytes on their seagrass substrate.

A range of studies summarized in reviews by van Montfrans et al. (1984), Orth and van Montfrans (1984) and Jernakoff et al. (1996) have indicated either that decreased epiphytic load caused by grazer removal tends to improve seagrass growth (e.g. Hootsman and Vermaat 1985; Howard and Short 1986; Phillipart 1995) or that there was inhibition of seagrass growth caused by increased epiphytic loads. These impacts were observed for a wide variety of seagrass species including *Zostera marina* and *Thalassia testudinum*, and *Halodule wrightii*. An important issue that remains is whether there is evidence that grazing can control epiphyte growth under high nutrient loading conditions, and whether there is any specific nutrient elevation level where grazer controls will likely be overwhelmed. Controlled experiments combining both nutrient elevation and grazer density manipulations remain relatively limited.

Although they examined both the effects of grazers and nutrient additions on seagrass and epiphyte production, Williams and Ruckelshaus (1993) did not conduct simultaneous experiments with both factors. Mesocosm treatments without the isopod grazer *Idotea resicata* had epiphyte biomass almost 300% higher than in tanks with grazers at field densities. However, the growth response of *Z. marina* after about two months was not significantly different, presumably because total epiphyte load in the ungrazed treatment was still below the critical threshold for seagrass growth impacts.

In a series of mesocosm experiments, Neckles et al. (1993) varied nutrient concentrations and epiphyte grazer densities to examine the relative effects of these factors on growth of *Z. marina*. Experiments were conducted in early and late summer, fall and spring, with nutrient enrichment levels and grazer density and relative composition all varying with season to better reflect natural conditions. Experimental outcomes also varied with season. Epiphyte biomass increased with nutrient enrichment in all experiments, although marginally so in the fall experiment. Grazer impacts were greatest in the two summer treatments, which also corresponded to the treatments with the highest density of grazers. The late summer experiment, with a grazer density of 11,400 m⁻², showed a 592% increase in epiphyte biomass in ungrazed treatments. The authors noted that seagrass blades in ungrazed treatments at this time of year had dense tunicate populations, suggesting that the grazers inhibited tunicate recruitment as well as presumably affecting algal epiphytes. The effects of nutrient enrichment were never large enough to overwhelm the impact of grazers. In all experiments the ungrazed, ambient nutrient level treatments always possessed epiphyte biomass greater than or equal to the grazed, nutrient enriched treatments. As the authors point out, the fact that absolute nutrient level, water temperature, grazer density, and grazer composition all varied simultaneously among the

experiments makes it impossible to identify the causes of the differential seasonal responses of epiphytes to grazers that were observed.

In addition to the factors identified by Neckles et al. (1993), mesocosm experiments have demonstrated that grazing impacts on epiphytes may be influenced by a variety of hydrodynamic factors. Murray et al. (2000) conducted a series of experiments with the brackish water macrophyte *Potamogeton perfoliatus* to examine the relative impacts of the frequency and timing of nutrient additions, the residence time of water within experimental systems, and relative trophic complexity of food chains in the mesocosms. By scaling macrophyte and epiphyte responses relative to the controls in each experiment, the magnitudes of response to treatments could be assessed. Grazing had the largest relative effect on macrophyte growth, except under high nutrient loads. With high levels of nutrients, changes from pulsed to continuous nutrient addition and from high to low water exchange rates, both led to larger relative responses in macrophyte growth.

In terms of the ability of grazers to control epiphyte biomass under elevated nutrient loads, amphipod grazers were able to decrease epiphytic biomass by 56% relative to controls under low nutrient addition conditions, which was associated with a 43% increase in macrophyte biomass (Murray et al. 2000). However, while the grazers reduced the magnitude of the epiphyte response under high nutrient loads (+63% for grazed versus +112% for ungrazed), the grazing impact had no ameliorating effect on the macrophyte response, which was -88% for macrophyte growth in both grazed and ungrazed treatments relative to controls.

Any factor that influences either the densities of grazers, such as predation, or the feeding efficiency of the grazers on epiphytes, such as hydrodynamics, may determine the level of impact that epiphytes may have on seagrasses. Schanz et al. (2002) observed that biomass of epiphytes on *Z. marina* was highest in sites exposed to water movement, and that there was little epiphyte coverage on seagrass in sheltered areas where abundance of the grazing snail *Hydrobia ulvae* was extremely high ($151 \times 10^3 \text{ m}^{-2}$). In situ flume experiments showed that snail density was negatively correlated with current velocity, while epiphyte cover was positively correlated with velocity. The authors propose a trophic cascade effect caused by hydrodynamics, where fast currents remove or inhibit feeding of micrograzers, thus releasing epiphytes from grazing pressure. However, Caine (1980) found an opposite pattern, with epiphyte biomass and abundance of the grazing amphipods *Caprella laeviscula* both being higher in quiet water sites versus sites with active wave action. On individual seagrass blades, grazer biomass and epiphyte biomass were also positively correlated. These differences suggest that species specific differences in the dominant grazers in differing locales may determine the influence of hydrodynamics. *Caprella*, which is adapted to a clinging existence, may be far less subject to high current speeds than small grazing snails. Given the wide range of consumption rates for different epiphyte grazers (reviewed by Jernakoff et al. 1996, Table 3), grazer community composition will clearly be critical to determining the ultimate level of effect on seagrass epiphytes.

7.5 Research Gaps

Epiphyte biomass appears to be a major response variable in determining the ability of seagrasses to grow and survive under in situ conditions. In early studies, determination of photosynthesis/ irradiance relationships for seagrasses were typically done in the laboratory with epiphytes removed from the seagrass shoots (e.g. Williams and McRoy 1982; Rice et al. 1983). More recent studies have shown that not only does the presence of epiphytes affect light quantity, but also spectral light quality can be altered. Effects of epiphytes on the light available to seagrasses is thus an important factor which must be quantified in order to be able to develop accurate seagrass-stressor response models for evaluating overall impacts of nutrients to seagrass systems.

However, the question of whether high epiphyte loads alone can directly result in seagrass loss does not yet appear to have been conclusively answered. Responses of seagrass ecosystems to nutrient enrichment typically involve multiple trophic pathways, with relative responses in phytoplankton, macroalgae and epiphytic algae all potentially occurring. High loadings of epiphytes clearly can substantially reduce available illumination to seagrass plants. In some systems, light reduction to seagrasses from epiphyte load may reach 60 to 80%, at least seasonally (Harden 1994; Dixon 2000). Epiphyte grazing studies generally show that removal of epiphytes enhances seagrass growth. These observations are strongly suggestive that persistent heavy epiphyte cover will lead to seagrass loss, but to date there is no experimental evidence that would identify epiphyte load as the single causative factor responsible for seagrass loss under high nutrient loads.

The role of epiphytic cover in affecting light availability, and hence seagrass distribution, may be an essential element to include in development of management criteria for protection of coastal seagrass beds. Tomasko (pers. comm.) has found that, for *Thalassia testudinum* in several southwest Florida embayments, there is considerable variation from bay to bay in the minimum light requirements for the species even over this relatively limited geographic region. Part of this variation appears to be spatial variation in the typical epiphytic load. The role of grazers in determining the ultimate impact of epiphyte increases in response to eutrophication still represents a significant source of uncertainty in the development of protective nutrient criteria for seagrasses. The technical guidance for ambient water quality criteria for Chesapeake Bay (U.S. EPA 2003) provides an explicit formulation for including epiphyte loads in estimating light available at the seagrass leaf surface. This is an important step forward, but the model formulations do not yet appear to have been extensively validated for other systems.

Mesocosm research has shown that different algal components may dominate in the biomass response to nutrient enrichment in spite of similar initial conditions, and that temperature, nutrient exposure regime and other factors such as grazing intensity may all influence the outcome of nutrient enrichment. The laboratory results help support observations that suggest that seagrass losses, even in different regions of the same limited system, may be caused by competition between seagrasses and different algal components (Short and Burdick 1996). Such results together suggest that if seagrass stress-response models are to be used to

evaluate whether sets of environmental conditions are adequately protective of seagrasses, such models must account for impacts from multiple pathways, and must account for effects of trophic cascades.

7.6 Literature Cited

- Ballantine, D. and H. J. Humm. 1975. Benthic algae of the Anclote estuary I. Epiphytes of seagrass leaves. *Florida Scientist* 38:148-162.
- Bintz, J. C., S. W. Nixon, B. A. Buckley, and S. L. Granger. 2003. Impacts of temperature and nutrients on coastal lagoon plant communities. *Estuaries* 26:765-776.
- Borowitzka, M. A. and R. C. Lethbridge. 1989. Seagrass Epiphytes. pp. 458-499. In A. W. D. Larkum, A. J. McComb and S. A. Shepherd (eds). *Biology of Seagrasses: A treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier, Amsterdam. pp. 841.
- Borum, J. 1985. Development of epiphyte communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Marine Biology* 87:211-218.
- Borum, J. 1987. Dynamics of epiphyton on eelgrass (*Zostera marina* L.) leaves: Relative roles of algal growth, herbivory, and substratum turnover. *Limnology and Oceanography* 32:986-992.
- Borum, J. and S. Wium-Andersen. 1980. Biomass and production of epiphytes on eelgrass (*Zostera marina* L.) in the Øresund, Denmark. *Ophelia*, Supplement 1:57-64.
- Borum, J., H. Kaas, and S. Wium-Andersen. 1984. Biomass variation and autotrophic production of an epiphyte-macrophyte community: II. Epiphyte species composition, biomass and production. *Ophelia* 23:165-179.
- Brandt, L. A. and E. W. Koch. 2003. Periphyton as a UV-B filter on seagrass leaves: a result of different transmittance in the UV-B and PAR ranges. *Aquatic Botany* 76:317-327.
- Brix, H. and J. E. Lyngby. 1985. Uptake and translocation of phosphorus in eelgrass (*Zostera marina*). *Marine Biology* 90:111-116.
- Brush, M. J. and S. W. Nixon. 2002. Direct measurements of light attenuation by epiphytes on eelgrass *Zostera marina*. *Marine Ecology Progress Series* 238:73-79.
- Bulthuis, D. A. and W. J. Woelkerling. 1983. Biomass accumulation and shading effects of epiphytes on leaves of the seagrass *Heterozostera tasmanica*, in Victoria, Australia. *Aquatic Botany* 16:137-148.
- Burkholder, J. M., K. M. Mason, and H. B. Glasgow Jr. 1992. Water column nitrate enrichment promotes decline of eelgrass *Zostera marina*: evidence from seasonal mesocosm experiments. *Marine Ecology Progress Series* 81:163-178.
- Burkholder, J. M., H. B. Glasgow Jr., and J. E. Cooke. 1994. Comparative effects of water-column nitrate enrichment on eelgrass *Zostera marina*, shoalgrass *Halodule wrightii*, and widgeongrass *Ruppia maritima*. *Marine Ecology Progress Series* 105:121-138.
- Caine, E. A. 1980. Ecology of two littoral species of caprellid amphipods (Crustacea) from Washington, USA. *Marine Biology* 56:327-335.
- Cambridge, M. L., A. W. Chiffings, C. Brittan, L. Moore, and A. J. McComb. 1986. The loss of seagrass in Cockburn Sound, Western Australia. II. Possible causes of seagrass decline. *Aquatic Botany* 24:269-285.

- Cebrian, J., S. Enriques, M. Fortes, N. Agawin, J. E. Vermaat, and C. M. Duarte. 1999. Epiphyte accrual on *Posidonia oceanica* (L.) delile leaves: implication for light absorption. *Botanica Marina* 42:123-128.
- Dixon, L. K. 2000. Establishing light limitations for the seagrass *Thalassia testudinum*: An example from Tampa Bay, Florida. pp. 9-32. In: S. A. Bortone (ed.), *Seagrasses: Monitoring, Ecology, Physiology and Management*. CRC Press, Boca Raton. pp. 318.
- Dixon, L. K. and G. Kirkpatrick. 1995. Light attenuation with respect to seagrasses in Sarasota Bay, Florida. Sarasota Bay National Estuary Program. Mote Marine Laboratory Report no. 407. pp. 53.
- Drake, L. A., F. C. Dobbs, and R. C. Zimmerman. 2003. Effects of epiphyte load on optical properties and photosynthetic potential of the seagrasses *Thalassia testudinum* Banks ex König and *Zostera marina* L. *Limnology and Oceanography* 48:456-463.
- Frankovich, T. A. and J. W. Fourqurean. 1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Marine Ecology Progress Series* 159:37-50.
- Hall, M. O. 1988. Dynamics and interactions of epiphytic macroalgae and meiofauna on the seagrass *Thalassia testudinum*. Ph. D. dissertation, University of South Florida, Tampa, pp. 170.
- Hall, M. O. and N. J. Eiseman. 1981. The seagrass epiphytes of the Indian River, Florida. I. Species list with descriptions and seasonal occurrences. *Botanica Marina* 24:139-146.
- Hanisak, M. D. 2001. Photosynthetically Active Radiation, Water Quality and Submerged Aquatic Vegetation in the Indian River Lagoon. Final Report for Contract No. 93W199 to the St. Johns River Water Management District, Palatka, Florida. pp. 502 .
- Harden, S. W. 1994. Light requirements, epiphyte load and light reduction for three seagrass species in the Indian River Lagoon, Fl. M.S. thesis, Florida Institute of Technology, Melbourne Fl. pp. 130.
- Harlin, M. M. 1975. Epiphyte - host relations in seagrass communities. *Aquatic Botany* 1:125-131.
- Harlin, M. M. 1980. Seagrass epiphytes. pp. 117-151. In: R. C. Phillips and C. P. McRoy (eds). *Handbook of Seagrass Biology: An Ecosystem Perspective*. Garland STPM Press, New York. pp. 353.
- Heijs, F. M. L. 1985. The seasonal distribution and community structure of the epiphytic algae on *Thalassia hemprichii* (Ehrenb.)Aschers. from Papua New Guinea. *Aquatic Botany* 21:295-324.
- Hootsmans, M. J. M. and J. E. Vermaat. 1985. The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. *Aquatic Botany* 22:83-88.
- Howard, R. K. and F. T. Short. 1986. Seagrass growth and survivorship under the influence of epiphyte grazers. *Aquatic Botany* 24:287-302.
- Humm, H. J. 1964. Epiphytes of the seagrass, *Thalassia testudinum*, in Florida. *Bulletin of Marine Science of the Gulf and Caribbean* 14:306-341.
- Jensen, P. R. and R. A. Gibson. 1986. Primary production in three subtropical seagrass communities: A comparison of four autotrophic components. *Florida Scientist* 49:129-141.

- Jernakoff, P., A. Brearley, and J. Nielsen. 1996. Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. *Oceanography and Marine Biology Annual Reviews* 34:109-162.
- Kita, T. and E. Harada, 1962. Studies on epiphytic communities. I. Abundance and distribution of microalgae and small animals on *Zostera* blades. *Publications of the Seto Marine Biological Laboratory* 10:245-257.
- Kopp, B. S. 1999. Effects of nitrate fertilization and shading on physiological and biomechanical properties of eelgrass (*Zostera marina* L.). Ph. D. Dissertation, University of Rhode Island, pp. 187.
- Lapointe, B. E., D. A. Tomasko, and W. R. Matzie. 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. *Bulletin of Marine Science* 54:696-717
- Lewis, J. B. and C. E. Hollingworth. 1982. Leaf epifauna on the seagrass *Thalassia testudinum*. *Marine Biology* 71:41-49.
- Lin, H.-J., S. W. Nixon, D. I. Taylor, S. L. Granger, and B. D. Buckley. 1996. Responses of epiphytes on eelgrass, *Zostera marina* L., to separate and combined nitrogen and phosphorus enrichment. *Aquatic Botany* 52:243-258.
- Moore, K. A. and R. L. Wetzel. 2000. Seasonal variations in eelgrass (*Zostera marina* L.) responses to nutrient enrichment and reduced light availability in experimental ecosystems. *Journal of Experimental Marine Biology and Ecology* 244:1-28.
- Morgan, M. D. and C. L. Kitting. 1984. Productivity and utilization of the seagrass *Halodule wrightii* and its attached epiphytes. *Limnology and Oceanography* 29:1066-1076.
- Murray, L., R. B. Sturgis, R. D. Bartleson, W. Severn, and W. M. Kemp. 2000. Scaling submersed plant community responses to experimental nutrient enrichment. pp. 241-257. In: S. A. Bortone (ed). *Seagrasses: Monitoring, Ecology, Physiology and Management*. CRC Press, Boca Raton. pp. 318.
- Nagle, J. S. 1968. Distribution of the epibiota of macroepibenthic plants. *Contributions in Marine Science* 13:105-144.
- Neckles, H. A., R. L. Wetzel, and R. J. Orth. 1993. Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina* L.) dynamics. *Oecologia* 93:285-295.
- Nelson, T.A. and J.R. Waaland. 1997. Seasonality of eelgrass, epiphyte and grazer biomass and productivity in subtidal eelgrass meadows subjected to moderate tidal amplitude. *Aquatic Botany* 56:51-74.
- Neverauskas, V. P. 1987. Accumulation of periphyton biomass on artificial substrates deployed near a sewage sludge outfall in South Australia. *Estuarine, Coastal and Shelf Science* 25:509-519.
- Neverauskas, V. P. 1988. Response of a *Posidonia* community to prolonged reduction in light. *Aquatic Botany* 31: 361-366.
- Orth, R. J. and J. van Montfrans. 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. *Aquatic Botany* 18:43-69.
- Penhale, P. and W. O. Smith, Jr. 1977. Excretion of dissolved organic carbon by eelgrass (*Zostera marina*) and its epiphytes. *Limnology and Oceanography* 22:400-407.
- Phillipart, C. J. M. 1995. Effect of periphyton grazing by *Hydrobia ulvae* on the growth of *Zostera noltii* on a tidal flat in the Dutch Wadden Sea. *Marine Biology* 122:431-437.

- Phillips, R. C. 1960. Observations of the ecology and distribution of the Florida seagrasses. Florida. State Board of Conservation Marine Laboratory Professional Paper Series No. Two. 72 pp.
- Rice, J. D., R. P. Trocine, and G. N. Wells. 1983. Factors influencing seagrass ecology in the Indian River Lagoon. *Florida Scientist* 46:276-286.
- Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquatic Botany* 3:55-63.
- Sand-Jensen, K. and J. Borum. 1984. Epiphyte shading and its effect on photosynthesis and diel metabolism of *Lobelia dortmanna* L. during the spring bloom in a Danish lake. *Aquatic Botany* 20:109-119.
- Sand-Jensen, K. 1990. Epiphyte shading: its role in resulting depth distribution of submerged aquatic macrophytes. *Folia Geobotanica et Phytotaxonomica, Praha*. 25:315-320.
- Sand-Jensen, K. and N. P. Revsbach. 1987. Photosynthesis and light adaptation in epiphyte-macrophyte associations measured by oxygen microelectrodes. *Limnology and Oceanography* 32:452-457.
- Schanz, A., P. Polte, and H. Asmus. 2002. Cascading effects of hydrodynamics on an epiphyte-grazer system in intertidal seagrass beds of the Wadden Sea. *Marine Biology* 141:287-297.
- Short, F. T. and D. M. Burdick. 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. *Estuaries* 19:730-739.
- Short, F. T., D. M. Burdick, and J. E. Kaldy III. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnology and Oceanography* 40:740-749.
- Silberstein, K., A. W. Chiffings, and A. J. McComb. 1986. The loss of seagrass in Cockburn Sound, Western Australia. III. The effect of epiphytes on productivity of *Posidonia australis* Hook. F. *Aquatic Botany* 24:355-371.
- Taylor, D. I., S. W. Nixon, S. L. Granger, and B. A. Buckley. 1999. Responses of coastal lagoon plant communities to levels of nutrient enrichment: a mesocosm study. *Estuaries* 22:1041-1056.
- Tomasko, D. A. and B. E. Lapointe. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies. *Marine Ecology Progress Series* 75:9-17.
- Tomasko, D. A., C. J. Dawes, and M. O. Hall. 1996. The effects of anthropogenic enrichment on turtle grass (*Thalassia testudinum*) in Sarasota Bay, Florida. *Estuaries* 19:448-456.
- Trocine, R. P., J. D. Rice, and G. N. Wells. 1981. Inhibition of seagrass photosynthesis by ultraviolet-B radiation. *Plant Physiology* 168:74-81.
- Twilley, R. R., W. M. Kemp, K. W. Staver, J. C. Stevenson, and W. R. Boynton. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects on production of plants and associated communities. *Marine Ecology Progress Series* 23:179-191.
- U.S. EPA. 2003. Ambient water quality criteria for dissolved oxygen, water clarity and chlorophyll *a* for the Chesapeake Bay and its tidal tributaries. U.S. EPA, Office of Water and Office of Science and Technology. EPA 900-R-03-002.

- van Katwijk, M. M., L. H. T. Vergeer, G. H. W. Schmitz, and J. G. M. Roelofs. 1997. Ammonium toxicity in eelgrass *Zostera marina*. Marine Ecology Progress Series 157:159-173.
- Van Montfrans, J., R. L. Wetzel, and R. J. Orth. 1984. Epiphyte-grazer relationships in seagrass meadows: consequences for seagrass growth and production. Estuaries 7:289-309.
- Wetzel, R. L. and H. A. Neckles. 1986. A model of *Zostera marina* L. photosynthesis and growth: simulated effects of selected physical-chemical variables and biological interactions. Aquatic Botany 26:307-323.
- Williams, S. L. and C. P. McRoy. 1982. Seagrass productivity: the effect of light on carbon uptake. Aquatic Botany 12:321-344.
- Williams, S. L. and M. H. Ruckelshaus. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. Ecology 74:904-918.

8.0 Macroalgal Interactions with the Seagrasses *Zostera* spp. and *Thalassia testudinum*

David R. Young

8.1 Background

The declining distributions of seagrasses, including *Zostera* and *Thalassia*, often are attributed to excessive accumulations of macroalgae, which in turn are attributed to anthropogenic nutrient loadings (Chapter 2). In this chapter we address the following questions:

1. What is the evidence from field surveys suggesting negative effects of macroalgae on *Zostera* and *Thalassia*?
2. Is there corresponding evidence from field manipulations or laboratory experiments?
3. Is there evidence of positive effects of macroalgae on *Zostera* and *Thalassia*?

Where available, information on the mechanisms involved in the effect(s) also is presented.

8.2 Field Evidence Suggesting Macroalgal Impacts on *Zostera*

There have been numerous reports in recent decades of an inverse relationship between the abundance of macroalgae (principally green macroalgae such as *Ulva*, *Chaetomorpha*, and *Cladophora* species) and the distribution and abundance of *Zostera* species and other seagrasses (Table 8.1). The general conclusion is that *Zostera* distributions have been impacted by increases in macroalgal abundance resulting from eutrophication of near shore marine/estuarine waters. The comprehensive summary *Seagrass Ecology* (Hemminga and Duarte 2000) states: “The wealth of reports on seagrass decline following eutrophication renders the negative effect of marine eutrophication on seagrass stands an indisputable fact, and indicates that it most likely is the main cause of seagrass decline worldwide.” Although there is some evidence that high levels of nitrate and ammonium can be directly toxic to seagrasses (Burkholder et al. 1992, 1994; Van Katwijk et al. 1997), most researchers have attributed this decline to light reduction caused by excess nutrient stimulation of phytoplankton, epiphytes, and/or macroalgae.

In one of the first reports of macroalgal effects, den Hartog and Polderman (1975) noted that in the Dutch Waddenzee, “*Ulva* especially can form thick deposits on the mud flats, suffocating underlying *Zostera* stands.” Two processes that could cause this “suffocation” are prevention of oxygenation of the bottom sediment by direct contact with the water column, and reduction in delivery of oxygen via the lacunae to the rhizosphere from reduced photosynthesis by the shaded eelgrass (Penhale and Wetzel 1983). Both conditions could lead to prolonged periods of sediment anoxia, with the excessive organic loadings from the *Ulva* mats yielding high concentrations of dissolved sulfide, a known phytotoxin, in the pore water (Goodman et al. 1995).

Table 8.1. Relationships between macroalgal abundance and the distribution or abundance of *Zostera marina*, *Z. noltii*, and *Thalassia testudinum*, in chronological order.

Algal Taxon	Effect	Location	Reference
<i>Zostera marina</i>			
<i>Ulva</i>	<i>Zostera</i> suffocated	Netherlands Coast	den Hartog and Polderman (1975)
<i>Chaetomorpha</i>	macroalgae replaced <i>Zostera</i>	North Sea	Nienhuis (1983)
macroalgae	<i>Zostera</i> declined	Coast of Poland	Plinski and Florczyk (1984)
macroalgae	no effect	Coast of Ireland	Whelan and Cullinane (1985)
<i>Ulva</i>	<i>Zostera</i> uprooted, buried	Northeast Pacific	Kentula and McIntire (1986)
<i>Ulva</i>	macroalgae replaced <i>Zostera</i>	Venice Lagoon	Sfriso et al. (1989)
macroalgae	macroalgae replaced <i>Zostera</i>	Coast of Denmark	Funen County Council (1991)
macroalgae	<i>Zostera</i> declined	Coast of Poland	Kruk-Dowgiallo (1991)
macroalgae	<i>Zostera</i> declined	Coast of Poland	Ciszewski et al. (1992)
macroalgae	macroalgae replaced <i>Zostera</i>	Northwest Atlantic	Valiela et al. (1992)
<i>Ulva</i>	<i>Zostera</i> declined	Northwest Atlantic	Short et al. (1993)
<i>Cladophora</i>	<i>Zostera</i> declined	Coast of Denmark	Thybo-Christesen et al. (1993)
<i>Ulva</i>	<i>Zostera</i> bed suffocated	SW Coast of England	den Hartog (1994)
macroalgae	macroalgae replaced <i>Zostera</i>	Northwest Atlantic	Lyons et al. (1995)
<i>Ulva</i> , <i>Chaetomorpha</i>	<i>Zostera</i> declined	North Sea	Nienhuis (1996)
macroalgae	macroalgae replaced <i>Zostera</i>	Coast of Portugal	Oliveira and Cabecadas (1996)
macroalgae	macroalgae replaced <i>Zostera</i>	Baltic Sea	Schramm (1996)
<i>Cladophora</i> , <i>Gracilaria</i>	decreased meadow area	Northwest Atlantic	Short and Burdick (1996)
<i>Ulva</i>	shading killed <i>Zostera</i>	Venice Lagoon	Coffaro and Bocci (1997)
<i>Ulva</i>	macroalgae replaced <i>Zostera</i>	Coast of Portugal	Flindt et al. (1997)
<i>Cladophora</i> , <i>Gracilaria</i>	shading killed <i>Zostera</i>	Northwest Atlantic	Hauxwell et al. (1998)
macroalgae	macroalgae replaced <i>Zostera</i>	Temperate Zone	Raffaelli et al. (1998)
macroalgae	loss of seagrass	Northwest Atlantic	Bricker et al. (1999)
macroalgae	macroalgae replaced <i>Zostera</i>	Northwest Atlantic	Valiela et al. (2000a)
macroalgae	macroalgae replaced <i>Zostera</i>	Northwest Atlantic	Bowen and Valiela (2001)
<i>Cladophora</i> , <i>Gracilaria</i>	removal increased <i>Zostera</i>	Northwest Atlantic	Deegan et al. (2002)
macroalgae	<i>Zostera</i> declined	Northwest Atlantic	Hughes et al. (2002)
macroalgae	macroalgae replaced <i>Zostera</i>	Coast of Denmark	Nielsen et al. (2002)
<i>Cladophora</i> , <i>Gracilaria</i>	macroalgae replaced <i>Zostera</i>	Northeast Atlantic	Hauxwell et al. (2003)
macroalgae	no displacement	Northeast Pacific	Kentula and DeWitt (2003)
<i>Ulva</i>	no effect	Northeast Pacific	Thom et al. (2003)
macroalgae	macroalgae replaced <i>Zostera</i>	Adriatic Coast of Italy	Curiel et al. (2004)

<i>Zostera noltii</i>			
<i>Ulva</i>	<i>Zostera</i> suffocated	Netherlands Coast	den Hartog and Polderman (1975)
<i>Ulva</i>	macroalgae replaced <i>Zostera</i>	Venice Lagoon	Sfriso et al. (1989)
macroalgae	little effect	Dutch Wadden Sea	Philippart and Dijkema (1995)
<i>Ulva</i>	macroalgae replaced <i>Zostera</i>	Spanish Atlantic Coast	Niell et al. (1996)
<i>Ulva</i> , <i>Chaetomorpha</i>	<i>Zostera</i> declined	North Sea	Nienhuis (1996)
<i>Ulva</i>	macroalgae replaced <i>Zostera</i>	Portuguese Atlantic	Oliveira and Cabecadas (1996)
<i>Ulva</i>	macroalgae replaced <i>Zostera</i>	Northwest Atlantic	Flindt et al. (1997)
<i>Ulva</i>	macroalgae replaced <i>Zostera</i>	Portuguese Atlantic	Pardal et al. (2000)
<i>Ulva</i>	macroalgae replaced <i>Zostera</i>	Portuguese Atlantic	Cardoso et al. (2004)
<i>Ulva</i>	macroalgae replaced <i>Zostera</i>	Portuguese Atlantic	Patricio et al. (2004)
<i>Thalassia testudinum</i>			
macroalgae	decreased productivity	Gulf of Mexico	Cowper (1978)
<i>Chaetomorpha</i> , <i>Acetabularia</i>	uprooted; stopped recolonization	Mexican Caribbean	Merino et al. (1992)
<i>Eucheuma</i>	possible competition	Gulf of Mexico	Perez-Enriquez (1996)
macroalgae	no effect	Gulf of Mexico	Bell and Hall (1997)
macroalgae	possible competitor	Columbian Caribbean	Angel and Polania (2001)
macroalgae	potential threat	Gulf of Mexico	Kopecky and Dunton (2006)

Nienhuis (1983) observed that eelgrass abundance in a southwest Netherlands' estuary dropped by about 50% between 1978 and 1980. He listed a number of possible causes including macroalgal competition, and suggested that the most plausible explanation for the decrease was an increase in organic matter deposition on the bottom following increased nitrogen loadings to the estuary, which in turn caused rapid anoxia of the sediments. This increase in organic matter deposition could have produced "a surplus of toxic substances," killing the root and rhizome system. Two potential phytotoxins which could have been produced in high concentrations under such circumstances are dissolved sulfide (Goodman et al. 1995) and ammonium (Van Katwijk et al. 1997; 2000).

A mixed bed of *Z. marina* and *Z. noltii* in Langstone Harbor, England was completely destroyed by a thick blanket of *Ulva* spp., due to prolonged anaerobic conditions under the algal mat with corresponding high levels of sulfide and ammonia (den Hartog 1994). However, Whelan and Cullinane (1985) found no significant interaction between macroalgae and eelgrass in southwest Ireland.

Although there was no evidence of causality, Thybo-Christesen et al. (1993) noted a significant change in the vegetation in Danish coastal waters, with the appearance of filamentous algal mats being associated with a substantial decrease in the abundance of eelgrass. Working in Venice Lagoon, Sfriso et al. (1989) found that high nutrient loads in the lagoon in the 1970s were followed in the 1980s by a major shift in macrophyte composition. *Z. marina* and *Z. noltii* beds were replaced by "nitrophile species," principally *Ulva rigida*. In some shallow areas of the

lagoons, this macroalga occupied 100% of the bottom at an abundance exceeding 10 kg/m² wet weight, leading to periodic occurrences of water column anoxia and extensive mortality of macrofauna.

Flindt et al. (1997) compared two other European estuaries with Venice Lagoon. In the Mondego River estuary of Portugal, major reductions of *Z. noltii* beds were observed, apparently as the result of blooms of the green macroalgae *Ulva* spp. (Pardal et al. 2000). In Denmark's Roskilde Fjord, which experienced increased nutrient loading from urbanization of the watershed, increased agricultural fertilization, and increased atmospheric deposition, eelgrass meadows also were substantially reduced. However, in this case the direct cause appears to have been increased biomass of phytoplankton and epiphytic algae. Coffaro and Bocci (1997) modeled the competition of resources by the green macroalgal species *U. rigida* and *Z. marina* in Venice Lagoon, concluding that both nitrogen availability and water velocity influenced the structure of the primary producer community, and that competition for light was a major factor in the interaction between the macroalgae and eelgrass.

Losses of eelgrass and other seagrass in recent decades also have been reported and extensively studied in the U.S.A. Orth and Moore (1983) analyzed extensive data sets on submerged aquatic vegetation (SAV) from Chesapeake Bay. They found that, in Virginia, the abundances of seagrass beds dominated by *Z. marina* and *Ruppia maritima* decreased sharply in the early 1970s; similar decreases in SAV in Maryland were observed. These authors suggested that this decline may be related to factors affecting the quantity and quality of light reaching the plants. However, they did not discuss a specific mechanism (e.g., macroalgal increases) for such an effect.

Valiela et al. (1992) conducted an extensive study of the sources and effects of nutrient enrichment in Waquoit Bay, Massachusetts. They concluded that increased development of watersheds there led to increased groundwater nutrient concentrations, which in turn led to increased abundances of macroalgae and major reductions in distributions of eelgrass. Continuing this research, Lyons et al. (1995) concluded that, in this bay, the abundance of macroalgae increased linearly with nitrogen loading while the abundance of eelgrass decreased exponentially. They also reported that, as salt marsh area increased, eelgrass biomass also increased, suggesting that salt marshes might serve as a buffer against watershed inputs of nutrients. Short and Burdick (1996) analyzed data from aerial photographs and ground surveys in the Waquoit Bay National Estuarine Research Reserve, relating the loss in eelgrass areal extent to housing development and groundwater loadings of nitrogen in the sub-basins of the watershed. The direct effect of these loadings varied from basin to basin, but included stimulation of phytoplankton, epiphytic growth on the eelgrass, and macroalgae. The authors concluded that in one area, "the main algal competitor causing a decline in eelgrass habitats was unattached macroalgae [sic] (*Gracilaria* sp., *Cladophora* sp.), which smothered and crowded out eelgrass plants."

Valiela et al. (1997) continued and expanded this work. The increase of nutrient loading in estuaries was found to increase macroalgal nitrogen uptake rate, tissue nitrogen content,

photosynthetic rate, and growth rate. Although the effects of such loadings are mitigated by fringing salt marshes and higher rates of tidal exchange, high nitrogen loadings and resultant macroalgal blooms can significantly alter estuarine ecosystems. Effects include interception of nutrients released from sediments, change in the flux of carbon through the food web, alteration of the oxygenation of the water and sediments, and changes in the benthic fauna. Valiela et al. (2000a; 2000b) subsequently reported a successful mathematical model of the watershed nitrogen loadings of Waquoit Bay. Hauxwell et al. (2003) extended their studies in Waquoit Bay, showing an exponential decrease in eelgrass shoot density and bed area as nitrogen loads increased. They recommended that these variables be used for routine monitoring of eelgrass health. They also noted that the relationship between nitrogen loading and eelgrass health was indirect; the direct effect was increased growth and standing stock of algae (water column algae, epiphytes, and macroalgae), causing light limitation of eelgrass. A major effect, however, was severe light limitation to newly recruiting shoots by shading from macroalgal canopies ≤ 15 cm in height.

There are few reports of the interaction between macroalgae and eelgrass on the Pacific Coast of the U.S.A. Phillips (1984) commented that large masses of loose macroalgae such as *Ulva* spp. commonly occur in seagrass meadows, especially where tidal currents are sluggish. In Netarts Bay on the Oregon coast, Kentula and McIntire (1986) found a decrease in shoot net primary production of *Z. marina* in mid-summer concurrent with a decrease in insolation and a rapid increase in the biomass of *U. prolifera*. They observed that as this macroalga drifted through the eelgrass meadow it became entangled with the eelgrass canopy, uprooting the plants. Where the *Ulva* was attached, sediment deposition was increased which partially buried the aboveground biomass of nearby eelgrass plants. Working in Yaquina Bay, Oregon, Kentula and DeWitt (2003) did not find any evidence of the displacement of eelgrass by macroalgae, but noted the potential for a negative interaction based on the fact that the biomass measured for the eelgrass and macroalgae were comparable. Similarly, Thom et al. (2003) did not find clear evidence of a decline in eelgrass distribution or abundance with increased green macroalgae in Coos Bay, Oregon, but they did suggest that green macroalgae such as *Ulva* spp. may negatively affect the eelgrass in the future.

8.2.1 Field Evidence Suggesting Macroalgal Impacts on *Thalassia*

There also have been several reports of an inverse relationship between the abundance of macroalgae and the distribution and abundance of *Thalassia* and other seagrass species (Table 8.1). Cowper (1978) found that drift algae competed for light with seagrasses, including *T. testudinum*, in Redfish Bay, Texas, with the algae having substantially higher growth rates than the seagrasses at irradiances less than 45% of surface irradiance. Merino et al. (1992) studied the relationship between *T. testudinum* and macroalgal communities (dominated by the genera *Chaetomorpha* and *Acetabularia*) on the Mexican Caribbean coast. They reported that as the algae became more common, the seagrass communities declined. In particular, the algae formed mats covering the bottom communities; then, as oxygen bubbles formed within the mats causing them to float, the remaining seagrass sprouts were uprooted. Perez-Enriquez (1996) found a negative association between the red seaweed *Eucheuma isiforme* and the seagrasses *T. testudinum* and *Syringodium filiforme* off the Peninsula of Yucatan, Mexico. However, in this

case the author suggested that these seagrasses might be affecting the distribution of the seaweed. In contrast, in Tampa Bay, Florida, Bell and Hall (1997) found no significant relationship between percent cover or biomass of drift algae and mean blade length, shoot density, or above-ground biomass of the dominant seagrass species *T. testudinum* and *Halodule wrightii*. Angel and Polania (2001) studied the distribution of *T. testudinum* and *S. filiforme* around San Andres Island in the Columbian Caribbean. They reported significant damage to the seagrass meadows around the island, suggesting a number of possible anthropogenic causes as well as possible competition for space by macroalgae. Working in two estuaries in the western Gulf of Mexico, Kopecky and Dunton (2006) found very high abundances of drift macroalgae which they characterized as a potential threat to *T. testudinum* and other seagrasses in those systems.

8.3 Evidence of Macroalgal Impacts on *Zostera* from Laboratory or Field Manipulation

Harlin and Thorne-Miller (1981) conducted field experiments in Rhode Island, adding ammonium, nitrate, or phosphate to the water column. They found that ammonium additions caused the appearance of dense mats of the free-floating green macroalgae *Ulva* and stimulated eelgrass growth. This growth response of *Z. marina* was greater in the area where current velocity reached 12 cm/sec, presumably because the boundary area around the eelgrass leaves in the higher velocity area was decreased, enhancing nutrient uptake. In contrast, the nitrate additions enhanced the growth of the green macroalgae but not the eelgrass, while phosphate additions stimulated growth of eelgrass but not green macroalgae. None of the nutrient supplements had a significant effect on epiphytic algae or phytoplankton in the test areas. The authors concluded that the rapid growth of green macroalgae in the nitrogen-rich waters probably limited the growth of adjacent seagrasses. In mesocosm experiments, Bintz et al. (2003) observed that the negative effect of elevated water temperature on eelgrass was significantly increased with inorganic nutrient additions, which enhanced the accumulation of macroalgae, especially at higher temperatures.

Short et al. (1995) enriched mesocosms with nitrogen and phosphorus via dissolution of a slow-release fertilizer and found that stimulation of three different algal forms (phytoplankton, epiphytes, and macroalgae) occurred in different replicate treatments. However, the enrichment effects on eelgrass shoot density, biomass, and leaf length were similar for all replicates. In each case, the negative effect of algae on eelgrass occurred primarily through shading, and eelgrass growth decreased linearly with reduced light. Taylor et al. (1995) also conducted mesocosm experiments on eelgrass in Rhode Island with various combinations of nutrients. They reported that in the controls phytoplankton levels remained low while macroalgae and epiphytes were abundant, but in the nutrient-enriched mesocosms phytoplankton blooms dominated. These mesocosm studies do not appear to have produced definitive results regarding the effect of macroalgae on eelgrass. This point was emphasized by Raffaelli et al. (1998), who commented on the absence of controlled manipulative field experiments to explore such effects.

Subsequently, Hauxwell et al. (1998) observed that benthic algal growth rates and biomass increased with nitrogen load in three Massachusetts estuaries, while abundance of

grazers decreased, resulting in negligible top-down control of macroalgal biomass. Then, using macroalgal enclosure or exclusion field experiments, Hauxwell et al. (2001) compared eelgrass productivity in two estuaries that had a six-fold difference in nitrogen loading rate. The authors concluded that macroalgal cover was the primary cause of eelgrass loss in the high-nitrogen estuary. Upon removal of macroalgae, shoot density, summer growth, and summer aboveground net production all increased significantly. They observed low sediment redox conditions and potentially toxic concentrations of ammonium in the porewater, and identified an approximate 9-12 cm critical macroalgal canopy height at which eelgrass declined. Working in Washington State, Nelson and Lee (2001) conducted similar field manipulations, finding that removal of the dominant green macroalgae *Ulvaria obscura* from eelgrass beds significantly reduced the loss of shoots during the summer bloom. They concluded that natural blooms of this macroalgae reduce eelgrass shoot density in the area.

Brun et al. (2003a; 2003b) conducted laboratory and field experiments in Cadiz, Spain on the effect of shading by *U. rigida* canopies on *Z. noltii*. They reported that productivity and elongation rates of the seagrass decreased when subjected to overlying mats of the green macroalgae. They also reported the mobilization of starch in both above- and below-ground tissues, accompanied by enhanced protein turnover and changes in metabolic pathways. Cummins et al. (2004) added *U. intestinalis* (at levels equivalent to a naturally occurring bloom) to a seagrass meadow composed of *Z. capricorni* and other genera in New South Wales, Australia. Three months later, considerable gaps resulted in the seagrass canopy.

In 1999-2000, Sullivan (unpub.) manipulated green macroalgae densities in 2-m² enclosures in Yaquina Bay estuary, Oregon to examine impacts on sediment and water column processes in *Z. marina* habitat. Macroalgae biomass was removed or added, with enclosure and non-enclosure controls. Porewater NH₄⁺ and PO₄⁻ increased with algae density in all habitats, while porewater nitrite and nitrate differed but did not respond to algal density. Water column nutrient and oxygen concentrations within algal canopies differed from open water levels. However, only the water column oxygen concentrations responded to algal manipulations. Macroalgal density affected seagrass density, with algae additions reducing shoot density relative to non-enclosure controls (Figure 8.1).

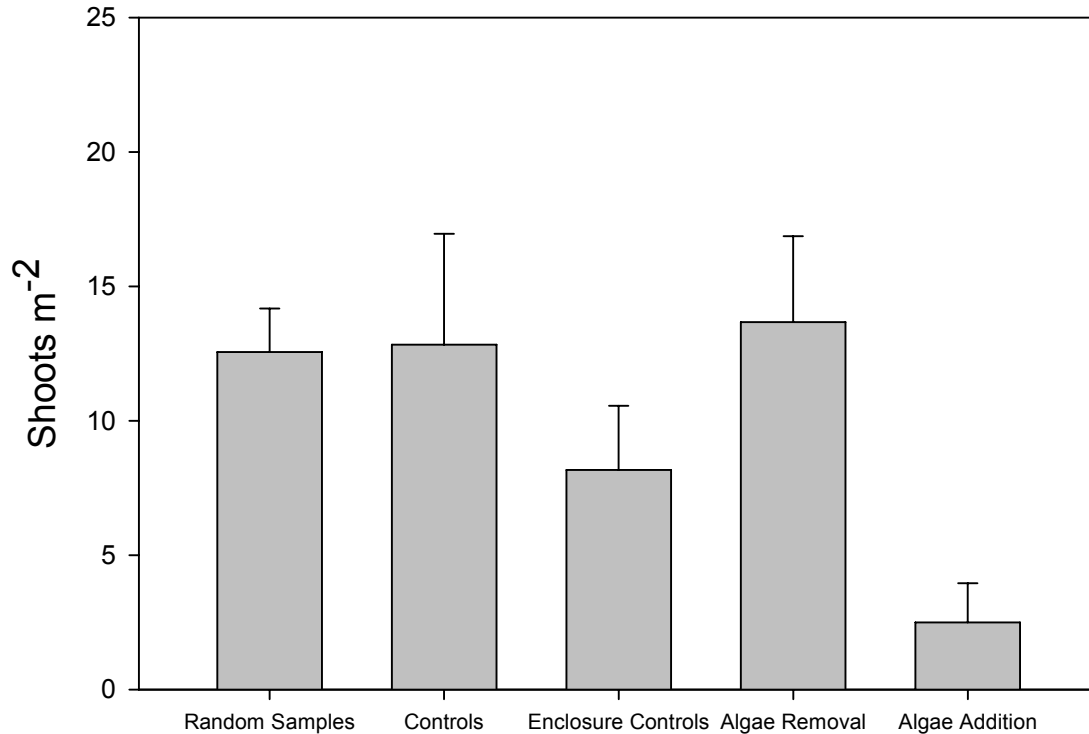


Figure 8.1. Effects of experimental benthic green macroalgal (*Ulva* spp.) manipulations on shoot density of *Zostera marina* in experimental enclosures as compared to controls, for Yaquina Bay, Oregon (G. Sullivan, unpub. data, The Wetlands Institute, Chicago IL). Algae addition treatment is significantly different from all other treatments except the enclosure controls (one-way ANOVA, square root transformed data, Holm-Sidak multiple comparisons, $p < 0.0001$).

8.3.1 Evidence of Macroalgal Impacts on *Thalassia* from Laboratory or Field Manipulation

McGlathery (1995) manipulated nutrient and grazing levels at a eutrophic and a mesotrophic/oligotrophic site in a Bermuda lagoon. Nutrient enrichment caused an increase in percent cover of the filamentous, mat-forming macroalga *Spyridea hypnoides* and a decline in the percent cover and above-ground biomass of *T. testudinum* at the eutrophic site. Holmquist (1997) manipulated algal mats (*Laurencia poiteau*) over study plots of *T. testudinum* in southwestern Florida Bay. The algal canopy heights were 40 cm versus 18 cm for the seagrass. After 6 months of algal cover, the density of *T. testudinum* fell to 12% of the original value, and after 18 months of recovery the density had increased to only about 25% of the initial density. Macia (2000) manipulated drift algae and sea urchins (*Lytechinus variegatus*) within cages containing *T. testudinum* in Biscayne Bay, Florida. Under normal grazing, the drift algae blooms that formed large mats covering the seagrass canopy in winter did not have a significant negative effect on the seagrass. However, with increased grazing pressure there was a synergistic effect of grazing and drift algae on seagrass shoot density. Davis and Fourqurean (2001) manipulated densities of the rhizophytic algae *Halimeda incrassata* in plots of *T. testudinum* in the upper

Florida Keys. They reported that the addition of the macroalgae had no significant impact on seagrass growth, but that the removal of the macroalgae significantly lowered the leaf tissue C:N ratio. The authors concluded that competition for nitrogen was the mechanism of the interaction. In comparison, Irlandi et al. (2004) did not find any significant effects of manipulated drift algae cover on *T. testudinum* at two different sites and seasons in Biscayne Bay, Florida. Further, Armitage et al. (2005) found no replacement of *T. testudinum* by macroalgae under nutrient enriched conditions in Florida Bay.

8.4 Positive Effects of Macroalgae on Eelgrass

There is little evidence in the literature of positive effects of macroalgae on eelgrass. A possible exception is for eelgrass in the estuarine intertidal zones of the Pacific Northwest and elsewhere. The accumulation of green macroalgae within and upslope of eelgrass meadows may help to retain water on the mudflats during periods of daylight low-tide intervals, thus reducing desiccation of the eelgrass plants. Boese et al. (2003) have documented desiccation damage in intertidal eelgrass and suggested that this may be a limiting factor for upper intertidal distribution. In Yaquina Bay, Oregon, acute desiccation stress is often observed in late spring and early summer when daylight spring-tides, sunny and/or windy weather combine. In contrast, in the late summer and fall, the presence of large amounts of macroalgae tends to cover exposed sheaths which may provide some protection. Annual eelgrass shoots may not be as susceptible to desiccation stress since their sheaths are often more flexible than perennial eelgrass shoots, and tend to lie flat on the sediment surface (van Katwijk et al. 2000; Boese, unpub. data).

8.5 Research Gaps

The reports cited above provide substantial evidence that, in numerous locations around the world, elevated concentrations of nutrients in near shore estuarine and marine waters have stimulated algal growth, including that of macroalgae, which interferes with the physiology (photosynthesis, respiration, reproduction, etc.) of eelgrass. The most frequently cited impact is shading. Quantitative relationships between macroalgal canopy height (or corresponding measures of abundance) and specific impacts on eelgrass plants (such as those provided by Hauxwell et al. 2001), for different water body characteristics (temperature, current velocity, turbidity, grazing pressure, etc.) are needed. Similarly, relationships between macroalgal abundance and the causative anthropogenic activity (e.g., normalized nitrogen load rate) are needed to recommend corrective actions.

8.6 Conclusions

The studies summarized here generally identify excessive accumulations of green macroalgae as a principal cause of the decline or disappearance of the eelgrass *Z. marina*. The primary mechanism of impact is shading of the eelgrass, thus reducing its photosynthesis. However, a secondary mechanism is that excessive macroalgal loading of the sediments may lead to elevated porewater concentrations of ammonium and/or dissolved sulfide that may contribute to eelgrass decline. There also are reports of drifting macroalgae becoming entangled

with eelgrass and uprooting it, or causing its burial via increased sediment deposition. On occasion these processes are lumped into the general terms outcompete, crowd out, suffocate, etc. Eutrophication of the near shore marine waters by anthropogenic inputs of nutrients (principally nitrogen) is most commonly cited as the direct cause of the macroalgal blooms impacting the eelgrass.

In summary, there appears to be a substantial body of evidence that increases in nitrogen loadings to estuaries are accompanied by increases in macroalgal abundances and decreases in seagrass distributions. This suggests that, conceptually, macroalgal abundance should be included in estuarine nutrient loading criteria intended to protect seagrasses in those systems. Hauxwell et al. (2001) provided quantitative guidance for at least part of such a strategy in Waquoit Bay, Massachusetts. They identified a macroalgal canopy height of 9-12 cm above which eelgrass declines. In one estuarine watershed of the Bay, a six-fold increase in the nitrogen loading rate over that in a “pristine” watershed corresponded to an increase in macroalgal canopy height from 2 cm to 9 cm, the threshold for a measurable decline in eelgrass distribution suggested by their study. It seems likely that such relationships between nutrient loading, macroalgal abundance, and seagrass distribution are site-specific. For example, systems with long residence times are likely to be much more vulnerable to increased loadings than are those that are rapidly flushed. The logical sequence appears to be first a determination of the relationship between macroalgal and seagrass abundances in a given system, and then a determination of the relationship between nutrient loading and macroalgal abundance for that system.

8.7 Literature Cited

- Angel, I. F. and J. Polania. 2001. Structure and distribution of seagrass meadows in San Andres Island, Columbia Caribbean. *Boletín Ecotropical: Ecosistemas Tropicales* 35:1-24.
- Armitage, A. R., T. A. Frankovich, K. L. Heck, Jr., and J. W. Fourqurean. 2005. Experimental nutrient enrichment causes complex changes in seagrass, microalgae, and macroalgae community structure in Florida Bay. *Estuaries* 28:422-434.
- Bell, S. S. and M. O. Hall. 1997. Drift macroalgal abundance in seagrass beds: investigating large-scale associations with physical and biotic attributes. *Marine Ecology Progress Series* 147:277-283.
- Bintz, J. C., S. W. Nixon, B. A. Buckley, and S. L. Granger. 2003. Impacts of temperature and nutrients on coastal lagoon plant communities. *Estuaries* 26:765-776.
- Boese, B. L., K. E. Alayan, E. F. Gooch, and B. D. Robbins. 2003. Desiccation index: a measure of damage caused by adverse aerial exposure on intertidal eelgrass (*Zostera marina*) in an Oregon (USA) estuary. *Aquatic Botany* 76:329-337.
- Bowen, J. L. and I. Valiela. 2001. The ecological effects of urbanization of coastal watersheds: historical increases in nitrogen loads and eutrophication of Waquoit Bay estuaries. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1489-1500.
- Bricker, S. B., C. G. Clement, D. E. Pirhalla, S. P. Orlando, and D. R. G. Farrow. 1999. National Estuarine Eutrophication Assessment: Effects of Nutrient Enrichment in the Nation's Estuaries. NOAA, National Ocean Service, Special Projects Office and the National Centers for Coastal Ocean Science, Silver Spring, MD, 71 pp.
- Brun, F. G., J. J. Vergara, G. Navarro, I. Hernández, and J. L. Pérez-Lloréns. 2003a. Effect of shading by *Ulva rigida* canopies on growth and carbon balance of the seagrass *Zostera noltii*. *Marine Ecology Progress Series* 265:85-96.
- Brun, F. G., I. Hernandez, J. J. Vergara, and J. L. Pérez-Lloréns. 2003b. Growth, carbon allocation and proteolytic activity in the seagrass *Zostera noltii* shaded by *Ulva* canopies. *Functional Plant Biology* 30:551-560.
- Burkholder, J. M., K. M. Mason, and H. B. Glasgow Jr. 1992. Water-column nitrate enrichment promotes decline of eelgrass *Zostera marina*: evidence from seasonal mesocosm experiments. *Marine Ecology Progress Series* 81:163-178.
- Burkholder, J. M., H. B. Glasgow Jr, and J. E. Cooke. 1994. Comparative effects of water-column nitrate enrichment on eelgrass *Zostera marina*, shoalgrass *Halodule wrightii*, and widgeongrass *Ruppia maritima*. *Marine Ecology Progress Series* 105:121-138.
- Cardoso, P. G., M. A. Pardal, A. I. Lillebø, S. M. Ferreira, D. Raffaelli, and J. C. Marques. 2004. Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. *Journal of Experimental Marine Biology and Ecology* 302:233-248.
- Ciszewski, P., L. Kruk-Dowgiallo, and L. Zmudzinski. 1992. Deterioration of the Puck Bay and biotechnical approaches to its reclamation. In: *Proceedings of the 12th Baltic Marine Biologists Symposium: physiological and biochemical strategies in Baltic organisms; new approaches in ecotoxicological research; changes in Baltic ecosystems, 1991*, Helsingor, Denmark, pp. 43-46.

- Coffaro, G. and M. Bocci. 1997. Resources competition between *Ulva rigida* and *Zostera marina*: a quantitative approach applied to the Lagoon of Venice. *Ecological Modelling* 102:81-95.
- Cowper, S. W. 1978. The drift algae community of seagrass beds in Redfish Bay, Texas. *Contributions in Marine Science* 21:125-132.
- Cummins, S. P., D. E. Roberts, and K. D. Zimmerman. 2004. Effects of the green macroalga *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary. *Marine Ecology Progress Series* 266:77-87.
- Curiel, D., A. Rismondo, G. Bellemo, and M. Marzocchi. 2004. Macroalgal biomass and species variations in the Lagoon of Venice (Northern Adriatic Sea, Italy): 1981-1998. *Scientia Marina* 68:57-67.
- Davis, B. C. and J. W. Fourqurean. 2001. Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum*. *Aquatic Botany* 71:217-232.
- Deegan, L. A., A. Wright, S. G. Ayvazian, J. T. Finn, H. Golden, R. R. Merson, and J. Harrison. 2002. Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12:193-212.
- Den Hartog, C. 1994. Suffocation of a littoral *Zostera* bed by *Enteromorpha radiata*. *Aquatic Botany* 47:21-28.
- Den Hartog, C. and P. J. G. Polderman. 1975. Changes in the seagrass populations of the Dutch Waddenzee. *Aquatic Botany* 1:141-147.
- Flindt, M. R., L. Kamp-Nielsen, J. C. Marques, M. A. Pardal, M. Bocci, G. Bendoricchio, J. Salomonsen, S. N. Nielsen, and S. E. Jørgensen. 1997. Description of the three shallow estuaries: Mondego River (Portugal), Roskilde Fjord (Denmark) and the Lagoon of Venice (Italy). *Ecological Modelling* 102:17-31.
- Funen County Council. 1991. Eutrophication of Coastal Waters. Coastal Water Quality Management in the County of Funen, Denmark, 1976-1990. Department of Technology and Environment, Denmark, 287 p.
- Goodman, J. L., K. A. Moore, and W. C. Dennison. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. *Aquatic Botany* 50:37-47.
- Harlin, M. M. and B. Thorne-Miller. 1981. Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. *Marine Biology* 65:221-229.
- Hauxwell, J., J. McClelland, P. J. Behr, and I. Valiela. 1998. Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. *Estuaries* 21:347-360.
- Hauxwell, J., J. Cebrián, C. Furlong, and I. Valiela. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 82:1007-1022.
- Hauxwell, J., J. Cebrián, and I. Valiela. 2003. Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series* 247:59-73.
- Hemminga, M. A. and C. M. Duarte. 2000. *Seagrass Ecology*. Cambridge University Press, Cambridge, United Kingdom. 298 pp.

- Holmquist, J. G. 1997. Disturbance and gap formation in a marine benthic mosaic: influence of shifting macroalgal patches on seagrass structure and mobile invertebrates. *Marine Ecology Progress Series* 158:121-130.
- Hughes, J. E., L. A. Deegan, J. C. Wyda, M. J. Weaver, and A. Wright. 2002. The effects of eelgrass habitat loss on estuarine fish communities of southern New England. *Estuaries* 25:235-249.
- Irlandi, E. A., B. A. Orlando, and P. D. Biber. 2004. Drift algae-epiphyte-seagrass interactions in a subtropical *Thalassia testudinum* meadow. *Marine Ecology Progress Series* 279:81-91.
- Kentula, M. E. and C. D. McIntire. 1986. The autecology and production dynamics of eelgrass (*Zostera marina* L.) in Netarts Bay, Oregon. *Estuaries* 9:188-199.
- Kentula, M. E. and T. H. DeWitt. 2003. Abundance of seagrass (*Zostera marina* L.) and macroalgae in relation to the salinity-temperature gradient in Yaquina Bay, Oregon, USA. *Estuaries* 26:1130-1141.
- Kopecky, A. L. and K. H. Dunton. 2006. Variability in drift macroalgal abundance in relation to biotic and abiotic factors in two seagrass dominated estuaries in the western Gulf of Mexico. *Estuaries and Coasts* 29:617-629.
- Kruk-Dowgiallo, L. 1991. Long-term changes in the structure of underwater meadows of the Puck Lagoon. *Acta Ichthyologica et Piscatoria (Supplement)* 21:77-84.
- Lyons, J., J. Ahern, J. McClelland, and I. Valiela. 1995. Macrophyte abundances in Waquoit Bay estuaries subject to different nutrient loads and the potential role of fringing salt marsh in groundwater nitrogen interception. *Biological Bulletin* 189:255-256.
- Maciá, S. 2000. The effects of sea urchin grazing and drift algal blooms on a subtropical seagrass bed community. *Journal of Experimental Marine Biology and Ecology* 246:53-67.
- McGlathery, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. *Marine Ecology Progress Series* 122:239-252.
- Merino, M., A. González, E. Reyes, M. Gallegos, and S. Czitrom. 1992. Eutrophication in the lagoons of Cancún, México. *Science of the Total Environment (Supplement)* 1992: 861-870.
- Nelson, T. A. and A. Lee. 2001. A manipulative experiment demonstrates that blooms of the macroalga *Ulvaria obscura* can reduce eelgrass shoot density. *Aquatic Botany* 71:149-154.
- Niell, F. X., C. Fernández, F. L. Figueroa, F. G. Figueiras, J. M. Fuentes, J. L. Pérez-Llorens, M. J. García-Sánchez, I. Hernández, J. A. Fernández, M. Espejo, J. Buella, M. C. García-Jiménez, V. Clavero, and C. Jiménez. 1996. Spanish Atlantic coasts. In: W. Schramm and P.H. Nienhuis (eds.). *Marine Benthic Vegetation: Recent Changes and the Effects of Eutrophication*. Springer-Verlag, Berlin, pp. 265-281.
- Nielsen, S. L., K. Sand-Jensen, J. Borum, and O. Geertz-Hansen. 2002. Depth colonization of eelgrass (*Zostera marina*) and macroalgae as determined by water transparency in Danish coastal waters. *Estuaries* 25:1025-1032.
- Nienhuis, P. H. 1983. Temporal and spatial patterns of eelgrass (*Zostera marina* L.) in a former estuary in The Netherlands, dominated by human activities. *Marine Technological Society Journal* 17(2):69-77.

- Nienhuis, P. H. 1996. The North Sea coasts of Denmark, Germany and The Netherlands. *In*: W. Schramm and P.H. Nienhuis (eds.). *Marine Benthic Vegetation: Recent Changes and the Effects of Eutrophication*. Springer-Verlag, Berlin, pp. 187-221.
- Oliveira, J. C. and G. Cabeçadas. 1996. Portugal. *In*: W. Schramm and P.H. Nienhuis (eds.). *Marine Benthic Vegetation: Recent Changes and the Effects of Eutrophication*. Springer-Verlag, Berlin, pp. 283-292.
- Orth, R. J. and K. A. Moore. 1983. Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. *Science* 222:51-53.
- Pardal, M. A., J. C. Marques, I. Metelo, A. I. Lillebø, and M. R. Flindt. 2000. Impact of eutrophication on the life cycle, population dynamics and production of *Ampithoe valida* (Amphipoda) along an estuarine spatial gradient (Mondego estuary, Portugal). *Marine Ecology Progress Series* 196:207-219.
- Patrício, J., R. Ulanowicz, M. A. Pardal, and J. C. Marques. 2004. Ascendency as an ecological indicator: a case study of estuarine pulse eutrophication. *Estuarine, Coastal and Shelf Science* 60:23-35.
- Penhale, P. A. and R. G. Wetzel. 1983. Structural and functional adaptations of eelgrass (*Zostera marina* L.) to the anaerobic sediment environment. *Canadian Journal of Botany* 61:1421-1428.
- Perez-Enriquez, R. 1996. Summer biomass, density and weight assessment of the red seaweed *Eucheuma isiforme* (Rhodophyta, Gigartinales) at Dzilam, Yucatan State, Mexico. *Botanica Marina* 39:251-253.
- Philippart, C. J. M. and K. S. Dijkema. 1995. Wax and wane of *Zostera noltii* Hornem. in the Dutch Wadden Sea. *Aquatic Botany* 49:255-268.
- Phillips, R. C. 1984. The Ecology of Eelgrass Meadows in the Pacific Northwest: A Community Profile. U.S. Fish and Wildlife Service, FWS/OBS-84/24, 85 pp.
- Plinski, M. and I. Florczyk. 1984. Changes in the phytobenthos resulting from the eutrophication of the Puck Bay. *Limnologica* 15:325-327.
- Raffaelli, D. G., J. A. Raven, and L. J. Poole. 1998. Ecological impact of green macroalgal blooms. *Oceanography and Marine Biology: an Annual Review* 36:97-125.
- Schramm, W. 1996. The Baltic Sea and its transition zones. *In*: W. Schramm and P.H. Nienhuis (eds.). *Marine Benthic Vegetation: Recent Changes and the Effects of Eutrophication*. Springer-Verlag, Berlin, pp. 131-163.
- Sfriso, A., B. Pavoni, and A. Marcomini. 1989. Macroalgae and phytoplankton standing crops in the central Venice Lagoon: primary production and nutrient balance. *Science of the Total Environment* 80:139-159.
- Short, F. T., D. M. Burdick, J. Wolf, and G. E. Jones. 1993. Eelgrass in Estuarine Research Reserves along the East Coast, U.S.A., Part I: Declines from Pollution and Disease and Part II: Management of Eelgrass Meadows. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Estuarine Research Reserve Program and Coastal Ocean Program, Silver Spring, MD, 107 p.
- Short, F. T., D. M. Burdick, and J. E. Kaldy III. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnology and Oceanography* 40:740-749.

- Short, F. T. and D. M. Burdick. 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. *Estuaries* 19:730-739.
- Taylor, D. I., S. W. Nixon, S. L. Granger, B. A. Buckley, J. P. McMahon, and H.-J. Lin. 1995. Responses of coastal lagoon plant communities to different forms of nutrient enrichment - a mesocosm experiment. *Aquatic Botany* 52:19-34.
- Thom, R. M., A. B. Borde, S. Rumrill, D. L. Woodruff, G. D. Williams, J. A. Southard, and S. L. Sargeant. 2003. Factors influencing spatial and annual variability in eelgrass (*Zostera marina* L.) meadows in Willapa Bay, Washington, and Coos Bay, Oregon, estuaries. *Estuaries* 26:1117-1129.
- Thybo-Christesen, M., M. B. Rasmussen, and T. H. Blackburn. 1993. Nutrient fluxes and growth of *Cladophora sericea* in a shallow Danish bay. *Marine Ecology Progress Series* 100:273-281.
- Valiela, I., K. Foreman, M. LaMontagne, D. Hersh, J. Costa, P. Peckol, B. DeMeo-Andreson, C. D'Avanzo, M. Babione, C.-H. Sham, J. Brawley, and K. Lajtha. 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. *Estuaries* 15:443-457.
- Valiela, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* 42:1105-1118.
- Valiela, I., G. Tomasky, J. Hauxwell, M. L. Cole, J. Cebrián, and K. D. Kroeger. 2000a. Operationalizing sustainability: management and risk assessment of land-derived nitrogen loads to estuaries. *Ecological Applications* 10:1006-1023.
- Valiela, I., M. Geist, J. McClelland, and G. Tomasky. 2000b. Nitrogen loading from watersheds to estuaries: verification of the Waquoit Bay Nitrogen Loading Model. *Biogeochemistry* 49:277-293.
- Van Katwijk, M. M., L. H. T. Vergeer, G. H. W. Schmitz, and J. G. M. Roelofs. 1997. Ammonium toxicity in eelgrass *Zostera marina*. *Marine Ecology Progress Series* 157:159-173.
- Van Katwijk M. M., D. C. R. Hermus, D. J. de Jong, R. M. Asmus, and V. N. de Jonge. 2000. Habitat suitability of the Wadden Sea for restoration of *Zostera marina* beds. *Helgoland Marine Research* 54:117-128.
- Whelan, P. M. and J. P. Cullinane. 1985. The algal flora of a subtidal *Zostera* bed in Ventry Bay, southwest Ireland. *Aquatic Botany* 23:41-51.

9.0 The Effects of Temperature and Desiccation on the Seagrasses *Zostera marina* and *Thalassia testudinum*

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9.1 Background

Temperatures elevated above the ambient range have long been recognized as having deleterious or fatal effects on marine organisms (e.g. Sachs 1864, working with *Vallisneria* and *Ceratophyllum*; Mayer 1914). Environmental temperature influences the rate of critical biological processes of organisms in general (Billings 1952; Vernberg 1978), including processes such as photosynthesis and respiration in seagrasses. This review examines and summarizes work characterizing the effects of natural and anthropogenically influenced variation in temperature and desiccation, cyclic and abnormal, on aspects of physiology, growth, reproduction and distribution of primarily the seagrasses *Zostera marina* and *Thalassia testudinum* in North America.

Larkum et al. (1989) summarized work involving temperature effects on seagrasses, emphasizing that the literature is rife with conflicting views on the relative importance of temperature and irradiance, attributable to the fact that water temperature is largely determined by the amount of incoming solar radiation, so that it is often difficult to separate the effects of each contribution. Anthropogenic alterations of the temperature environment through thermal effluent discharge has been shown to have major and non-predictable impacts on marine benthic communities (Schiel et al. 2004), and may interact with other stressors such as nutrient elevation through multiple mechanisms; these stresses can negatively impact seagrass populations.

Thorhaug, Segar and Roessler (1973) documented the dramatic effect of heated power plant effluent dilution on the local distribution and health of *Thalassia testudinum* (turtlegrass) in a subtropical habitat. Power plant effluents ~5° C above the ambient temperature of ~30° C completely denuded a ~9 ha expanse of seagrass. Concentric to that zone of initial dilution, at temperatures 3-4° C above ambient, plants showed “severe” damage. In the zone at ~1-2° C above ambient temperature, there was elevated productivity (see also Thorhaug, Blake and Schroeder 1978).

Aerial exposure and resulting desiccation stress is probably the most important factor limiting the upper intertidal distribution of seagrass species. Although this is not directly an anthropogenic stressor, alterations in estuarine bathymetry which increase elevations in intertidal areas would reduce seagrass populations by increasing the frequency and duration of aerial exposure. For example, high rates of sedimentation from logging in coastal watersheds with steep slopes such as found in the Pacific Northwest can reduce average depth within coastal embayments (Komar 1997; McManus et al. 1998; Styllas 2001). Reduced light due to eutrophication and turbidity in subtidal eelgrass beds would also serve to restrict potential

distribution of eelgrass to shallower areas where desiccation stress may be important on a seasonal basis.

9.2 Temperature-driven geographic, regional and spatial distribution

Setchell (1929) was the first to comprehensively examine the effects of temperature on characteristics of populations of *Zostera marina* L., including growth rate, onset of reproduction, senescence, and germination of seeds. Based on field observations, he proposed an optimal temperature window of 10 - 20°C, outside of which growth apparently ceased. He proposed vegetative growth occurred chiefly between 10 - 15°C, and reproductive activity between 15 - 20°C. He noted that along the geographic range, reproduction began earlier in southern populations and progressed northward. He found marked differences in plants in subtidal versus intertidal populations, and attributed these to temperature differences.

Although morphological differentiation may be attributed to complex influences (see below) subsequent work has confirmed many of these early observations (Phillips and Backman 1983). Comparison of flowering events along a latitudinal gradient from North Carolina to Canada indicated that reproduction occurred earlier in the south and at successively later dates with increasing latitude (Silberhorn et al. 1983). Puget Sound populations were found to have temperature optima of between 7.5 to 12.5°C, but tolerated temperature extremes of 6.5 to 18°C (Phillips 1972). *Zostera* populations can persist under more extreme temperature regimes. For example, Bering Sea populations experience temperatures from -6 to ~30°C, and even to 35°C in exposed intertidal pools (Zieman and Wetzel 1980; Biebl and McRoy 1971). At the southern extreme of the population range, the species apparently shifts its reproductive strategy based on the temperature range experienced. Perennial forms of *Z. marina* are found in northern Baja California (11-27°C), while the annual form is characteristic of the southern peninsula (12-32°C) (Ibarra-Obando et al. 1997; Meling-Lopez and Ibarra-Obando 1999), and in the Sea of Cortez (Phillips and Backman 1983).

Glynn (1968) suggested that temperature probably limited the northern distribution of *Thalassia testudinum* in Florida, although there were regional differences. In the Gulf of Mexico, *T. testudinum* is apparently capable of enduring a warm temperate climate, whereas along Florida's east coast exposure to temperatures of 35 - 40°C will kill the leaves.

Subtidal and tidepool populations of *Zostera* sp. in Alaska differ in a range of characteristics that have been attributed to differences in temperature regimes (McRoy 1970). Subtidal plants were aseasonal with high root/rhizome biomass, low shoot density, few or no flowering shoots, and long, wide leaves; tidepool beds had low root/rhizome biomass, high shoot density with a large number of flowering shoots and short, narrow leaves, and exhibited marked seasonal cycles of biomass. Similar contrasts were observed for other Pacific coast locations (Phillips et al. 1983b).

Analysis of seagrass $\delta^{13}\text{C}$ values indicates that seagrasses tend to become more ^{13}C depleted from tropical (warmer) to temperate (cooler) regions (Hemminga and Mateo 1996).

Variation (in order of relative importance) of source of carbon, irradiance and temperature on CO₂ availability in seawater may partly explain this latitudinal trend, but gradients in day length may also be involved.

Evans (1983) examined the occurrence of two thermally disjunct populations of *Z. marina* in the Woods Hole, MA area (27° C vs. 20-22° C). When grown under identical conditions at 15°C, the two isolates maintained growth differences. Their P_{max} data under experimental culture indicated that increased photosynthetic performance at elevated temperatures was not a good predictor of ecological success, e.g., when transplanted to a habitat with a different temperature regime. Phillips and Lewis (1983) reciprocally transplanted *Z. marina* over temporal, spatial and ecogenetic gradients in North America; they demonstrated that initial leaf widths of transplanting stock are not a good predictor of success. Puget Sound populations, coming from the mid-range of west-coast geographic and genetic distribution, and low temperature variance habitat, exhibited broad adaptive tolerance; Alaskan stock, originating in a highly variable thermal habitat, did not survive in Puget Sound. Olesen and Sand-Jensen (1993) concluded that Danish *Z. marina* acclimated to winter conditions by altering biomass allocation, i.e., increasing leaf surface area and reducing weight proportionally and respiration of non-photosynthetic tissues. Pollard and Greenway (1993) showed that *Z. capricorni* from warm, turbid Australian waters had higher than expected photosynthetic efficiencies than the same species from a relatively high light environment; plants accommodated to low-light turbid waters, at high water temperatures (29-33° C) reached H_{sat} with small incremental light increases. One quarter of gross production was expended as respiration.

9.2.1 Implications of climate change

The IPCC (2001) summary of historical data and predictions for climate change yields the following: The global average sea-surface temperature has increased since 1861 (beginning of “reliable” measurements) about $0.6 \pm 0.2^\circ \text{C}$, which includes a great deal of variability - most of the warming occurred in two periods, 1910-1945 and 1976-2000. Analyses of proxy data for the northern hemisphere indicate that the increase in temperature in the 20th century is likely to have been the largest of any century during the past 1,000 years. The increase in sea-surface temperature has been about one half that of the air temperature increase ($\sim 0.2^\circ \text{C}$ per decade) between 1950 and 1993. Tide gauge data show that global average sea level rose between 0.1 and 0.2 m during the 20th century, and that the global ocean heat content has increased since the late 1950s, the period for which adequate observations of sub-surface ocean temperatures have been available. According to NOAA's 2006 Annual Climate Review (NOAA 2006), the 2006 average annual temperature for the contiguous U.S. was the warmest on record, nearly identical to that of 1998, and $\sim 1.2^\circ \text{C}$ above the 20th Century mean of $\sim 11.7^\circ \text{C}$. The past nine years (1997-2006) are among the 25 warmest years on record, a span unprecedented in the historical record.

Short and Neckles (1999) suggest that a variety of factors such as increases in seawater temperature, resultant rise in sea level, changing water depth and tidal range, and increased salinity intrusion all will impact seagrasses as an effect of global warming. The direct effect of temperature increases will tend to alter the geographic distribution of seagrasses, and will result

in changes in the patterns of sexual reproduction. Another proposed effect of global warming is an increase in UV. However, *Z. capricorni* in Australia has been shown to acclimate readily to elevated UV and PAR by production of UV-blocking agents and, despite the enhancement of inhibitory effects of high PAR and UV-B by temperature stress, the relatively small temperature changes associated with climate change are unlikely to force widespread damage to the majority of eelgrass populations (Beardall et al. 1998).

9.3 Effects of temperature on phenology and reproduction

Each of the three reproductive phenophases (initiation of bud, anthesis, and appearance of fruit) of *Z. marina* vary significantly in their dates of occurrence along latitudinal gradients in North America (Phillips et al. 1983b). The time and temperature at which onset of reproductive phases occur differs between populations apparently representing different genotypes on the east and west coasts at the same latitude (see also Gambi 1988; Phillips and Lewis 1983; Buia and Mazzella 1991; Inglis and Lincoln-Smith 1998; Phillips et al. 1983b; Silberhorn et al. 1983; and Churchill and Riner 1978).

Flowering of *Thalassia testudinum* is largely controlled by water temperature, optimally in the range of ~20-26° C, while lower spring temperatures in the range of 10-18°C cause delayed flowering, with subsequent dehiscence of immature fruit (Phillips 1960; Moffler and Durako 1987; McMillan 1982). Thus there tends to be increasing failure of sexual reproduction as one approaches the northern limit of distribution (Witz and Dawes 1995). Zieman (1975) observed that seedling success was an exceptionally rare event, having documented the failure to survive of germinated seeds, and that most *Thalassia* growth and spreading is likely due to vegetative reproduction, suggesting that most expansion was clonal, citing McMillan and Moseley (1967).

Phillips et al. (1983a) noted a higher incidence of sexual reproduction in response to temperature at the geographic extremes of *Zostera* distribution than in the temperate central range, where temperatures are relatively moderate. Dawes, Phillips and Morrison (2004) observed that beds of *Thalassia testudinum* in more tropical regions contain a greater number of distinct genets (i.e., genetic variants) than do beds at higher latitudes, which may reflect success of seed production (and, hence, successful sexual reproduction), due to seasonal temperature effects (see also Davis et al. 1999; Witz 1994; Witz and Dawes 1995; Kirsten et al. 1998). They cite the example of lower winter water temperatures (i.e., 10-18° C) in the Tampa Bay area (a relatively “northern” population of *Thalassia*) as a possible cause of later flowering, resulting in loss of immature fruits in response to rapidly rising late spring temperatures. They credit Gessner (1970) with the general concept that sexual reproduction was less likely to be successful when aquatic plants encounter less-than-optimal temperatures - genetic variance at the cost of higher reproductive failure.

Time of the initial appearance of visible floral buds of *Z. marina* is quite variable within a location. Over a four year period, Phillips et al. (1983b) noted ranges of temperature of 6-21 °C in Rhode Island, 10-20° C in Halifax, N.S., while Puget Sound temperatures varied only from 8-

10° C over two sites. Distinguishable primordial anthers and pistils have been found in Chesapeake Bay populations in February at 3° C (Silberhorn et al. 1983), while Churchill and Riner (1978) observed microscopically visible buds in January in New York populations at water temperatures of 0.5-3° C. From these and other accounts (see especially Nienhus 1983; and Zimmerman et al. 1995; below, and Section 9.4), we may infer that the appearance of initial activity with respect to temperature and date may reflect the degree of success of the previous growth season, i.e., available stored energy from the rhizome (from depleted to plentiful), and the date of onset of significant increase in solar-induced diurnal temperature cycling. Burke et al. (1996), discussing carbohydrate reserves in eelgrasses, cite the agreement of their data on east coast *Z. marina* non-structural carbohydrate (nsc) reserve drawdown as fall progresses to winter with San Francisco Bay population data (Zimmerman et al. 1995), conditioned by high-turbidity-caused low light levels. Note that many authors cited elsewhere in this review observe the initiation and onset of growth of flowering buds in *Zostera* at very low temperatures in the dead of winter, precisely when nsc reserves would be at their lowest in most habitats. Zimmerman et al. (1995) also notes that plants with the highest level of nsc reserves show the highest level of asexual reproduction (i.e., transplant success = vegetative growth) at winter/spring onset of growth; there is a significant correlation of high nsc and growth with low turbidity and consequent higher light availability. de Cock (1981) suggested that the development of reproductive shoots is not inhibited by temperatures below 15° C (see Setchell 1929), but that maturation of inflorescences and timing of anthesis may be suppressed at lower temperatures. Ramage and Schiel (1998) noted that in New Zealand populations of *Z. novazelandica* in intertidal platforms, flowering shoots were more numerous in the low intertidal zone than in upper zones, and two times more in patches bordering tidepools than in patches not bordering tidepools; *Z. novazelandica* cultured at 5° C had ~3 times the number of inflorescences than those at 15° C, while none was formed at 25° C (see also McRoy's (1970) Alaskan observations with respect to submergent and emergent *Z. marina*).

Anthesis and pollination occur as temperatures rise from winter minima, with considerable interannual variation observed over a four year period, following a latitudinal gradient northward (Phillips et al. 1983b). Silberhorn et al. (1983) showed first evidence of Chesapeake Bay *Z. marina* pollen release at 14.3° C, stigma loss at 16° C in late April, with pollination essentially complete by mid-May.

Fruiting and seed dispersal in *Z. marina* are typically complete by late May to early June, consistently occurring in a temperature range from 20-25° C across a wide latitudinal gradient (de Cock 1980; Phillips et al. 1983b; Silberhorn et al. 1983); more northerly distributions may tend to fruit later in the season, and within lower temperature bands, e.g., Phillips (1983a; 1983b) for Puget Sound, and Harrison and Mann (1975) for Nova Scotia.

Nienhuis (1983) and Verhagen and Nienhuis (1983), modeling changes in biomass and distribution of *Z. marina* in the Netherlands, concluded that those changes could be attributed to temperature-induced changes in seed production: low water temperatures during the growing season caused a reduction in biomass, numbers of generative shoots and number of seeds; high water temperatures from August to late autumn would stimulate the production of vegetative

shoots. This vigorous growth tended to exhaust below-ground resources, leading to a reduction of biomass and numbers of generative shoots in the succeeding summer and thus diminished seed production. Zimmerman et al. (1995) determined that if carbohydrate reserves were low in below-ground organs, survival of transplants during winters dominated by high turbidity (and consequent low light) and low temperatures would be severely compromised.

A number of authors addressed the phenomenon of germination dormancy (Orth and Moore 1983; McMillan 1983; Loques et al. 1990). Mid-to northerly populations of *Z. marina* tend to exhibit temperature-mediated dormancy, reflecting the considerable change in seasonal temperature. More southerly populations (Sonora, Mexico, French Mediterranean), with seasonal temperature variation, exhibited salinity-mediated dormancy, or showed no dormancy at all.

Conclusions regarding temperature effects on germination have changed over time, reflecting broader geographic investigations. Phillips and Menez (1988) determined that water temperature, and not salinity, was the primary germination control. Hootsmans et al. (1987) experimentally determined that *Z. marina* seedling survival peaked at 10° C and 10-20‰, *Z. noltii* survived best at 10° C and 1‰, and both species showed maximal germination at 30° C and 1‰ salinity. In contrast, Moore et al. (1993) and Brenchley and Probert (1998) demonstrated that *Z. marina* and *Z. capricorni* germination was highest at low temperatures and under anaerobic conditions, and lowest under aerobic conditions.

El Niño events may have local or regional effects on seagrasses. Seddon et al. (2000) reported that *Z. muelleri* and *Z. mucronata* (= *Z. muelleri* subsp. *mucronata*) were among a number of intertidal and shallow subtidal Australian seagrasses that were drastically affected by high water temperatures associated with the 1993 El Niño event. Nelson (1997) concluded that intertidal eelgrass plants would tend to decline as a result of increased photoinhibition and desiccation due to increased temperature and light during El Niño episodes. Thom et al. (2003) found that warmer winters and cooler summers associated with the transition from *el Niño* to *la Niña* ocean conditions corresponded with an increase in eelgrass abundance and flowering.

Harrison (1982a) attributed a decline of *Z. marina* in the upper portion of a tidal flat drainage channel to impacts of warmed water receding with the ebbing tide, while flowering peaked earlier than the subtidal population. Phillips and Backman (1983) report that *Z. marina* in the Sea of Cortez, Mexico, completed all reproductive activities before the putative lethal upper limit for the species is reached (30° C), which suggests that the ultimate response to high water temperature is to behave as a true annual.

Burkholder et al. (1992) found adverse effects of water column nitrate enrichment in *Z. marina* in mesocosms were exacerbated by increasing or high temperatures. The meristematic portion of the shoot disintegrated after several weeks of exposure when water temperatures were held at 4° C above the 10 year (local) mean. Touchette and Burkholder (2002), using similar exposure scenarios, found that cellulose accumulation in below-ground structures was substantially below that for *Z. marina* grown at ambient temperatures; higher cellulose content is

shown to allow significant increase in new shoot productivity. Touchette et al. (2003), further exploring this phenomenon, noted that *Z. marina* grown under such conditions, typically that of the southern latitudinal limits of distribution, exhibited morphological and physiological symptoms of decline. Significantly reduced shoot density, leaf and root production, and altered internal C and N content, support the premise that in more southerly distributions, growth is inhibited by high temperature stress. The response of *Z. marina* to these conditions may be a reliable predictor for the impact of warming trends in climate change scenarios.

9.4 Effects of temperature on physiology

McMillan (1978) demonstrated that *Z. marina* collected from Alaska and Washington produced leaves of significantly different widths under three different temperature regimes in culture, indicating some characteristics of seagrass phenology can be modified by temperature.

Drew (1979) found that for a range of seagrass species, including *Z. marina*, light-saturated gross photosynthetic rates increased in direct proportion to temperature increase up to a point between 30-35°C, above which thermal damage caused a rapid reduction. Noting that respiration rates were not so dramatically affected, he concluded that effects on gross and net photosynthetic rates differed only in slope. Bulthuis (1985, 1987) comprehensively reviewed temperature effects on photosynthesis and growth of seagrasses. He found general agreement that the photosynthetic capacity of seagrasses (most seagrass genera represented) is reduced at 35-40°C. Within the limits of physiological tolerance (5-30°C), the rate of photosynthesis at light saturation, the dark respiration rate and the light compensation point more than double as temperature increases within the range experienced by most temperate zone seagrasses. The optimum temperature for photosynthesis decreases from 25-35°C at light saturation to as low as 5°C as irradiance decreases. Marsh et al. (1986) demonstrated that ratios of maximum photosynthetic rates to respiration rates were highest at 5°C and declined markedly at higher and lower temperatures in *Z. marina*. Even short-term (15 min) leaf exposure to high temperatures (e.g., ≥30°C) reduced net photosynthesis, increased respiration and led to a reduction in P:R ratios. Burke et al. (1996), Thayer et al. (1975) and Evans et al. (1986) support the thesis that 25°C may be an important threshold in that they note a negative carbon balance when water clarity conditions are low enough to reduce photosynthetic rates below that at light-saturation. Such conditions tend to compromise the ability of *Z. marina* to survive suboptimal weather scenarios (rainy, turbid springtime conditions, paralleling those of the early 1930's severe declines), especially if carbon reserves had been exhausted the previous summer under high temperature/high light conditions. Zimmerman et al. (1995) note that daily H_{sat} requirements for *Z. marina* range from 2.5 to 4 hours; for subtidal habitats, biweekly tidal cycling when high turbidity exists could severely stress deeper plants by severely limiting available light.

Sand-Jensen and Borum (1983) concluded that leaf productivity in *Z. marina* is limited by temperature, in that increasing temperatures increase maintenance costs by increasing dark respiration rates. However, Zimmerman et al. (1989) concluded from laboratory experiments that since *Z. marina* shows evidence of thermal acclimation, seasonal changes in ambient temperature may not significantly affect light-saturated photosynthesis (H_{sat}) requirements and

whole-plant C balance. Rapid mortality at high temperatures during summer may result instead from thermal disruption of metabolism.

The impact of temperature on photosynthesis and respiration may also be affected by both salinity variations and preadaptation. Biebl and McRoy (1971) showed that both subtidal and intertidal forms of *Z. marina* from Alaska maintained plasmatic resistance for short term (24 hr.) exposures over a range of salinities (0-3.0x, i.e., 1.0x = 31, 3.0x = ~93) and between -6°C and 34°C. Within these limits, photosynthesis increased with temperature in the intertidal plants up to 35° C, but up to only 30° C in the subtidal form. McRoy (1970) also demonstrated that the plants from tidepools shifted their entire temperature-respiration relationship toward the consumption of more oxygen in summer for any given temperature. None of the experiments showed effects of enzyme denaturation at 30° C, failing to support the 30° C lethal limit proposed by Setchell (1929).

In a comparison among species, Lutova and Feldman (1981) demonstrated that the thermostability of selected cell functions and enzymes in *Z. noltii* is approximately 4-5° C higher than that of *Z. marina*, consistent with a shallower distribution pattern. Physiological responses to temperature in *Z. marina* and *Ruppia maritima* in lower Chesapeake Bay are suggested as a partial basis for the difference in depth distribution of the species (Evans et al. 1986). Dennison (1987) showed that southern populations of *Z. marina* exhibit bimodal seasonal patterns of net photosynthesis, due to high respiration during summer months, while northern populations exhibit a more unimodal seasonal pattern, presumably due to temperature differences between southern and northern populations.

Pérez-Lloréns and Niell (1993, 1994) reported on the ability of two morphotypes of *Z. noltii* (in southern Spain) to photosynthesize in air (in the intertidal); the photosynthetic rates of the narrow-leaved variety (higher in the intertidal) were higher in air than the wider-leaved variety (lower in the intertidal), suggesting local adaptation to elevated insolation and temperature, as well as resistance to desiccation (see also McMillan 1984).

Investigations on *Thalassia testudinum* in Florida, the Gulf coast, and Caribbean have revealed that temperatures in excess of ~32° C will interfere with maintenance of ionic condition (Schroeder 1975), and that physiological changes such as chlorophyll *a* fluorescence values will occur prior to observable morphometric changes (Byron and Fourqurean 2004). Capone and Taylor (1980) found that C₂H₂ (acetylene) reduction rates were halved by a decrease of 10° C and that rates of N₂ fixation varied ~20-fold, being maximal in late summer and minimal in January. Zieman (1970) determined that net leaf productivity was significantly temperature dependent, with optimal growth occurring from 23-31° C (see also Barber and Behrens 1985).

Borum et al. (2005) and Rudnick et al. (2005) reviewed the mass die-off of *Thalassia* beds in Florida Bay in the 1980s (Robblee et al. 1991 and others), concluding that toxicity was caused by sulfide invasion of the rhizome, which was preceded by hypoxia caused by accelerated respiration in response to temperatures elevated above the seasonal ambient level.

Sand-Jensen and Borum (1983) (*Z. marina* in Danish waters) and Kerr and Strother (1985, 1989) (*Z. muelleri* in Australian waters) concluded that leaf productivity and photosynthetic ability respectively either were not affected by water temperature, or could be maintained under extreme conditions; secondary mechanisms such as those affecting dark respiration rates and rates of mineralization of the sediments were more likely to be affected.

Vergeer et al. (1995) demonstrated that *Z. marina* under culture produced lower levels of phenolic compounds when grown at high temperature, while those subjected to high light intensity increased production of phenols. Phenolic compounds are good bactericides and fungicides, which might offer some protection against infection of *Z. marina* by *Labyrinthula zosterae*, the putative cause of eelgrass wasting disease. However, infection with *Labyrinthula* itself proves also to have pronounced effects on the production of phenolic compounds (ibid.), confounding the protective effect of lower temperatures.

Interactive effects of global warming with other anthropogenic factors may be particularly stressful to seagrass populations. Mesocosm experiments with eelgrass (Bintz et al. 2003) which combined nutrient enrichment with sustained temperature elevation to 4° C above a 9-year mean caused significant declines in number of leaves per shoot, shoot surface area and shoot growth rate. The authors concluded that widespread eelgrass declines in the Northeast U.S. may be due to the combination of nutrient enrichment of coastal waters and the increasing frequency of warmer than average summer water temperatures. Johnson et al. (2003) conclude that persistent replacement of *Z. marina* by widgeongrass (*Ruppia maritima*) in two bays in the San Diego area during and following the 1997-1998 ENSO event foretell the possibility of widespread long-range habitat conversions if average water temperatures increase 1.5 - 2.5° C due to global warming.

Warmer than usual water temperatures have been proposed as a cause for the wide scale loss of eelgrass in the 1930's in Europe due to wasting disease. Giesen et al. (1990) propose a combination of high water temperatures, below-average sunshine and increased turbidity of coastal waters may have caused eelgrass to succumb to the saprophyte *Labyrinthula macrocystis* (cf. *L. zosterae*). Elevated water temperatures may have provided a higher overwintering survival rate for the parasite (see also Vergeer et al. 1995).

9.5 Effects of temperature on leaf growth, density and biomass

In Pacific coast populations, the relative proportion of vegetative compared to reproductive biomass is correlated to the length of growing season with temperatures between 15 and 20° C, although irradiance level is an important co-factor (Felger and McRoy 1974).

Poumian-Tapia and Ibarra-Obando (1999) demonstrated that seasonal changes in above-ground biomass and leaf area index (LAI) of *Z. marina* from a Mexican coastal lagoon were associated with water temperature.

At the other end of the temperature spectrum, Harrison and Mann (1975) discounted temperature as an important factor in eelgrass growth for a subtidal population in Nova Scotia, as most of the vegetative growth occurred at temperatures less than 10° C, concluding that this population may be adapted to very different temperature regimes than the optimal range proposed by Setchell (1929). Wium-Andersen and Borum (1984) also concluded that Setchell's growth regulation by temperature theory was not supported by their observations of *Z. marina* populations in Denmark, observing that ~75% of seasonal variance in leaf growth rate could be attributed to variation in surface irradiance, while only ~6% could be attributed to variation in temperature. Concurrently, Borum (1980), showed experimentally that temperature-dependent light-saturated photosynthesis only occurred at mid-day in the uppermost part of the leaf canopy.

A recent comprehensive review of eelgrass research in San Francisco Bay, CA. (Wyllie-Echeverria and Fonseca 2003) supported the original proposals of Setchell (1922, op. cit.) regarding the effects of temperature on the biotic responses of eelgrass (e.g., Phillips et al. 1983; Merkel and Associates 1999 (cited in Wyllie-Echeverria and Fonseca 2003); and Zimmerman et al. 1995). They conclude that transplantation and restoration efforts pay particular attention to season and temperature regimes in planning and scheduling, as many wintertime transplants were significantly inhibited by a combination of high turbidity and low temperatures.

Kirkman et al. (1982) (New South Wales, Australia) demonstrated a closer relationship for *Z. capricorni* productivity to water temperature than to solar radiation. The partial correlation coefficients between growth and water temperature were 0.95 (holding instantaneous solar radiation fixed) and 0.77 (holding solar radiation lagged by 1 month fixed), indicating an association between growth and water temperature not accounted for by solar radiation or solar radiation lagged by 1 month.

Marbà et al. (1996) found leaf and shoot growth in Mediterranean *Z. marina* populations to be associated primarily with average irradiance ($R^2 = 0.43$ leaf, 0.70 shoot), temperature variation was secondary ($R^2 = 0.57$ leaf, 0.10 shoot); *Z. noltii*, growing in the same area, but elevated in the intertidal with respect to *Z. marina*, was co-dependent on temperature ($R^2 = 0.62$ leaf, 0.32 shoot) and light ($R^2 = 0.64$ leaf, 0.37 shoot), although the light relationship lagged by ~1 month.

Harrison (1982a), Phillips and Backman (1983), Orth and Moore (1986), and Evans et al. (1986) all provide evidence that temperatures in excess of 30° C lead to declines in condition, i.e., loss of leaf or meristematic tissue or defoliation, or suppression of growth. Growth often resumes as temperatures fall below the 30° C threshold (often into the early fall season), explaining bimodal biomass peaks observed especially at the southern end of the distribution of seagrass populations in the northern hemisphere. Within single estuarine systems, biomass measures may follow gradients of both salinity and temperature, illustrated by the Yaquina Bay (Oregon) distribution of *Z. marina*, where summer coastal upwelling and large tidal prism "pumping" provides relatively cool, nutrient-rich water to the lower estuary, while temperatures increase upstream, reflecting watershed runoff influence. Biomass measures (shoots per unit area, plant size) are greatest near the ocean, tapering off proceeding upstream into warmer water.

During the summers of 1998-99, the overlying water column downstream was, on average, colder, more saline, less turbid, had more available light and higher dissolved inorganic nitrogen (DIN) than upstream. Temperature was negatively (but not significantly) correlated with *Z. marina* and green macroalgal cover $R = -0.52$ and -0.47 , respectively, $p > 0.1$); summertime DIN and phosphate concentrations were very poorly correlated with either seagrass or macroalgal cover $R < 0.18$, $p > 0.1$) (Kentula and DeWitt 2003).

Vegetative (leaf) growth in *Thalassia testudinum* is positively correlated with temperature, with the range 20-30° C being optimal for growth (Phillips 1960; Macauley, Clark, and Price 1988; Fletcher and Fletcher 1995; Irlandi et al. 2002; Tomasko and Hall 1999). Leaf length and width both decrease when stressed by elevated temperature (Linton and Fisher 2004). Zieman (1975) reported that leaf growth rates for *T. testudinum* in Biscayne Bay, Florida (data collected in 1969-70), was highest when the temperature was between 28-31° C and salinities ~30, and at stressed habitats, the minimum growth rates were when salinity was low (13-15) and temperature was highest (34-35° C).

9. 6 Desiccation Effects on Seagrasses

9.6.1 Minimal depth limit

Seagrasses in general are not tolerant of exposure to aerial conditions (excepting *Zostera japonica*, cf. *Z. americana*, *Z. nana*, *Z. noltii*? - see den Hartog and Kuo, 2006), suggesting that the shallowest distribution should be at a depth below the MLW (Koch 2001). This relationship has clearly been shown in tropical seagrasses where aerial exposure associated with extreme tides results in seasonal losses of above-ground biomass (Vermaat et al. 1993; Erftemeijer and Herman 1994; De Iongh et al. 1995; Stapel et al. 1997). In an extreme case the upper margin of a *Zostera noltii* bed was described as “burned” following such an exposure (van Lent et al. 1991). For intertidal *Z. capensis* in South African estuaries (Adams and Bate 1994), “scorched” leaves did not recover and were sloughed off, but regrowth from the basal meristem quickly replaced the lost tissue. For the temperate zone eelgrass, *Zostera marina*, numerous authors have implied that desiccation is the probable cause for changes in seagrass abundance and morphology across the tidal gradient (Bayer 1979; Jacobs 1979; Kentula and McIntire 1986; Keddy 1987; Koch and Beer 1996). *Thalassia testudinum* starts to become exposed at about a 15-cm water depth, because the blades are somewhat rigid (Phillips 1960). This exposure results in desiccation, which is often more severe in winter than in summer in subtropical habitats, where winter “spring” tides, high insolation and low-humidity polar air combine to enhance desiccation of tidally-exposed plants (Strawn 1953, 1961; Phillips 1960). Desiccation could be further accelerated in winter due to increased transpiration resulting from higher wind speeds (Holmquist et al. 1989).

Intertidal *Z. marina* is not found in the northern (where presumed ice scouring) and southern extremes of its range (with high summer temperatures) (Phillips et al. 1983b), respectively, preclude its growth. However, in the central portions of its range it is often present intertidally, where it can be found in greater density than subtidal populations. In these central ranges it is often found in three zones which have been defined by plant growth characteristics

and related to the degree of tidal exposure. For example Bayer (1979) and Boese et al. (2003) found and defined these zones in Yaquina Bay (Newport, OR, semi-diurnal tide, range ~2.4 m) as: 1) a subtidal and lower intertidal perennial zone (below 0.25 m MLLW) which consists mainly of perennial shoots which grow vegetatively from below-ground rhizomes which persists throughout the year, 2) a transition zone between 0.25-0.75 MLLW consisting of annual shoots and perennial patches, and 3) an upper intertidal zone (0.75 to 1.5 m MLW) which is characterized by annual shoots which grow from seeds and are absent in winter. Roughly the same growth pattern is representative of eelgrass from the Wadden Sea (Netherlands), where the perennial bed was never observed above 0.20 m above MLW, followed by the transition zone (bare sediment) and a mid-intertidal zone of annual plants (van Katwijk et al. 2000).

Occasionally *Z. marina* annuals and perennials are found above these zones, and are associated with micro-topographical features (e.g. tide pools, drainage channels) which would tend to retain water longer during ebb tides. Thus it appears that the upper limit for *Z. marina* is controlled not directly by tidal elevation but by the duration of water coverage (Kentula and McIntire 1986; Jacobs 1979). It is also possible that eelgrass biomass can structurally retard water loss by trapping water during ebb tides as has been reported for turtle grass in Florida Bay (Powell and Schaffner 1991). They observed that water was retained by dense turtle grass for up to eight hours during low tides and prevented desiccation. Intertidal macroalgae may play a somewhat similar role, as we have observed the low tide trapping of water during periods of high macroalgae accumulations in Yaquina Bay (Boese unpubl. data). It is also possible that the presence of epiphytes on the leaves of seagrass may reduce the desiccating effects of aerial exposure. Penhale and Smith (1977) noted that *Z. marina* plants, which had epiphytes removed, lost five times the amount of dissolved organic carbon following exposure to 1 h of laboratory desiccating conditions, when compared to plants with encrusting epiphytes. This suggested to them that the encrusted epiphytes trapped water interstitially during the receding tide, which diminished or prevented desiccation damage during aerial exposure.

The zonal differences between *Z. marina* annual and perennial forms appear to be due to morphological differences. van Katwijk et al. (2000) noted in the intertidal areas of the Wadden sea that eelgrass annuals when exposed during low tide tend to lie flat on the moist sediment surface as opposed to perennials which had stiffer sheaths that could not lie flat on the sediment. These upright sheaths tended to desiccate rapidly when exposed. These observations were confirmed by Boese et al. (2003), who noted the same phenomena in Yaquina Bay eelgrass.

Studies done on *Z. noltii* and *Z. japonica* have observed that these two eelgrass species are more tolerant of desiccation stress than *Z. marina* and can grow higher in the intertidal zone (Harrison 1982a; Harrison 1982b; Leuschner et al. 1998). Both of these species have smaller leaves and appear to sustain photosynthesis at lower leaf water content than *Z. marina* (Leuschner et al. 1998). Similar morphological differences have been noted in tropical seagrass species with tolerance to high temperature and aerial exposure, correlating with smaller and narrower leaves (McMillan 1984). Although *Z. marina* is less tolerant of desiccation, exposed leaves are capable of photosynthesis as long as leaves are moist, and are also able to recover from mild desiccation when leaves are re-wetted (Leuschner and Rees 1993).

9.6.2 Effect of tidal amplitude

The interaction between tidal exposure and light availability are the principal forcing factors determining the depth range within which seagrass can survive. As waters become more turbid seagrasses will be limited to shallow waters where they increasingly are affected by aerial exposure (Koch 2001). Assuming a low tolerance of desiccation, the minimum depth (Z_{\min}) was defined by Koch (2001) as half the tidal amplitude. Tidal amplitude in this case was defined as the difference between mean high and mean low water in areas with diurnal tides and as the difference between mean higher high water and mean lower low water in areas with semi-diurnal tides (Koch 2001). If the maximum depth that seagrass can grow (Z_{\max}) is due to light limitation, then no seagrass can survive if $Z_{\max} \leq Z_{\min}$. Thus as the tidal range increases, the depth range where seagrasses can occur is linearly decreased (Koch 2001).

This theoretical relationship is supported by the results of Koch and Beer (1996). That study attempted to explain the disappearance of *Z. marina* from the western portions of Long Island Sound while it persisted in the eastern portions. Light attenuation had increased due to eutrophication and the greater tide range in the western portion of the sound appeared to narrow the depth range within which *Z. marina* could grow, making this shallow population vulnerable to storm events (Koch and Beer 1996). Koch and Beer (1996) concluded that regulatory management of seagrass should take into account tides as well as light.

9.6.3 Effects of desiccation

At the population level, aerial exposure and associated desiccation stress affects *Z. marina* in a variety of ways. With increasing intertidal exposure, shoot density is reduced, leaves become narrower, canopy height is reduced, annual plants become more prevalent and flowering increases; these effects are associated with perennial eelgrass meadows becoming progressively more patchy with increasing tide height (Bayer 1979; Jacobs 1979; Kentula and McIntire 1986; Harrison 1982a; Keddy 1987; Ruckelshaus 1994; Koch and Beer 1996; Boese and Robbins unpublished data).

At the individual shoot level, desiccation reduces the plant's photosynthetic ability (Leuschner and Rees 1993), and leaves become physically damaged (van Katwijk et al. 2000; Boese et al. 2003). The progression of damage is an initial drying of the leaf in and immediately adjacent to the exposed sheaths, followed by gradual loss of pigment over a 7- 14 d interval. These non-pigmented areas often occur in bands across individual leaves which probably affect translocation of photosynthetic products, and weaken the leaf making it more vulnerable to breakage. Desiccation-induced breakage can contribute to the reduced canopy height often observed in high intertidal plants (Boese et al. 2003).

Desiccating events are episodic, and often associated with daylight spring tides during the summer, as illustrated in the seasonal losses of intertidal seagrass that occur in the tropics (Vermaat et al. 1993; Erftemeijer and Herman 1994; De Iongh et al. 1995; Stapel et al. 1997; van Lent et al. 1991). Similar episodic event have been observed in Yaquina Bay, Oregon during

daylight low tides in the spring and early summer, although winter low tide exposures to freezing temperatures may result in similar damage (Boese et al. 2003).

9.7 Research Gaps

There is a general lack of research on intertidal seagrass populations and how desiccation stress directly affects individual shoots and populations. Development of plant and population level models of the effects of exposure on eelgrass would be useful.

With respect to temperature effects, knowledge of site-specific temperature “windows” regarding vegetative growth, the initiation of reproduction (anthesis, pollination, seed set and dispersal), and upper thresholds for inhibition of growth, leaf loss and dark respiration seem to be the criteria that would be required for any restoration or preservation effort. Elevated levels of nitrogen, either as nitrate or ammonia, in combination with even slightly elevated above norm water temperatures could be held as a violation of acceptable habitat conditions. Additional multifactorial, mesocosm experiments with varying temperature and nitrogen concentrations could help define acceptable boundaries from a regulatory standpoint.

9.8 Literature Cited

- Adams, J. B. and G. C. Bate. 1994. The tolerance to desiccation of the submerged macrophytes *Ruppia cirrhosa* (Petagna) Grande and *Zostera capensis* Setchell. *Journal of Experimental Marine Biology and Ecology* 183:53-62.
- Barber, B. J. and P. J. Behrens. 1985. Effects of elevated temperature on seasonal *in situ* leaf productivity of *Thalassia testudinum* Banks ex König and *Syringodium filiforme* Kützing. *Aquatic Botany* 22:61-69.
- Bayer, R. D. 1979. Intertidal zonation of *Zostera marina* in the Yaquina estuary, Oregon. *Syesis* 12:147-154.
- Beardall, J., S. Beer, and J. A. Raven. 1998. Biodiversity of marine plants in an era of climate change: Some predictions based on physiological performance. *Botanica Marina* 41:113-123.
- Biebl, R. and C. P. McRoy. 1971. Plasmatic resistance and rate of respiration and photosynthesis of *Zostera marina* at different salinities and temperatures. *Marine Biology* 8:48-56.
- Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. *Quarterly Review of Biology*. 27:251-265.
- Bintz, J. C., S. W. Nixon, B. A. Buckley, and S. L. Granger. 2003. Impacts of temperature and nutrients on coastal lagoon plant communities. *Estuaries* 26:765-776.
- Boese, B. L., K. Alayan, E. Gooch, and B. D. Robbins. 2003. Desiccation index: A direct measure of the effects of tidal exposure on eelgrass (*Zostera marina*) in an Oregon estuary. *Aquatic Botany* 76:329-337.

- Borum, J. 1980. Biomasse og productionsforhold hos ålegræs (*Zostera marina* L.) og det tilknyttede epifytsamfund. M.S. Thesis, University of Copenhagen. 114 pp. (cited in Wium-Andersen and Borum, 1984)
- Borum, J., O. Pedersen, T. M. Greve, T. A. Frankovich, J. C. Zieman, J. W. Fourqurean, and C. J. Madden. 2005. The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. *Journal of Ecology* 93:148-158.
- Brenchley, J. L. and R. J. Probert. 1998. Seed germination responses to some environmental factors in the seagrass *Zostera capricorni* from eastern Australia. *Aquatic Botany* 62:177-188.
- Buia, M. C. and L. Mazzella. 1991. Reproductive phenology of the Mediterranean seagrasses *Posidonia oceanica* (L.) Delile, *Cymodocea nodosa* (Ucria) Aschers., and *Zostera noltii* Hornem. *Aquatic Botany* 40:343-362.
- Bulthuis, D. A. 1985. The effects of temperature on photosynthesis and growth of seagrasses. *Estuaries* 8:14A.
- Bulthuis, D. A. 1987. Effects of temperature on photosynthesis and growth of seagrasses. *Aquatic Botany* 27:27-40.
- Burke, M. K., W. C. Dennison, and K. A. Moore. 1996. Non-structural carbohydrate reserves of eelgrass *Zostera marina*. *Marine Ecology Progress Series* 137:195-201.
- Burkholder, J. M., K. M. Mason, and H. B. Glasgow Jr. 1992. Water column nitrate enrichment promotes decline of eelgrass *Zostera marina*: Evidence from seasonal mesocosm experiments. *Marine Ecology Progress Series* 81:163-178.
- Byron, D. A. and J. W. Fourqurean. 2004. Fluorescence responses of *Thalassia testudinum* to variations in salinity and temperature in Florida Bay. Abstract: 33rd Annual Marine Benthic Ecology Meeting, Mobile, AL, March 25-28, 2004.
- Capone, D. G. and B. F. Taylor. 1980. N₂ fixation in the rhizosphere of *Thalassia testudinum*. *Canadian Journal of Microbiology* 26:998-1005.
- Churchill, A. C. and M. I. Riner. 1978. Anthesis and seed production in *Zostera marina* L. from Great South Bay, New York, US. *Aquatic Botany* 4:83-93.
- Davis, J. L., D. L. Childers, and D. N. Kuhn. 1999. Clonal variation in a Florida Bay *Thalassia testudinum* meadow: molecular genetic assessment of population structure. *Marine Ecology Progress Series* 186:127-136.
- Dawes, C. J., R. C. Phillips, and G. Morrison. 2004. Seagrass Communities of the Gulf Coast of Florida: Status and Ecology. Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute and the Tampa Bay Estuary Program. St. Petersburg, FL. iv + 74 pp.
- de Cock, A. W. A. M. 1980. Flowering, pollination and fruiting in *Zostera marina* L. *Aquatic Botany* 9:201-220.
- de Cock, A. W. A. M. 1981. Influence of temperature and variations in temperature on flowering in *Zostera marina* L. under laboratory conditions. *Aquatic Botany* 10:125-131.
- de Iongh, H. H., B. J. Wenno, and E. Meelis. 1995. Seagrass distribution and seasonal biomass changes in relation to dugong grazing in the Moluccas, East Indonesia. *Aquatic Botany* 50:1-20, 1995.

- den Hartog, C., and J. Kuo. 2006. Taxonomy and Biogeography of Seagrasses. pp. 1-23. In: Larkum, A.W. D., R.J. Orth and C.M. Duarte (Eds.) Seagrasses: Biology, Ecology and Conservation. Springer-Verlag, Berlin.
- Dennison, W. C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany* 27:15-26.
- Drew, E. A. 1979. Physiological aspects of primary production in seagrasses. *Aquatic Botany* 7:139-150.
- Erftemeijer, P. L. A. and P. M. J. Herman. 1994. Seasonal changes in environmental variables, biomass, production and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. *Oecologia* 99:45-59.
- Evans, A. S. 1983. Growth and photosynthetic responses to temperature of two populations of *Zostera marina*. *Biological Bulletin (Woods Hole)* 165:508. (Abstract, General Scientific Meetings of the Marine Biological Laboratory, August 16-19, 1983, Woods Hole, MA.)
- Evans, A. S., K. L. Webb, and P. A. Penhale. 1986. Photosynthetic temperature acclimation in coexisting seagrasses, *Zostera marina* L. and *Ruppia maritima* L. *Aquatic Botany* 24:185-197.
- Felger, R. and C. P. McRoy. 1974. Seagrasses as potential food plants. In: Somers, G. F. (Ed.) Seed-Bearing Halophytes as Food Plants. Proceedings of a Conference, University of Delaware, June 10-11, 1974. Univ. Delaware Sea Grant DELU-W-74-001, NOAA Office of Sea Grant, U.S. Dept Commerce, Grant no. 2 35223; DEL SG 3 75.
- Fletcher, S. W. and W. W. Fletcher. 1995. Factors affecting changes in seagrass distribution and diversity patterns in the Indian-River-Lagoon complex between 1940 and 1992. *Bulletin of Marine Science* 1:49-58.
- Gambi, M.C. 1988. Flowering in a *Zostera marina* bed of San Juan Island (Washington, U.S.A.) during winter. *Aquatic Botany* 30:267-272.
- Gessner, F. 1970. Temperature: Plants. Pp. 363-406 in Kinne, O. (ed.). *Marine Ecology: A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters. Volume 1. Environmental Factors. Part 1.* Wiley-Interscience, London, England. 681 pp.
- Giesen, W. B. J. T., M. M. van Katwijk, and C. den Hartog. 1990. Temperature, salinity, insolation and wasting disease of eelgrass (*Zostera marina* L.) In the Dutch Wadden Sea in the 1930's. *The Netherlands Journal of Sea Research* 25:395-404.
- Glynn, P. W. 1968. Mass mortalities of echinoids and other reef flat organisms coincident with midday low water exposures in Puerto Rico. *Marine Biology* 1:226-243
- Harrison, P. G. 1982a. Spatial and temporal patterns in abundance of two intertidal seagrasses, *Zostera americana* den Hartog and *Zostera marina* L. *Aquatic Botany* 12:305-320.
- Harrison P. G. 1982b. Seasonal and year-to-year variations in mixed intertidal populations of *Zostera japonica* Aschers. & Graebn. and *Ruppia maritima* L. S.L. *Aquatic Botany*. 14:357-371.
- Harrison, P. G. and K. H. Mann. 1975. Chemical changes during the seasonal cycle of growth and decay in eelgrass (*Zostera marina*) on the Atlantic coast of Canada. *Journal of the Fisheries Research Board of Canada* 32:615-621.
- Hemminga, M.A. and M.A. Mateo. 1996. Stable carbon isotopes in seagrasses: Variability in ratios and use in ecological studies. *Marine Ecology Progress Series* 140:285-298.

- Holmquist, J. G., G. V. N. Powell, and S. M. Sogard. 1989. Sediment, water level and water temperature characteristics of Florida Bay's grass-covered mud banks. *Bulletin of Marine Science* 44:348-364.
- Hootsmans, M. J. M., J. E. Vermaat, and W. van Vierssen. 1987. Seed-bank development, germination and early seedling survival of two seagrass species from the Netherlands: *Zostera marina* L. and *Zostera noltii* Hornem. *Aquatic Botany* 28:275-285.
- Ibarra-Obando, S. E., C. -F. Boudouresque, and M. Roux. 1997. Leaf dynamics and production of a *Zostera marina* bed near its southern distributional limit. *Aquatic Botany* 58:99-112.
- Inglis, G. J. and M. P. Lincoln-Smith. 1998. Synchronous flowering of estuarine seagrass meadows. *Aquatic Botany* 60:37-48.
- Irandi, E., B. Orlando, S. Macia, P. Biber, T. Jones, L. Kaufman, D. Lirman, and E. T. Patterson. 2002. The influence of freshwater runoff on biomass, morphometrics, and production of *Thalassia testudinum*. *Aquatic Botany* 72:67-78.
- IPCC. 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change [Houghton, J.T., Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C.A. Johnson (eds.)]. Cambridge University Press, Cambridge, U.K. and New York, NY, USA, 881 pp. http://www.grida.no/climate/ipcc_tar/wg1/005.htm.
- Jacobs, R. P. W. M. 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. *Aquatic Botany* 7:151-172.
- Johnson, M. R., S. L. Williams, C. H. Lieberman, and A. Solbak. 2003. Changes in the abundance of the seagrasses *Zostera marina* L. (eelgrass) and *Ruppia maritima* L. (wideongrass) in San Diego, California, following an El Niño event. *Estuaries* 26:106-115.
- Keddy, C. J. 1987. Reproduction of annual eelgrass: Variation among habitats and comparison with perennial eelgrass (*Zostera marina* L.). *Aquatic Botany* 27:243-256.
- Kentula, M. E. and C. D. McIntire. 1986. The autecology and production dynamics of eelgrass (*Zostera marina* L.) in Netarts Bay, Oregon. *Estuaries* 9:188-199.
- Kentula, M. E. and T. H. DeWitt. 2003. Abundance of seagrass (*Zostera marina* L.) and macroalgae in relation to the salinity-temperature gradient in Yaquina Bay, Oregon, USA. *Estuaries* 26:1130-1141.
- Kerr, E. A. and S. Strother. 1985. Effects of irradiance, temperature and salinity on photosynthesis of *Zostera muelleri*. *Aquatic Botany* 23:177-183.
- Kerr, E. A., and S. Strother. 1989. Seasonal changes in leaf growth rate of *Zostera muelleri* Irmisch ex Aschers. in south-eastern Australia. *Aquatic Botany* 33:131-140.
- Kirkman, H., I. H. Cook, and D. D. Reid. 1982. Biomass and growth of *Zostera capricorni* Aschers. in Port Hacking, N.S.W., Australia. *Aquatic Botany* 12:57-67.
- Kirsten, J. H., C. J. Dawes, and B. J. Cochrane. 1998. Randomly amplified polymorphism detection (RAPD) reveals high genetic diversity in *Thalassia testudinum* Banks ex König (Turtlegrass). *Aquatic Botany* 61:269-287.
- Koch, E. W. 2001. Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation requirements. *Estuaries* 24:1-17.
- Koch, E. W. and S. Beer. 1996. Tides, light and the distribution of *Zostera marina* in Long Island Sound, USA. *Aquatic Botany* 53:97-107.

- Komar, P. D. 1997. Sediment Accumulation in Tillamook Bay, Oregon, a Large Drowned-River Estuary. Report for the Tillamook Bay National Estuary Project, May, 1997. 23 pp. (<<http://www.tbnep.org/reports/sedimentation.html>>).
- Larkum, A. W. D., A. J. McComb, and S. A. Shepherd. 1989. Biology of Seagrasses. A treatise on the biology of seagrasses with special reference to the Australian region. Aquatic Plant Studies 2. Elsevier, New York. Pp. 656-659.
- Leuschner, C. and U. Rees. 1993. CO₂ gas exchange of two intertidal seagrass species, *Zostera marina* L. and *Zostera noltii* Hornem., during emersion. Aquatic Botany 45:53-62.
- Leuschner, C., S. Landwehr, and U. Mehlig. 1998. Limitation of carbon assimilation of intertidal *Zostera noltii* and *Z. marina* by desiccation at low tide. Aquatic Botany 62:171-176.
- Linton, D., and T. Fisher (Eds.). 2004. Caribbean Coastal Marine Productivity Program: 1993-2003. CARICOMP. ISBN 976 610 624 X.
- Loques, F., G. Caye, and A. Meinesz. 1990. Germination in the marine phanerogam *Zostera noltii* Hornemann at Golfe Juan, French Mediterranean. Aquatic Botany 38:249-260.
- Lutova, M. I. and N. L. Feldman. 1981. Genotypic temperature adaptations of cellular functions and proteins in two *Zostera* species. Oecologia 49:92-95.
- Macauley, J. M., J. R. Clark, and W. A. Price. 1988. Seasonal changes in the standing crop and chlorophyll content of *Thalassia testudinum* Banks ex König and its epiphytes in the Northern Gulf of Mexico. Aquatic Botany 31:277-287. EPA/600/J-88/280, (ERL,GB 611). (Available from NTIS, Springfield, VA: PB89-209803).
- Marbà, N., J. Cebrian, S. Enríquez, and C.M. Duarte. 1996. Growth patterns of western Mediterranean seagrasses: Species-specific responses to seasonal forcing. Marine Ecology Progress Series 133:203-215.
- Marsh, J. A., W. C. Dennison, and R. S. Alberte. 1986. Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). Journal of Experimental Marine Biology and Ecology 101:257-267.
- Mayer, A. G. 1914. The effects of temperature upon tropical marine organisms. Carnegie Institute of Washington, Papers of the Tortugas Laboratory, 6:1-24.
- McManus, J., P. D. Komar, G. Bostrom, D. Colbert, and J. J. Marra. 1998. Sediment Sources and the History of Accumulation in Tillamook Bay, Oregon. Final Report, The Tillamook Bay National Estuary Project Sedimentation Study. 59 pp., Appendix. (<<http://www.tbnep.org/reports/sedimentation.html>>).
- McMillan, C. 1978. Morphogeographic variation under controlled conditions in five seagrasses, *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*, *Halophila engelmannii*, and *Zostera marina*. Aquatic Botany 4:169-189.
- McMillan, C. 1982. Isozymes in seagrasses. Aquatic Botany. 14:231-243.
- McMillan, C. 1983. Seed germination for an annual form of *Zostera marina* from the Sea of Cortez, Mexico. Aquatic Botany 16:105-110.
- McMillan, C. 1984. The distribution of tropical seagrasses with relation to their tolerance of high temperatures. Aquatic Botany 19:369-380, 1984.
- McMillan, C. and F. N. Moseley. 1967. Salinity tolerances of five marine spermatophytes of Redfish Bay, Texas. Ecology 48:503-506.

- McRoy, C. P. 1970. On the biology of eelgrass in Alaska. PhD Dissertation, Univ. Alaska, College, AK. Pp. 132-156. 71-25,292 - University Microfilms, Ann Arbor, MI.
- Meling-Lopez, A. E. and S. E. Ibarra-Obando. 1999. Annual life cycles of two *Zostera marina* L. populations in the Gulf of California: contrasts in seasonality and reproductive effort. *Aquatic Botany* 65:59-69.
- Merkel and Associates. 1999. Richmond Harbor Navigation Improvement Project, Post-dredging eelgrass survey. Prepared for Tetra Tech, Inc. San Francisco, CA. 22 pp. (cited in Wyllie-Echeverria and Fonseca 2003).
- Moffler, M. D. and M. J. Durako. 1987. Reproductive biology of the tropical-subtropical seagrasses of the southeastern United States. Pp. 77-88 in Durako, M. J., R. C. Phillips, and R. R. Lewis III (eds.). *Proceedings of the Symposium on Subtropical-Tropical Seagrasses of the Southeastern United States*. Florida Marine Research Publications No. 42. Florida Marine Research Institute, St. Petersburg, Florida. 209 pp.
- Moore, K. A., R. J. Orth, and J. F. Nowak. 1993. Environmental regulation of seed germination in *Zostera marina* L. (eelgrass) in Chesapeake Bay: effects of light, oxygen and sediment burial. *Aquatic Botany* 45:79-91.
- Nelson, T. 1997. Interannual variance in a subtidal eelgrass community. *Aquatic Botany* 56:245-252.
- Nienhuis, P. H. 1983. Temporal and spatial patterns of eelgrass (*Zostera marina* L.) in a former estuary in the Netherlands, dominated by human activities. *Marine Technology Society Journal* 17:69-77.
- NOAA. 2006. 2006 Annual Climate Review. U.S. Summary. <<http://www.ncdc.noaa.gov/oa/climate/research/2006/ann/us-summary.html>>
- Olesen, B. and K. Sand-Jensen. 1993. Seasonal acclimatization of eelgrass *Zostera marina* growth to light. *Marine Ecology Progress Series* 94:91-99.
- Orth, R. J. and K. A. Moore. 1983. Seed germination and seedling growth of *Zostera marina* L. (eelgrass) in the Chesapeake Bay. *Aquatic Botany* 15:117-131.
- Orth, R. J. and K. A. Moore. 1986. Seasonal and year-to-year variations in the growth of *Zostera marina* L. (eelgrass) in the lower Chesapeake Bay. *Aquatic Botany* 24:335-341.
- Penhale P.A. and W. O. Smith Jr. 1977. Excretion of dissolved organic carbon by eelgrass (*Zostera marina*) and its epiphytes. *Limnology and Oceanography* 22:400-407.
- Pérez-Lloréns, J. L. and F. X. Niell. 1993. Temperature and emergence effects on the net photosynthesis of two *Zostera noltii* Hornem. morphotypes. *Hydrobiologia* 254:53-64.
- Pérez-Lloréns, J. L. and F. X. Niell. 1994. Photosynthesis in air: Comparative responses to different temperatures of two morphotypes of *Zostera noltii* Hornem. from Palmones River estuary (southern Spain). *Verhandlungen der Internationalen Vereinigung für Limnologie* 25:2265-2269.
- Phillips, R. C. 1960. Observations on the ecology and distribution of the Florida seagrasses. Professional Paper Series. Florida Board of Conservation 2:1-72.
- Phillips, R. C. 1972. Ecological life history of *Zostera marina* L. (eelgrass) in Puget Sound, Washington. PhD Thesis, University of Washington, Seattle. 73-3771 University Microfilms, Ann Arbor, MI, pp. 32 & 121.
- Phillips, R. C. and T. W. H. Backman. 1983. Phenology and reproductive biology of eelgrass (*Zostera marina* L.) at Bahia Kino, Sea of Cortez, Mexico. *Aquatic Botany* 17:85-90.

- Phillips, R. C., W. S. Grant, and C.P. McRoy. 1983a. Reproductive strategies of eelgrass (*Zostera marina* L.). *Aquatic Botany* 16:1-20, 1983.
- Phillips, R. C. and R. L. Lewis III. 1983. Influence of environmental gradients on variations in leaf widths and transplant success in North American seagrasses. *Marine Technology Society Journal* 17:59-68.
- Phillips, R. C., C. McMillan, and K.W. Bridges. 1983b. Phenology of eelgrass, *Zostera marina* L., along latitudinal gradients on North America. *Aquatic Botany* 15:145-146.
- Phillips, R. C. and E. G. Menez. 1988. Seagrasses. *Smithsonian Contributions to the Marine Sciences - Number 34*. Smithsonian Institution Press, Washington, D.C., pp. 15-18.
- Pollard, P. C. and M. Greenway. 1993. Photosynthetic characteristics of seagrasses (*Cymodocea serrulata*, *Thalassia hemprichii* and *Zostera capricorni* in a lowlight environment, with a comparison of leaf-marking and lacunal-gas measurements of productivity. *Australian Journal of Marine and Freshwater Research* 44:127-139.
- Poumian-Tapia, M. and S. E. Ibarra-Obando. 1999. Demography and biomass of the seagrass *Zostera marina* in a Mexican coastal lagoon. *Estuaries* 22:837-847.
- Powell, G. V.N. and F. C. Schaffner. 1991. Water trapping by seagrasses occupying bank habitats in Florida Bay. *Estuarine, Coastal and Shelf Science*. 32:43-60.
- Ramage, D. L. and D. R. Schiel. 1998. Reproduction in the seagrass *Zostera novazelandica* on intertidal platforms in southern New Zealand. *Marine Biology* 130:479-489.
- Robblee, M. B., T. R. Barber, P. R. Carlson, M. J. Durako, J. W. Fourqurean, L. K. Muehlstein, D. Porter, L. A. Yarbro, R. T. Zieman, and J. C. Zieman. 1991. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress Series* 71:297-299.
- Ruckleshaus, M. H. 1994. Ecological and genetic factors affecting population structure in the marine angiosperm, *Zostera marina* L. PhD Dissertation, University of Washington, Seattle.
- Rudnick, E. T., P. B. Ortner, J. A. Browder, and S. M. Davis. 2005. A conceptual ecological model of Florida Bay. *Wetlands* 25:870-883.
- Sachs, J. 1864. Ueber die obere Temperturgränze der Vegetation. *Flora N. R.* 22:139-215.
- Sand-Jensen, K. and J. Borum. 1983. Regulation of growth of eelgrass (*Zostera marina* L.) in Danish coastal waters. *Marine Technology Society Journal* 17:15-21.
- Schiel, D. R., J. R. Steinbeck, and M. S. Foster. 2004. Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology* 85:1833-1839.
- Schroeder, P. B. 1975. Thermal stress in *Thalassia testudinum*. Ph.D. Dissertation, University of Miami, Coral Gables, Florida. 157 p.
- Seddon, S., R. M. Connolly, and K. S. Edyvane. 2000. Large-scale seagrass dieback in northern Spencer Gulf, South Australia. *Aquatic Botany* 66:297-310.
- Setchell, W. A. 1929. Morphological and phenological notes on *Zostera marina* L. *University of California Publications in Botany*, 14:389-452, 59 fig.
- Short, F. T. and H. A. Neckles. 1999. The effects of global climate change on seagrasses. *Aquatic Botany* 63(3-4):169-196.
- Silberhorn, G. M., R. J. Orth, and K. A. Moore. 1983. Anthesis and seed production in *Zostera marina* L. (eelgrass) from the Chesapeake Bay. *Aquatic Botany* 15:133-144.

- Stapel, J., R. Manuntun, and M.A. Hemminga. 1997. Biomass loss and nutrient redistribution in an Indonesian *Thalassia hemprichii* seagrass bed following seasonal low tide exposure during daylight. *Marine Ecology Progress Series* 148:251-262.
- Strawn, K. 1953. A study of the dwarf-seahorse, *Hippocampus regulus* Ginsburg, at Cedar Key, Florida. M.S. Thesis, University of Florida, Gainesville, Florida. 114 pp.
- Strawn, K. 1961. Factors influencing the zonation of submersed monocotyledons at Cedar Key, Florida. *Journal of Wildlife Management* 25:178-189.
- Styllas, M. N. 2001. Sediment accumulation and human impacts in Tillamook Bay, Oregon. Thesis, Master of Science in Oceanography, Oregon State University, Corvallis, Oregon. (<<http://www.tbnep.org/reports/sedimentation.html>>).
- Thayer, G. W., D. A. Wolfe, and R. B. Williams. 1975. The impact of man on seagrass systems. *American Scientist* 63:288-296.
- Thom, R. M., A. B. Borden, S. Rumrill, D. L. Woodruff, G. D. Williams, J. A. Southard, and S. L. Sargeant. 2003. Factors influencing spatial and annual variability in eelgrass (*Zostera marina* L.) meadows in Willapa Bay, Washington, and Coos Bay, Oregon, estuaries. *Estuaries* 26:1117-1129.
- Thorhaug, A., N. Blake, and P. B. Schroeder. 1978. The effect of heated effluents from power plants on seagrass (*Thalassia*) communities quantitatively comparing estuaries in the subtropic to the tropics. *Marine Pollution Bulletin* 9:181-187.
- Thorhaug, A., D. A. Segar, and M. A. Roessler. 1973. Impact of a power plant on a subtropical estuarine environment. *Marine Pollution Bulletin* 4:166-169.
- Tomasko, D. A. and M. O. Hall. 1999. Productivity and biomass of the seagrass *Thalassia testudinum* along a gradient of freshwater influence in Charlotte Harbor, Florida. *Estuaries* 22:592-602.
- Touchette, B. W. and J. M. Burkholder. 2002. Seasonal variations in carbon and nitrogen constituents in eelgrass (*Zostera marina* L.) as influenced by increased temperature and water-column nitrate. *Botanica Marina* 45:23-34.
- Touchette, B. W., J. M. Burkholder, and H. B. Glasgow Jr. 2003. Variations in eelgrass (*Zostera marina* L.) morphology and internal nutrient composition as influenced by increased temperature and water column nitrate. *Estuaries* 26(1):142-155.
- van Katwijk M. M., D. C. R. Hermus, D. J. de Jong, R. M. Asmus, and V. N. de Jong. 2000. Habitat suitability of the Wadden Sea for restoration of *Zostera marina* beds. *Helgolander Marine Research*. 54:117-128.
- van Lent, F., P. H. Nienhuis, and J. M. Verschuure. 1991. Production and biomass of the seagrasses *Zostera noltii* Hornem. and *Cymodocea nodosa* (Ucria) Aschers. at the Band d'Arguin (Mauritania, NW Africa) a preliminary approach. *Aquatic Botany* 41:353-367.
- Vermaat, J. E., J. A. J. Beijer, M. J. M. Hootsmans, and C. J. M. Philippart. 1993. Leaf dynamics and standing stocks of intertidal *Zostera noltii* Hornem. and *Cymodocea nodosa* (Ucria) Ascherson on the Band d'Arguin (Mauritania). *Hydrobiologia* 258:59-72.
- Vernberg, F. J. 1978. Multiple-Factor and Synergistic Stresses in Aquatic Systems. Pp. 726-747, In: Thorp, J. H. and J. W. Gibbons (Eds.). *Energy and Environmental Stress in Aquatic Systems. Selected papers from a Symposium held at Augusta, Georgia, November 2-4, 1977.* Technical Information Center, U. S. Department of Energy. CONF-771114.

- Vergeer, L. H. T., T. L. Aarts, and J. D. de Groot. 1995. The 'wasting disease' and the effect of abiotic factors (light intensity, temperature, salinity) and infection with *Labyrinthula zosterae* on the phenolic content of *Zostera marina* shoots. *Aquatic Botany* 52:35-44.
- Verhagen, J. H. G. and P. H. Nienhuis. 1983. A simulation model of production, seasonal changes in biomass and distribution of eelgrass (*Zostera marina*) in Lake Grevelingen. *Marine Ecology Progress Series* 10:197-195.
- Witz, J. J. A. 1994. Flowering frequency, sex distribution, density and age of short shoots in three west-central Florida *Thalassia testudinum* Banks ex König (Hydrocharitaceae) meadows. M.S. Thesis. University of South Florida, Tampa, Florida.
- Witz, M. J. A., and C. J. Dawes. 1995. Flowering and short shoot age in three *Thalassia testudinum* meadows off west-central Florida. *Botanica Marina* 38:431-436.
- Wium-Andersen, S. and J. Borum. 1984. Biomass variation and autotrophic production of an epiphyte-macrophyte community in a coastal Danish area: I. Eelgrass (*Zostera marina* L.) biomass and net production. *Ophelia* 23:33-46.
- Wyllie-Echeverria, S. and M. Fonseca. 2003. Eelgrass (*Zostera marina* L.) research in San Francisco Bay, California from 1920 to the present. Literature Review. NCCOS S.F. Bay Eelgrass (*Zostera marina*) Project. February, 2003; pp. 20;
<http://response.restoration.noaa.gov/cpr/watershed/sanfrancisco/sfb_html/resources/bibs.html>.
- Zieman, J. C. 1970. The effects of a thermal effluent stress on the sea-grasses and macroalgae in the vicinity of Turkey Point, Biscayne Bay, Florida. Ph.D. dissertation. University of Miami, Coral Gables, FL. 129 pp.
- Zieman, J. C. 1975. Seasonal variation of Turtle Grass, *Thalassia testudinum* König, with reference to temperature and salinity effects. *Aquatic Botany* 1:107-123.
- Zieman, J. C. and R. G. Wetzel. 1980. Productivity in Seagrasses: Methods and Rates. pp. 101-279. In: Phillips, R.C. and C.P. McRoy (Eds.) *Handbook of Seagrass Biology: An Ecosystem Perspective*. Garland STPM Press, New York.
- Zimmerman, R. C., J. L. Reguzzoni, S. Wyllie-Echeverria, M. Josselyn, and R. S. Alberte. 1995. Assessment of environmental suitability for growth of *Zostera marina* L. (eelgrass) in San Francisco Bay. *Aquatic Botany* 39:353-366.
- Zimmerman, R. C., R. D. Smith, and R. A. Alberte. 1989. Thermal acclimation and whole-plant carbon balance in *Zostera marina* (eelgrass). *Journal of Experimental Marine Biology and Ecology* 130:93-109.

10.0 The Effects of Bioturbation and Bioirrigation on Seagrasses

Theodore H. DeWitt

10.1 Background

Marine and estuarine fauna can diminish or enhance seagrass condition simply as a result of their burrowing, sediment re-working, feeding activities (e.g., bioturbation), or their ventilation of burrows and tubes (e.g., bioirrigation). Compared to other limiting or facilitating factors, little mention is made of bioturbation or bioirrigation in the seagrass literature prior to the early 1980's (i.e., prior to Suchanek 1983). Since then, however, several studies (see below) and one review (Short and Wyllie-Echeverria 1996) present compelling evidence that these processes may profoundly affect the local distribution, abundance, and productivity of seagrasses.

Generally speaking, bioturbation negatively affects seagrasses (although it may do the reverse in some circumstances), whereas bioirrigation has positive or neutral effects. These processes are ecologically distinct from other important plant-animal interactions that can affect seagrasses, such as herbivory and epifaunal colonization of seagrass leaves. Bioturbation is the biogenic transport of particulate matter (inorganic and organic) within the sediment column, resulting from burrowing, excavation, and feeding activities of infaunal and epifaunal invertebrates, demersal fish and marine mammals, and birds. Bioturbation includes the vertical and horizontal mixing of particulate matter and associated porewater within the sediment column, the deposition of sediment from depth to the sediment surface (or sediment water interface), and the resuspension of bedded sediments into the water column. The negative impacts of bioturbation on seagrasses are mediated through burial, shading, erosion, or damage to roots. Bioirrigation is the biogenic pumping of water and solutes from waters overlying the seafloor into the sediment column due to organismal activities within burrows or tubes (i.e., ventilation for respiration, feeding, defecation, or excavation) and passive ventilation of burrows or tubes caused by the Bernoulli-effect of bottom currents flowing over burrow openings (Allanson et al. 1992). The positive effects of bioirrigation to seagrasses, while less studied than the negative effects of bioturbation, potentially include oxygenation of sediments, import of nitrogen-rich particulate matter into the sediment (via suspension feeding), stimulation of organic matter remineralization, and enhancement of oxidation or removal of toxic substances in sediments (i.e., hydrogen sulfide, ammonia) (see reviews by Aller 1988; Kristensen 1988; Pearson 2001). Bioturbation can have similar impacts on sediment geochemistry as bioirrigation (i.e., enhancement of organic matter remineralization, oxygenation of sediments, and burial of sediment organic matter) and, therefore can potentially benefit seagrasses under some circumstances.

Bioturbation and bioirrigation may affect the impact of other stressors, particularly nutrient enrichment, on seagrasses. Little research has been conducted to specifically examine interactions between bioturbation/bioirrigation, nutrient enrichment and seagrass condition, although hypotheses regarding consequences of such interactions can be proposed. Both

bioturbation and bioirrigation can reduce the adverse impacts of eutrophication by increasing the rates of organic matter burial, below-ground decomposition, and nutrient cycling; by oxygenating sediment porewater; and by increasing the flux of dissolved metabolites and nutrients from sediments into the water column. Bioturbation can potentially increase the adverse effects of nutrient enrichment by decreasing water column light levels (i.e., by increasing turbidity as a result of sediment resuspension) or by acting as an independent stressor on nutrient-stressed plants. These interactions, their relevance to seagrass management, and gaps in scientific knowledge are discussed in the final section of this chapter.

As with all limiting or facilitating factors, the energetic and spatial magnitude of bioturbation and bioirrigation determine the importance (and the direction of the effect) of these processes on seagrasses. At low intensity, neither process is likely to have measurable effects on seagrasses. The research reviewed here focuses only on those cases where significant correlations or experimental evidence suggest a cause and effect relationship.

10.2 Role of Bioturbation in Limiting Seagrass Populations

Bioturbation by burrowing shrimp, sting rays, crabs, polychaete worms, and echinoderms have been reported to adversely affect seagrass recruitment, growth, and survival by burial or uprooting of seeds, seedlings, shoots and patches of seagrass (Table 10.1 and Figure 10.1). Dugongs and manatees mix and resuspend sediments as they forage for seagrass leaves and rhizomes (Packard 1984; Preen 1995; Domning 2001), but the impact of their bioturbation on seagrasses has not been evaluated; thus, it would be premature to include sirenians as bioturbators in this review. In some cases, cause and effect were inferred from disjunct distributions of populations of bioturbators and seagrasses, and observations of burial of seagrass shoots by excavated sediments where populations overlapped. Stronger evidence was provided in several studies featuring field or laboratory experiments in which seagrasses were transplanted into sediments containing different densities of bioturbators, or cages were erected to exclude bioturbators from seagrasses. The effects of each group of bioturbators on seagrasses are reviewed first, followed by a summary of the mechanisms by which bioturbation disturbs seagrasses.

10.2.1 Burrowing Shrimp Bioturbation

The most frequently reported bioturbator-seagrass interactions are those involving thalassinid burrowing shrimp (Arthropoda: Decapoda: Thalassinidae) as the bioturbators. Burrowing shrimp have been reported to variously affect seagrass recruitment (Dumbauld and Wyllie-Echeverria 2003), shoot growth, productivity and survival (Suchanek 1983; Harrison 1987; Molenaar and Meinesz 1995; Siebert and Branch 2007), population distribution (Suchanek 1983; Harrison 1987; Pranovi et al. 1996; Siebert and Branch 2005; Dumbauld and Wyllie-Echeverria 2003), and community structure (Duarte et al. 1997). Post-larval stages of burrowing shrimp live in extensive burrow galleries excavated in estuarine and marine sediments, have prodigious rates of sediment turnover (reviewed by Rowden and Jones 1993), and are important ecosystem engineering species in many coastal systems because of their influence on benthic

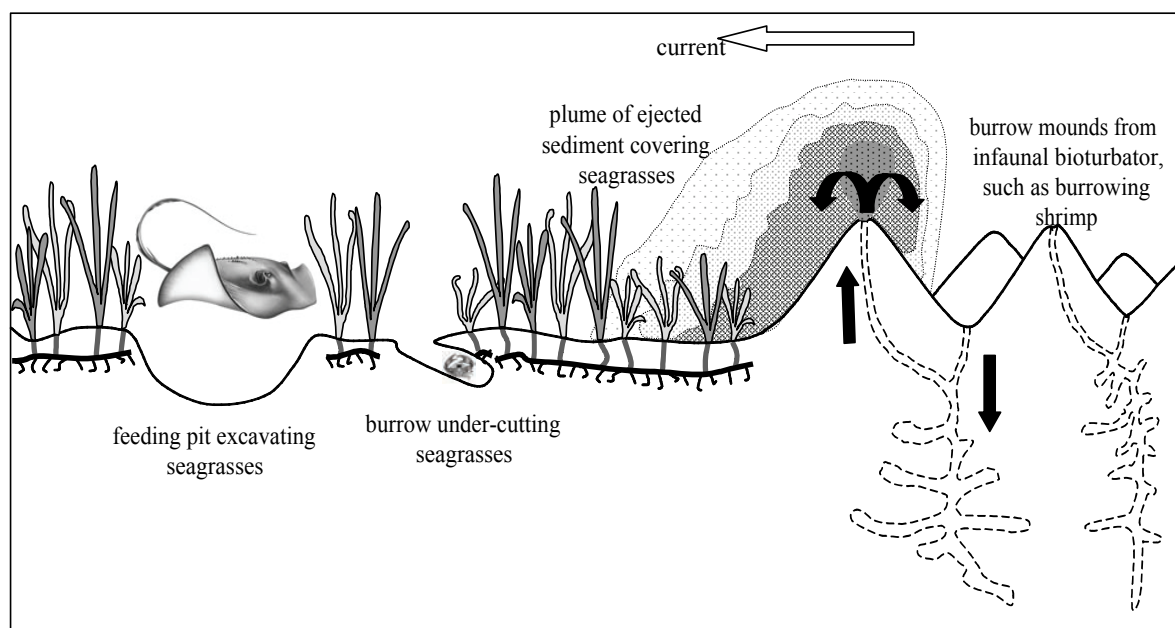


Figure 10.1. Illustration of some of the adverse effects of bioturbation on seagrasses (adapted from Suchanek 1983, Figure 4). Arrows show paths of sediment subduction, advection and resuspension as result of sediment reworking by burrowing shrimp.

Table 10.1 Summary of sources of significant bioturbation impacts for different seagrasses

Bioturbation Source	Seagrass Species	Reference
Burrowing shrimp	<i>Zostera marina</i> , <i>Z. japonica</i>	Thompson and Pritchard 1969
	<i>Z. marina</i> , <i>Z. japonica</i>	Harrison 1987
	<i>Z. japonica</i>	Dumbauld and Wyllie-Echeverria 2003
	<i>Z. japonica</i> , <i>Z. capricorni</i>	Berkenbusch et al. 2007
	<i>Z. noltii</i>	Pranovi et al. 1996
	<i>Z. capensis</i>	Siebert and Branch 2005, 2006
	<i>Z. capensis</i>	Angel et al. 2006
	<i>Posidonia oceanica</i>	Molenaar and Meinesz 1995
	<i>Halodule uninervis</i>	Duarte et al. 1997
	<i>Thalassia testudinum</i>	Suchanek 1983
	<i>T. hemprichii</i>	Duarte et al. 1997
	<i>Syringodium isoetifolium</i>	Duarte et al. 1997

	<i>Cymodocea rotundata</i>	Duarte et al. 1997
	<i>C. serrulata</i>	Duarte et al. 1997
Stingrays	<i>Z. marina</i>	Orth 1975
	<i>Z. marina</i>	Merkel 1990
	<i>Z. marina</i> , <i>H. wrightii</i>	Townsend and Fonseca 1998
	<i>H. wrightii</i>	Fonseca et al. 1994
	<i>T. testudinum</i>	Ogden 1980
	<i>T. testudinum</i>	Zieman 1982
	<i>T. testudinum</i>	Valentine et al. 1994
	<i>Syringodium sp.</i>	Fonseca et al. 1998
Crabs	<i>Z. capricorni</i> (=novazelandica)	Woods and Schiel 1997
	<i>Z. marina</i>	Davis and Short 1997
	<i>Z. marina</i>	Davis et al. 1998
	<i>T. testudinum</i>	Valentine et al. 1994
Polychaetes	<i>Z. noltii</i>	Phillipart 1994
	<i>Z. marina</i>	Luckenbach and Orth 1999
	<i>Z. marina</i>	Davis and Short 1997
	<i>Zostera</i> spp.	Hughes et al. 2000
Echinoderms	<i>Z. marina</i>	Backman 1984

community structure and geochemical processes (Berkenbusch and Rowden 2003 and 2007; DeWitt et al. 2004; Tamaki 2004; Siebert and Branch 2006; Berkenbusch et al. 2007). Burrowing shrimp species occur along virtually all coasts world-wide (Dworschak 2000) and frequently occur in habitats that can sustain seagrass populations.

Suchanek (1983) conducted the first published study that connected burrowing shrimp bioturbation with a decrease in seagrass condition and abundance. He noted a negative correlation in the spatial distribution of subtidal ghost shrimp (*Callinassa* spp.) and turtlegrass (*Thalassia testudinum*) in two bays on St. Croix (US Virgin Islands). Subtidal populations of four ghost shrimp species live in those bays, and one species (*C. rathbunae*) turns over ~2.6 kg sediment m⁻² d⁻¹, producing large mounds (ca. 19 cm height) of ejected sediment, at densities of ~6-7 mounds m⁻². Turtlegrass productivity and percent cover decreased in proportion with increasing density of ghost shrimp mounds (Figure 10.2.A). Shoots and leaves of *T. testudinum* transplanted into areas of high ghost shrimp density steadily decline in abundance over a five month period whereas turtlegrass transplanted into areas with low shrimp densities were “lush

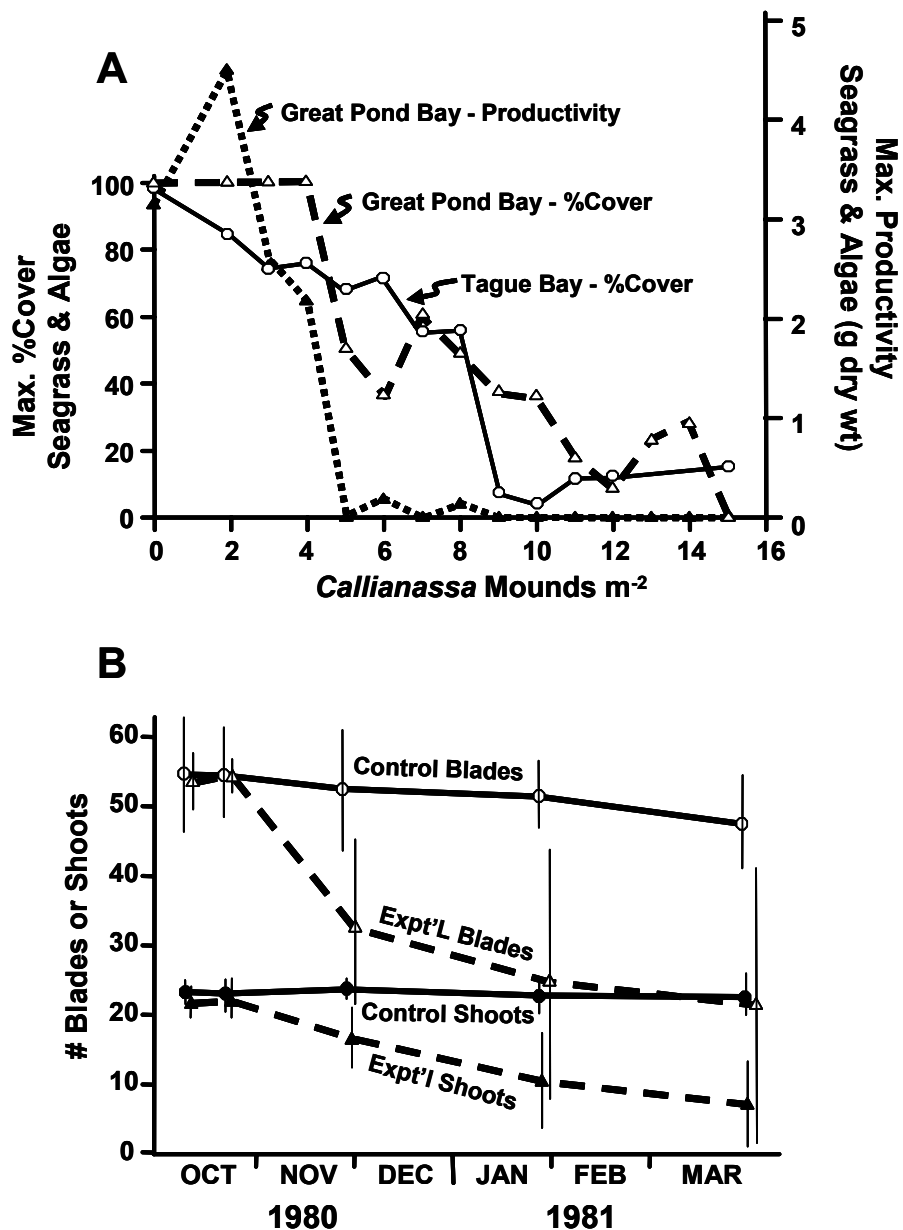


Figure 10.2. Effects of bioturbating burrowing shrimp (*Callianassa* spp.) on turtle grass (*Thalassia testudinum*) on subtidal sand flats on St. Croix island (US Virgin Islands); from Suchanek (1983). A. Field data showing inverse relationships between burrowing shrimp abundance and seagrass percent cover at Tague Bay (solid line) and Great Pond Bay (dashed line), and with seagrass productivity (dotted line) at Great Pond Bay. B. Results of a field experiment showing temporal change in number of seagrass blades and shoots (mean \pm 1 SE) from turtle grass transplanted into areas with high densities (experimental; dashed line) or low densities (control; solid line) of burrowing shrimp. Reproduced with permission from Journal of Marine Research and T.H. Suchanek.

and healthy” (Figure 10.2.B). Suchanek (1983) proposed that burial by excavated sediments, or shading due to either turbidity or deposition of fine-grained resuspended sediment onto leaves were the likely mechanisms causing decreased turtlegrass productivity and survival. He concluded that burrowing shrimp could severely limit *T. testudinum* distribution and negatively affect the habitat and energetic value of Caribbean seagrass beds. Whereas Suchanek (1983) characterized the direct effects of *Callianassa* spp. on turtlegrass, Wanless et al. (1988) reported an indirect effect of bioturbation by these shrimp on *T. testudinum*, positing that hurricane transported sediments from shrimp’s mounds (which had a characteristic sediment grain size distribution) contributed to the smothering of seagrasses.

In subtidal sandy habitats (specifically the French Mediterranean), Molenaar and Meinesz (1995) reported that populations of the shrimp *C. tyrrhena* reduced survival of *Posidonia oceanica* transplanted by ~40% relative to sands not inhabited by burrowing shrimp. They proposed that the transplants were buried by sediments excavated by *C. tyrrhena*, which is a prodigious bioturbator; at densities of 16 shrimp m⁻², they deposit ~600 g m⁻² d⁻¹ of sand on the seafloor (Ott 1976 in Molenaar and Meinesz 1995). Pranovi et al. (1996, F. Pranovi, personal communication) observed a sharp decrease in the presence of the seagrass, *Z. noltii*, in Venice Lagoon (Italy) during the early 1990’s and a coincident increase in the abundance of the mud shrimp, *Upogebia pusilla*; this pattern was also found in spatial surveys conducted in the lagoon. Bioturbation by the shrimp was proposed as a mechanism to explain the distribution patterns, but no experiments were conducted to test the hypothesis (F. Pranovi, personal communication).

Callianassid burrowing shrimp can limit the intertidal distribution of seagrasses. In Langebaan Lagoon (west coast of South Africa), Branch et al. (2003) and Siebert and Branch (2005) observed that the seagrass, *Z. capensis*, was relegated to the upper intertidal when co-occurring on tide flats with the ghost shrimp *C. kraussi*. Using an elegant field experiment, Siebert and Branch (2006) demonstrated that patches of seagrass increased in area when transplanted into lower intertidal areas from which the shrimp had been extirpated. However, if high densities of ghost shrimp were present, the seagrass shoots died and the patches declined in size. Sediment resuspension and deposition were much greater in shrimp-dominated habitats than in the seagrass beds, and smothering and burial by shrimp-excavated sediments were suspected to be main mechanisms that limited the lower limit of *Z. capensis* distribution (Siebert and Branch, 2005, 2006). However, they also found that these callianassid shrimp did not colonize areas immediately down-slope of the seagrass bed, nor open patches within the seagrass meadow; processes causing these patterns are discussed later in this section. In Papanui Inlet (South Island, New Zealand), Berkenbusch et al. (2007) reciprocally transplanted ghost shrimp (*C. filholi*) or small patches of seagrass (*Z. capricorni*) into field enclosures containing the other species (i.e., seagrass or shrimp, respectively), and compared the abundances of manipulated shrimp and seagrass relative to untransplanted, enclosed patches of ghost shrimp and seagrass (i.e., control treatments) over 6 months. In the presence of ghost shrimp, *Z. filholi* biomass and shoot density decreased. Bioturbation was considerably higher in enclosures containing ghost shrimp; burial by excavated sediments was presumably the mechanism causing the demise of *Z. filholi* transplants. However, in seagrass-dominated enclosures, transplanted ghost shrimp abundances declined whereas the seagrass abundance was unchanged relative to the

unmanipulated control treatment. They inferred that the density of the root mat prevented the ghost shrimp from burrowing into the sediment, as reported or inferred in other studies (i.e., Brenchley 1982; Harrison 1987; Siebert and Branch 2006).

Interactions between intertidal burrowing shrimp and seagrasses in NE Pacific estuaries have been the subject of several studies, particularly focused on the Callianassid ghost shrimp (*Neotrypaea* [= *Callianassa*] *californiensis*) and the native eelgrass *Z. marina* and the invasive Japanese eelgrass *Z. japonica*. The outcomes of the interactions, however, were not unidirectional. In British Columbia (Canada), Harrison (1987) observed negative correlations in the abundances of *Z. marina*, *Z. japonica* and ghost shrimp, and proposed that ghost shrimp bioturbation could prevent the seagrasses from colonizing unvegetated sediments. *Z. japonica* shoots transplanted into dense patches *N. californiensis* disappeared within a few weeks due to burial by sediments excavated by the shrimp. He proposed that interactions between ghost shrimp and *Zostera* spp. could limit the distribution of seagrasses, but that the seagrasses also could limit the shrimp's distribution if the water column was sufficiently clear to allow early lateral growth of the seagrasses in early Spring (see section 10.4). Dumbauld and Wyllie-Echeverria (2003) reported that burrowing shrimp bioturbation was an important factor determining recruitment success for *Z. japonica* seedlings in intertidal sediments of Willapa Bay estuary (Washington, USA). They observed that, following the eradication of burrowing shrimp (predominantly the ghost shrimp, *N. californiensis*) by pesticide application, *Z. japonica* and *Z. marina* often colonized intertidal habitats, whereas seagrass seedlings were sparse or absent from ghost shrimp dominated areas. They measured no significant difference in vertical distribution, viability or germination success of *Z. japonica* seeds among experimental plots (shrimp-dominated sediments treated, or not, with pesticide to kill the shrimp), but decreased growth and loss of *Z. japonica* seedlings in plots containing ghost shrimp. Burial or light limitation due to sediment resuspension were suggested as the mechanisms that reduced seedling growth and survival. They proposed that bioturbation could affect *Zostera* seed germination if seeds were buried to >12 cm depth under sediment in light of Bigley's (1981) finding that the hypocotyls of sprouts fail to reach the sediment surface if germinated below that depth. Dumbauld and Wyllie-Echeverria (2003) concluded that "seedling survival is important for recruitment from the seed bank and while shrimp may cause some loss and decreased germination success, the effect of bioturbation on seedling survival, in part due to the coincident timing of shrimp activity and sprouting in early spring, is more important at the population level." (pg. 37).

Thompson and Pritchard (1969) noted that the upper intertidal limit of *Z. marina* in Oregon matched the lower limit of dense ghost shrimp populations and that seasonal expansion of either species of eelgrass on sand flats was correlated with declines in the abundance of ghost shrimp. In contrast to Dumbauld and Wyllie-Echeverria (2003), Thompson and Pritchard (1969) found that ghost shrimp densities declined in experimentally created plots of *Z. japonica*. Berkenbusch et al. (2007) reported much the same result from a field study in which ghost shrimp or small patches of Japanese eelgrass were reciprocally transplanted into field enclosures containing the other species (i.e., *Z. japonica* or shrimp, respectively). In all cases, the patches of *Z. japonica* grew whereas the abundance of *N. californiensis* declined. They suggested that a combination of rapid growth by the eelgrass and relatively low bioturbation by *N. californiensis*

(as compared to its New Zealand counterpart, *C. filholi*) allowed the invasive eelgrass to be the superior competitor in these experiments. In laboratory experiments, Brenchley (1982) found that the root and rhizome mat of *Z. marina* greatly inhibited burrowing by the burrowing shrimp *N. californiensis* and *Upogebia pugettensis*. For presumably the same reasons, Harrison (1987) observed that *N. californiensis* were largely unsuccessful at colonizing dense *Z. marina* patches on a British Columbia tide flat. The key difference between the studies of Dumbauld and Wyllie-Echeverria (2003) and those of Thompson and Pritchard (1969) and Berkenbusch et al. (2007) is the life history stages of the seagrasses that were brought into conflict with the ghost shrimp. Synthesizing the results of experimental studies on interactions between *N. californiensis* and *Zostera* spp. in NE Pacific estuaries, it appears that bioturbation by ghost shrimp can suppress the germination of eelgrass seeds and the survival of seedlings (at least for *Z. japonica* and probably for *Z. marina*), but that established patches of adult eelgrass are resistant to adverse impacts from ghost shrimp probably because the root and rhizome mat inhibits burrowing by the shrimp.

Thom et al. (2003) found burrowing shrimp co-existing with intertidal *Z. marina* in Coos Bay (Oregon, USA) and Willapa Bay (Washington, USA) estuaries, and found no evidence for negative interactions between these organisms. However, they did not report which species of burrowing shrimp they encountered in the eelgrass beds, and it is possible that they saw the burrows of the mud shrimp, *Upogebia pugettensis*, rather than *N. californiensis*. *Upogebia pugettensis* is common in *Z. marina* beds in estuaries of California, Oregon and Washington (USA), including Coos Bay and Willapa Bay, whereas *N. californiensis* is relatively uncommon in eelgrass beds (T. H. DeWitt, unpublished data). However, *N. californiensis* is common in high intertidal beds of *Z. japonica* (Dumbauld and Wyllie-Echeverria 2003; T. H. DeWitt, personal observation). No research has been published investigating why these two species of burrowing shrimp have different patterns of coexistence with *Z. marina*; possible reasons include different rates of sediment turnover (which are lower for *U. pugettensis*) and thus less disturbance to eelgrass by mud shrimp (T. H. DeWitt, personal observation), different capabilities to burrow through the eelgrass root and rhizome mat (Brenchley 1982), or increased susceptibility of *N. californiensis* to predation in lower intertidal and subtidal eelgrass habitats (Posey 1986). In South Africa, Siebert and Branch (2005, 2006) found high densities of the mud shrimp *U. africana* coexisting with *Z. capensis* in the upper intertidal where both species apparently found refuge from interactions with the ghost shrimp, *C. kraussi*). Upogebiid shrimp are less vigorous bioturbators than Callianassid burrowing shrimp largely because Upogebiids are primarily suspension feeders and thus do not need to constantly excavate and ingest organic-rich sediments as do deposit-feeding Callianassids.

In contrast to the suppression of populations of seagrasses in single-species meadows, burrowing shrimp bioturbation can increase seagrass species diversity within mixed-species meadows. Cumulative disturbance by burrowing shrimp to several species of tropical seagrasses in the Silaqui and Santiago Islands (Philippines) was estimated to be greater than the disturbance caused by sediment transport associated with hurricanes and typhoons (Duarte et al. 1997). They conducted a field experiment to measure the effects of episodic deposition of sediment on the growth, survival, and demography of seven seagrass species (*Thalassia hemprichii*, *Enhalus*

acoroides, *Cymodocea rotundata*, *C. serrulata*, *Halodule uninervis*, *Syringodium isoetifolium*, and *Halophilla ovalis*, listed by relative abundance). Seagrass species responded variably to sediment deposition treatments, one (*E. acoroides*) was relatively unaffected by any of the deposition treatments; two (*T. hemprichii*, *C. rotundata*) exhibited sharp declines in response to the moderate and high sediment deposition treatments; three (*H. uninervis*, *S. isoetifolium*, *C. serrulata*) declined initially and then recovered in all deposition treatments; and one (*H. ovalis*) opportunistically increased in abundance in most treatments. Differential responses to sediment loading was proposed be an important mechanism for maintaining high seagrass species diversity in this meadow by having the greatest negative impact on abundant seagrass species (presumably competitive dominant species, although that was not tested directly), and opening space for colonization by competitively subordinate seagrass species. Duarte et al. (1997) noted that natural disturbances affecting sediment transport ranged in scale from sub-meter (burrowing shrimp) to 10^3 m (hurricanes and typhoons), with the frequency of occurrence being approximately inverse of their size (i.e., monthly for burrowing shrimp mound duration vs. “rarely” for hurricanes and typhoons). Hence, the cumulative disturbance of small-scale but frequent sediment reworking by burrowing shrimp resulted in an estimated twice-yearly reworking of the seagrass meadow. The scale and frequency of disturbance by burrowing shrimp bioturbation was sufficient to cause major growth and population responses by the seagrasses in this tropical meadow, and sustain higher seagrass species diversity than under conditions of very low or very high disturbance (sensu the intermediate disturbance hypothesis; Sousa 1984).

In summary, disturbance from burrowing shrimp bioturbation (particularly Callianassid ghost shrimp) significantly disturbs several species of seagrasses including those with deep rhizomes (e.g., *Thalassia testudinum*), can affect all life stages of seagrasses (e.g., seeds, seedlings and shoots), can limit the distribution and abundance of seagrasses in some locations, and can modify the biodiversity of seagrasses in mixed species meadows. In some cases, the early life stages of seagrasses are more susceptible to burrowing shrimp bioturbation than are adult life stages. The interaction between seagrasses and burrowing shrimp is not, however, always tilted in favor of the bioturbator. Dense root mats have been shown or suggested to prevent Callianassid ghost shrimp from burrowing into sediments within established eelgrass beds, and Upogebiid mud shrimp coexist with *Zostera* in at least two regions. Finally, the outcome of shrimp-seagrass interactions can be tilted to favor the shrimp if water quality (particularly, turbidity) slows seagrass growth (see section 10.4).

10.2.2 Stingray Bioturbation

Stingrays (Vertebrata: Chondrichthyes: Myliobatiformes) forage for benthic invertebrate prey by excavating sediments using jets of water blown from the mouth and plunger-like suction created with the pectoral disc (Martin 2003). In the process, they excavate broad, shallow pits of width approximately that of a ray’s disc width and depths of ~10-20 cm (Valentine et al. 1994), often removing seagrass shoots and rhizomes in the process. Schools of cownose rays (*Rhinoptera bonasus*) destroyed large areas of one *Z. marina* meadow (ca. $4 \text{ km}^2 \text{ y}^{-1}$) and were suspected of causing similar damage at six other sites in Chesapeake Bay (Virginia, USA) (Orth 1975). Similarly, southern stingrays (*Dasyatis americanus*) and spotted eagle rays (*Aetobatis*

narinari) were observed to damage turtlegrass (*T. testudinum*) habitat while feeding (Ogden 1980; Zieman 1982 in Valentine et al. 1994).

Valentine et al. (1994) documented the persistence of large unvegetated patches within *T. testudinum* meadows in St. Joseph Bay (Florida, USA) that appeared to be created by herbivory or bioturbation, possibly by stingrays. Three stingray species (*R. bonasus*, *D. americanus*, and *D. sabina*) released within large experimental cages (72 m²) over turtlegrass beds were observed to dig feeding pits and dislodge *T. testudinum* shoots. However, only the largest individuals of the southern stingray (*D. americanus*; disc width >90 cm) dug pits sufficiently deep to damage seagrass rhizomes and cause a decrease in below-ground biomass. Based on the scarcity of large southern stingrays and paucity of large sting ray pits recorded in field surveys, Valentine et al. (1994) concluded that stingrays were unable to create the persistent bare patches in these *T. testudinum* meadows.

By contrast, Townsend and Fonseca (1998) determined that large bioturbation pits, possibly created by stingrays, were deeper (mean 4 cm, maximum 12 cm) than the rhizome depth of the predominant seagrasses (*Z. marina* and *Halodule wrightii*; 1 to 5 cm) in mixed-species seagrass meadows (North Carolina, USA). Many smaller pits, possibly created by crabs, were also deeper than the rhizomes. Therefore bioturbators could damage seagrass beds through disruption of rhizomes and roots, or dislodge seeds or seedlings. Pits occupied only ~1% of the area, but owing to the frequency of pit formation and persistence of pits, Townsend and Fonseca (1998) estimated that every square meter of seafloor was disturbed at a rate of 1.2 y⁻¹. They suggest that disturbance by bioturbation is an important process creating patchiness in seagrass beds and disrupting linkages among seagrass patches, increasing the risk of erosion of the seagrass patches by currents and waves (Fonseca and Bell 1998). Thus, bioturbation may be important for generating and maintaining landscape-scale distribution patterns of seagrasses.

In addition to affecting extant populations of seagrasses, bioturbation by stingrays has been identified as an important source of disturbance for seagrass restoration. Bioturbation by foraging round stingrays (*Urolophus halleri*) was identified as a potential hindrance to restoration of eelgrass (*Z. marina*) in San Diego Bay (California, USA) (Merkel 1990). Transplanted eelgrass protected by stingray exclusion barriers (i.e., fences, stakes, erosion mats) had higher short-term (23 d) survival than unprotected planting units in soft sediments where ray feeding pits were abundant (Merkel 1990). Stingrays caused a loss of >50% of seagrass (*H. wrightii*) transplant units in Tampa Bay (Florida, USA), and cages constructed of 2.5 cm mesh galvanized chicken wire improved *H. wrightii* survival to 60% relative to <1% survival in uncaged controls (Fonseca et al. 1994). Stingrays' impacts to transplanted seagrass can occur very rapidly; Fonseca et al. (1998) reported 100% loss of *Halodule* sp. and *Syringodium* sp. transplants within 24 h of planting where stingray-exclusion cages were not used.

10.2.3 Crab Bioturbation

A handful of studies have reported that bioturbation by crabs and lobsters (Arthropoda: Decapoda) can damage seagrass shoots, rhizomes and roots, eroding edges of seagrass beds or opening space within beds, and thereby affecting seagrass distribution and abundance. Valentine

et al. (1994) determined that bioturbation by stone crabs (*Menippe* spp.) was the most likely cause of open patches in *T. testudinum* meadows in St. Joseph Bay, although stingrays had at first appeared to be the culprits (see above). Stone crabs were most common along margins of seagrass beds, where they build large burrows at oblique angles just under the turtle grass rhizosphere. Burrowing undermines the edge of the seagrass bed, causing sections of the grass mat to dislodge from the sediments. This often results in the in-filling or collapse of the stone crab burrows, requiring continual burrow maintenance by the crabs (e.g. extension under the new edge of the seagrass bed) and thus enlarging the area of seagrass disturbed by the crabs. As Valentine et al. (1994) point out, stone crab burrowing appears to create a positive feedback loop for recession of the edge of *T. testudinum* beds. Stone crabs caused twice as much recession in the edges of turtlegrass patches, compared to seagrass margins without crabs. Damage to turtlegrass rhizomes due to bioturbation may have long-lasting consequences because of slow rhizome growth and patch recolonization (Williams 1990).

On rocky intertidal platforms (Kaikoura, New Zealand), burrowing crabs (*Macrophthalmus hirtipes*) are responsible for significant erosion of the edges of seagrass patches (*Z. novazelandica*) (Woods and Schiel 1997). *M. hirtipes* burrows, found predominantly at the edges of the seagrass patches, persist longer in seagrass patches than on open mudflats, possibly because the interconnecting rhizomes and roots reduce cave-ins of burrow walls. As with stone crabs, burrowing by *M. hirtipes* appears to disrupt the sediment-binding properties of *Z. novazelandica*'s rhizome-root mat, dislodging the seagrass, requiring the crabs to extend their burrows further into the seagrass patch, etc., setting up a positive feedback loop that perpetuates erosion of the bed margin. Once the seagrass patches began to decline at their edges, the interiors of crab burrows were exposed, creating a greater surface area for further erosion by waves and currents. The area immediately surrounding the burrow is rapidly undermined and torn away, ultimately accelerating the erosion of the seagrass patch margin. In addition to being disturbed through this crab's bioturbation, *Z. novazelandica* leaves, roots and rhizomes are eaten by the omnivorous *M. hirtipes* (Woods and Schiel 1997).

These two studies illustrate two important points about the effects of bioturbator impacts on seagrasses. First, bioturbation impacts to the edges of seagrass patches may be more damaging than those in the middle of the patches because exposure of the edge may make the patch more vulnerable to subsequent erosion by water movement. Second, damage to seagrass patch edges may set up a positive feedback process that accelerates erosion of the seagrass patch, either by increased bioturbation or by hydrodynamic forces.

Davis and Short (1997) and Davis et al. (1998) reported that non-native green crabs (*Carcinus maenas*) disturbed eelgrass transplants (*Z. marina*) at restoration sites in Great Bay Estuary (New Hampshire, USA). Garbary and Miller (2006) reported that bioturbation by green crabs was responsible for the nearly total loss of eelgrass from Antigonish Harbour (Nova Scotia, Canada). Davis et al. (1998) observed that green crabs damaged naturally occurring and transplanted eelgrass shoots by tearing or cutting the sheath bundle during their burrowing activities and while foraging for infaunal prey. Mesocosm experiments demonstrated that disturbance by green crabs resulted in loss of 39% of transplanted *Z. marina* shoots within 1 wk

of exposure to the crabs (Davis et al.1998). Cages alone were not successful at keeping *C. maenas* away from transplants, but using crab traps in addition to exclusion cages improved the survival rate of transplanted eelgrass (Davis and Short 1997).

Bioturbation associated with horseshoe crabs (*Limulus polyphemus*) foraging activity in Great Bay Estuary (New Hampshire, USA) uprooted unprotected established plants and transplanted shoots of *Z. marina* (Davis and Short 1997); wire mesh cages successfully protected transplants from disturbance by horseshoe crabs. Other epibenthic crabs (such as *Callinectes sapidus*, *Cancer magister*), and lobsters (*Homarus americanus*) also burrow into sediments within seagrass patches, and may excavate open space in the form of small pits in seagrass beds (Townsend and Fonseca 1998; Valentine et al.1994; Short and Wyllie-Echeverria 1996; Short et al. 2001). However, the extent to which bioturbation by these crabs significantly affects seagrasses distribution or survival has not been reported.

10.2.4 Polychaete Bioturbation

Four studies reported that bioturbation by polychaete worms (Annelida: Polychaeta) can adversely affect seagrass populations, two of which provided experimental evidence to support that hypothesis. Beneficial aspects of polychaete bioturbation have also been reported, and will be discussed in a later section. Phillipart (1994) reported that populations of *Z. noltii* and the lugworm, *Arenicola marina*, maintained non-overlapping distributions on tide flats of the Dutch Wadden Sea (Terschelling, The Netherlands). The species' distributions met at an abrupt border, even though both had similar substrate and emersion limitations. Seagrass shoots transplanted into tide flat plots containing high lugworm density (ca. 68 worms m⁻²) soon had sediments deposited upon them from the worms' fecal castings and material excavated from burrows. Shoots transplanted into plots from which lugworms had been excluded had substantially higher biomass and abundance (cover) than in plots where lugworms were absent. In the presence of lugworms, *Z. noltii* shoots completely disappeared within 6 wk. Phillipart (1994) suggests that increased bioturbation, associated with the population expansion of *A. marina* between 1970 and 1990, may have been a major contributor to decline in *Z. noltii* on Wadden Sea tide flats. In contrast, van Katwijk and Hermus (2000) report that lugworm bioturbation did not affect the survival of transplanted *Z. marina* shoots on wave-exposed Dutch Wadden Sea tide flats. This result was inferred from shoot survival in a series of exclosures designed to reduce wave and current effects that also excluded lugworms and other large macrofauna. However, van Katwijk and Hermus' (2000) study did not include treatments that manipulated bioturbation independently of hydrodynamics, and thus, any effects of bioturbators were confounded with those of water movement.

Sediment reworking by the head-down deposit-feeding polychaete, *Clymenella torquata*, had both detrimental and beneficial effects on the dispersal and survival of *Z. marina* seeds in Chesapeake Bay (Virginia, USA) (Luckenbach and Orth 1999). In laboratory flumes, lateral transport of eelgrass seeds was reduced in the presence of "medium" and "high" densities of the worms (192 and 288 worms m⁻², respectively). Worm bioturbation caused the sediment surface to have an enhanced topographic relief, and seeds became passively trapped within small biogenic depressions or pits. Subsequently, many trapped seeds were buried by sediments

reworked (defecated) by *C. torquata*. Trapping reduced the dispersal of eelgrass seeds, which potentially slows the expansion of seagrass populations. However, seeds buried by *C. torquata* bioturbation were not buried too deeply for germination and they were protected from herbivory (Luckenbach and Orth 1999).

Hughes et al. (2000) proposed that the polychaete, *Nereis diversicolor*, may have contributed to the loss of coastal seagrasses (*Zostera* spp.) and to difficulties in restoring seagrass beds in south-east England (United Kingdom). In field and laboratory experiments, shoots of *Z. noltii* that were protected from *N. diversicolor* had higher biomass, higher survival, and less damage to roots than unprotected transplants (Figure 10.3). Worms apparently damaged *Z. noltii* roots by burrowing and leaves by herbivory. However, the authors noted that bioturbation-induced damage to roots may have been an experimental design artifact, and thus the role of bioturbation in this worm-seagrass interaction is uncertain.

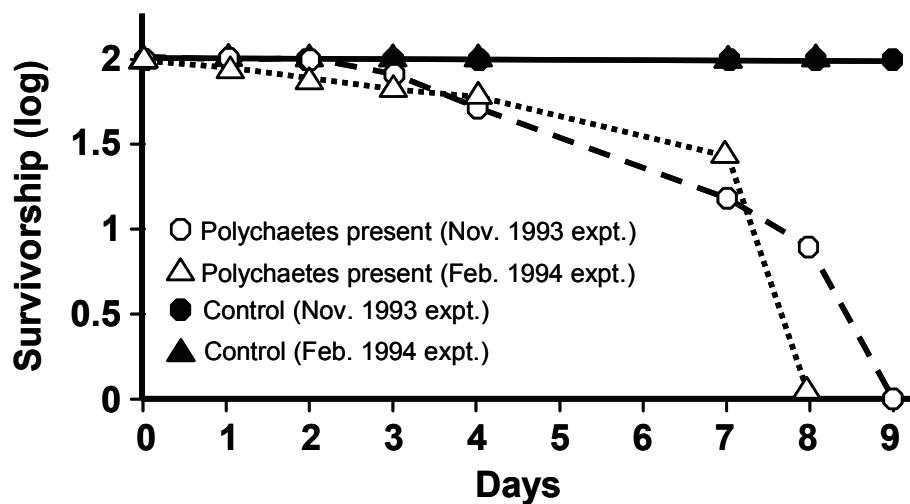


Figure 10.3. Results of two laboratory experiments showing decreased survivorship of seagrass (*Zostera noltii*) planted into sediments containing polychaetes (*Nereis diversicolor*; open circles and triangles, and dashed or dotted line) or devoid of worms (controls; filled circles and triangles, and solid lines) (modified from Figure 6 of Hughes et al. 2000).

Davis and Short (1997) noted that bioturbation by an ecologically similar polychaete, *Neanthes virens*, may have been responsible for 99% loss of subtidal transplanted *Z. marina* shoots. The worms appeared to pull the distal ends of seagrass leaves into their burrows, forcing the rest of the leaves flat against the sediment surface, after which the leaves were buried by bioturbated sediments leading to shoot death. No experiments were conducted to test the hypothesis that eelgrass shoot death was clearly caused by activities of *N. virens*, although their natural history observations presented a plausible mechanism.

10.2.5 Echinoderm Bioturbation

Sea cucumbers and sand dollars (Echinodermata: Holothuroidea and Echinoidea, respectively) have been observed to disturb seagrasses during their burrowing and feeding activities. However, only two studies have experimentally examined whether bioturbation by echinoderms can affect seagrass growth, survival, or populations. Burrowing sea cucumbers (*Holothuria arenicola*) in the Bahamas were observed to smother turtlegrass (*T. testudinum*) with defecated sediments (Mosher 1980, in Valentine et al. 1994); however, whether this adversely affected the seagrass was not discussed. In field experiments, Backman (1984) demonstrated that dense populations of sand dollars (*Dendraster excentricus*) uprooted eelgrass (*Z. marina*) and inhibited colonization of unvegetated habitats in Puget Sound, Washington.

Sand dollars (*Mellita quinquiesperforata*) were frequently observed in unvegetated patches within subtropical turtlegrass meadows of St. Joseph Bay (Florida, USA) and elsewhere (Valentine et al. 1994, and references therein). To test the hypothesis that bioturbation from burrowing activities of *M. quinquiesperforata* were responsible for the long-term persistence of these open spaces by preventing recolonization by *T. testudinum*, Valentine et al. (1994) measured the rate of change in the size of the turtlegrass perimeter surrounding open patches from which all sand dollars were periodically removed or patches containing undisturbed populations of sand dollars (ca. 5-15 m⁻²). Over a two year period, perimeters of replicate open patches expanded or contracted by up to 20%, but independently of sand dollar abundance, and at the conclusion of the study, no significant difference in mean patch perimeter was detected between these treatments (accounting for initial patch size). Valentine et al. (1994) concluded that sand dollars were ineffective at controlling open-space recolonization by *T. testudinum*; they ultimately determined that bioturbation by burrowing stone crabs was responsible for erosion of the edges of turtlegrass beds and therefore the biogenic creation of open space in those seagrass meadows (see above).

Although there are few studies of echinoderm bioturbation impacts on seagrasses, Valentine et al. (1994) point out that sediment reworking by other burrowing echinoids (i.e., spatangoid urchins) can exceed that of sand dollars (Thayer 1983), that they can occur in high densities in the vicinity of seagrass meadows (Chester 1969, in Valentine et al. 1994), and may therefore be a source of disturbance for tropical seagrasses. Most echinoderms are found only in marine waters. Thus, bioturbation by echinoderms is more likely to occur along open coasts rather than in estuaries.

10.2.6 Mechanisms of Bioturbation-Induced Disturbance to Seagrasses

Relatively little is known about the actual mechanism by which the seagrasses are harmed, compared to observations and experiments that demonstrate the net effects of bioturbators on seagrass shoot growth and survival. The most commonly reported mechanisms in the studies reviewed above were burial of seagrass shoots and seeds, uprooting of shoots and patches, undermining edges of seagrass patches, damaging roots or rhizomes, and shading by deposition of resuspended sediments onto leaves. Indirect mechanisms by which bioturbators were reported to damage seagrasses include reducing water column light availability because of increased turbidity from resuspended fine sediments (Suchanek 1983), burial by storm-

transported sediments previously excavated by bioturbators (Wanless et al. 1988), and increased susceptibility to hydrodynamic erosion (Valentine et al. 1994; Woods and Schiel 1997).

Rarely were the magnitudes or effects of those disturbance processes confirmed experimentally. In very few studies were the magnitudes of the disturbing process measured (e.g., burial rate, burrowing rate, sediment deposition rate, light reduction, etc.). In all of the studies reviewed above, the mechanism of disturbance was inferred from short-term observations of bioturbator activity (i.e., burrowing, digging, sediment expulsion), the condition of seagrasses (i.e., partial burial, uprooted shoots, exposed roots and rhizomes, sediment on leaves), biogenic structures in the environment (i.e., burrows, mounds, and pits), or feeding habits of the bioturbators (i.e., absence of herbivory). Transplant experiments have provided the strongest evidence that organisms that are bioturbators can decrease seagrass growth or survival, but few studies independently tested that the proposed disturbance mechanism, presented at the magnitude affected by the bioturbators, could cause the growth and survival responses seen in the seagrasses (but see Duarte et al. 1997). Furthermore, few of the studies quantified the spatial scale over which the disturbance could be expected to occur. Ideally, this would require a comparison of the landscape and regional distributions of the bioturbator species, of the seagrass species, and of the habitat suitable for sustainable seagrass growth, and experimental demonstration of the responses of seagrasses to bioturbation at random locations throughout that landscape. No study has put it all together, measuring the natural rates and magnitudes of the causal process of disturbance (i.e., burial, etc), measuring the responses of appropriate seagrass life history stages to those levels of disturbance, and determining the spatial scales over which bioturbation could affect seagrass populations. That is perhaps a tall order, but not inappropriate given the inferred ecological importance of bioturbator impacts to seagrass populations and the functions of seagrass habitats, as stated in most of the papers (for example, “bioturbation by *Callianassa* has a direct effect on seagrass beds but may indirectly influence a multitude of faunal relationships both within grass beds and in nearby communities such as coral reefs, mangroves, and the deep sea”, Suchanek 1983, p. 296).

10.3 Role of Bioturbation and Bioirrigation in Enhancing Seagrass Populations

Bioturbation and bioirrigation can benefit seagrass populations and communities in two ways: 1) modification of sediment geochemistry to create conditions favorable for seagrass growth, and 2) facilitation of seagrass recruitment and colonization. Relatively few studies have been conducted on processes that may facilitate seagrass population growth. However, as interest increases in expanding or restoring seagrass populations, study of the role of these natural facilitating processes in improving the condition of seagrass meadows can be expected to also increase.

10.3.1 Modification of Sediment Geochemistry

Bioirrigation and bioturbation increase the exchange of solutes and organic matter between the water column and the sediment column, strongly affecting sedimentary microbial processes such as organic matter decomposition, ammonification, nitrification-denitrification, and sulfide oxidation-reduction (Aller 1988; Kristensen 1988; Hopkinson et al. 1999; Fukukawa

2001). To the extent that these sediment geochemical processes limit seagrass growth and survival (Chapter 6), bioirrigation and bioturbation can stimulate processes favorable for seagrass growth (e.g., fertilization), reduce conditions harmful to seagrass survival (i.e., eutrophication, hypoxia), and reduce toxic substances within the rhizosphere (i.e., hydrogen sulfide, ammonia).

The role of bioturbating and bioirrigating benthic fauna in elevating sediment nutrient concentrations is well documented (Aller 1988; Kristensen 1988; Schaffner et al. 1992; Hopkinson et al. 1999; Felder 2001; Eyre and Ferguson 2002; Webb and Eyre 2004). Bioturbation and bioirrigation transfer organic matter from the sediment surface and water column into the sediment column, enhancing aerobic remineralization of sedimentary organic matter, thereby increasing sediment porewater nutrient concentrations, and enhance dissolved nutrient efflux back to the water column. Rates of bioturbation, deposit feeding, and suspension feeding typically increase in response to increasing organic matter concentration, at least up to some threshold where ingestion rate is maximized or organic matter loading causes toxicity (i.e., hypoxia or toxic contaminants associated with organic matter) (Jumars and Wheatcroft 1988; Wheatcroft and Martin 1996; Prins et al. 1997; DeWitt et al. 2004). However, little research has been conducted to investigate the occurrence of these processes in seagrass beds (particularly increasing nutrient availability) and their role in elevating seagrass productivity or growth. Thayer and Fonseca (1984) suggested that under conditions of nutrient limitation, “nitrogen availability [for eelgrass, *Z. marina*]...may be limited by the requirements of the heterotrophic community responsible for the decomposition of organic matter in sediments” (p. 31). Phillipart (1994) suggested that low densities of juvenile lugworms (*Arenicola marina*) might be beneficial to *Z. noltii* as a result of the worms’ bioturbating activities increasing nutrient fluxes, as reported by Huettel (1990). Reusch et al. (1994) and Reusch and Williams (1998) demonstrated that the mussels, *Mytilus edulis* and *Musculista senhousia*, respectively, caused porewater concentrations of ammonium and phosphate to increase dramatically, and both papers suggested that these suspension feeders fertilized beds of *Z. marina*. Peterson and Heck (1999, 2001a, 2001b) demonstrated that the suspension feeding mussel (*Modiolus americanus*) enhanced productivity of turtlegrass (*T. testudinum*) through fertilization of sediments under nutrient-limited conditions in St. Joseph Bay (Florida, USA). The mechanism by which mussels fertilized seagrass beds was basically the same in all five papers: mussels ingested nitrogen-rich seston and transferred this material to the sediment surface via deposition of feces and pseudofeces; particulate organic nitrogen in the fecal matter was microbially remineralized into dissolved inorganic nitrogen through ammonification and nitrification; and the dissolved inorganic nitrogen was absorbed by seagrass roots and transformed into new tissue. Suspension feeding and deposit feeding benthic invertebrates (i.e., bioirrigators and small-scale bioturbators) are common in seagrass beds, sometimes in great abundance (Orth et al. 1984; Beal 1994; Bachelet et al. 2000; Bowden et al. 2001), and it is highly likely that they also fertilize sediments and seagrasses (Peterson and Heck 1999, 2001a, 2001b; Peterson et al. 2003).

Bioirrigation also acts to enhance oxygenation of sediments and to advect toxic solutes back to the water column (Aller 1988, 1994; Fukukawa 2001; Meile et al. 2001). Feeding and respiratory currents generated by burrowing infauna exchanges burrow water with overlying

water. Typically, overlying water has higher concentrations of dissolved oxygen and lower concentrations of nutrients, hydrogen sulfide, CO₂ and other porewater constituents than burrow water. Sediment porewater adjacent to the burrows diffusively exchanges with burrow waters (Aller 1988; Kristensen 1988), and thus ventilation of burrows results in increased porewater oxygen concentrations, and decreased concentrations of nutrients, hydrogen sulfide, etc. (Kristensen 1988; Aller 1994; Furukawa 2001). Elevated levels of ammonium and hydrogen sulfide have adverse effects on seagrasses as discussed in Chapters 3 and 6. Thus, the presence of bioirrigators has the potential to increase the survival and growth of seagrasses by reducing toxic concentrations of those compounds in sediment porewater. Little research has been conducted on this interaction between bioirrigators and seagrasses. Using a physiologically-based stress-response model for *Thalassia testudinum*, Eldridge and Kaldy (2004) suggests that bioirrigation has a very large impact on turtlegrass patch growth due to the oxidation of sediments in the root zone. This effect remains to be investigated experimentally with this and other seagrass species.

10.3.2 Enhancing Seagrass Recruitment and Colonization

While bioturbation can act to inhibit seagrass recruitment by burial of seeds (Luckenbach and Orth 1999; Dumbauld and Wylie-Echeverria 2003), burial of seeds by bioturbation can also increase seagrass recruitment by protecting those seeds from herbivory (Luckenbach and Orth 1999), by trapping seeds in shallow-water sediments that might otherwise be transported by currents to deep waters (i.e., below the species' photic zone) (Orth et al. 1994), or by transporting seeds to geochemical microenvironments that stimulate germination (Moore et al. 1993).

Bioturbation may also benefit seagrasses by modifying sedimentary habitats such that seagrasses could recolonize them. Extending processes described above, bioturbation can oxygenate and remediate sediments that are anoxic or hypoxic due to high organic matter loading (e.g., eutrophication) and are toxic to seagrasses (van Katwijk et al. 1997; Koch and Erskine 2001), possibly resulting in geochemical conditions tolerable to seagrass colonization, particularly if remineralization and burial exceed organic matter loading (Aller 1988; Fukukawa 2001). Bioturbation can also facilitate restoration of sediment texture altered by episodic sedimentation. Norkko et al. (2002) reported that bioturbation facilitated the recovery of macrofaunal communities following the experimental deposition of terrigenous clay onto tide flats, simulating massive sediment runoff associated with poor land management. Duarte et al. (1997) noted that sediment reworking by burrowing shrimp reduced the thickness of sediment layers experimentally deposited on seagrass patches; this may have benefited seagrasses in those patches to some extent given that several of the seagrass species were adversely affected by sediment deposition. Aside from the comment in Duarte et al. (1997), I know of no studies specifically demonstrating the role of bioturbation in modifying sediments and thereby facilitating seagrass colonization. Whether this is a reflection of the lack of investigation into this process, or because it rarely occurs, is unknown; however, I believe the process is plausible and potentially important for seagrass persistence in eutrophic systems.

Disturbance by bioturbation can create open space within areas monopolized by dominant space competitor(s). Those areas are then available for colonization by weaker

competitors. This is an example of the intermediate disturbance hypothesis, which predicts that in communities structured by competition, biodiversity is greatest under conditions of intermediate disturbance, and reduced under conditions of low disturbance (where the dominant competitor(s) dominate all resources) or high disturbance (where only the most disturbance-tolerant species persist) (Sousa 1984; Dial and Roughgarden 1998). As discussed in section 10.2.1, Duarte et al. (1997) observed that bioturbation by burrowing shrimp could be partially responsible for maintaining high seagrass diversity in Philippine seagrass meadows by creating open patches within dense *Thalassia hemprichii* stands that could be colonized by more opportunistic species of seagrass. A similar scenario may maintain diversity in mixed-species seagrass beds of south Florida (B.J. Peterson, personal communication).

10.4 Effects of Interactions Between Bioturbation/Bioirrigation and Water Quality on Seagrasses

Previous sections have described how bioturbation can act to limit or facilitate the growth of seagrass populations; a third seagrass response could be “no effect”. (To the best of my knowledge, bioirrigation only has neutral or facilitating effects on seagrasses). As with other environmental factors that can be limiting or facilitating to seagrasses (i.e., nutrients, temperature, light), the direction of the seagrass response will to some extent be determined by the magnitude and timing of the bioturbation, and on the presence of other limiting factors (“stressors”). Low intensity bioturbation (such as that caused by small species, young life stages of large species, species with low sediment reworking rates, or by low population densities of large bioturbators) would be likely to have neutral direct effects or could facilitate seagrass condition by stimulating nutrient cycling and organic matter remineralization. High intensity bioturbation (such as that caused by species with high sediment reworking rates, by large-bodied bioturbators, or by dense populations of bioturbators) would be likely to directly disturb one or more life history stages of seagrasses. Variation in seasonality of sediment reworking rates among bioturbators could have important consequences for seagrasses. Seagrasses whose growth rates were seasonally synchronous with the reworking rates of bioturbators would have a better chance of growing away (vertically or horizontally) from the disturbance. Seagrasses encountering bioturbators that had no seasonal variation in sediment reworking rates would be less able to grow away from the disturbance during low growth seasons (i.e., winter).

Other factors (such as water quality) that limit seagrass condition could affect the outcome of interactions between bioturbators, bioirrigators, and seagrasses. Little is known about the effects of interactions between bioturbation/bioirrigation and water quality on seagrass growth or survival. The issue has been addressed in only three studies. Phillipart (1994) suggested that, following the historical decline of *Zostera* spp. in the Wadden Sea due to disease and eutrophication, expansion of populations of bioturbating lugworms may have prevented recovery of seagrass populations. Similarly, Hughes et al. (2000) suggested that expansion of populations of the bioturbating polychaete *Nereis diversicolor* may have hindered natural and intentional restoration of *Zostera* spp. populations in south-east England following their decline due to wasting disease and eutrophication. In these two cases, the bioturbator-water quality interaction is temporally out of phase, with bioturbation impacts expressed after impacts of poor

water quality and wasting disease (which itself may be linked to poor water quality, Hawkins et al. 1999). One could argue that it is not valid to consider these cases as examples of the interaction; however, the net detrimental effect to seagrass populations (if true) would be likely a consequence of both sources of disturbance acting sequentially.

Over a 15 year period, Harrison (1987) observed an increase in the size of seagrass beds (*Zostera marina* and *Z. japonica*.) on a British Columbia (Canada) tide flat, and a decrease in the area dominated by burrowing shrimp (*Neotrypaea californiensis*), following the construction of a breakwater. The breakwater greatly reduced currents over the tide flat, and water clarity increased substantially. Transplant experiments demonstrated that survival and growth of *Z. japonica* was sharply reduced in presence of high densities of burrowing shrimp; however, the shrimp were not successful at burrowing through the root-rhizome mat of extant seagrass beds (see section 10.2.1). Burrowing shrimp bioturbation activity was seasonal, being greatest in the summer and early fall, and least in the winter and early spring, probably in response to temperature (Fritz 2002). Harrison (1987) proposed that the increase in water clarity allowed the seagrass patches to start growing laterally earlier in the spring than when the water had been turbid. Each year, the seagrass patches expanded gradually over shrimp beds, smothering seasonally-quiescent shrimp that could not burrow through the seagrass bed. Lateral expansion of the seagrass bed stopped as shrimp bioturbation increased, which reduced survival and growth of seagrass shoots at the shrimp-seagrass boundary. However, there was a net gain in area for the seagrass beds. The converse of this interaction hypothesis is that when water clarity was reduced, burrowing shrimp bioturbation limited growth of *Zostera* spp. patches. No experiments were conducted to test this interaction hypothesis (other than the previously discussed transplant experiments), and it is possible that the seagrass bed expansion occurred only because of the increase in water clarity. In any case, the hypothesis illustrates one way in which water quality and bioturbation may interact to limit seagrass populations.

Bioturbation and bioirrigation may help to offset adverse impacts of poor water quality (such as eutrophication and sedimentation) that could otherwise be detrimental to seagrasses. The capability of bioturbators and bioirrigators to enhance nutrient cycling and organic matter remineralization, and to oxygenate sediments, were discussed in Section 10.3.1. Similarly, the capability of bioturbators to facilitate restoration of benthic communities following episodic sedimentation events was discussed in Section 10.3.2. To the extent that some benthic invertebrates are suspension feeders as well as bioturbators or bioirrigators, feeding by populations of those organisms could potentially increase water clarity, increase light availability, and thus enhance seagrass growth.

Several studies have demonstrated the capacity of populations of benthic suspension feeders to daily filter large proportions (i.e., >33%) of the water column within embayments and substantially reduce the concentration of phytoplankton (for bivalves see Dame and Prins 1998; for burrowing shrimp see DeWitt et al. 2004 and Griffen et al. 2004). Other investigators have speculated that reduction of populations of suspension feeders could contribute to an increase in turbidity and, consequently, reduce populations of submerged aquatic vegetation (SAV). Newell (1988) and Ulanowicz and Tuttle (1992) suggested that over harvesting of oyster (*Crassostrea*

virginica) populations may have contributed to the decline of seagrasses in Chesapeake Bay. Phelps (1994) suggested that the rise and fall of SAV in the upper Potomac R. estuary (Washington, D.C., USA) during 1980-1991 was caused in part by changes in water clarity due to filter feeding by increasing and then declining populations of the invasive Asiatic bivalve, *Corbicula fluminea*. Only one study has explicitly examined whether benthic suspension feeders could remove sufficient particulate material to increase the light field enough to affect seagrass growth and survival. Newell and Koch (2004) developed a model to test whether the filtering capacity of oysters (*C. virginica*) and hard clams (*Mercenaria mercenaria*) at various population densities could affect *Ruppia maritima* growth in Chesapeake Bay. They determined that filtering by high densities of oysters, as occurred historically, could have reduced turbidity sufficiently to enhance seagrass growth. However, hard clams had much lower filtration rates than oysters, and in their model, high population densities of the clams were unable to reduce turbidity enough to benefit *R. maritima*.

Clearly not all benthic suspension feeders have the capability to substantially reduce turbidity, and the best example of an organism that does have this ability (i.e., oysters) is not a bioturbator/bioirrigator. Newell and Koch (2004) concluded that the potential for benthic suspension feeders to reduce turbidity and enhance seagrass growth is limited to those invertebrates that 1) are able to sustain high filtration rates under conditions of high turbidity (which can clog the filtering mechanisms of some species) and 2) occur at high population density within or adjacent to seagrass beds. One group of bioirrigating infauna that does have the potential to significantly reduce turbidity are suspension-feeding upogebiid burrowing shrimp. Populations of *Upogebia pusilla* (Dworschak 1981) and *U. pugettensis* (DeWitt et al. 2004; Griffen et al. 2004) are estimated to daily remove 60-100% of phytoplankton from the water over their habitats. Whereas *U. pugettensis* have similar individual and population filter capacities to oysters (*Crassostrea gigas*; Griffen et al. 2004), then populations of Upogebiid burrowing shrimp may be able to reduce turbidity sufficiently to benefit seagrass growth.

Note that the mechanism by which benthic suspension feeders improve water quality for seagrass growth is primarily the result of feeding rather than bioturbation or bioirrigation per se. But, suspension feeding is not uncommon among bioturbating and bioirrigating crustaceans (amphipods, thalassinids) and bivalves. Furthermore, particles entrained in water passing through *U. pugettensis* burrows (e.g., during bioirrigation) can become trapped on the burrow walls and thus removed from the water column (Griffen et al. 2004). Those authors estimate that ~40% of particle removal by the suspension-feeding and bioirrigating burrowing shrimp, *U. pugettensis*, is caused by burrow-wall entrapment. While this process likely occurs for many other bioirrigating infauna, it has not been studied for other species. But, to the extent that *U. pugettensis* populations have the potential to significantly reduce turbidity, then burrow-wall entrapment of particles is an important mechanisms by which bioirrigating infauna (or Upogebiids at least) can reduce turbidity sufficiently to benefit seagrasses.

10.5 Implications for Seagrass Protection and Restoration

Narrative or numerical criteria for protection of seagrasses may need to incorporate a safety margin to account for the adverse effects of bioturbation when large bioturbators co-occur with anthropogenic stressors that adversely affect seagrasses. As discussed in Section 10.4, bioturbators can potentially increase the adverse effects of nutrient enrichment by decreasing water column light levels (i.e., by increasing turbidity as a result of sediment resuspension) or by acting as an independent stressor on nutrient-stressed plants. However, these interactions have been specifically examined in only a very few studies and consequently are poorly understood. An initial step to account for adverse interactions between water quality and bioturbators would be development of guidelines to identify the magnitude of risk of seagrass loss caused by the presence of bioturbators. Those guidelines could simply be 1) determining whether large bioturbating organisms (similar to those listed in Table 10.1) are present within areas habitable by seagrasses, and 2) if present, categorizing the population density of bioturbators as lower, equal, or higher than the densities reported to damage seagrasses. Short et al. (2002) recommend using similar information as part of their Transplant Suitability Index to rank sites for their potential for successful seagrass (*Z. marina*) restoration. Determination of an appropriate safety margin to account for bioturbator-stressor interactions will require additional information on how those interactions magnify adverse effects of the stressor alone.

To complicate matters, bioirrigators and bioturbators can reduce some adverse effects of poor water quality, particularly those caused by nutrient enrichment (i.e., reducing turbidity or phytoplankton concentration; oxygenating sediments; flushing ammonia, H₂S, or other toxins from sediments; see Sections 10.3 and 10.4). Thus, the presence of bioirrigators and bioturbators in or near seagrass beds may help explain seemingly anomalous situations wherein seagrasses are observed growing under conditions of poor water or sediment quality. Knowledge of the abundance of bioirrigators and bioturbators may thus be a useful covariate for interpreting outliers in field-based stress-response data sets, and thereby improve the scientific basis for establishing numerical protective criteria for seagrasses.

Bioturbation has been a significant detriment to seagrass bed restoration primarily due to uprooting of transplanted shoots (i.e., stingrays: Merkle 1990; Fonseca et al. 1994, 1998; crabs: Davis and Short 1997; Davis et al. 1998; polychaetes: Davis and Short 1997; Hughes et al. 2000; see discussions above). Additionally, manipulative experiments have demonstrated that other bioturbators taxa can kill transplanted shoots or seedlings (i.e., burrowing shrimp: Suchanek 1983; Molenaar and Meinesz 1995; Dumbauld and Wyllie-Echeverria 2003; Siebert and Branch 2006; Berkenbusch et al. 2007; echinoderms: Backman 1984) and therefore can potentially affect seagrass restoration. Physical barriers, such as cages or fences, have been used to exclude bioturbating stingrays and crabs from seagrass restoration sites, at least on a small scale (Merkel 1990; Fonseca et al. 1998). Physical barriers may also be useful for excluding echinoderms, however they are unlikely to be useful for excluding burrowing shrimp or polychaetes because these organisms are relatively small bodied and live underground. Pesticide application to kill polychaetes or burrowing shrimp can enhance survival of seagrasses (de Deckere et al. 2001;

Dumbauld and Wylie-Echeverria 2003), although use of broad-spectrum pesticides to control indigenous infauna is controversial (Feldman et al. 2000).

Alternatively, the presence of bioirrigators or low-intensity bioturbators may enhance the success of seagrass restoration in sediments with high organic matter concentrations by virtue of their oxygenating sediments and increasing the efflux of toxic hydrogen sulfide or ammonia from sediment porewater, and thereby increase the probability of seagrass growth or survival. Also, suspension-feeding, bioirrigating benthic fauna can reduce turbidity sufficiently to enhance seagrass growth. Newell and Koch (2004) suggest that enhancement of population densities of suspension feeders with high filtration rate could enhance restoration of seagrass beds. While their example was for epibenthic oysters, the principle holds for bioirrigating or bioturbating infauna such as Upogebiid burrowing shrimp or other bivalves that also have high filtration rates (Gerritsen et al. 1994; Dame and Prins 1998; Griffen et al. 2004).

10.6 Knowledge Gaps & Research Needs

Compared to other abiotic processes, little is known about the importance of bioturbation and bioirrigation as either limiting factors or facilitators of seagrass population growth. The three critical knowledge gaps concerning the negative and positive effects of bioturbation and bioirrigation on seagrass populations are: 1) effects of bioirrigation on seagrasses, particularly with respect to oxygenating root zone sediments, 2) interactions between bioturbation/bioirrigation and abiotic limiting factors (especially anthropogenic stressors), and 3) scaling the effects of bioturbator/bioirrigator populations to seagrasses,.

Recent models of seagrass-sediment interactions (Eldridge and Morse 2000; Eldridge and Kaldy in press) suggest that bioirrigation can profoundly affect seagrass growth and survival through oxidation of the root zone. To the extent that seagrass growth or survival is limited by the concentration of toxic metabolites (such as ammonium or hydrogen sulfide) in porewater, and that oxidation of those metabolites is limited by the exchange of porewater with oxygenated overlying water, then bioirrigators have the potential to increase the growth and survival of seagrasses by enhancing the oxidation of those toxic metabolites. While these geochemical processes have been empirically demonstrated for unvegetated sediments, their impacts on seagrasses have not been investigated experimentally in the field or laboratory.

As summarized in Section 10.4, various authors (Harrison 1987; Phillipart 1994; Hughes et al. 2000) have suggested that co-occurrence of bioturbators and poor water quality might have an increased adverse effect on seagrass populations, compared to the effect of either stressor alone. Other research suggests that the populations of bioirrigators or bioturbators might reduce one or more adverse effects of nutrient enrichment to seagrass populations (see Section 10.3). Further investigation of these interactions, particularly for benthic invertebrate bioturbators and bioirrigators that are common in habitats that suitable for seagrasses. The potential for bioturbation or bioirrigation to reduce adverse effects of certain pollutants may be valuable for protection or restoration of seagrass populations.

Little is known about scaling the effects of bioturbator or bioirrigator populations to seagrasses. While several investigators have discussed the potential for dense populations of specific bioturbators or bioirrigators to affect seagrasses, the density-dependence of those effects have not been studied. Trivially, no effect would be expected in the absence of bioturbator/bioirrigators, but at what population density of those animals would effects to seagrasses be expected to occur? Secondly, one might expect that the effects of bioturbation and bioirrigation might scale with the animal body size, and thus with the size- or age-structure of the animal populations. Finally, the spatial and temporal scale over which the effects of bioturbation/bioirrigation are exerted upon seagrass populations have not been examined. Direct effects of bioturbation might be largely local (i.e., limited to the area disturbed by the animals). However, nutrient efflux or suspension feeding by bioirrigators potentially affect water quality parameters (and hence, seagrass growth) over a larger area than that which the animals occupy. Related to this is the question of the geographic ubiquity of bioturbator-seagrass and bioirrigator-seagrass interactions. Whereas study sites investigating these interactions were specifically selected for all of the studies reviewed above, no one has surveyed randomly selected sites within seagrass beds to assess the frequency or magnitude of bioturbation and bioirrigation. Understanding how the effects of bioturbator or bioirrigator populations scale relative to seagrass populations will be critical for estimating the risks or benefits that seagrass populations obtain from the presence of those animals.

10.7 Literature Cited

- Allanson, B. R., D. Skinner, and J. Imberger. 1992. Flow in prawn burrows. *Estuarine, Coastal and Shelf Science* 35:253-266.
- Aller, R. C. 1988. Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. pp. 301-338. In: T. H. Blackburn and J. Sorensen (eds.), *Nitrogen Cycling in Coastal Environments*, John Wiley and Sons.
- Aller, R. C. 1994. Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. *Chemical Geology* 114:331-345.
- Angel, A., G. M. Branch, R. M. Wanless, and T. Siebert. 2006. Causes of rarity and range restriction of an endangered endemic limpet, *Siphonaria compressa*. *Journal of Experimental Marine Biology and Ecology* 330:245-260.
- Bachelet, G., X. De Montaudouin, I. Auby, and P. Labourg. 2000. Seasonal changes in macrophyte and macrozoobenthos assemblages in three coastal lagoons under varying degrees of eutrophication. *ICES Journal of Marine Science* 57:1495-1506.
- Backman, T. W. H. 1984. Phenotypic expressions of *Zostera marina* L. ecotypes in Puget Sound, Washington. Ph.D. dissertation, University of Washington, Seattle, Washington. pp. 178.
- Beal, B. F. 1994. Effects of seagrass (*Zostera marina*) cover on growth and survival of softshell clams (*Mya arenaria*). *Journal of Shellfish Research* 13:311-312, 1994.
- Berkenbusch, K. and A. A. Rowden. 2003. Ecosystem engineering – moving away from ‘just-so’ stories. *New Zealand Journal of Ecology* 27:67-73.
- Berkenbusch, K. and A. A. Rowden. 2007. An examination of the spatial and temporal generality of the influence of ecosystem engineers on the composition of associated assemblages. *Aquatic Ecology* 41:129-147.
- Berkenbusch, K., A. A. Rowden, and T.E. Myers. 2007. Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages. *Journal of Experimental Marine Biology and Ecology* 341: 70-84.
- Bigley, R. E. 1981. The population biology of two intertidal seagrasses, *Zostera japonica* and *Ruppia maritima* at Roberts Bank, British Columbia. M.S. Thesis. University of British Columbia, Vancouver, BC, Canada. pp. 205.
- Bowden, D. A., A. A. Rowden, and M. J. Attrill. 2001. Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of *Zostera marina* seagrass beds. *Journal of Experimental Marine Biology and Ecology* 259:133-154.
- Brenchley, G. A. 1982. Mechanisms of spatial competition in marine soft-bottom communities. *Journal of Experimental Marine Biology and Ecology* 60:17-33.
- Chesher, R. H. 1969. Contributions to the biology of *Meoma ventricosus* (Echinoidea: Sptangoida). *Bulletin of Marine Science* 19:72-110.
- Dame, R. F. and T. C. Prins. 1998. Bivalve carrying capacity in coastal ecosystems. *Aquatic Ecology* 31:409–421.
- Davis, R. C. and F. T. Short. 1997. Restoring eelgrass, *Zostera marina* L., habitat using a new transplanting technique: The horizontal rhizome method. *Aquatic Botany* 59:1-15.
- Davis, R. C., F. T. Short, and D. M. Burdick. 1998. Quantifying the effects of green crab damage to eelgrass transplants. *Restoration Ecology* 6:297-302.

- de Deckere, E. M. G. T., T. J. Tolhurst, and J. F. C. de Brouwer. 2001. Destabilization of cohesive sediments by infauna. *Estuarine, Coastal and Shelf Science* 53:665-669.
- DeWitt, T. H., A. F. D'Andrea, C. A. Brown, B. D. Griffen, and P. M. Eldridge. 2004. Impact of burrowing shrimp populations on nitrogen cycling and water quality in western North American temperate estuaries. pp. 107-118. In: A. Tamaki (ed.), *Proceedings of the Symposium on Ecology of Large Bioturbators in Tidal Flats and Shallow Sublittoral Sediments – from Individual Behavior to Their Role as Ecosystem Engineers*. University of Nagasaki, Japan.
- Dial, R. and J. Roughgarden. 1998. Theory of marine communities: The intermediate disturbance hypothesis. *Ecology* 79:1412-1424.
- Domning, D.P. 2001. Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166:27-50.
- Duarte, C. M., J. Terrados, N. S. R. Agawin, M. D. Fortes, S. Bach, and W. J. Kenworthy. 1997. Response of a mixed Philippine seagrass meadow to experimental burial. *Marine Ecology Progress Series* 147:285-294.
- Dumbauld, B. R. and S. Wyllie-Echeverria. 2003. The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. *Aquatic Botany* 77:27-42.
- Dworschak, P. C. 1981. The pumping rates of the burrowing shrimp *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea). *Journal of Experimental Marine Biology and Ecology* 52:25-35.
- Dworschak, P. C. 2000. Global diversity in the Thalassinidea (Decapoda). *Journal of Crustacean Biology* 20:238-245.
- Eldridge, P. M. and J. E. Kaldy. 2004. Stress response model for the tropical seagrass *Thalassia testudinum*: the interactions of light, temperature, sedimentation and geochemistry. *Estuaries* 27:923-937.
- Eldridge, P. M. and J. W. Morse. 2000. A diagenetic model for sediment-seagrass interactions, *Marine Chemistry* 70:89-103.
- Eyre, B. D. and A. J. P. Ferguson. 2002. Comparison of carbon production and decomposition, benthic nutrient fluxes and denitrification in seagrass, phytoplankton, benthic microalgae and macroalgae-dominated warm-temperate Australian lagoons. *Marine Ecology Progress Series* 229:43-59.
- Felder, D. L. 2001. Diversity and ecological significance of deep-burrowing macrocrustaceans in coastal tropical waters of the Americas (Decapoda: Thalassinidea). *Interciencia* 26:440-449.
- Feldman, K. L., B. R. Dumbauld, T. H. DeWitt, and D. C. Doty. 2000. Oysters, crabs, and burrowing shrimp: Review of an environmental conflict over aquatic resources and pesticides in Washington state's (USA) coastal estuaries. *Estuaries* 23:141-176.
- Fonseca, M. S. and S. S. Bell. 1998. The influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Ecology Progress Series* 171:109-121.
- Fonseca, M. S., W. J. Kenworthy, F. X Courtney, and M.O. Hall. 1994. Seagrass planting in the southeastern United States: Methods for accelerating habitat development. *Restoration Ecology* 2:198-212.

- Fonseca, M. S., G. W. Thayer, and W. J. Kenworthy. 1998. Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. NOAA Coastal Ocean Program Decision Analysis Series No. 12. NOAA Coastal Ocean Office, Silver Spring, MD. 222 pp.
- Fritz, C. E. 2002. A seasonal study of sediment reworking by *Neotrypaea californiensis* in Yaquina Bay, Oregon. Masters Thesis, Oregon State University, Corvallis, Oregon.
- Fukukawa, Y. 2001. Biogeochemical consequences of macrofauna burrow ventilation. *Geochemical Transactions*. 2:83-91.
- Garbary, D.J., and A.G. Miller. 2006. Green crabs (*Carcinus maenas*) as the grim reaper: destruction of eelgrass beds in Nova Scotia. *Journal of Shellfish Research* 25:728.
- Gerritsen J., A. F. Holland, and D. Irvine. 1994. Suspension feeding bivalves and the fate of primary production: an estuarine model applied to Chesapeake Bay. *Estuaries* 17:403-416.
- Griffen, B. D., T. H. DeWitt, and C. Langdon. 2004. Particle removal rates by the mud shrimp *Upogebia pugettensis*, its burrow, and a commensal clam: effects on estuarine phytoplankton abundance. *Marine Ecology Progress Series* 269:223-236.
- Harrison, P. G. 1987. Natural expansion and experimental manipulation of seagrass (*Zostera* spp.) abundance and the response of infaunal invertebrates. *Estuarine, Coastal and Shelf Science* 24:799-812.
- Hawkins, S. J., J. R. Allen, and S. Bray. 1999. Restoration of temperate marine and coastal ecosystems: nudging nature. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9:23-46.
- Hopkinson, Jr., C. S., A. E. Giblin, J. Tucker, and R. H. Garritt. 1999. Benthic metabolism and nutrient cycling along an estuarine salinity gradient. *Estuaries* 22:863-881.
- Huettel, M. 1990. Influence of the lugworm *Arenicola marina* on porewater nutrient profiles in sand flat sediments. *Marine Ecology Progress Series* 62:241-248.
- Hughes, R. G., D. Lloyd, L. Ball, and D. Emson. 2000. The effects of the polychaete *Nereis diversicolor* on the distribution and transplanting success of *Zostera noltii*. *Helgoland Marine Research* 54:129-136.
- Jumars, P. A. and R. A. Wheatcroft. 1988. Responses of benthos to changing food quality and quantity, with a focus on deposit feeding and bioturbation. pp. 235-253. In: W. H. Berger, V. S. Smetacek, and G. Wefer (eds.). *Productivity of the Ocean: Present and Past*. Wiley-Interscience, New York. pp. 470.
- Koch, M. S. and J.M. Erskine. 2001. Sulfide as a phytotoxin to the tropical seagrass *Thalassia testudinum*: interactions with light, salinity and temperature. *Journal of Experimental Marine Biology and Ecology* 266:81-95.
- Kristensen, E. 1988. Benthic fauna and biogeochemical processes in marine sediments: microbial activities and fluxes. pp. 275-299. In: T. H. Blackburn and J. Sorensen (eds.), *Nitrogen Cycling in Coastal Environments*. John Wiley and Sons, New York.
- Luckenbach, M. W. and R. J. Orth. 1999. Effects of a deposit-feeding invertebrate on the entrapment of *Zostera marina* L. seeds. *Aquatic Botany* 62:235-247.
- Martin, R. A. 2003. The Amazing Sensory Talents of Batoids. World Wide Web Publication. www.elasmo-research.org/education/topics/s_batoid_senses.htm

- Meile, C., C. M. Koretsky, and P. Van Cappellen. 2001. Quantifying bioirrigation in aquatic sediments: An inverse modeling approach. *Limnology and Oceanography* 46:164-177.
- Merkel, K. W. 1990. Eelgrass transplanting in south San Diego Bay, California. pp. 28-42 In: S. Wyllie-Echverria, R. S. Hoffman and K. W. Merkel (eds.), *Proceedings of the California Eelgrass Symposium*, Chula Vista, California, May 27 and 28, 1988. Sweetwater River Press, National City, California.
- Molenaar, H. and A. Meinesz.. 1995. Vegetative reproduction in *Posidonia oceanica*: Survival and development of transplanted cuttings according to different spacings, arrangements and substrates. *Botanica Marina* 38:313-322.
- Moore, K. A., R. J. Orth, and J. F. Nowak. 1993. Environmental regulation of seed germination in *Zostera marina* L. (eelgrass) in Chesapeake Bay: Effects of light, oxygen and sediment burial. *Aquatic Botany* 45:79-91.
- Mosher, C. 1980. Distribution of *Holothuria areicola* Semper in the Bahamas with observations on habitat, behavior and feeding activity (Echinodermata: Holoturoidea). *Bulletin of Marine Science* 30:1-12.
- Newell, R. I. E. 1988. Ecological Changes in Chesapeake Bay: Are they the result of overharvesting the American oyster (*Crassostrea virginica*), p. 536–546. In M. Lynch (ed.), *Understanding the Estuary: Advances in Chesapeake Bay Research*. Chesapeake Research Consortium Publication 129, Gloucester Point, Virginia. Download from www.vims.edu/GreyLit/crc129.pdf.
- Newell, R. I. E. and E. W. Koch. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27:793–806.
- Norkko, A., S. F. Thrush, J. E. Hewitt, V. J. Cummings, J. Norkko, J. I. Ellis, G. A. Funnell, D. Schultz, and I. MacDonald. 2002. Smothering of estuarine sandflats by terrigenous clay: the role of wind-wave disturbance and bioturbation in site-dependent macrofaunal recovery. *Marine Ecology Progress Series* 234:23-41.
- Ogden, J. C. 1980. Faunal relationships in Caribbean seagrass beds. , pp. 171-198. In: R. C. Phillips and C. P. McCoy (eds.), *Handbook of Seagrass Biology: An Ecosystem Perspective*, Garland STPM Press, New York.
- Orth, R. J. 1975. Destruction of eelgrass, *Zostera marina* by the Cownose Ray, *Rhinoptera bonasus*, in the Chesapeake Bay. *Chesapeake Science*. 16:205-208.
- Orth, R. J., K. L. Heck Jr., and J. van Montfrans. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationship. *Estuaries* 7:339-350.
- Orth, R. J., M. W. Luckenbach, and K. A. Moore. 1994. Seed dispersal in a marine Macrophyte: Implications for colonization and restoration. *Ecology* 75:1927-1939.
- Ott, J. A., B. Fuchs, R. Fuchs, and A. Malasek. 1976. Observations on the biology of *Callianassa stebbingi* Borrodaille and *Upogebia litoralis* Risso. *Senckenbergiana Maritime* 8:61-79.
- Packard, J.M. 1984. Impact of manatees *Trichechus manatus* on seagrass communities in eastern Florida. *Acta Zoologica Fennica* 172:21-22.
- Pearson, T. H. 2001. Functional group ecology in soft-sediment marine benthos: the role of bioturbation. pp. 233-267. In: R. B. Gibson, M. Barnes and R. J. A. Atkinson. *Oceanography and Marine Biology Annual Reviews*. Vol. 39. Taylor & Francis Ltd..

- Peterson B. J. and K. L. Heck, Jr. 1999. The potential for suspension feeding bivalves to increase seagrass productivity. *Journal of Experimental Marine Biology and Ecology* 240:37–52.
- Peterson B. J. and K. L. Heck, Jr. 2001a. Positive interactions between suspension feeding bivalves and seagrass—a facultative mutualism. *Marine Ecology Progress Series* 213:143–155.
- Peterson B. J. and K. L. Heck, Jr. 2001b. An experimental test of the mechanism by which suspension feeding bivalves elevate seagrass productivity. *Marine Ecology Progress Series* 218:115–125.
- Peterson, B. J., K. L. Heck, Jr., and J. W. Fourqurean. 2003. Organisms as resource providers: a tale of two suspension feeders in seagrass communities. *Gulf of Mexico Science* 21:120.
- Phelps, H. L. 1994. The asiatic clam (*Corbicula fluminea*) invasion and system-level ecological change in the Potomac River estuary near Washington, D.C. *Estuaries* 17:614–621.
- Phillipart, C. J. M. 1994. Interactions between *Arenicola marina* and *Zostera noltii* on a tidal flat in the Wadden Sea. *Marine Ecology Progress Series* 111:251–257.
- Posey, M. H. 1986. Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis*. *Marine Ecology Progress Series* 31:15–22.
- Pranovi, F., D. Curiel, A. Rismondo, and M. Marzocchi. 1996. Seagrass meadow distribution in relation to the presence of *Upogebia pusilla* (Crustacea, Decapoda) in the Lagoon of Venice. *Biologia Marina Mediterranea*. 4:169–171. (Italian with English abstract)
- Preen, A. 1995. Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. *Marine Ecology Progress Series* 124:201–213.
- Prins, T. C., A. C. Smaal, and R. F. Dame. 1997. A review of the feedbacks between bivalve grazing and ecosystem processes. *Aquatic Ecology* 31:349–359.
- Reusch, T. B. H., A. R. O. Chapman, and J. P. Gröger. 1994. Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. *Marine Ecology Progress Series* 108:265–282.
- Reusch, T. B. H. and S. L. Williams. 1998. Variable responses of native eelgrass *Zostera marina* to non-indigenous bivalve *Musculista senhousia*. *Oecologia* 113:428–442.
- Rowden, A. A. and M. B. Jones. 1993. Critical evaluation of sediment turnover estimates for Callianassidae (Decapoda: Thalassinidea). *Journal of Experimental Marine Biology and Ecology* 173:265–272.
- Schaffner, L. C., P. Jonsson, R. J. Diaz, R. Rosenberg, and P. Gapcynski. 1992. Benthic communities and bioturbation history of estuarine and coastal systems: Effects of hypoxia and anoxia. pp. 1001–1016. In: R. A. Vollenweider, R. Marchetti, and R. Viviani (eds), *Marine Coastal Eutrophication*, Elsevier, London.
- Short, F. T., R. C. Davis, B. S. Kopp, C. A. Short, and D. M. Burdick. 2002. Site-selection model for optimal transplantation of eelgrass *Zostera marina* in the northeastern US. *Marine Ecology Progress Series* 227:253–267.
- Short, F. T., K. Matso, H. M. Hoven, J. Whitten, D. M. Burdick, and C. A. Short. 2001. Lobster use of eelgrass habitat in the Piscataqua River on the New Hampshire/Maine border, USA. *Estuaries* 24:277–284.
- Short, F. T. and S. Wyllie-Echeverria. 1996. Natural and human induced disturbances of seagrasses. *Environmental Conservation* 23:17–27.

- Siebert, T., and G. M. Branch. 2005. Interactions between *Zostera capensis*, *Callianassa kraussi* and *Upogebia africana*: deductions from field surveys in Langebaan Lagoon, South Africa. *African Journal of Marine Science* 27: 345-356.
- Siebert, T., and G. M. Branch. 2007. Ecosystem engineers: interactions between eelgrass *Zostera capensis* and the sandprawn *Callianassa kruassi* and their indirect effects on the mudprawn *Upogebia africana*. *Journal of Experimental Marine Biology and Ecology* 338: 253-270.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Suchanek, T. H. 1983. Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation. *Journal of Marine Research* 41:281-29.
- Tamaki, A. 2004. Ghost shrimps, snails, and clams on intertidal sandflats in the Ariake Sound estuarine system: seeking for unified perspectives on their population explosions and declines. pp. 107-118. In: A. Tamaki (ed.), *Proceedings of the Symposium on Ecology of Large Bioturbators in Tidal Flats and Shallow Sublittoral Sediments – from Individual Behavior to Their Role as Ecosystem Engineers*. University of Nagasaki, Japan.
- Thayer, G. W. 1983. Sediment-mediated biological disturbance and the evolution of marine benthos. pp. 479-625. In: M. J. S. Tevesz and P. L. McCall (eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Plenum, New York.
- Thayer, G. W. and M. S. Fonseca. 1984. The ecology of eelgrass meadows of the Atlantic coast: a community profile. US Fish & Wildlife Service, FWS/OBS-84/02.
- Thom, R. M., A. B. Borde, S. Rumrill, D. L. Woodruff, G. D. Williams, J. A. Southard, and S. L. Sargeant. 2003. Factors influencing spatial and annual variability in eelgrass (*Zostera marina* L.) meadows in Willapa Bay, Washington, and Coos Bay, Oregon, estuaries. *Estuaries* 26:1117-1129.
- Thompson, L. D. and A. W. Pritchard. 1969. Osmoregulatory capacities of *Callianassa* and *Upogebia* (Crustacea: Thalassinidae). *Biological Bulletin* 136:114-129.
- Townsend E. C. and M. S. Fonseca. 1998. Bioturbation as a potential mechanism influencing spatial heterogeneity of North Carolina seagrass beds. *Marine Ecology Progress Series* 169:123-132.
- Ulanowicz, R. and J. H. Tuttle. 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. *Estuaries* 15:298–306.
- Valentine, J. F., K. L. Heck, Jr., P. Harper, and M. Beck. 1994. Effects of bioturbation in controlling turtlegrass (*Thalassia testudinum* Banks ex Koenig) abundance: Evidence from field enclosures and observations in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology* 178:181-192.
- van Katwijk, M. M. and D. C. R. Hermus. 2000. Effects of water dynamics on *Zostera marina*: transplantation experiments in the intertidal Dutch Wadden Sea. *Marine Ecology Progress Series* 208:107–118.
- van Katwijk, M. M., L. H. T. Vergeer, G. H. W. Schmitz and J. G. M. Roelofs. 1997. Ammonium toxicity in eelgrass *Zostera marina*. *Marine Ecology Progress Series* 157:159-173.

- Wanless, H. R., L. P. Tedesco, and K. M. Tyrrell. 1988. Production of subtidal tubular and surficial tempestites by Hurricane Kate, Caicos Platform, British West Indies. *Journal of Sedimentary Petrology* 58:739-750.
- Webb, A. P. and B. D. Eyre. 2004. Effect of natural populations of burrowing thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification. *Marine Ecology Progress Series* 268:205-220.
- Wheatcroft, R. A. and W. R. Martin. 1996. Spatial variation in short-term (^{234}Th) sediment bioturbation intensity along an organic-carbon gradient. *Journal of Marine Research* 54: 763-792.
- Williams, S. L. 1990. Experimental studies of Caribbean seagrass bed development. *Ecological Monographs* 60:449-469.
- Woods, C. M. C. and D. R. Schiel. 1997. Use of seagrass *Zostera novazelandica* (Setchell, 1933) as habitat and food by the crab *Macrophthalmus hirtipes* (Heller 1862) (Brachyura: Ocypodidae) on rocky intertidal platforms in southern New Zealand. *Journal of Experimental Marine Biology and Ecology* 214:49-65.
- Zieman, J. C. 1982. The ecology of seagrasses of south Florida: A community perspective. U.S. Fish and Wildlife Service, Office of Biological Services. Washington, D.C. FWS OBS-82 25. 158 pp.

11.0 Research Gaps in Relation to Setting Protective Criteria

Walter G. Nelson

11.1 Overview

The U.S. EPA sponsored a workshop in Baltimore, Maryland in 2003 entitled: Towards a National Basis for Protective Criteria for Submerged Aquatic Vegetation, in conjunction with the National Conference on Coastal and Estuarine Habitat Restoration. A group of more than 60 scientists and resource managers from 21 coastal states discussed the scientific knowledge base and the challenges in developing a national framework for protection of submerged aquatic vegetation. Through a series of regional presentations on the status of SAV research, followed by break-out discussion groups, several key questions were addressed. The principal questions were: Does our current state of scientific knowledge allow drafting of a national guidance for setting criteria protective of SAV, or are there still critical research gaps? Does it appear possible to set criteria on a regional basis, or is it likely that criteria will have to be set on a system or even sub-system basis? I will address these two questions in reverse order.

The US EPA produced a National Strategy for the Development of Regional Nutrient Criteria (US EPA, 1998), which proposed an operational approach for developing nutrient criteria guidance for the states at a regional level, rather than at a national level. The Nutrient Strategy proposed the use of the Level III Ecoregional classification system as the regional framework for development of nutrient criteria. A variety of guidance documents recommending ambient water quality criteria for different water body types (e.g. wetlands, US EPA 2000; lakes and reservoirs, US EPA, 2001) have been developed for various Level III or sublevel III ecoregions. The tradeoffs of developing protective criteria at larger, aggregated ecological scales versus individual water bodies is clearly one of accuracy and relevance of a criterion versus the data collection effort needed for establishing a criterion at an individual aquatic system level (Chapter 1, Figure 1.3). The tremendous backlog at the state level in the development of Total Maximum Daily Load (TMDL) values for individual stream segments is a graphic expression of the potential disadvantages of trying to develop criteria at the system or sub-system scale. On the other hand, if a criterion developed at regional scale is not applicable or protective of individual systems or sub-systems, then it is of little practical use.

The consensus of workshop participants was that establishing adequately protective criteria for SAV even on a regional basis would be difficult, given the inherent variability of estuarine systems at such scales. Apart from the scientific and technical issues of regional scale criteria, participants from the coastal management community noted that most resource management of estuaries occurs at the local scale. Thus, criteria established at the local scale and with local input will tend to resonate better with the public. Establishment of effective criteria at a spatial scale which avoids a “Balkanization” of standards may be possible. The guidance document for Chesapeake Bay water quality criteria (US EPA 2003) illustrates one possible approach to establishing criteria for seagrasses, where criteria within this large and

complex system are determined based on four separate salinity regimes, but are applicable throughout the Bay.

In contrast to the development of what was at least a general consensus on an appropriate scale for setting seagrass criteria (subregional, system, or sub-system), the workshop participants identified a wide range of issues relating to the knowledge base needed to establish protective criteria. There were questions raised concerning the utility of using classical water quality criteria based on ambient concentrations of nutrients, versus attempting to frame criteria in terms of loadings to the system. If a nutrient concentration or loading criterion is established, should it be set at levels that insure survival of seagrasses or should it be set at more stringent levels to insure that seagrasses thrive? These questions of general principle have not yet been definitely resolved.

11.2 Summary of Research Gaps Identified

11.2.1 Light

The review of light information proposed that one present gap in current approaches to establishing light requirements for seagrass populations is the ability to adequately account for the effects of varying periods of diminished irradiance on seagrass survival. An alternative is to determine a benchmark level of leaf sucrose representing the ability of the plant to maintain a positive carbon balance. Additional studies are needed on the rates of translocation of sucrose from rhizomes to shoots in *Zostera marina* during times of negative carbon balance to assess the importance of this mechanism of mitigating low light conditions. Physiological studies of P vs. I, sucrose content *et cetera*, should always be accompanied with a range of normalizing measures.

11.2.2 Nutrients

The question of whether either nitrate or ammonium is directly toxic to seagrasses needs resolution. Apparently contradictory results have been reported, but a potential interactive effect of temperature has been suggested, and should be examined for all seagrasses. There is little apparent relationship between nutrient inputs and the rate and type of dominant primary producers (Nixon et al. 2001), making it difficult to predict whether a criterion will be protective. (See also 11.2.7).

11.2.3 Salinity

While nutrient additions may have greater impact on eelgrass populations in high salinity areas, (van Katwijk et al. 1999), the interactions of nutrient effects with salinity have not been widely studied. Additional information on the effect of increasing the variance in salinity on *Z. marina* would be helpful, especially in terms of variation of population response.

11.2.4 Hydrodynamic Factors

Hydrodynamic factors clearly influence the survival and distribution of seagrasses, and more data may be needed to define current velocity and wave tolerance ranges for various species and systems. Relative differences in sensitivity of various life stages (e.g. seedlings) to hydrodynamic factors may be needed. Because many aspects of hydrodynamic influences on

seagrasses are determined by natural factors (wind speed, depth), it is most likely that hydrodynamic influences would be considered in terms of whether sufficient safety margins are present in setting water quality criteria. Hydrodynamics considerations are clearly critical in planning seagrass restoration projects.

11.2.5 Sediment Characteristics

Grain size of the substratum influences the distribution and health of *Zostera marina*, although there remain uncertainties concerning the mechanisms. In general, we need a better understanding of how sediment pore water concentration of potentially toxic substances, such as ammonium and dissolved sulfides, interact with the effects of varying light levels in determining plant survival. Such information would be helpful in insuring that protective criteria based on water quality variables alone would be adequately protective.

11.2.6 Epiphytes

Epiphytes influence available light quality and quantity and may partly determine the ability of seagrasses to grow and survive. The role of epiphytic cover in affecting light availability may be an essential element to include in development of management criteria for protection of coastal seagrass beds. The technical guidance for ambient water quality criteria for Chesapeake Bay (U.S. EPA 2003) provides an explicit formulation for including epiphyte loads in estimating light available at the seagrass leaf surface. Model formulations need to be validated for other systems. Mesocosm research has shown that different algal components may dominate in the biomass response to nutrient enrichment in spite of similar initial conditions, and that temperature, nutrient exposure regime and other factors such as grazing levels may all influence the outcome of nutrient enrichment. Thus, models used for development of seagrass criteria must be able to account for impacts from multiple pathways, and must account for effects of trophic cascades.

11.2.7 Macroalgal interactions

Quantitative relationships between macroalgal canopy height (or corresponding measures of abundance) and specific impacts on eelgrass plants (such as those provided by Hauxwell et al. 2001), for different water body characteristics (temperature, current velocity, turbidity, grazing pressure, etc.) are needed. Similarly, relationships between macroalgal abundance and the causative anthropogenic activity (e.g., normalized nitrogen load rate) are needed to recommend corrective actions. It seems likely that such relationships between nutrient loading, macroalgal abundance, and seagrass distribution are site-specific, but this supposition needs to be confirmed.

11.2.8 Desiccation and Temperature Impacts

For a region such as the west coast, where intertidal seagrass can be a large percentage of the total population, better knowledge of desiccation effects on individual shoots and populations is needed to support multi-stressor, seagrass stress-response models. Better definition of the interactive effects of temperature and nutrient effects is a critical need, both for site specific permitting of heated discharge waters, and to be able to set protective criteria under conditions of global warming.

11.2.9 Bioturbation

The effects of bioturbation and bioirrigation on seagrass populations and how they interact with anthropogenic stressors remain poorly known. Failure to account for both the positive and negative effects of organisms in the sediment, e.g. alteration of sediment oxygen levels and sediment resuspension rates, could result in criteria either overly conservative or insufficiently protective of seagrasses.

11.3 Conclusions

The current review confirms that there is a great deal of scientific information currently available concerning the responses of *Zostera marina* and *Thalassia testudinum* to a wide range of environmental factors. A main theme that has emerged from the review is that the interactive effects among factors influencing seagrass survival remain relatively poorly known, especially across broader regional scales. This appears true even for such fundamental environmental characteristics as salinity and temperature and their interactions in the expression of nutrient or sediment impacts on SAV, although research is beginning to fill this gap.

Clearly of concern is whether current modeling approaches, whether empirical or mechanistic, are adequate to predict the response of seagrasses to even single stressors. The independent reviews of nutrients (Chapter 3), epiphytes (Chapter 7) and macroalgal interactions (Chapter 8) all identified the concern that there is currently a high level of uncertainty in being able to predict the trophic pathway for expression of nutrient impacts on seagrasses. Thus water quality criteria based on nutrient concentrations may not be adequately protective of seagrass resources. Alternate standards based on water clarity or water column chlorophyll *a* criteria may not be adequately protective if the principle expression of nutrient impacts occur through the epiphyte or macroalgal pathways. These same concerns were also identified by scientists and managers at the Baltimore workshop.

Current protective criteria for seagrasses (e.g. US EPA 2003) are water column based. The review of sediment influences (Chapter 6) suggests that there are important influences on plant survival through sediment associated mechanisms that may not be adequately captured by water quality criteria alone. The review of effects of light limitation (Chapter 2) suggested there may be advantages to looking for integrative, plant based metrics such as sucrose content that relate to the ability of seagrasses to survive within a temporally varying environment. The Baltimore workshop similarly proposed the possibility of using such integrative measures, specifically the Nutrient Pollution Indicator (NPI) (Lee et al. 2004). Such measures may be an appropriate method to integrate water column and sediment impacts into single protective criteria.

In conclusion, there remain some fundamental research needs which would greatly improve the ability to set protective criteria for seagrasses. However, there is also a considerable scientific knowledge base that can be used in establishing criteria for protection of seagrasses. The concept of protective criteria is actually one that embodies principles of adaptive management. Initial criteria may be based on incomplete data or modeling approaches, but it is

expected that as better data and approaches become available, they will be applied to improve the protective criteria. Various localized efforts have made significant progress in establishing seagrass protective criteria, e.g. Tampa Bay, Chesapeake Bay. While there are still many issues in moving from local criteria to guidance for criteria across multiple systems, it would appear that creation of a first level guidance is certainly feasible with the knowledge currently available.

11. 4 Literature Cited

- Hauxwell, J., J. Cebrián, C. Furlong, and I. Valiela. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 82:1007-1022.
- Lee, K. S., F. T. Short, and D. M. Burdick. 2004. Development of a nutrient pollution indicator using the seagrass, *Zostera marina*, along nutrient gradients in three New England estuaries. *Aquatic Botany*, 78: 197–216.
- Nixon, S., B. Buckley, S. Granger, and J. Bintz. 2001. Responses of very shallow marine ecosystems to nutrient enrichment. *Human and Ecological Risk Assessment* 7:1457-1481.
- U.S. EPA. 1998. National Strategy for the Development of Regional Nutrient Criteria. U.S. EPA, Office of Water. EPA 822-R-98-002.
- U.S. EPA. 2000. Ambient Water Quality Criteria Recommendations. Information Supporting the Development of State and Tribal Nutrient Criteria. Wetlands in Nutrient Ecoregion XIII. U.S. EPA, Office of Water, Office of Science and Technology. EPA 822-B-00-023.
- U.S. EPA. 2001. Ambient Water Quality Criteria Recommendations. Information Supporting the Development of State and Tribal Nutrient Criteria. Lakes and Reservoirs in Nutrient Region III. U.S. EPA, Office of Water, Office of Science and Technology. EPA 822-B-01-008.
- U.S. EPA. 2003. Ambient Water Quality Criteria for Dissolved Oxygen, Water Clarity and Chlorophyll *a* for the Chesapeake Bay and Its Tidal Tributaries. U.S. EPA, Office of Water and Office of Science and Technology. EPA 900-R-03-002.
- van Katwijk, M. M., G. H. W. Schmitz, A. P. Gasseling, and P. H. van Avesaath. 1999. Effects of salinity and nutrient load and their interaction on *Zostera marina*. *Marine Ecology Progress Series* 190:155-165.



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