ERDC/EL SR-21-6

Environmental Laboratory

US Army Corps
of Engineers®
Engineer Research and
Development Center

Ecosystem Management and Restoration Research Program (EMRRP)

Environmental Factors Affecting Coastal and Estuarine Submerged Aquatic Vegetation (SAV)

Eve Eisemann, Catherine Thomas, Matthew Balazik, Damarys Acevedo-Mackey, and Safra Altman

September 2021

Ecosystem Management and Restoration
and Research Program (EMRRP)

ERDC/EL SR-21-6
September 2021

Environmental Factors Affecting Coastal and Estuarine Submerged Aquatic Vegetation (SAV)

Eve Eisemann, Catherine Thomas, Matthew Balazik,
Damarys Acevedo-Mackey, Safra Altman

Environmental Laboratory
US Army Engineer Research and Development Center
3909 Halls Ferry Road
Vicksburg, MS 39180--6133

Final report

Prepared for Ecosystem Management and Restoration Research Program
Vicksburg, MS 39180-6199

Under Funding Account Code U4368952, AMSCO Code 031342

Abstract

Submerged aquatic vegetation (SAV) growing in estuarine and coastal marine systems provides crucial ecosystem functions ranging from sediment stabilization to habitat and food for specific species. SAV systems, however, are sensitive to a number of environmental factors, both anthropogenic and natural. The most common limiting factors are light limitation, water quality, and salinity, as reported widely across the literature. These factors are controlled by a number of complex processes, however, varying greatly between systems and SAV populations. This report seeks to conduct an exhaustive examination of factors influencing estuarine and coastal marine SAV habitats and find the common threads that tie these ecosystems together. Studies relating SAV habitats in the United States to a variety of factors are reviewed here, including geomorphological and bathymetric characteristics, sediment dynamics, sedimentological characteristics, and water quality, as well as hydrologic regime and weather. Tools and methods used to assess each of these important factors are also reviewed. A better understanding of fundamental environmental factors that control SAV growth will provide crucial information for coastal restoration and engineering project planning in areas populated by SAVs.

Contents

Figures and Tables

Figures

Tables

Preface

The work reported herein was conducted at the US Army Engineer Research and Development Center (ERDC) under Funding Account Code U4368952 and AMSCO Code 031342 for the Ecosystem Management and Restoration Research Program (EMRRP). The work was performed by the Wetlands and Coastal Ecology Branch and the Environmental Engineering Branch, of the Ecosystem Evaluation and Engineering Division, ERDC, Environmental Laboratory (ERDC-EL), and by the Coastal Engineering Branch, of the Navigation Division, ERDC, Coastal and Hydraulics Laboratory (ERDC-CHL).

At the time of publication, Ms. Patricia Tolley was Chief of the Wetlands and Coastal Ecology Branch, and Ms. Brooke Petery was Acting Chief of the Environmental Engineering Branch; Mr. Mark Farr was Chief of the Ecosystem Evaluation and Engineering Division of ERDC-EL; Dr. Trudy Estes was Program Manager of EMRRP, and Mr. Warren Lorentz was the Acting Technical Director. The Acting Deputy Director of ERDC-EL was Dr. Brandon Lafferty, and the Acting Director was Dr. Jack Davis. Ms. Lauren Dunkin was Chief of the Coastal Engineering Branch; Dr. Jackie Pettway was Chief of the Navigation Division; the Deputy Director of ERDC-CHL was Jeffrey R. Eckstein and the Director was Dr. Ty V. Wamsley.

COL Teresa A. Schlosser was Commander of ERDC, and Dr. David W. Pittman was the Director.

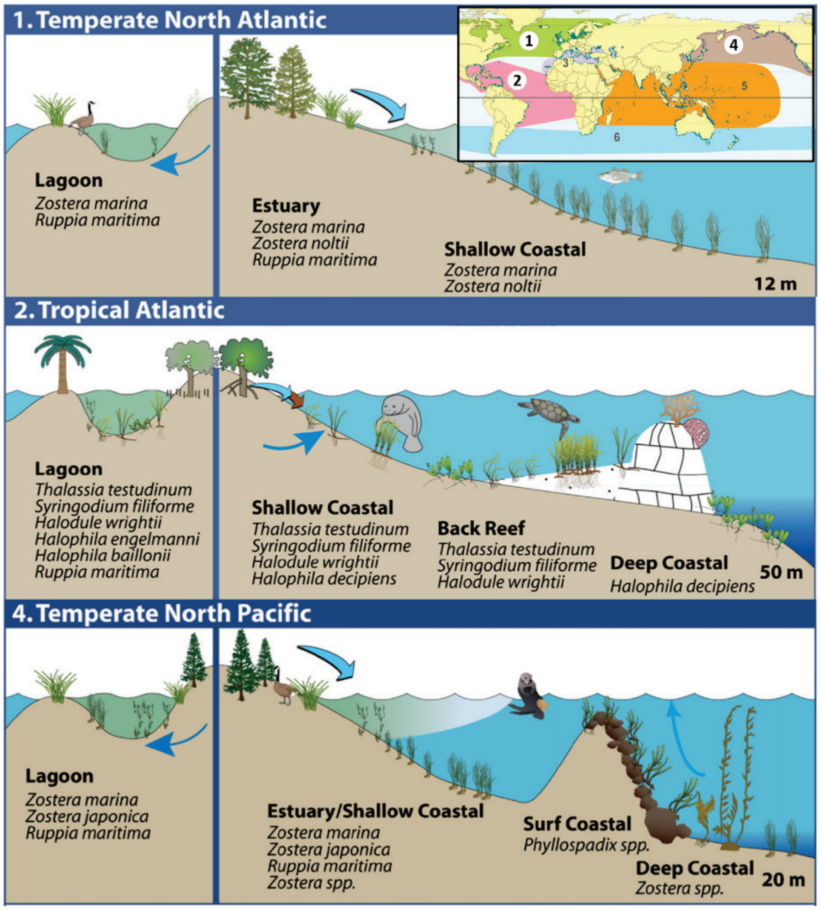
1 Introduction

Background

Submerged aquatic vegetation (SAV) in coastal systems provides a variety of critical ecosystem functions, including carbon sequestration, sediment stabilization, wave energy reduction, water-quality improvement, and habitat creation for diverse communities and important species across the nation. A number of factors are placing coastal SAV ecosystems at risk globally, including sediment starvation, subsidence, and water-quality issues, (Kirwan and Megonigal 2013; Orth et al. 2006). Many of these factors are also influenced by human activities. Improving the condition of these degraded coastal systems often requires targeted restoration efforts; however, these efforts often lack sufficient information or key data for effective project planning. The success of these restoration efforts hinges on creating a sustainable physical environment suitable for the growth of the targeted species as well as ecosystem development. This targeting may involve placement of soil or sediment substrate to raise the surface elevation or improve soil conditions to support desired habitat.

One type of SAV, seagrass, dominates in coastal and estuarine systems and is of particular ecological importance, providing food and critical habitat for numerous species. Seagrasses inhabit three defined bioregions in North America, the Temperate North Atlantic (in estuaries and lagoons), the Tropical Atlantic (in back reefs and on shallow banks) (Figure 1a), and the Temperate North Pacific (in estuaries, lagoons, and the coastal surf zone) (Figure 1c; Short et al. 2007). Seagrass is currently in decline globally owing to the aforementioned factors influencing its habitat (Eleuterius 1987; Kirwan and Megonial 2013; Orth et al. 2006). Identifying the specific conditions to promote seagrass and other coastal SAV recovery and growth is mentioned as one of the "important yet essentially unanswered questions" globally in the US Geological Survey's (USGS) report *Seagrass Status and Trends in the Mississippi Sound from 1940–2002* (Moncreiff 2007, 79).

Figure 1. Bioregion where seagrass submerged aquatic vegetation (SAV) occurs in North America. SAV's location on the globe is shown in the top-right inset. Important physical characteristics of each respective biozone are outlined along with seagrass species that occur there (depths represent maximum reported depth, figure modified from Short et al. 2007, 8).



The important factors for SAV survival are more thoroughly studied and understood in estuarine and other well-protected environments. These environments are typically characterized by shallow bathymetry, fine-grained substrate, and relatively low-energy conditions, where wave exposure and light are identified as primary limiting factors for SAV growth (Boer 2007; Koch 2001; Livingston, Mcglynn and Niu 1998). Along sandy barrier islands, SAV habitat has been related to the barrier island's stability and size, but there is a need to better study and quantify the conditions that promote SAV recovery and growth here (Carter et al. 2011; Eleuterius 1987; Pham, Biber and Carter 2014). SAV in these environments face dynamic conditions and additional threats not experienced in other SAV systems, like rapid burial and erosion as well as high-energy wave events (Pham, Biber and Carter 2014).

Most studies use a method of SAV mapping to understand environmental factors important for this habitat. SAV growth is mapped in coastal and estuarine waters using field and remote-sensing methodologies. Hyperspectral, multispectral, and RGB (red, green, and blue) aerial imagery can show locations of potential SAV beds, which can then be ground truthed to verify presence or absence and species (Carter et al. 2011; Reif et al. 2011). Understanding the spatial pattern of SAV growth and how it changes over time can provide valuable information about habitat requirements (Carter et al. 2011). Studies outlining findings relating the physical environment to SAV growth and the methods used to draw these conclusions are outlined in this report. Knowledge of these important habitat-controlling factors can be applied to develop suitability or similar predictive models (DeMarco et al. 2018). Such models can be applied to consider SAV impacts when designing restoration or other coastal projects.

Objective

This work seeks to investigate and establish correlations between SAV living in the coastal zone, including shallow marine and estuarine environments, and a variety of factors in its environments. The ultimate focus of this work is on geomorphological features and substrate characteristics, from which guidance can be developed for the selection of appropriate substrate material and conditions to support a variety of coastal SAV growth. This guidance will enable

- rapid assessment to determine whether available source material is appropriate for a given restoration
- identification of appropriate locations for restoration efforts and site conditions that must exist or be created for restoration success
- identification of potential issues at sites where restoration has not been successful or where an ongoing restoration effort requires adaptive management to increase its likelihood of success
- improvement of the efficiency and success of coastal vegetation restoration efforts, which will aid planners and managers during the planning stage.

This literature review synthesizes available information on multiple parameters that are critical for coastal SAV growth. The review also outlines site conditions documented in the literature leading to varying levels of success for coastal SAV growth and establishment. This effort investigated and compiled established correlations between the different geomorphological parameters, sediment characteristics, and coastal vegetation growth. This report, therefore, establishes the current state of knowledge and identifies gaps needing future field efforts.

Approach

A literature search was conducted to synthesize available information on multiple parameters for coastal and marine SAV growth. The parameters considered in the literature search included geomorphological conditions, topography and bathymetry, hydrological regime, sedimentology, physical processes, and water quality. For each of these parameters, the following aspects were investigated: vegetation characteristics and requirements, sediment characteristics and requirements, factors affecting vegetation growth, and tools and methods typically used for assessment. Finally, published relationships and correlations are either described or compiled into a table.

2 Geomorphology and Bathymetry

Submerged aquatic vegetation (SAV) habitat characteristics and requirements

Geomorphological and bathymetric characteristics of a coastal environment can heavily influence whether it is a suitable habitat for SAV. Coastal and estuarine SAV species primarily occur in relatively shallow water environments where they have sufficient light and protection from waves (with the exception of *Phyllospadix* spp. along the rocky Pacific coast) (Eleuterius 1987; Short et al. 2007; Yates, Morrison and Greening 2011). In North America, these requirements place coastal SAV in bays, estuaries, behind barrier islands, or in most other protected, shallow, coastal environments (Short et al. 2007).

According to the literature reviewed, coastal geomorphological and bathymetric environments suitable for SAV growth are broken down into five general groups (Table 1a–c). These groups include back barrier platforms and shoals, bays and lagoons, estuaries, areas adjacent to rocky islands, and the swash zone. Many of these environments overlap with each other. Many bays can also be classified as estuaries (Mobile Bay, Alabama, and the Columbia River Estuary are two examples). Bays are grouped with sounds here, so this environment includes bodies of water that have a greater marine contribution to water and morphology than estuaries. Barrier islands frequently serve as the landform separating sounds and lagoons from the marine environment, so the back barrier could be considered either part of the bay or the lagoon behind it. In New England and along the West Coast, rocky islands frequently occur within estuaries and bays. Table 1 provides species and habitat characteristics for SAV in major US examples of these environments as well as references for each.

Back-barrier platforms and shoals: These landforms typically exist along coastlines with ample sand supply, where wave and other nearshore processes maintain subaerially exposed sandy barrier islands along with associated subaqueous platforms and shoals. These features frequently provide protection from waves to a back-barrier lagoon area, where marshes and SAV are often found.

Larger barrier islands provide more protection from wave and current energies such that the area behind the island is more conducive for seagrass growth and survival (Fonseca 1996; Fonseca and Bell 1998; Koch 2001; Koch et al. 2006b; Fonseca, Koehl and Kopp 2007). Thus, the overall size of a barrier island plays a huge factor in the establishment and long-term survival of seagrasses.

Barrier islands provide the primary protection for coastal seagrass beds along the Mississippi-Alabama coastlines—for example, whether these beds exist in estuaries or directly around the islands (Moncreiff 2007). The geomorphology of barrier islands can change slowly or rapidly, affecting seagrass distribution (Short et al. 2007). In the past few decades, as the Petit Bois barrier island (Mississippi) decreased in size by 40%, the seagrass beds behind the island also decreased significantly (Carter et al. 2011). Examples listed in the table include the Mississippi-Alabama Barrier Islands, Louisiana Chandeleur Barrier Islands, and North Carolina Barrier Islands.

Bays and lagoons: This grouping also includes sounds. These are all semienclosed, large bodies of water with significant marine influence. Bays, lagoons, and sounds are similar environments, characterized for the purposes of this report as a body of relatively open water protected from waves by barrier islands, spits, or other landforms.

The morphology of these water bodies varies widely, with some shallow enough or with water clear enough to support SAV throughout, while others only maintain fringing SAV. SAV typically only occurs along mainland shorelines in the Mississippi Sound, for example where wave energy is minimized and the depth is shallow enough for sufficient light penetration. In the Puget Sound, on the other hand, the water is clear enough to allow SAV growth at greater depths within the sound. Examples listed in the table include Long Island Sound of New York, Connecticut, and Rhode Island; Mississippi Sound of Mississippi and Alabama; Pamlico Sound, North Carolina; and Puget Sound, Washington.

Estuaries: Estuaries are characterized by the meeting of a freshwater source (river) and the marine environment, often supporting fringing marshes and tidal creeks, especially in coastal zones with a low gradient and a significant tidal range (trailing-edge, for example, US Gulf Coast and East Coast). Estuaries can have qualities like bays and lagoons and often fall into both categories, but they are generally better protected from coastal waves. Estuaries typically support finer-grained and organic-rich bottom substrates, often contributing to an increase in suspended matter (sediment and organic) and subsequently turbidity.

Higher levels of turbidity can reduce the habitable depth for seagrasses because of reduced light penetration. Turbidity and other impacts on light availability are discussed in section 4 of this report. SAV typically exists in estuaries in the intertidal or subtidal zones along fringing marshes and within tidal creeks and tributaries. Major examples of estuaries shown in the table include Mobile Bay, Alabama; the Chesapeake Bay of Delaware, Maryland, and Virginia; and Yaquina Bay, Oregon.

Adjacent to rocky islands: Rocky islands occur along leading-edge (tectonically active) or glacially influenced coastlines. In the United States, these coastline types are found along the West Coast and in New England, respectively. Rocky islands may be present within some of the larger coastal systems mentioned above, like bays and estuaries.

SAV occurs typically in shallow areas on a protected side of rocky islands or around rocky islands within an estuary. The enclosing water body may be sheltered from waves, allowing the island to add extra protection for SAV habitats. Rocky coastal zones tend to have coarser-grained sediments and often clearer water. A trend in increased depth of SAV habitat is clear in these environments (Table 1). Examples of rocky-island SAV habitats listed in the table include Naragansett Bay, Rhode Island, and the Puget Sound, Washington.

Swash zone: The swash zone is the area along the coast where waves crash and the energy is the highest. The majority of SAV cannot tolerate these conditions.

Plants in the genus *Phyllospadix* provide the only exception to the typical low-energy, soft-bottom environmental requirements for SAV. These seagrasses attach to rocks in rocky intertidal and subtidal swash zones along the West Coast and can withstand higher and more constant wave energy (Wyllie-Echeverria and Ackerman 2003).

Factors affecting SAV growth

Geomorphology and bathymetry influence SAV habitat primarily in that they control and are controlled by other important environmental parameters like light availability, erosion and deposition, water quality, currents, and temperature. The primary limiting factors for SAV in the coastal zone are water quality, light availability, and physical exposure (energy) (Beck, Lruczynski and Sheridan 2007).

A significant body of work addresses how these factors correlate with SAV growth (see Carter, Rybicki and Landwehr 2000; Duarte et al. 2007; Heck et al. 2000). Information on most of these specific parameters are provided in their respective sections of this report. In this section, the specific geomorphological and bathymetric characteristics of the environments where SAVs are observed will be discussed. Geomorphology and bathymetry are interrelated, as SAV-suitable depth ranges will vary according to geomorphologically controlled factors such as wave exposure, grain size, and turbidity, and bathymetric features could also be considered part of geomorphology. These factors not only affect where SAVs grow regionally but also their local and patch-scale distributions (Thayer, Kenworthy and Fonseca 1984). For example, seagrass SAV tends to grow on elevated sections of the sea bottom, 5–45 cm above the average surrounding bathymetry (Eleuterius 1987). In the case of small-scale variations, it may be hard to distinguish whether the original bathymetry controls the growth of SAV or the SAV is influencing the bathymetry by sequestering sediment. In the case of restorations, experiments have shown that varying the geomorphological characteristics of a seagrass planting site can lead to different rates of growth and levels of establishment success across a variety of environments deemed suitable for that species (Thayer, Kenworthy and Fonseca 1984).

Among all of the environments categorized in the previous section, excluding the rocky nearshore swash zone (*Phyllospadix* spp. only), the geomorphology and bathymetry of each setting meets basic environmental requirements, making them conducive to coastal SAV growth. These basic requirements are outlined in the following sections, each focusing on a specific important element for SAV growth.

Relatively shallow water: The water-depth limitation for SAV growth is primarily a light-limitation issue, of which some species are more tolerant. Suspended matter (sediment and organics) in the water column as a primary control on depth range is clear when SAV bed depths in relatively low- and high-turbidity areas are compared (see the Mississippi Sound versus the Florida Keys in Table 1). Water depth may change in some areas because of subsidence or tectonic shifts, affecting SAV habitability. For example, seagrass SAV died in areas deepening because of subsidence caused by oil, gas, and water extraction along coastal Texas (Pulich and Onuf 2007).

Protection from waves and currents: SAV generally grows in sheltered areas like coastal lagoons, bays, and estuaries, because they are sheltered from energetic waves and often exist landward of barrier islands or coral reefs (Fonseca 1996; Koch et al. 2006a; Short et al. 2007; Pilkey, Cooper and Lewis 2009). These types of sheltered environments provide protection against the current, wave, and wind energies that cause sediment resuspension and consequently increase turbidity and deposition (Koch 2001).

Exposure of SAV to current and wave energy depends largely on the local geomorphology and can affect plant establishment and growth. Too much energy can prevent SAV from establishing altogether (Robins and Bell 2000).

Most SAV requires some sort of protection from coastal waves, but different species require varying levels of protection. *Halodule wrightii*, for example, is the only species observed to populate the semiexposed north shore of back bay Matagorda Bay, while other species of SAV only inhabit sections of the bay with very limited fetch relative to the dominant wind direction (Adair, Moore, and Onuf 1994). Only the *Phyllospadix* species are able to tolerate significant waves on a regular basis (Wyllie-Echeverria and Ackerman 2003).

Storms events can damage SAV beds, but studies show that, when growing in a typically suitable environment, seagrasses have evolved to handle the acute damage from large storms (Michot et al. 2002; Heck and Byron 2006; Carter et al. 2011). For example, in 1969, Hurricane Camille destroyed hundreds of hectares of seagrass beds in Mississippi and Chandeleur Sounds. The barrier islands protecting Chandeleur Sound remained intact, while Ship Island was cut in two and a new inlet formed. The seagrass beds in still-protected Chandeleur Sound recovered more quickly than those behind the split Ship Island (Eleuterius 1987).

The chronic increase in current and wave energy because of increased exposure may contribute to SAV losses. For example, the growth of Camille Cut (the new Ship Island inlet) may have been a factor in the reduction of seagrass areas behind Ship Island in the Mississippi Sound (USACE 2014a, 2014b). In addition, following Hurricane Camille, seagrass species diversity behind Ship Island decreased.

Slow and limited deposition and erosion: Established SAV beds can tolerate deposition and erosion that occurs at an average rate slow enough for the SAV to adjust to over time, but SAV can be buried and killed by sedimentation caused by shifting coastal geomorphology or rapid deposition caused by storm events (Short and Neckles 1999; Short et al. 2007). SAV along the back-barrier platform of Ship Island, Mississippi, has been observed to tolerate ~5 cm/yr of sand deposition, but SAV was unable to establish in zones of frequent overwash that experience higher average depositional rates (Eisemann et al. 2019). SAV slowly repopulates with different species along the Chandeleur Islands, Louisiana, changing SAV community dynamics and potentially reducing diversity (Franze 2002; Poirrier and Handley 2007).

Shifting of sand is a primary factor influencing the size, shape, and distribution of seagrass beds in Mississippi Sound (Eleuterius 1987). In Mississippi Sound, most beds form meadows parallel to and between sand bars that run perpendicular to the island shoreline. The increased elevation around the seagrass beds is due to deposition of sediment caused by seagrass stems and leaves (Koch et al. 2006b).

Tools for assessment

Assessing how geomorphological and bathymetric characteristics are related to SAV growth can be done in a number of ways. One way is to note the general environment while conducting a study (for example, enclosed estuary versus barrier island). SAV mapping can be conducted by using aerial imagery where patches are visible through the water column. Imagery types useful for this application include hyperspectral, multispectral, natural color, and black and white (Carter et al. 2011; Reif et al. 2011). Field surveys and ground truthing can provide verification for aerial imagery results or provide another method for mapping SAV. SAV location and characteristics can then be compared with geomorphological and bathymetric data to assess their relationship to these factors.

To rigorously quantify bathymetry and topography, and subsequently geomorphological characteristics, aerial LiDAR from planes or drones can be employed. LiDAR elevations can reveal static characteristics like the location and elevation of islands and shoals as well as how these features change (Anderson, Carter, and Funderburk 2016; Eisemann et al. 2018b). This type of information, coupled with information about local SAV growth, can reveal how these factors are related (Eisemann et al. 2019). Advancements in LiDAR technology allow bathymetry measurements up to ~10 m[1] deep in some coastal environments, depending on water clarity (Mitchell, Thayer and Hayman 2010). Water depth is also frequently measured using transducer sonar units mounted on boats. Sonar can map bathymetry in areas too deep for LiDAR to penetrate. Coastal geomorphological changes can also be observed using repeated aerial photography and shoreline locations over time (Carter et al. 2011).

Published relationships

Various species of SAV grow in every coastal region of the United States, and numerous studies record the presence of SAV species in a wide range of coastal systems, as described in the previous sections. A thorough, but surely nonexhaustive, list of published studies documenting SAV present in coastal regions around the United States and associated geomorphological and bathymetric characteristics of those habitats follows (Table 1a–c).

---

[1] For a full list of the spelled-out forms of the units of measure used in this document, please refer to *US Government Publishing Office Style Manual*, 31st ed. (Washington, DC: US Government Publishing Office, 2016), 248–52, https://www.govinfo.gov/content/pkg/GPO-STYLEMANUAL-2016/pdf/GPO-STYLEMANUAL-2016.pdf.

Table 1a. Growth environments and characteristics for a variety of SAV species occurring along the Tropical North Atlantic coast of the United States (see Figure 1). This region includes the Gulf of Mexico coastline and the Atlantic coast of Florida. Some reports did not provide water depths, and some only provided information relative to tidal levels. The available data are presented here, and when information was not available, the cell contains a dash (—).

Region or environment	Plant species	Geomorphological and bathymetric characteristics	Water depth	Reference
Galveston Bay, TX	shoal grass (*Halodule wrightii)* star grass (*Halophila engelmannii*) turtle grass (*Thalassia testudinum*)	Back-barrier bay back-barrier platforms estuaries	—	Pulich and Onuf (2007)*
Laguna Madre, TX	manatee grass (*Syringodium filiforme*) turtle grass (*T. testudinum)* shoal grass (*Halodule wrightii*)	Back-barrier bay back-barrier platforms estuaries	—	Pulich and Onuf (2007)*
Galveston and Matagorda Bays, TX	star grass (*Halophila engelmannii*) turtle grass (*T. testudinum*) water celery (*Vallisneria americana*	Back-barrier platforms	Subtidal	Adair et al. (1994)
Galveston and Matagorda Bays, TX	shoal grass (*Halodule wrightii*) wigeon grass (*Ruppia maritima*) waternymph (*Najas guadalupensis*)	Back-barrier platforms, occasionally along northern bay shoreline	Lower intertidal and upper subtidal	Adair et al. (1994)
Matagorda Bay, TX	shoal grass (*Halodule wrightii*	Northern bay shoreline	—	Adair et al. (1994)
Chandeleur Sound, LA	turtle grass (*T. testudinum*) manatee grass (*S. filiforme*) shoal grass (*Halodule wrigthii*) star grass (*Halophila engelmani*)*i* wigeon grass (*R. maritima*)	Shallow back-barrier platforms and shoals	—	Poirrier and Handley (2007)*
Chandeleur Sound, LA	wigeon grass (*R. maritima*) shoal grass (*Halodule wrightii*)	shoreline marshes (*R. maritima*) washover fans (both)	—	Franze (2002)
Mississippi Sound, MS and AL	shoal grass (*Halodule wrightii*)	Back barrier platforms	2 m and less, 1.3 m and less	Moncreiff et al. (1998)* Carter et al. (2011)
Mississippi Sound, AL	wigeon grass (*R. maritima*)	bay and river mouths (low salinity areas)	—	Stout and Lelong (1981)*
Perdido Bay, AL	shoal grass (*Halodule wrightii*) turtle grass (minor, *T. testudinum*)	Back-barrier platforms	—	Stout and Lelong (1981)* Lelong (1988)*
Mobile Bay, AL	water celery (*V. americana*) wigeon grass (*R. maritima*)	Estuaries (mostly fresh to brackish)	—	Stout and Lelong (1981)*
Southwest FL Shelf and Big Bend Coast	Paddle grass (*Halophilia decipiens*)	Continental shelf	9–30+ m	Continental Shelf Associates Inc. (1989)*

Region or environment	Plant species	Geomorphological and bathymetric characteristics	Water depth	Reference
Florida Keys	star grass (*Halophilia engelmanni*	Bays continental shelf	Up to 20 m	Iverson and Bittaker (1986)
Big Bend Coast, FL	shoal grass (*Halodule wrightii*)	Shallow nearshore shoals exposed during low tide	Between high tide and lower low tide elevation	Iverson and Bittaker (1986)
Big Bend Coast, FL	turtle grass (*T. testudinum*) manatee grass (*S. filiforme*) shoal grass (*Halodule wrightii*)	Shallow areas not exposed during low tide	Deeper than low low tide elevation	Iverson and Bittaker (1986)**
Florida Estuaries	general	Estuaries	~1 m	Carlson and Madley (2007)*
Big Bend Coast, FL	wigeon grass (*R. maritima*)	River mouths (low salinity areas)	—	Iverson and Bittaker (1986)
Big Bend Coast, FL	manatee grass (*S. filiforme*)		Up to 6–8 m	Iverson and Bittaker (1986)
Florida Keys	manatee grass (*S. filiforme*)	Bays continental shelf	Up to 8–10 m	Iverson and Bittaker (1986)
Atlantic Florida Coast	shoal grass (*Halodule wrightii*)	Shallow nearshore areas, intertidal	—	Thayer et al. (1984)

* Information or source derived from Seagrass Status and Trends in The Northern Gulf of Mexico: 1940–2002 (Handley et al. 2007).

** These beds grew alongside sponges, and macroalgae, sponges, gorgonians, corals, and bryozoans colonized the outer edges of beds (Iverson and Bittaker 1986).

Table 1b. Growth environments and characteristics for a variety of SAV species occurring along the Temperate North Atlantic coast of the United States (see Figure 1). Some reports did not provide water depths, and some only provided information relative to tidal levels. The available data are presented here, and when information was not available, the cell contains a dash (—).

Region or environment	Plant species	Geomorphological and bathymetric characteristics	Water depth	Reference
Central New England (Waquoit Bay, Narragansett Bay)	eelgrass (*Zostera marina*)	Adjacent to rocky islands, within embayments and coves, along edges of salt-marsh ponds	Typically 1–2 m water depth, Range: +2 to −12 m relative to mean sea level (within tidal range)	Short et al. (1993) Moore and Short (2006)
Central New England (Great Bay)	wigeon grass (*Ruppia maritima*)	Deep salt-marsh pans and estuary drainage channels	Up to 4 m	Short et al. (1993)
Pamlico Sound and Back Sound, NC	eelgrass (*Z. marina*) shoal grass (*Halodule wrightii*) wigeon grass (*R. maritima*)	Marsh embayments, adjacent to shoals and islands in the sound	Up to 1.2 m	Short et al. (1993) Thayer et al. (1984)
Chesapeake Bay	*seagrass (Zostera sp.)*	Fringing edges of marshy lower estuary	<2 m	Moore et al. (2000)
Chesapeake Bay	seagrass (*Ruppia* sp.)	Fringing edges of marshy upper and central estuary, lower estuary tributaries	<2 m	Moore et al. (2000)
Chesapeake Bay	pondweed (*Potamogeton* sp.)	Fringing edges of marshy upper estuary and estuary tributaries	<2 m	Moore et al. (2000)
Chesapeake Bay	freshwater SAV	Far upper estuary and estuary tributaries	<2 m	Moore et al. (2000)
Long Island Sound	eelgrass (*Z. marina*) wigeon grass (*R. maritima*)	General—Long Island Sound	—	Holst et al. (2003)
Long Island Sound	eelgrass (*Z. marina*)	Tidal creeks, harbors, small bays, protected areas all along Long Island Sound coast (historical) Similar environments, primarily only east of the Connecticut River (modern)	0.5–3.5 m mean low water	Holst et al. (2003)

Table 1c. Growth environments and characteristics for a variety of SAV species occurring along the Temperate North Pacific coast of the US (see Figure 1). Some reports did not provide water depths, and some only provided information relative to tidal levels. The available data is presented here, and when information was not available the cell contains a dash (-).

Region or environment	Plant species	Geomorphological and bathymetric characteristics	Water depth	Reference
US Pacific Coast	seagrass (*Phyllospadix* sp.)	Exposed, rocky coastlines (attaches to rocks)	Subtidal and intertidal	Short et al. (2007) Wyllie-Echeverria and Ackerman (2003)
US Pacific North West	seagrass (*Zostera* sp.)	estuaries and bays, soft-bottom, intertidal and subtidal	Subtidal and intertidal	Wyllie-Echeverria and Ackerman (2003)
AK Coast, south of arctic circle (largest population: Izembek Lagoon, AK)	eelgrass (*Z. marina*)	Coastal lagoons and bays, found under sea ice sometimes	~1.3 m water depth	McRoy, 1969 Short et al. (2007) Wyllie-Echeverria and Ackermann (2003)
Puget Sound, WA	eelgrass (*Z. marina*)	Adjacent to rocky islands, within embayments, offshore of pocket beaches, all within sound	Intertidal and shallow sub-tidal, +1 to −8.8 m mean low low water	Dowty et al. (2005) Berry et al. (2003)
Yaquina Bay, OR	eelgrass (*Z. marina*)	Estuaries and enclosed bays	0 to +2.3 m (mean low low water to high tide mark)	Shafer et al. (2016)
WA, OR, CA	dwarf eelgrass (*Z. Japonica*, introduced)	Estuaries and enclosed bays	0 to +2.3 m mean low low water	Short et al. (2007) Shafer et al. (2016)
US Pacific Coast Continental Shelf	eelgrass (*Z. marina*)	Shallow continental shelf waters	—	Wyllie-Echeverria and Ackerman (2003)
Areas with coverage smaller than 5 km^2: Netarts Bay, OR; Yaquina Bay, OR; Tillamook Bay, OR; Coos Bay, OR; Tomales Bay, CA; San Francisco Bay, CA; San Diego Bay, CA	eelgrass (*Z. marina*) dwarf eelgrass (*Z. Japonica*, introduced)	Bays and estuaries	—	Wyllie-Echeverria and Ackerman (2003)
Grays Harbor, WA	eelgrass (*Z. marina*)	Bays and estuaries	—	Philips (1984)
Willapa Bay, WA	eelgrass (*Z. marina*) dwarf eelgrass (*Z. Japonica*, introduced)	Bays and estuaries	—	Wyllie-Echeverria and Ackerman (2003)
Humboldt Bay, CA	eelgrass (*Z. marina*)	Bays and estuaries	—	Harding et al. (1975)

3 Physical Processes (Sediment Dynamics)

SAV habitat characteristics and requirements

SAV growth can considerably influence physical processes such as water movement and sediment dynamics in estuarine and marine environments, and, conversely, these dynamics can impact SAV habitat when severe enough (Visser et al. 2015). Madsen et al. (2001) suggest that meadow-forming SAV species (such as *Zostera*, *Halodule*, *Thalassia*, and *Vallisneria*) have a significantly different effect on currents and sediment movement than canopy-forming SAV species (such as *Hydrilla*, *Myriophyllum*). A higher proportion of biomass is distributed near the water-sediment interface in SAV meadows. Meadow-forming SAV is therefore effective at sediment stabilization (Abdelrhman 2003). Alternatively, the biomass of canopy-forming SAV is greatest near the water surface and least at the sediment-water interface, thus allowing more sediment resuspension. Nonetheless, both types of SAV can play an important role in reducing wind-generated sediment resuspension by dampening wave activity and redirecting currents (James, Barko and Butler 2004). To date, limited data are available that quantitatively determine SAV tolerance to various physical processes. The primary physical processes affecting SAV growth include sediment erosion, resuspension, deposition, and subsidence (Madsen et al. 2001).

Factors affecting growth

Sediment erosion and resuspension

Erosion in estuarine and marine environments generally occurs via waves, severe storms, and anthropogenic activities that disturb sediments (Leonardi et al. 2016; Xue et al. 2009). Despite the ability of SAV to reduce sediment erosion, a decrease in SAV bed elevation may be observed depending on the extent to which sediment is eroded. In some circumstances, large swaths of SAV can be removed during severe erosion events, but plants are typically able to quickly repopulate the area if it remains habitable (Carter et al. 2011). New dredging activities typically avoid SAV growth areas, but the original establishment of channels often cut through SAV habitat, permanently reducing habitable area (Carlson and Madley 2007; Pulich and Onuf 2007). Frequent boat traffic can also cause SAV habitat loss via propeller scarring and fishing and crabbing activities that involve dragging gear (Holst et al. 2003; Carlson and Madley, 2007).

Natural erosion patterns typically observed in estuarine and protected marine environments do not adversely affect SAV growth and distribution (Madsen et al. 2001). Some research suggests that a certain amount of local erosion is important for healthy SAV growth, as buried detritus may be removed and resuspended into the water column to maintain carbon-nitrogen balance in sediment (Dauby et al. 1995). Conversely, nutrients also enter the water column via resuspension. Cowan, Pennock, and Boynton (1996) reported that the sediment-water exchange of nutrients can provide up to 80% of phosphorus and nitrogen required by phytoplankton. The resulting growth of phytoplankton increases light attenuation along with the suspended particles. Some reports have attributed SAV dieback to increased turbidity during sediment resuspension events (Chesapeake Bay Program 2012; Orth et al. 2004). Turbidity caused by sediment erosion has been reported to be temporary depending on the settling velocity of the particles, and it will often pass before causing lasting effects (Madsen et al. 2001).

Sediment deposition

Sediment deposition has been shown to have very little effect on SAV under normal, fair-weather conditions (Madsen et al. 2001). Severe storm events can quickly deposit large volumes of sediment, bury SAV, or cover photosynthetically active portions of the plants with settled particles (James, Barko and Butler 2004). Erosion of materials from land and redeposition into the shallow-water zone can smother SAV beds (Beck, Lrucznski, and Sheridan 2007). An example of this includes wash-over deposits, which are devoid of SAV behind some barrier island systems (Eisemann 2016). Sediment accumulation accommodation capacity in SAV beds can be somewhat determined by plant morphology: tall, canopy-forming SAV is not as susceptible to sediment burial as meadow-forming SAV (Koch 2001; Potouroglou et al. 2017). In either case, slow sediment deposition can increase elevation of SAV beds over time. Higher SAV bed elevation may cause a shift in plant distribution, where deeper areas become colonized and diebacks may be observed in shallower, intertidal areas as SAV becomes exposed during low tide. As observed with sediment erosion, sediment deposition is generally part of a natural cycle in which increases in SAV bed elevation can gradually increase exposure to surface currents and waves (Koch 2001). Sediments then eventually erode away because of more intense wave impacts, leading to the subsequent reduction in SAV bed elevation (Madsen et al. 2001). Anthropogenic deposition can also impact SAV beds, as sediments placed during dredging activities are often rapidly deposited and thick enough to smother SAV or prevent it from establishing in an otherwise suitable area (Carlson and Madley 2007).

Subsidence

Coastal subsidence refers to the sum of shallow and deep subsidence that causes the downward displacement of the land (Cahoon, Reed, and Day 1995). Relative sea-level rise along the Texas coast, in part attributed to subsidence from oil, gas, and groundwater removal, is likely the cause of observed SAV loss in specific areas (Pulich and Onuf 2007). Direct data are limited regarding the effects of subsidence on SAV growth and distribution; however, subsidence will increase depths and consequently light attenuation above SAV beds, influencing the habitable zone as it did in Texas.

Tools for assessment

In determining changes in coastal environments, several remote-sensing technologies provide reliable tools for data collection and continuous monitoring. Analytical tools for determining both erosion and deposition include topographic light detection and ranging (LiDAR), bathymetric LiDAR, and orthorectified aerial or satellite imagery. USGS (2017) reports the use of interferometric synthetic aperture radar (InSAR) to measure elevation changes. At present, the InSAR is reportedly the most effective means of measuring changes in large-scale land surface altitude, as high-density measurements over large areas are made by using radar signals from Earth-orbiting satellites (USGS 2017). LiDAR, particularly airborne LiDAR bathymetry (ALB), is an efficient, high-resolution, laser-based tool to monitor geomorphology in coastal environments (Long et al. 2010).

Published relationships

Water movement, the presence of SAV, and sediment dynamics are all strongly correlated in coastal systems, as each factor is contingent on the other. The number of available studies quantitatively correlating the theoretical relationships are limited, however. Koch and Gust (1999) noted tide-dominated environments where SAV blades and stands exhibit a unidirectional lean, directing friction velocities of the moving water above the SAV canopy, ultimately reducing current velocity within the SAV bed. Environments dominated by waves, however, tended to show an increase in potential sediment erosion in SAV beds as the constant changing of blade directions allowed for greater interactions between the SAV bed and the water column (Madsen et al. 2001).

4 Sedimentology

SAV habitat characteristics and requirements

Sediment characteristics in aquatic environments play a critical role in the biogeochemical cycling of inorganic and organic matter (Griffiths et al. 2017), greatly contributing to the overall health of SAV. As discussed in section 2, the presence of SAV can also affect sediment dynamics and consequently the sedimentology within the system it inhabits (Tinoco et al. 2017). The complexity of substrate properties relative to SAV growth and distribution is generally site- and species-specific and is therefore difficult to generalize. Several studies have investigated SAV growth and distribution in sediment of various characteristics to determine threshold limits and optimal growth parameters for healthy SAV environments (Boer 2007; Czerny and Dunton 1995; Duerte et al. 2007). The primary sedimentology factors affecting SAV growth and distribution in estuarine and marine sediments include grain size, organic matter content, pore-water nutrients, and sulfides.

Factors affecting growth

Grain size

Sediment grain size is an important characteristic that directly affects the physical, as well as chemical and biological, properties of the substrate (Barth 2011). Observations from previous studies demonstrate that the primary impact of sediment grain size on SAV growth is related to the plant's ability to establish roots securely into substrate (Ailstock, Shafer, and Magoun 2010; Handley and Davy 2002). Li et al. (2012) analyzed the relationship between SAV growth and particle size distribution and found that smaller grain size sediments encouraged faster growth and development, while SAV growth in a coarse sand and gravel media led to uprooting and dislodgement of the plant. These findings are consistent with those from Koch and Beer (1996) and Denny (1980), in which the primary relationship between substrate particle size and SAV growth was the ability of the roots to penetrate and remain anchored in the sediment. Koch (2001) simulated sediment grain sizes using various sizes of glass beads, in which *Ruppia maritima* was found to exhibit maximum growth in fine to medium-coarse media. Most SAV species have been reported to grow in a wide range of substrates, from coarse sand to mud (Anderson 1972).

SAV growth can also be affected by the geochemical processes that occur in sediment of certain grain sizes (Koch 2001). The presence of fine-grained material (silt, clay) in sediment influences pore-water geochemistry, ultimately affecting nutrient availability. As clay and silt become dominant relative to sand, the pore-water exchange at the sediment-water interface decreases, because sediment pores are considerably smaller and have less connectivity (Huettel, Berg, and Kostka 2014). Koch (2001) concluded that reductions in pore water and pore-water exchange increases nutrient concentrations and phytotoxins (phenols, organic acids, hydrogen sulfide, or reduced iron and manganese) in high-salinity sediments. SAV is sustained in sediment with low pore-water exchange in oligohaline or mesohaline environments, since phytotoxin concentrations are not as elevated as those found in high-salinity systems (Capone and Kiene 1988). Conversely, pore-water exchange in coarse sediments is much higher than in finer sediment, and thus nutrient availability is reduced (Huettel, Berg, and Kostka 2014). A coarse-sediment substrate will remain more oxygenated, and phytotoxins are reduced as a result of the increased exchange of solutes through advective porewater seepage, providing an advantageous environment for SAV growth in high-salinity environments (Koch 2001). The effect of sediment grain size on SAV growth in both marine and estuarine environments have been shown to be species specific; however, different species vary in their response to substrate conditions (Batiuk et al. 1992; Leschen, Ford, and Evans 2010; Dunton 1990). Table 2 lists the published sediment grain sizes colonized by healthy SAV in either natural or simulated marine and estuarine environments.

Table 2. Sediment grain sizes colonized by healthy SAV in natural and simulated estuarine and marine environments as reported in literature.

Environment	Species	Fines (%)	Reference
Freshwater to estuarine	*Vallisneria americana*	6.0–10.0	Batiuk et al. (1992)
		14.0 (clay)	Hutchinson (1975)
		48.0 (silt)	Hutchinson (1975)
Estuarine	*Ruppia maritima*	1.8–9.2	Livingston et al. (1998)
		11.0–14.0	Dunton (1990)
Estuarine to marine	*Halodule wrightii*	1.8–9.2	Livingston et al. (1998)
		14.0	Dunton (1994)
		8.1–28.8	Dunton (1990)
		10.2–12.4	Murphey and Fonseca (1995)
		0.8–14.7	Hoskin (1983)

Environment	Species	Fines (%)	Reference
			Grady (1981)
Marine	*Syringodium filiforme*	1.8–9.2	Livingston et al. (1998)
		7.3–9.9	Hoskin (1983)
		1.9	Wood et al. (1969)
	Thalassia testudinum	22.0	Lee and Dunton (1996)
		23.0–35.0	Kaldy and Dunton (2000)
		4.8	Wood et al. (1969)
		14.6	Scoffin (1970)
		2.2–17.1	Koch (2001)
		1.0–34.0	Burrell and Schubel (1977)
		12.2–34.1	Hoskin (1983)
		0.8–14.7	Grady (1981)
	Zostera marina	35.0	Leschen et al. (2010)
		2.3–56.3	Koch (2001)
		13.0	Krause-Jansen et al. (2011)
		14.0	Marshall and Lukas (1970)
		15.0	Orth (1977)

Organic matter

Sediment organic matter content is typically defined as the percentage by mass of organic material (nonlithological) composing sediment. The accumulation of organic matter in SAV beds is primarily attributed to the burial of decaying rhizomes and roots or the trapping of decaying plant shoots or leaves over time (Brenner et al. 2006). In a range of salinity environments, numerous studies have reported that optimal SAV growth occurs in substrates with <5% organics (Murphey and Fonseca 1995; Dan et al. 1998; Moore, Shields, and Jarvis 2010). The mechanism by which SAV growth is affected by sediments with high organic matter content is not thoroughly understood, but it is suggested to be associated with nutrient bioavailability (Koch 2001). As nutrients become associated with organic deposits, its bioavailability is reduced, particularly in fine-grained substrates (Pollman et al. 2017). A small number of SAV species, including *Zostera marina* and *Posidonia oceanica*, were reported to grow in substrates containing between 6.5% and 16.4% organic matter (Koch 2001). It is noteworthy, however, that SAV species tolerant of high organic matter content exhibited a positive correlation between leaf size and percentage of organic matter. Lee and Dunton (2000) concluded that the increased photosynthetic activity due to the larger leaf surface area produces more oxygen in the rhizosphere that, in turn, neutralizes detrimental effects associated with organic carbon content. Although the organic matter threshold of <5% has been concluded as a safe limit for most SAV species in high-salinity environments (Barko and Smart 1983), tolerance of organic matter content is species and site specific. Table 3 summarizes the range of organic matter content in sediment colonized by healthy SAV species as reported from previous studies.

Table 3. Sediment organic matter (%) ranges in healthy SAV beds presented in previous studies.

Environment	Species	Organic matter (%)	Reference
Freshwater to estuarine	*Vallisneria americana*	2.0–8.0	Moore et al. (2010)
		0.3–5.56	Kreiling et al. (2007)
		1.0–5.3	Batiuk et al. (1992)
		<6.5	Hutchinson (1975)
Estuarine	*Ruppia maritima*	<2	Ward et al. (1984)
		3.25	Kemp et al. (1984)
Estuarine to marine	*Halodule Wrightii*	0.77–3.62	Murphey and Fonseca (1995)
Marine	*Syringodium filiforme*	2.5	Wood et al. (1969)
	Thalassia testudinum	0.5–2.3	Koch (2001)
		3.5–4.9	Wood et al. (1969)
	Zostera marina	0.77–3.62	Murphey and Fonseca (1995)
		1.25	Marshall and Lukas (1970)
		1.25	Orth (1977)
		0.41–1.38	Dan et al. (1998)
		0.4–5.3	Koch (2001)
		6.37–7.57	Short et al. (1993)

Nutrients

In estuarine and marine aquatic environments, several studies show that limited nutrients in sediment do not prevent SAV from colonizing certain areas (Koch 2001; Boer 2007; Bintz et al. 2003). Nonetheless, nutrients can be a limiting factor in optimal SAV growth. Although SAV can take up nutrients from the water column, most nutrients are absorbed from the substrate (Gu and Hoyer 2005; Shivers 2010). Nutrient availability is generally correlated with sulfide production in the substrate (Lamers et al. 2013). In the presence of sulfide, the stable metal-sulfide precipitants formed with plant micronutrients prevent uptake by the roots in reducing environments. Metals such as copper, zinc, cadmium, and nickel form stable, typically insoluble sulfide compounds, whereas sodium and potassium form weakly stable, typically insoluble compounds (Wright and Reddy 2009). At present, limited information is available regarding optimal nutrient concentrations in healthy SAV beds in estuarine and marine environments.

Sulfides

Sulfides in aquatic environments are produced by "sulfate-reducing bacteria during organic carbon oxidation and nutrient mineralization" (Pollard and Moriarty 1991, 11). The microbial population of marine systems function similarly to those of freshwater environments in organic carbon degradation and nutrient regeneration. However, "distinct physiological groups of bacteria dominate carbon catabolism in each system" (Capone and Kiene 1988, 725). High sulfate concentrations present in seawater cause sulfate reduction to exceed methoanogenesis, which increases as salinity decreases (Capone and Kiene 1988). Although the activity of sulfate-reducing bacteria stimulates plant growth as nutrients are mineralized, the concurrent uptake of sulfide by the plants can be detrimental (Pollman et al. 2017). The biogeochemical factors that determine sediment sulfide levels are iron, organic matter, and oxygen (Pollman et al. 2017).

Sulfide toxicity to SAV can be increased under eutrophic conditions. As phytoplankton population increases and light availability is reduced, photosynthesis rates are lowered, which leads to reduced oxygen production in the rhizosphere. Oxygen produced by macrophyte roots can inhibit activity of sulfate-reducing bacteria, allowing SAV to thrive in saline sediments or prevent restricted plant growth. Oxygen released by SAV roots can also directly oxidize sulfides, limiting their toxic effects (Lee 1999; Pezeshki and DeLaune 2012). Additionally, iron in the sediment can sufficiently sequester dissolved sulfides to form precipitates (Lamers et al. 2013).

Sediment sulfide thresholds under varying light conditions are presumably different among SAV species. Previous studies report adverse effects on photosynthesis and growth upon exposure to sulfide at concentrations between 1000–2000 µM (Carlson, Yarbro, and Barber 1994). Eldridge and Morse (2000) suggest that sulfide in marine sediments may be toxic to SAV at concentrations above 1000 µM. Table 4 summarizes the reported effects of sulfide on various SAV species. As observed from the data presented, sulfide toxicity to SAV may be largely contingent on (1) plant biomass, which governs oxygen production in the rhizosphere; (2) water clarity, which determines the photosynthesis rate; (3) sediment organic matter content, and (4) salinity. Sufficient data regarding sulfide threshold limits in sediments providing toxicity results of various SAV species in estuarine and marine sediments are yet to be published.

Table 4. Sediment sulfide concentrations (µM) tolerated by healthy SAV.

Environment	Species	Sulfide concentration (µM)	SAV condition	Reference
Marine	*Thalassia testudinum*	Up to 1000 to 2000	Healthy to dying	Lee and Dunton (2000) Carlson et al. (1994) Eldridge and Morse (2000) Carlson et al. (1994)
	Zostera marina	400 to 2000	Reduced photosynthesis to root degeneration	Smith et al. (1998) Pregnall et al. (1984)

Tools for assessment

Sampling and analytical approaches for sediment characterization may vary depending on analysis type and data acquisition time. In some instances, field sampling and on-site data collection may be required for monitoring purposes, whereas total characterization of a particular site may require more in-depth laboratory testing. Thus, analytical tools to measure sediment grain size, organic matter content, nutrients, and sulfides for both laboratory and field use will be discussed.

Sediment Grain Size

When determining sediment grain size, particle-size analysis and bulk density measurements are important to obtain not only to separate particle sizes but also to estimate sand, silt, and clay volumes. Laser diffraction analysis of the substrate can further differentiate and measure silts and clays with a great degree of reproducibility on small samples (Zobeck 2004).

Organic Matter Content

For organic matter measurements, analytical instruments, measuring total carbon (TC), total inorganic carbon (TIC), and total organic carbon (TOC) are highly reliable sources of organic carbon determination in sediments.

Nutrients

Two primary sample types can be assessed to characterize potential nutrient availability in sediments: pore waters and sediment mineralogy. Micronutrients and other metals in pore waters can be analyzed using inductively coupled plasma mass spectrometry (ICP-MS) and optical or atomic emission spectroscopy (O/AES). Total nitrogen can be determined on-site using a portable near infrared spectroscopic meter.

Sulfides

Acid volatile sulfides (AVS) can be measured using a colorimetric method after sulfide is volatilized after the addition of acid and converted to a gas at room temperature. Hydrogen sulfide is purged from the sample using an inert gas and trapped in a sodium hydroxide solution, which is then analyzed via colorimetry with a mixed-diamine reagent (MDR). The sulfide binds to the reagent-forming methylene blue, which is measured using a spectrometer. In many cases, AVS and simultaneously extracted metals (SEM) are performed together in marine sediments to characterize the formation of AVS-SEM metal toxicants. The redox potential, related to the state of sulfides in the pore water, can be measured using an electrode instrument.

Published relationships

Several studies demonstrated correlations between sedimentological characteristics (organic matter, salinity, sulfide generation, and sediment grain size) and SAV growth (Koch 2001; Cammen 1982; Marchand et al. 2006). As salinity increases from mesohaline to euhaline environments, sulfate levels are elevated, increasing the potential for sulfide conversion within the sediment. Sulfide generation is strongly correlated to organic matter, since the magnitude and distribution of various microbial activities is determined by the amount of organic material present in the substrate (Rui et al. 2016). Organic matter in the sediment becomes a food source for the bacteria, which increases respiratory activity and the reduction of sulfate. Moreover, sulfide levels in sediment can also be correlated with grain size. It is important to note that the extent to which sulfide penetrates the sediment from the water is based on the grain size of the substrate (Huettel and Webster 2001). When sulfate levels in the overlying water column are low, sediment sulfide concentrations are low as well. When sulfate concentrations in the water column are high, however, sediment sulfide content can vary from high to low depending on the sediment grain size (Pollman et al. 2017).

5 Water Quality

Water quality is critical for SAV health, and poor water quality is hypothesized to be the major cause for the loss of seagrasses around the world (Beck, Lruczynski, and Sheridan 2007; Lee, Parks, and Kim 2007). While reduced light availability is typically the main factor causing reductions in SAV abundance, increases in water temperature and carbon dioxide concentration, both attributed to poor water quality, seem to also have negative impacts on SAV survival.

Factors affecting growth

Light availability

Light availability for photosynthesis is the main driver for seagrass SAV survival (Orth and Moore 1983; Cambridge et al. 1986). Seagrass health is considered an indicator for light availability and water clarity in an area. Water clarity is an important water-quality characteristic that determines the distribution of all SAV, as it directly affects the light availability to the aquatic ecosystem. Seagrass SAV distribution is limited by the amount of light that reaches the bottom of the water column (Dennison et al. 1993). Water clarity requirements of seagrasses have been identified in previous studies detailing the minimum light requirements needed to support seagrass growth in a range of salinity zones (Dennison et al. 1993, Steward et al. 2005; Burd and Dunton 2001). The combination of increased freshwater runoff and nutrient input reduces light availability, which hinders SAV growth. Lefcheck et al. (2018) found a strong correlation between reduced nutrient input and increasing SAV coverage in the Chesapeake Bay, Virginia.

Because light availability controls the depths at which SAV can grow, as addressed in section 1, researchers have developed relationships on how deep an SAV species can grow on the basis of light attenuation (Duarte 1991, Duarte et al. 2007). In accordance with the Beer-Lambert Law, the light extinction coefficient or attenuation factor of light through water is described by the equation

$$I_d = I_o e^{-K_z D}, \tag{1}$$

where I_d is light intensity at depth, I_o is light intensity at the surface, *e* is the natural base log, K_z is the light extinction coefficient, and *D* is depth of the light intensity measurement in meters. Light intensity is measured by Watts per square meter. By including light intensity at the depth and the surface, the above equation can be solved for the light extinction coefficient

$$K_z = \left(\ln I_o - \ln I_d\right) * D^{-1}. \qquad (2)$$

After K_z is calculated, *ln* is the natural log, and the light intensity required (I_r) to photosynthesize for any given seagrass species in various K_z environments can be determined with the equation

$$D = \left(\ln I_o - \ln I_r\right) * K_z^{-1}. \qquad (3)$$

Photocells are required to measure light intensity, but are expensive and rarely available to most researchers. Secchi depth (S_d) measurements are more commonly used to measure light intensity (Duarte et al. 2007). S_d can be accurately converted to K_z (Poole and Atkins 1929; Graham 1966; Idso and Gilbert 1974; Duarte 1991) using the equation

$$K_z = \frac{1.7}{S_d}. \qquad (4)$$

By using published relationships between S_d or K_z with known depth of seagrass colonization (Z_c), the depth a species of seagrass can grow according to water clarity can be determined (Duarte 1991; Nielsen et al. 2002; Duarte et al. 2007) (Table 5). Duarte (1991) and Duarte et al. (2007) described the negative relationship between the depth of colonization of a seagrass species (Z_c) and the light extinction coefficient (K_z). Using data from 424 published reports describing K_z and Z_c, Duarte et al. (2007) found a very strong ($r^2 = 0.61$, $p < 0.001$) negative relationship between K_z and Z_c. The negative linear relationship using all the published data reported by Duarte et al. (2007) is

$$\log Z_c\left(m\right) = 0.07\left(\pm 0.019\right) - 1.03\left(\pm 0.04\right) K_z\left(m^{-1}\right). \qquad (5)$$

There was considerable variation in the Z_c for the same species in different geographic areas (Table 5), which is explained by water turbidity (Duarte et al. 2007). Regions with lower light extinction coefficient values had deeper known depths of colonization.

Another way of describing the depth limits of seagrass growth and colonization in relation to water clarity is through examination of the percentage of surface light that reaches the bottom. Percent light through the water (PLW) is the amount of surface light that reaches the depth where seagrasses grow. The PLW is expressed as

$$PLW = e^{[(-K_e)(D_e)]} \times 100, \tag{6}$$

where K_z and D again are the light extinction coefficient and depth of the light measurement in meters, respectively. PLW is only one aspect of the light available for a seagrass to photosynthesize.

Another major aspect that can affect light availability is the presence of epiphytic algae growing on the blades or leaves of the seagrass. Percent light at the leaf (PLL) is the amount of light available for the plant to use for photosynthesis. PLL is expressed as

$$PLL = \left(PLW\right)\left(e^{[(-K_e)(B_e)]}\right) \times 100, \tag{7}$$

where B_e is epiphyte coverage of the leaf and K_e is the biomass-specific epiphytic light attenuation coefficient (Twilley et al. 1985; Vermaat and de Bruyne 1993; Kemp, Bartleson, and Murray 2000). The required percentage of surface light that reaches the leaf blade for survival and growth varies not only between species but also for the same species in different regions (Lee, Park, and Kim 2007) (Table 6). In addition, surface light requirements vary with species-specific salinity requirements. For example, in the Chesapeake Bay, Carter, Rybicki, and N. Landwehr (2000) found that most freshwater SAV species require 13% surface light, while Kemp et al. (2004) stated that species in brackish water require 22% surface light.

In clear waters like those of the Mediterranean Sea, the seagrass *Halophila stipulacea* is able to grow at depths of 145 m (Short et al. 2007). There are very few instances where seagrasses inhabit areas deeper than 2 m in the continental United States. The historical distribution of most seagrasses in the continental United States is usually confined to depths less than 5 m (Short et al. 2007). In areas of clear water along the US coast, like Big Bend and the Florida Keys, seagrasses grow at depths of 20 m (Iverson and Bittaker 1986; Mattson et al. 2007). Discussion of specific colonization depths and other bathymetric topics are covered in section 1.

Turbidity and Total Suspended Solids

Numerous factors affect light attenuation. Two factors commonly associated with light attenuation are turbidity and total suspended solids (TSS). Many people use the terms turbidity and TSS interchangeably, which is incorrect. TSS are particles bigger than 2 µm suspended in a fluid that tend to settle out of suspension if left undisturbed by external forces. External forces that suspend sediments are water currents, wave energy, bioturbation, or anthropogenic mechanical forces such as from a dredge or propeller. Common particles that contribute to TSS are gravel, sand, silt, and large species of algae. TSS is typically measured by pouring a known amount of water sample through filter paper, usually a 2 µm filter, and weighing what is captured. The typical unit for TSS is mg/L. Turbidity, however, is the clarity of a liquid. Turbidity is typically expressed in nephelometric turbidity units (NTU), which is actually a qualitative value and not a quantitative one like TSS. While TSS plays a major factor, turbidity is also affected by colored dissolved organic material, inorganic compounds, clay, small algae, salt, and any other compounds that dissolve in water. TSS is usually considered the main cause of turbidity; however, water stained by tannins from leaves will have a very high NTU reading but be completely void of TSS. Turbidity is measured by the amount of light scattered at right angles when a light is shined into a fluid and therefore takes into account compounds that are dissolved in the water. As NTU increases, the fluid is considered cloudier and has higher light attenuation. Legal standards for drinking water in the United States is <1.0 NTU, and anything >50 NTU is completely opaque.

Nutrients

As discussed in section 3, SAV requires a certain amount of nutrients in the environment to thrive and takes up most from its substrate. SAV can thrive in relatively nutrient-poor environments, and nutrient overloading is a more common issue faced in the coastal environment (Koch 2001). Excess nutrient runoff from land into the water can cause major negative impacts on SAV survival throughout the world (Orth and Moore 1983; Cambridge et al. 1986; Pulich and White 1991; Duarte et al. 2007; Lee et al. 2007; Short et al. 2007). Duarte (2002) listed light attenuation caused by eutrophication as the leading cause in declines of most coastal seagrass communities. Nutrient loading is specifically listed as a major threat to seagrass communities in the Gulf of Mexico (Beck, Lruczynski and Sheridan 2007), Chesapeake Bay (Chesapeake Bay Foundation 2000), and Long Island Sound (LISHRI 2015). Excess nutrients in the water, particularly phosphorus and nitrogen, can cause the overgrowth of phytoplankton. High concentrations of phytoplankton in the water column increase light attenuation, reducing light availability to SAV as previously discussed. The negative effects of increased nutrients can be exacerbated by additional epiphytic algae growth on blades or leaves, which further reduces light available for seagrasses to photosynthesize.

Salinity

Coastal and marine SAV can tolerate various levels of salinity, but typically prefer concentrations between 25 and 40 parts per thousand (ppt) (Eleuterius 1987; Koch et al. 2006a; Touchette 2007; Merino, Carter and Merino 2009; Collier et al. 2014) (Table 8). There are a number of freshwater SAV species, but the focus of this report is marine and coastal SAV, dominated by seagrasses. Seagrasses can exist in low-salinity environments but are usually outcompeted by species intolerant of hypersaline water (Touchette 2007). Marine seagrass physiology has evolved to handle the hyperionic and hyperosmotic stress of a saltwater environment (Mahajan and Tuteja 2005). Seagrasses create hyperosmotic fluid along their outer cell walls to stop desiccation with salt-secreting glands to remove salt from their tissue (Liphschitz and Waisel 1974) and by ion transport (Flowers, Troke and Yeo 1977).

Seagrasses can survive episodes outside of their optimal salinity concentrations, but chronic hyper- or hyposalinity events can cause seagrass die-offs. Hypersalinity events are very rare compared to hyposalinity events. Hypersalinity usually occurs in enclosed bays that are starved of freshwater inputs because of use for municipal purposes (Fourquean and Robblee 1999). Hyposalinity episodes in coastal areas are typically caused by natural freshwater runoff from storm events or can be anthropogenically triggered by the use of flood-control structures (for example, Bonnet Carre Spillway, Louisiana) (Moncreiff 2007). Hyposalinity episodes are considered the biggest threat to the survival of

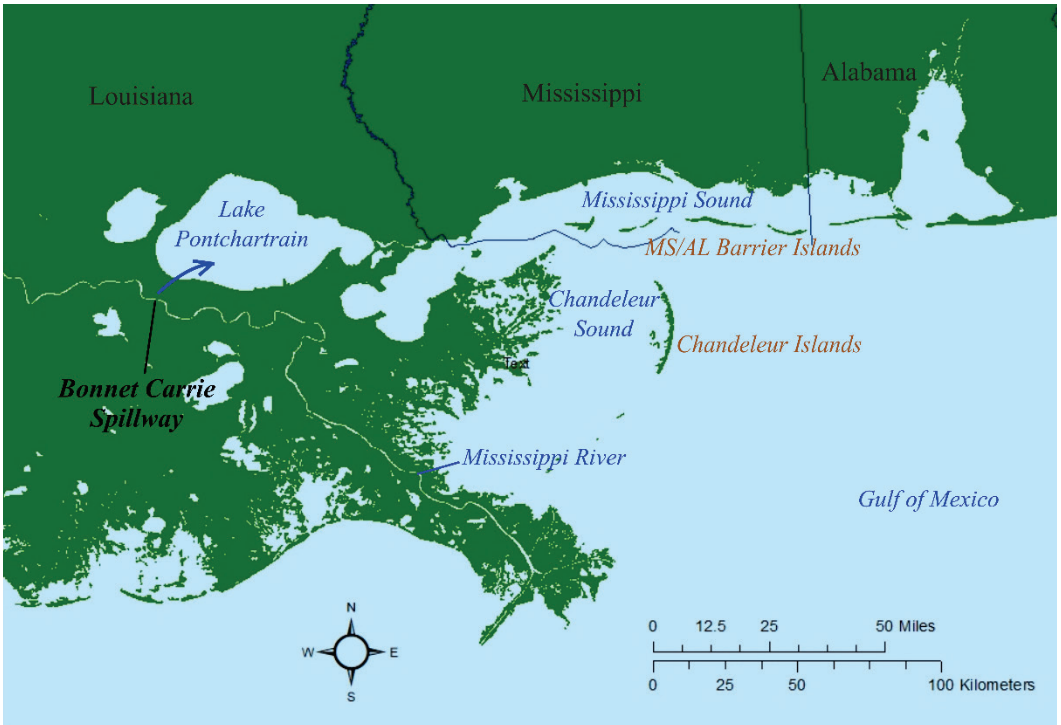
Halophila johnsonii (Torquemada, Durako and Lizaso 2005; Kahn and Durako 2008), which is the only marine plant protected under the endangered species act (Kenworthy 1997). Hyposalinity is thought to cause seagrass die-offs around the world (Eleuterius 1987; Furnas 2003; Lirman and Cropper 2003; Collier et al. 2014). Kahn and Durako (2006) found that the seedling tolerance to changes in salinity concentrations are less than those for mature plants. Seagrass species vary in their abilities to survive fluctuating salinities. In a mesocosm study using seagrass from Biscayne Bay, Florida, Lirman and Cropper (2003) found that *Thalassia testudiumn* and *Syringodium filiforme* survived but struggled when salinities dropped below 25 ppt, while *Halodule wrightii* flourished in salinities as low as 5 ppt. The increased tolerance to hyposalinity of *Halodule wrightii* may explain why it seems to be dominating areas with highly modified watersheds that experience more pulsed freshwater input. Species-specific salinity tolerance is often presented with salinity threshold values, but salinity tolerance is complex and also depends on the duration and intensity of salinity fluctuations.

Salinity case study: Mississippi Sound

Salinity levels in the Mississippi Sound fluctuate due to storm events that cause freshwater runoff (Eleuterius 1987). In the Mississippi Sound, Eleuterius and Miller (1976) reported that rainfall hindered seagrass growth and that seagrass growth was best during drought years. Prior to 1987 there were four species of seagrasses in Mississippi Sound: *T. testudinum, S. filiforme, Halophila engelmannii*, and *Halodule wrightii*. Currently *Halodule wrightii* and *R. maritima* are the only seagrasses inhabiting the Mississippi Sound. The shift to a monotypic seagrass occurred by 1987 and is likely due to decreased salinities in Mississippi Sound because of the major modifications to the Mississippi River. Of the four species that occurred, *Halodule wrightii*, was the most tolerant to low-salinity environments (McMillan and Moseley 1967; McMahan 1968). *R. maritima*, a brackish water plant that can handle salinity of 0 ppt (Touchette 2007; Merino, Carter, and Merino 2009), started to expand into the Mississippi Sound when distribution of other seagrasses declined.

The opening of the Bonnet Carrie spillway, a flood-control structure in southern Louisiana that empties Mississippi River water into the coastal zone, likely has numerous cascading effects on the seagrasses of Mississippi Sound (Figure 2). Between its construction in 1931 and 2020, the spillway has been opened 15 times, ranging in duration from 13 to 79 days (mean 40.6 days) to alleviate pressure on levees in New Orleans, Louisiana (USACE 2014c; USACE 2020). The spillway was opened three times in the 1970s, with the most notable release occurring in 1973, when the spillway was open for 75 days. In 1973, the water north of Petit Bois and Horn Island was fresh for over three months (Eleuterius 1987). Seagrasses in the Mississippi Sound flowered in April–June, coinciding with the releases of the spillway. Seagrasses flower for only a short period of time, and prolonged exposure to fresh water can cause flower failure or severe reductions in bloom time (Torquemada and Lizaso 2011; Collier et al. 2014). It is possible that these three releases through the spillway were the main driver for the decline in three species of seagrasses that no longer occur in Mississippi Sound (Eleuterius 1987).

Figure 2. The location of the Bonnet Carrie Spillway in relation to the Mississippi Sound and other coastal water bodies. The direction of water movement from the Mississippi River into Lake Pontchartrain is indicated with a blue arrow (northeast). From there, water makes its way towards the coastal sounds and the Gulf of Mexico.



Temperature

Similar to terrestrial vegetation species, temperate to subtropical SAV productivity tends to vary seasonally, with high productivity in the spring and summer and low productivity during the winter and fall (Dunton 1994; Lee, Park and Kim 2005). An overview by Lee, Park, and Kim (2007) documents that the optimal temperature range for photosynthesis is 12°C–

26°C for temperate species and 23°C–32°C for tropical species (Table 9). It is hard to isolate the effects of temperature and light regime on seagrass growth, since both are important factors (Lee and Dunton 1996; Lee, Park and Kim 2007).

As the global climate changes, ocean water temperature changes may impact coastal SAV. Ocean water temperatures are hypothesized to increase between 2.6°C and 4.2°C by 2100 (Collins et al. 2013). Water temperature is a primary driver of seagrass growth and life history (Lee, Park and Kim 2007), so elevating water temperatures are a concern for seagrass survival. Coastal SAV evolved when global water temperatures and carbon dioxide concentrations were higher (Beer and Koch 1996) relative to current levels, so some suggest climate change may help seagrasses (Orth et al. 2006). This conclusion is not a widely accepted opinion, however.

Duarte (2002) suggested that increasing water temperatures would have negative impacts on seagrass survival. Numerous studies followed to corroborate that suggestion. Carlson and Madley (2007) stated that warm-water discharge from power plants resulted in losses of seagrass in Biscayne Bay and St. Joseph Sound, Florida. A mesocosm study by Bintz et al. (2003) and a field study by Oviatt (2004) both suggested increasing summer water temperatures are a major driving factor for reduced *Z. marina* abundance in the northeast United States. The trend of reduced *Z. marina* abundance because of increasing water temperatures was also noted in several European countries (Rasmussen 1977). *Z. muelleri* experienced increased leaf loss and shoot mortality when exposed to water temperature 5°C above its optimal growth temperature of 27°C (York et al. 2013). A strong correlation between flowering events associated with temperature stress, reduced vertical rhizome growth, and increased shoot mortality of *P. oceanica* meadows have been documented (Marba and Duarte 2010). These events have increased with warming in the Mediterranean Sea despite pristine environments void of problems from light attenuation (Marba and Duarte 1997; Diaz-Almela et al. 2006; Marba and Duarte 2010).

Carbon dioxide concentration

The drastic increase in fossil fuel use during the industrial revolution has led to an increase in atmospheric carbon dioxide by ~40%, and possibly 300% by 2100 (Portner et al. 2014). The increase in atmospheric carbon dioxide is causing the ocean pH to decrease (that is, become more acidic), affecting biochemical processes (Fabry et al. 2008). Seagrasses are photoautotrophs, and it is suggested that increases in partial pressure of carbon dioxide (pCO_2) in the aquatic environment will increase photosynthetic rates of marine autotrophs (Mackey et al. 2015). Zimmerman et al. (1995, 1997) and Palacios and Zimmerman (2007) conducted 45 d and 1 y laboratory studies looking at the effects of elevated aqueous carbon dioxide concentration on *Z. marina*. Both studies showed that elevated carbon dioxide levels increase leaf photosynthetic rates, shoot density, leaf size, and leaf sugar content while decreasing light requirements to conduct the previously described processes. These studies go on to say that very low aqueous carbon dioxide concentrations may be a limiting factor to the growth of seagrass. Researchers suggest that direct injection of carbon dioxide into the ground of seagrass areas may be a useful technique for sequestering carbon dioxide (Mackey et al. 2015). A review by Koch et al. (2013) reported that over 85% of seagrasses use a C_3 pathway for photosynthesis,[2] and an increase aqueous pCO_2 will increase seagrass growth. However, Koch et al. (2013) stated the need to look at the response of elevated carbon dioxide along with increasing water temperatures. A study that looked at the combined effects of elevated carbon dioxide and water temperature at the time of this report was conducted by Repolho et al. (2017) on *Z. noltii*. When examining the combined effects, *Z. noltii* showed no signs of increased growth, and the combination had a net deleterious effect on growth and survival. This study suggests the increase in growth typically seen in seagrass due to increases in carbon dioxide availability is negated by elevated water temperatures, and the global trend may reflect the same.

Tools for assessment

TSS and turbidity

TSS can be measured by pouring a known volume of water through preweighed filter paper and then weighing the filter paper to determine the weight of suspended solids in the water. New sonde technology allows TSS to be measured in the field. A number of instruments, like the YSI IQ Sensor Net ViSolid Probe and the laser in situ scattering transmissometer

---

[2] For a full list of the spelled-out forms of the chemical elements used in this document, please refer to *US Government Publishing Office Style Manual*, 31st ed. (Washington, DC: US Government Publishing Office, 2016), 265, https://www.govinfo.gov/content/pkg/GPO-STYLEMANUAL-2016/pdf/GPO-STYLEMANUAL-2016.pdf.

(LISST) use optics and reflected light to determine the amount of suspended solids in the water sample. Turbidity can simply be measured using a Secchi disk. As the black and white disk is lowered, the depth at which the disk is no longer visible is recorded; this is known as the Secchi depth. Turbidity can also be measured with sondes that determine the amount of light refracted at right angles from a light source. Several probes are made that can measure turbidity in a liquid. By coupling turbidity measurements with sediment grab samples in the field, TSS can be determined without any additional sensors if it is assumed that the suspended material has similar characteristics as the sediment. Newly developed techniques calculate turbidity parameters from aerial photography or satellite imagery (Matthews 2011; Dogliotti et al. 2015).

Photosynthetically active radiation

Several companies have sondes with photo sensors to measure the amount of light energy of a particular wavelength reaching a certain depth of water. The most commonly used photo sensor is the LI-192 Underwater Quantum Sensor by LI-COR.

Published relationships

The relationship between environmental factors and seagrass productivity is critical for seagrass conservation and management. Seagrass growth dynamics relative to environmental factors vary among species because of unique physiological and morphological adaptations (Lee, Park and Kim 2007). Correlations between optimal seagrass growth and abiotic environmental factors (including light penetration, nutrients, salinity, and temperature) are presented in Tables 5–9.

Table 5. The colonization depth (Z_c) in meters of some seagrasses found in North America. *N* is the number of published relationships for each species used to determine Z_c information. Modified from Duarte 1991 and Duarte et al. 2007. *Introduced to the West Coast of the United States.

Region	Species	N	Mean Z_c	Standard error	Minimum depth	Maximum depth
Temperate	*Ruppia maritima*	2	0.9	—	0.8	1.0
	*Zostera japonica**	1	0.9	—	0.9	0.9
	Z. marina	386	3.3	0.1	0.5	10.0
	Halodule wrightii	6	1.8	0.3	1.1	2.7
	Halophilia decipiens	2	26.8	—	24.3	29.3

Region	Species	N	Mean Z_c	Standard error	Minimum depth	Maximum depth
Subtropical to tropical	*Syringodium filiforme*	6	1.8	0.3	1.1	2.7
	Thalassia testudinum	6	1.3	0.1	1.1	1.7

Table 6. Minimal light requirements of seagrass studies conducted in North America. Variation in light requirements likely has to do with photo-acclimation to specific areas. Adapted from Lee, Park and Kim 2007.

Region	Species	Latitude	Minimum light (%)	Reference
Temperate	*Zostera marina*	41° N	12–13	Koch and Beer (1996)
		41° N	19	Dennison et al. (1993)
Subtropical to tropical	*Halophila decipiens*	23° N	9	Dennison et al. (1993)
		17° N	4	Dennison et al. (1993)
	Halophila engelmanni	23° N	24	Dennison et al. (1993)
	Halodule wrightii	27° N	18	Dunton (1994)
		27° N	15–20	Burd and Dunton (2001)
		27° N	24–37	Kenworthy and Fonseca (1996)
		27° N	20	Steward et al. (2005)
		27° N	18	Dunton (1994)
		27° N	20	Czerny and Dunton (1995)
		28° N	18	Dunton (1994)
		25°–30° N	17	Dennison et al. (1993)
	Syringodium filiforme	23° N	19	Dennison et al. (1993)
		25°–30° N	17–18	Dennison et al. (1993)
		27° N	24–37	Kenworthy and Fonseca (1996)
	Thalassia testdinum	18° N	24	Dennison et al. (1993)
		23° N	24	Dennison et al. (1993)
		25° N	13	Fourqurean and Zieman (1991)
		27° N	20	Czerny and Dunton (1995)
		27° N	>14	Lee and Dunton (1997)
		25°–30° N	15	Dennison et al. (1993)

Table 7. Water column nutrient concentrations found in a SAV beds. Bolded numbers are study means. Table adapted from Lee, Park and Kim 2007. A dash signifies parameter was not evaluated (-).

Region	Plant Species	Latitude	Water column (µM)			Reference
			NH^+_4	$NO^-_3 + NO^-_2$	PO^{3-}_4	
Temperate	*Zostera marina*	37° N	3–20	—	0.5–1.6	Moore et al. (1996)
		43° N	3.21–8.26	—	0.50–0.74	Short et al. (1995)
		48° N	1.9	—	—	Williams and Ruckelshaus (1993)
		48° 32’11”N	0.05–1.69	24.3	0.37–2.46	Nelson and Waaland (1997)

Region	Plant Species	Latitude	Water column (µM)			Reference
			NH^+_4	***$NO^-_3 + NO^-_2$***	***PO^{3-}_4***	
Subtropical to tropical	*Halodule wrightii*	24°–25°N	6.8–80.7	—	—	Powell et al. (1989)
		24° N	1.64	2.32	—	Tomasko and Lapointe (1991)
		24°33′-24°51′ N	11.64–53.07 (22.79)	—	0.14-1.27 (0.40)	Lapointe et al. (1994)
		24°–25° N	6.8–80.7	—	—	Powell et al. (1989)
		26° N	0–3.1	0-3.0	—	Kaldy and Dunton (2000)
		26°09′ N	1.22 ±0.08	0.84±0.06	—	Lee and Dunton (1996)
		27°49′ N	1.16 ±0.06	0.84±0.05	—	Lee and Dunton (2000)
		29°8′ N	0.25–1.8	0.02-0.5	0-0.29	Heck et al. (2000)

Table 8. Reported salinity tolerance in parts per thousand (ppt) for survival of selected seagrass species in the United States. Where upper or lower limits are not specified *and up* or *up to* terminology is used. Variation in tolerances likely has to do with the acclimation of a species in a certain area.

Region	Species	Reported salinity tolerance (ppt)	Sources
Temperate	*Ruppia maritima*	0–60	Phillips 1960
		<35–70	Koch et al. 2007
		0–100	Kantrud 1991
		0–35	Strazisar 2013
	Zostera japonica	5 *and up*	Kaldy and Shafer 2012
	Z. marina	6 *and up*	Salo et al. 2014
Subtropical to tropical	*Halophila johnsonii*	8 *and up*	Griffin and Durako 2012
		10 *and up*	Kahn and Durako 2008
		20–40	Torquemada et al. 2005
	Halodule wrightii	0-60	Texas Parks and Wildlife 1999
		Up to 70	Koch et al. 2007
		5–45	Lirman and Cropper 2003
		Up to 72	McMillian and Mosley 1967
		5–80	McMahan 1968
	Syringodium filiforme	4–45	Lirman and Cropper 2003
		Up to 45	McMillan and Mosley 1967
	Thalassia testdinum	5–45	Lirman and Cropper 2003
		20–40	Zieman 1982
		Up to 45	McMillian and Mosley 1967
		36–70	Koch et al. 2007

Table 9. Optimum water temperatures for photosynthesis (p) and growth (g) for seagrasses according to studies conducted in North America. Table adapted from Lee, Park and Kim 2007.

Region	Plant Species	Latitude	Range (°C)	Optimal (°C)	Reference
Temperate	*Phyllospadix torreyi*	34°16′ N	10–23	23 (p)	Drew (1979)
		38°20′ N	12–21	13 (g)	Drysdale and Barbour (1975)
Tropical/ Subtropical	*Ruppia maritima*	37°25′ N	1–28	28 (p)	Wetzel and Penhale (1983)
		37°16′ N	8–30	23 (p)	Evans et al. (1986)
	Zostera marina	37°25′ N	1–28	22 (p)	Wetzel and Penhale (1983)
		37°16′ N	8–30	19 (p)	Evans et al. (1986)
		37° N	0–30	16 (g)	Evans et al. (1996)
		34° N	15–29	22 (p)	Penhale (1977)
		34°16′ N	4–21	21 (p)	Drew (1979)
		40°31′5″ N	0–20	16–20 (p)	Dennison (1987)
		40°31′5″ N	0–35	25–30 (p)	Marsh et al. (1986)
	Halophila decipiens	28°08′44″ N	10–30	30 (p)	Dawes et al. (1989)
	Halophila johnsonii	25°55′ N	15–35	30 (p)	Dawes et al. (1989)
		27°28′40″ N	10–30	25–30 (p)	Ralph (1998)
	Halodule wrightii	27°21′ N	12–30	30 (p)	Dunton and Tomasko (1994)
		27°49′–28°15′ N	17–29	25-28 (p)	Dunton (1996)
	Syringodium filiforme	27° N	11.9–32.3	23–29 (g)	Barber and Behrens (1985)
		28° N		28 (g)	Gilbert and Clark (1981)
		27°32′2″ N	9–32	32 (g)	Fry and Virnstein (1988)
	Thalassia testudinum	26°24' N	15–30	30 (g)	Kaldy and Dunton (2000)
		27°49′ N	13–31	29 (g) 29 (p)	Lee and Dunton (1996) Herzka and Dunton (1997)
		27° N	11.9–32.3	23–31 (g)	Barber and Behrens (1985)
		25° N	19.0–35.5	28–31 (g)	Zieman (1975)
		26°50′ N	14–33	30 (g)	Tomasko and Hall (1999)
		26°08′ N	15–31	27 (p)	Herzka and Dunton (1997)
		26°08′05″ N	10–32	31 (p)	Herzka and Dunton (1998)

6 Hydrologic Regime and Weather

Factors affecting growth

Water level and wave energy

Seagrasses lack structural elements to support and protect themselves outside of water. Most seagrasses are excluded from the intertidal zone because of exposure to waves and desiccation (Koch and Beer 1996). Exceptions to this rule are the three *Phyllospadix* species that grow along the rocky West Coast of North America (Short et al. 2007). Of the species found on the US East Coast and Gulf of Mexico, *Halodule wrightii* is the most tolerant to above-water exposure (Yates, Morrison and Greening 2011). Seagrass growth is also limited by high wave energy (Dan et al. 1998; Robbins and Bell 2000). Wave energy usually forces seagrasses to inhabit water deeper than the wave's mixing depth, which is half of the wavelength (Chambers 1987). The area affected by the mixing depth typically has continuous water and sediment movement, leading to high TSS levels, both of which hinder seagrass establishment (Koch 2001).

Seagrasses have the ability to attenuate wave energy (Fonseca and Cahalan 1992; Koch et al. 2006b) by forming meadows that reduce more energy than canopy-style seagrass (Verduin and Backhaus 2000). If the meadows are effective enough at reducing wave energy, seagrasses can spread to shallower waters because of a reduction in wave energy. As long as the leading edge of the seagrass bed remains in place, the area behind becomes easier and allows for more seagrass to establish (Koch 2001). Waves can sometimes benefit seagrasses by removing epiphytic growth that can cover the leaves, which reduces their photosynthetic ability. (Kendrick and Burt 1997; Koch 2001; Koch et al. 2006b). Wave energy also reduces self-shading by keeping the leaves moving back and forth. (Koch 2001).

Kelly, Fonseca, and Whitfield (2001) generated a model to select areas for seagrass restoration efforts using a number of hydrologic factors. The amount of fetch, known as the relative exposure index, was found to be a major factor for restoration. Areas of high fetch were estimated to have low restoration chances, while areas leeward of islands, or other protective features, had a higher chance of restoration success.

Currents

Current and wave energy exchanges the water around leaves, aiding in nutrient and carbon diffusion, which lead to better growth (Nikora, Goring and Biggs 2002). Similar to waves, current also rids the leaf surface area of epiphytic organisms. Areas that are too quiescent tend to be poor habitat for seagrasses (Koch 2001). For SAV survival, nutrients and gases must pass between the SAV external tissues and the surrounding water and sediment. The diffusive boundary layer acts as a barrier between the plant tissues and surrounding environment. Water current strength plays a significant role in the size of the diffusive boundary layer. Weak currents are associated with large diffusive boundary layers. Larger diffusive boundary layers make it harder for plants to uptake nutrients through the leaves from passing water (Fonseca and Kenworthy 1987). When water is stagnant around SAV surface tissue, the partial pressure of nutrients and gases is reduced, decreasing diffusion (Koch et al. 2006b). Water currents are usually 2 to 10 times slower in seagrass beds compared to adjacent bare areas, hypothesized to be due to the seagrass (Carter et al. 1988; Rybicki et al. 1997). While the current reduction is usually beneficial for establishing seagrass further down current, the leading seagrass area may reduce the current too much, making the diffusive boundary layer too great for seagrass growth. The current velocity required varies by species because of variation in leaf shape. The critical diffusive boundary layer distance for *Cymodeca nodosa* is 98 µm and 298 µm for *T. testudinum* (Koch 1994). In general, most seagrasses prefer sustained current velocities between 5 and 100 cm/s (Koch 2001). For example, in the Chesapeake Bay, seagrass species require a minimum sustained current of 3–16 cm/s to survive, with a maximum of 50–180 cm/s (Chesapeake Bay Foundation 2000).

Storms

The impacts of storms on seagrass communities seem to be highly variable, with frequent weak storms causing larger impacts than infrequent strong storms. Large storm events initially appear to be very destructive to seagrasses because of removal of aboveground leaf material, covering of plants by shifting sediments, increased light attenuation, and uprooting of the plants (Preen, Long, and Coles 1995; Short and Neckles 1999; Cabello-Pasini, Lara-Turrent and Zimmerman 2002; Michot et al. 2002). Specific to Mississippi Sound, Eleuterius and Miller (1976) and Eleuterius (1987) described the destruction of 1400 ha of seagrass beds due to Hurricane Camille in 1969. However, a more recent study by Carter et al. (2011) looking at historical aerial photos suggested Hurricane Camille was not as destructive as originally thought, as the grasses were able to recover after initial damages were incurred.

Seagrasses seem to be adapted to withstand acute damage caused by strong storms such as hurricanes (Dawes et al. 1995; Franze 2002; Carter et al. 2011). Rasheed (2004) found multiple species of seagrass can use asexual reproduction to recolonize areas disturbed by experimental disturbance. Byron and Heck (2006) conducted seagrass surveys post Hurricane Ivan in 2004 and Hurricane Katrina in 2006 along coastal Alabama. Posthurricane surveys showed no change in seagrass coverage because of Katrina, and 82% of the seagrass beds were still established after Ivan. Michot et al. (2002) found no negative effects on seagrass coverage in Guatemala and Honduras from Hurricane Mitch in 1998.

Climate change

The direct effects due to wind, such as leaf blade damage and burial of aboveground biomass by sediment movement, may not be as detrimental to seagrasses as previously thought. Climate change with cascading effects of chronic freshwater and nutrient inputs from increased rain because warmer temperatures are more likely to be detrimental than acute burial or shifting sediment. As described in the hydrologic section, fresh water can hinder seagrass reproduction or cause death. Increases in the amount of routine storm freshwater runoff is a chronic problem for seagrasses, known as osmotic shock (IPCC 2013). Climate change may lead to higher frequency and increasing strength of storms, which may cause more flooding and nutrient loading throughout the US territories. The increase of fresh water into seagrass habitat will lower salinities and hinder the growth of true seagrasses (IPCC 2013). This lowered salinity will allow species typically found in brackish water to spread.

7 Summary and Discussion

Geomorphology and bathymetry

SAV habitats occur across a wide range of coastal environments whose water quality, sedimentology, hydrologic regime, and many other factors interplay with the geomorphology and bathymetry of the area. The basic requirements for SAV growth, outlined in this report, must be accommodated in each environment, limiting the types of coastal environments where SAV can thrive. These environments can be roughly categorized according to their geomorphological and bathymetric characteristics into back-barrier platforms and protected shoals; bays, lagoons, and sounds; estuaries; adjacent to rocky islands; and swash zone. The vast majority of coastal SAVs grow in protected areas, leaving only a few species tolerant of swash-zone conditions.

Physical properties and sediment dynamics

The primary sediment-dynamics controlling factors for SAV growth are erosion, resuspension, deposition and subsidence. Tide-dominated environments tend to show increased deposition in SAV beds, while wave-dominated environments are more susceptible to erosion within SAV beds (Madsen et al. 2001). Most natural deposition and erosion do not negatively influence SAV growth, or if they do, the SAV is able to easily recover. In overall higher-energy environments, however, (for example, barrier island systems with large inlets), large erosion and deposition events have been observed to kill SAV. Anthropogenic erosion and deposition, including dredging, dredge material placement, recreation, and fishing, can also cause SAV death.

Sedimentology

The sedimentology of the substrate in which SAV is growing plays a variety of roles in SAV health. The primary influencing factors include grain size, organic matter content of the sediment, and nutrient content of the pore waters. These factors interact to influence SAV habitability.

Finer-grained substrates reduce pore-water exchange within the water column, particularly when the sediment is clay rich. These sediments hold nutrients in the pore water more efficiently but can also foster reducing conditions, making the sediment unsuitable for SAV growth. A highly compacted or very clay-rich substrate can be difficult for SAV roots to penetrate.

Coarse-grained materials (typically sand) allow for increased pore-water exchange and remain more oxygenated beneath the sediment-water interface. With a very high rate of pore-water exchange, nutrients can become quickly depleted, and if the grain size is too course, SAV may have a hard time anchoring effectively. Coastal and marine SAV has been observed growing in substrates ranging from ~2%–50% fines, with different species tolerating various parts of that range best.

Water quality

The quality of the water in which SAV grows is one of the most important deciding factors for SAV habitat. In fact, most studies report that light limitation, related to water clarity, is *the* primary limiting factor (Orth and Moore 1983; Cambridge et al. 1986). Water clarity is affected by suspended particulate, both organic and inorganic, and is controlled by a variety of processes.

Coastal and marine SAV does not require high nutrient concentrations to thrive and takes up of these most from the substrate (Koch 2001). Dissolved nutrient overloading from runoff produces very detrimental effects on coastal SAV communities (Orth and Moore 1983; Cambridge et al. 1986; Pulich and White 1991; Duarte et al. 2007; Lee, Park and Kim 2007; Short et al. 2007).

Salinity naturally fluctuates in the coastal environment, and coastal SAV is adapted to a certain level of variation. But extreme reductions in salinity can heavily damage seagrass SAV populations in particular (Furnas 2003; Lirman and Cropper 2003; Collier et al. 2014). The opening of the Bonnet Carre Spillway in Louisiana in 1973, for example, led to mass seagrass death and reduction in diversity (Eleuterius 1987; Moncreiff 2007).

As the global climate changes, these environments will see continued increases in dissolved carbon dioxide concentrations as well as water temperatures. Increased dissolved carbon dioxide concentrations tends to increase SAV growth (Zimmerman et al. 1995, 1997; Palacios and Zimmerman 2007). Coupled with an increase in water temperature, however, the net effects will likely be deleterious (Repolho et al. 2017).

Hydrologic regime and weather

Marine and coastal SAV require a minimum amount of water flow for circulation, to supply fresh nutrients and remove waste. If currents or waves become too strong, however, the SAV may be damaged. The ideal energy level varies between species and regions, but typical coastal SAV species require habitats deeper than strong wave orbitals, or protected from waves completely, with current velocities between 5 and 100 cm/s (Koch 2001).

Occasional storm events causing larger than usual waves and higher current velocities can temporarily damage SAV, but they will often recover quickly. High-energy conditions can even remove harmful epiphytic algae from photosynthetic surfaces of the SAV. If severe storms become too frequent, or overall wave exposure is increased, permanent SAV loss is often observed.

Discussion and conclusions

This review provides a summary of the most important controlling factors for coastal and marine SAV habitats and how each of these ties into the system as a whole. It is widely reported that the main controlling factor for SAV habitats in the coastal zone is light limitation, influenced by the complex interaction of water quality, energy (waves and currents), sedimentology, and geomorphology. This complexity illustrates why all of these factors are important to consider when attempting to understand a particular habitat. Measuring light availability alone will not reveal the root cause of limitations or benefits, as it could be caused by a variety of factors. Many coastal projects, including engineering and restoration efforts, affect SAV habitat. Planning for all coastal projects conducted near or in SAV habitat should address how it will affect that habitat, and all potentially limiting factors described in this report must be considered.

Of course, not every factor mentioned in this report is important in every system, so steps must be taken to narrow down and understand controlling factors in a given system. Consider first the specific areas where SAV is currently or was historically present in a particular location. Can any spatial patterns be recognized in the present or through time?

Consider next the dominant characteristics of the given environment. Is it an open bay, a marshy estuary fringe, a back barrier, an open nearshore environment, a rocky bay, or adjacent to islands? Each of these environments has a specific set of characteristics as it relates to SAV habitats, as discussed in section 1. Consider the limiting factors of these specific environments and their individual characteristics and decide whether they are impacting SAV in the area. Each environment's unique hydrologic regime and controlling factors related to currents and waves may come into play. What causes the highest, potentially SAV-limiting energy in the area? Is it waves during storms, or the tides, storm surge, or possibly boat wakes? Various substrate types exist in differing environments, and each will see differing patterns of erosion and deposition or impacts due to sediment characteristics. Each may also face varying water-quality issues, from nutrient overload and other pollution issues, or salinity fluctuations. Human activities such as dredging, fishing, and recreational boating may also affect the environment.

Bringing together current or historical patterns of SAV in the area and narrowing down the controlling factors is the first step to making the most important and effective decision when it comes to restoration, replanting, conservation, or mitigation during local projects. Planning for coastal engineering projects can benefit from a similar method. A basic understanding of the major limiting factors for SAV in that area, as well as a few small changes in planning, could possibly prevent mass SAV loss or unwanted SAV growth.

Bibliography

Abdelrhman, M. 2003. Effect of eelgrass Zostera marina canopies on flow and transport. *Marine Ecology Press Series*. 248:67-83.

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(2):110-121.

Ailstock, M., D. Shafer, and A. Magoun. 2010. Effects of planting depth, sediment grain size, and nutrients on *Ruppia maritima* and *Potamogeton perfoliatus* seedling emergence and growth. *Restoration Ecology*, 18(4):574-583.

Anderson, C., G. Carter, and W. Funderburk. 2016. The use of aerial RGB imagery and LIDAR in comparing ecological habitats and geomorphic features on a natural versus man-made barrier island. *Remote Sensing*, 8:602-619. doi:10.3390/rs8070602

Anderson, R. 1972. Submerged vascular plants of the Chesapeake Bay and tributaries. *Chesapeake Science*, 13:87-89.

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.

Barko, J., and M. Smart. 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. *Journal of Ecology*. 71:161-17.

Barth, N. 2011. Impact of breakwaters on sediment characteristics and submerged aquatic vegetation. University of Maryland. Master's Thesis.

Batiuk, A., R. Orth, K. Moore, W. Stevenson, J. Stevenson, L. Staver, V. Carter, N. Rybicki, R. Hickman, S. Kollar, S. Bieber, and P. Heasly. 1992. Submerged Aquatic Vegetation Habitat Requirements and Restoration Targets: A Technical Synthesis. USEPA-CBP 68-WO-0043. Annapolis, Maryland: US Environmental Protection Agency.

Beck, M., W. Lruczynski, and P. Sheridan. 2007. Conclusions *in* Handley, L., Altsman, D., and DeMay, R., eds., 2007, Seagrass Status and Trends in the Northern Gulf of Mexico: 1940–2002: US Geological Survey Scientific Investigations Report 2006–5287, 267 p. https://pubs.usgs.gov/sir/2006/5287/pdf/Conclusions.pdf

Beer, S., and E. Koch. 1996. Photosynthesis of seagrasses vs. marine macroalgae in globally changing CO2 environments. *Marine Ecology Progress Series* 141:199-204.

Berry, H. D., A. T. Sewell, S. Wyllie-Echeverria, B. R. Reeves, T. F. Mumford, Jr., J. R. Skalski, R. C. Zimmerman, and J. Archer. 2003. Puget Sound Submerged Vegetation Monitoring Project: 2000-2002 Monitoring Report. Nearshore Habitat Program, Washington State Department of Natural Resources, Olympia, Washington. 60pp. plus appendices. Available online: http://www2.wadnr.gov/nearshore.

Bintz, J., S. Nixon, B. Buckley, and S. Granger. 2003. Impacts of temperature and nutrients on coastal lagoon plant communities. *Estuaries* 26:765. doi:10.1007/BF02711987

Boer, W. F. 2007. Seagrass-sediment interactions, positive feedbacks and critical thresholds for occurrence: a review. *Hydrobiologia*, 591, 5-24.

Brenner, M., D. Hodell, B. Leyden, J. Curtis, W. Kenney, B. Gu, and J. Newman. 2006. Mechanisms of organic matter and phosphorus burial in sediments of a shallow, subtropical, macrophyte-dominated lake. *Journal of Paleolimnology*, 35(1):129-148.

Burd, A., and K. Dunton. 2001. Field verification of a light-driven model of biomass changes in the seagrass *Halodule wrightii*. *Marine Ecology Progress Series* 209:85-98.

Burrell, C., and J. Schubel. 1977. Seagrass ecosystem oceanography, p. 196-232. In C. P. McRoy and C. Helfferich (eds.), Seagrass Ecosystems. Marcel Dekker, Inc, New York.

Byron, D., and K. Heck, Jr. 2006. Hurricane effects on seagrasses along Alabama's Gulf Coast. *Estuaries and Coasts* 29:939-942.

Cabello-Pasini, A., C. Lara-Turrent, and R. Zimmerman. 2002. Effect of storms on photosyhthesis, carbohydrate content and survival of eelgrass populations from a coastal lagoon and the adjacent open ocean. *Aquatic Botany*, 74:149-164.

Cahoon, D., D. Reed, and J. Day. 1995. Estimating shallow subsidence in microtidal salt marshes of the southeastern United States: Kaye and Barghoorn revisited. *Marine Geology*, 128(1-2):1-9.

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.

Cammen, L. 1982. Effect of particle size on organic carbon content and microbial abundance within four marine sediments. *Marine Ecology Progress Series*, 9:273-280.

Capone, D., and R. Kiene. 1988. Comparison of microbial dynamics in marine and freshwater sediments: Contrasts in anaerobic carbon catabolism. *Limnology and Oceanography*, 33(4):725-749.

Carlson, P., L. Yarbro, and T. Barber. 1994. Relationship of sediment sulfide to mortality of *Thalassia testudinum* in Florida Bay. *Bulletin of Marine Science*, 54:733-74.

Carlson Jr, P., and K. Madley. 2007. Statewide summary of Florida, Seagrasses. *In* Handley, L., Altsman, D., and DeMay, R., eds., 2007, Seagrass Status and Trends in the Northern Gulf of Mexico: 1940–2002: US Geological Survey Scientific Investigations Report 2006–5287, 267 p. https://pubs.usgs.gov/sir/2006/5287/pdf/StatewideSummaryforFlorida.pdf

Carter, G., K. Lucas, P. Biber, G. Criss, and G. Blossom. 2011. Historical changes in seagrass coverage on the Mississippi barrier islands, northern Gulf of Mexico, determined from vertical aerial imagery (1940-2007). Geocarto International 26:663-673. Doi:1.1080/1016049.2011.620634

Carter, V., J. Barko, Godshalk, and N. Rybicki. 1988. Effects of submersed macrophytes on water quality in the tidal Potomac River, Maryland. Maryland. *Journal of Freshwater Ecology*, 4:493-501.

Carter, V., R. Rybicki, and N. Landwehr. 2000. Light requirements for SAV survival and growth, p. 11-33. In R. Batiuk, R. Orth, K. Moore, J. C. Stevenson, W. Dennison, L. Staver, V. Carter, N. Rybicki, R. Hickman, S. Kollar, and S. Bieber (eds.), Chesapeake Bay Submerged Aquatic Vegetation Water Quality and Habitat-Based Requirements and Restoration Targets: A Second Technical Synthesis. CBP/ TRS 245/00. EPA 903-R-00-014. US EPA, Chesapeake Bay Program, Annapolis, Maryland.

Chambers, P. 1987. Nearshore occurrence of submerged aquatic macrophytes in relation to wave action. Canadian Journal of Fisheries and Aquatic Sciences 44:1666-1669. doi:10.1139/f87-204

Chesapeake Bay Foundation 2000. Chesapeake Bay submerged aquatic vegetation water quality and habitat-based requirements and restoration targets: A second technical synthesis. http://www.fwspubs.org/doi/suppl/10.3996/082016-JFWM-068/suppl_file/10.3996082016-jfwm-068.s7.pdf.

Chesapeake Bay Program. 2012. Underwater bay grasses in the Chesapeake Bay and rivers in 2011. http://www.chesapeakebay.net/documents/BackgrounderFINAL3_27_12.pdf.

Collier, C., C. Villacorta-Rath, K. Dijk, M. Takahashi, and M. Waycott. 2014. Seagrass proliferation precedes mortality during hypo-salinity events: a stress-induced morphometric response. *PLoS ONE* 9(4): e94014. doi: 10.137/journal.pone.0094014

Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, et al. 2013. Long-term climate change: Projections, commitments and irreversibility. In: Stocker, T.F., et al. (Eds.). *Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge and New York: Cambridge University Press.

Continental Shelf Associates, Inc., 1989, Southwest Florida nearshore benthic habitat study, narrative report: New Orleans, La., US Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Regional Office, OCS study MMS 89-0080, 55 p.

Cooper, J., D. Lewis, and O. Pilkey. 2007. Fetch-limited barrier islands: overlooked coastal landforms. *The Geological Society of America* 3. doi:10.1130/GSAT01703A.1

Cowan, J., J. Pennock, and W. Boynton. 1996. Seasonal and interannual patterns of sediment-water nutrient and oxygen fluxes in Mobile Bay, Alabama (USA); Regulating factors and ecological significance. *Marine Ecology Progress Series*, 141:229-245.

Czerny, A., and K. Dunton. 1995. The effects of in situ light reduction on the growth of two subtropical seagrasses, *Thhalassia testudinum* and *Halodule wrightii*. *Estuaries* 18:418-427.

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.

Dauby, P., A. Bale, N. Bloomer, C. Canon, R. Ling, A. Norro, J. Robertson, A. Simon, J. Theate, A. Watson, and M. Frankignoulle. 1995. Particle fluxes over a Mediterranean seagrass bed: A one year case study. *Marine Ecology Progress Series*, 126:233-246.

Dawes, C., C. Lobban, and D. Tomasko. 1989. A comparison of the physiological ecology of the seagrasses *Halophila decipiens* Ostenfeld and *H. johnsonii* Eiseman from Florida. *Aquatic Botany*, 33:149-154.

Dawes, C., S. Bell, R. Davis, E. McCoy, H. Mushinshy, and J. Simon. 1995. Initial effects of Hurricane Andrew on the shoreline of southwest Florida. *Journal of Coastal Research*, 21:103-110.

DeMarco, K., B. Couvillion, S. Brown, and M. La Peyre. 2018. Submerged aquatic vegetation mapping in coastal Louisiana through development of a spatial likelihood occurrence (SLOO) model. *Aquatic Botany*, 151:87-97.

Dennison, W. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany*, 27:15-26.

Dennison, W., R. Orth, K. Moore, J. Stevenson, V. Carter, S. Kollar, P. Bergstrom, and R. Batiuk. 1993. Assessing water quality with submersed aquatic vegetation. *Bioscience,* 43:86-94. Doi.10.2307/1311969

Denny, P. 1980. Solute movement in submersed angiosperms. *Biological Reviews*, 55:62-92.

Diaz-Almela, E., N. Marba, E. Alvarez, E. Balestri, J. Ruiz-Fernandez, and C. Duarte. 2006. Patterns of seagrass (*Posidonia oceanica*) flowering in the Western Mediterranean. *Marine Biology*, 148:723-742.

Dogliotti, A., K. Ruddick, B. Nechad, D. Doxaran, and E. Knaeps. 2015. A single algorithm to retrieve turbidity from remotely-sensed data in all coastal and estuarine waters. *Remote Sensing of Environment*, 156:157-168.

Dowty, P., B. Reeves, H. Berry, S. Wyllie-Echeverria, T. Mumford, A. Sewell, P. Milos, and R. Wright. 2005. “Puget Sound submerged vegetation monitoring project: 2003-2004 monitoring report.” Nearshore Habitat Program, Washington State Department of Natural Resources, Olympia, Washington.

Drew, E. 1979. Physiological aspects of primary production in seagrasses. *Aquatic Botany*, 7:139-150.

Drysdale, F. R., and M. G. Barbour. 1975. Response of the marine angiosperm *Phyllospadix torreyi* to certain environmental variables: a preliminary study. *Aquat. Bot.*, 1:97–106.

Duarte, C. 1991. Seagrass depth limits. *Aquatic Botany*, 40:363-377.

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

Duarte, C., N. Marba, D. Krause-Jensen, and M. Sanchez-Camacho. 2007. Testing the predictive power of seagrass depth limit models. *Estuaries and Coasts*, 30:652-656.

Dunton, K. 1990. Production ecology of *Ruppia maritima* and *Halodule wrightii* in two subtropical estuaries. *Journal of Experimental Marine Biology and Ecology*, 143:147-164.

Dunton, K. 1994. Seasonal growth and biomass of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradiance. *Marine Biology*, 120: 479-489.

Dunton, K. 1996. Photosynthetic production and biomass of the subtropical seagrass *Halodule wrightii* along an estuarine gradient. *Estuaries*, 19:436-447.

Dunton, K., and D. Tomasko. 1994. In situ photosynthesis in the seagrass *Halodule wrightii* in a hypersaline subtropical lagoon. *Marine Ecology Progress Series*, 107:281-293.

Eisemann, E. 2016. Modern fair-weather and storm sediment transport around Ship Island, Mississippi: Implications for coastal habitats and restoration efforts. *Master's Thesis*. 260. https://aquila.usm.edu/masters_theses/260

Eisemann, E., D. Wallace, M. Buijsman, and T. Pierce. 2018b. Response of a vulnerable barrier island to multi-year storm impacts: LiDAR-data-inferred morphodynamic changes on Ship Island, Mississippi, USA. *Geomorphology,* 313:58-71. doi:10.1016/j.geomorph.2018.04.001

Eisemann, E. R., S. Altman, D. Acevedo-Mackey, and M. K. Reif. 2019. “Relating Seagrass Habitat to Geomorphology and Substrate Characteristics Around Ship Island, MS.” EMRRP Technical Notes Collection. ERDC/TN EMRRP-EBA-24. Vicksburg, MS: US Army Engineer Research and Development Center.

Eldridge, P., and J. Morse. 2000. A diagenetic model for sediment-seagrass interactions. *Marine Chemistry*, 70:89-103.

Eleuterius, L. 1987. Seagrass ecology along the coasts of Alabama, Louisiana, and Mississippi. *Florida Marine Research Publications*, 11-24.

Eleuterius, L., and G. Miller. 1976. Observations on sagrasses and seaweeds in Mississippi Sound since Hurricane Camille. *Journal of Mississippi Academy of Sciences*, 21:58-63.

Evans, A., K. Webb, and P. Penhale. 1986. Photosynthetic temperature acclimation in two coexisting seagrasses, *Zostera marina* L. and *Ruppia maritima* L. *Aquatic Botany*, 24:185-197.

Fabry, V., B. Seibel, R. Feely, and J. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science*, 65:414-432. doi:10.1093/icesjms/fsn048

Flowers, T., P. Troke, and A. Yeo. 1977. The mechanisms of salt tolerance in halophytes. *Annual Review of Plant Physiology*, 28:89-121. doi:10.1146/annurev.pp.28.060177.000513

Fonseca, M. 1996. The role of seagrasses in nearshore sedimentary processes a review. In *Estuarine shores: Evolution environments and human alteration*. K.F. Nordstrom and C.T. Roman, ed., 261-286. John Wiley and Son Ltd.

Fonseca, M., and J. Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuarine Coastal and Shelf Science*, 35:565-576. Doi:10.1016/S0272-7714(05)80039-3

Fonseca, M., and S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Progress Series*, 171:109-121.

Fonseca, M., and W. Kenworthy. 1987. Effects of current on photosynthesis and distribution of seagrass. *Aquatic Botany,* 27:59-78.

Fonseca, M., M. Koehl, and B. Kopp. 2007. Biomechanical factors contributing to self-organization in seagrass landscapes. *Journal of Experimental Marine Biology and Ecology*, 340:227-246. Doi:10.1016/j.jembe.2006.09.015

Fourqurean, J., and M. Robblee. 1999. Florida Bay: A brief history of recent ecological changes. *Estuaries,* 22:345-357.

Fourqurean, J., and J. Zieman. 1991. Photosynthesis, respiration and whole plant carbon budget of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series*, 69:161-170.

Franze, C. D. 2002. Barrier island seagrass and geomorphic interactions: a case study of hurricane damage and efficacy of restoration efforts, at the Chandeleur Islands: New Orleans, La., University of New Orleans, M.S. thesis, 69 p.

Fry, B., and R. Virnstein. 1988. Leaf production and export of the seagrass *Syringodium filiforme* Kutz. in Indian River Lagoon, Florida. *Aquatic Botany*, 30:261-266.

Furnas, M. 2003. Catchment and corals: terrestrial runoff of the Great Barrier Reef. Townville Queensland: Australian Institute of Marine Science. 334 p.

Gilbert, S., and K. Clark. 1981. Seasonal variation in standing crop of the seagrass *Syringodium filiforme* and associated macrophytes in the northern Indian River, Florida. *Estuaries,* 4:223-225.

Grady, J. 1981. Properties of seagrass and sand flat sediments from the intertidal zone of St. Andrews Bay, Florida. *Estuaries,* 4:335-344.

Graham, J. 1966. Secchi disc observations and extinction coefficients in the central and eastern North Pacific Ocean. *Limnology and Oceanography*, 11:184-190.

Griffin, N., and M. Durako. 2012. The effect of pulsed versus gradual salinity reduction on the physiology and survival of *Halophila johnsonii* Eiseman. *Marine Biology*, 159: 1439–1447.

Griffiths, J., M. Kadin, F. Nascimento, T. Tamelander, A. Tornroos, S. Bonaglia, E. Bonsdorff, V. Bruchert, A. Gardmark, M. Jarnstrom, J. Kotta, M. Lindegren, M. Nordstrom, A. Norkko, J. Olsson, B. Weigel, R. Zydelis, T. Blenckner, S. Niiranen, and M. Winder. 2017. The importance of benthis-pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biology*, 23(6):1-18.

Gu, B., and M. Hoyer. 2005. Community Structure and Environmental Conditions in Florida Shallow Lakes Dominated by Submerged Aquatic Vegetation, Lake and Reservoir Management, 21:4, 403-410.

Handley, L., D. Altsman, and R. DeMay, eds. 2007. Seagrass Status and Trends in the Northern Gulf of Mexico: 1940–2002: US Geological Survey Scientific Investigations Report 2006–5287, 267 p.

Handley, R., and A. Davy. 2002. Seedling root establishment may limit *Najas marina* L. to sediments of flow cohesive strength. *Aquatic Botany*, 73:129-136.

Harding, L. W. Jr., J. H. Butler, and R. E. Heft. 1975. Standing stock and production of eelgrass (*Zostera marina* L.) in Humboldt Bay, California. United States.

Heck Jr, K., and D. Byron. 2006. Post Hurricane Katrina damage assessment of seagrass resources of the Mississippi Islands, Gulf Islands National Seashore. Gulf Breeze, Florida, USA: Gulf Islands National Seashore, 1-29.

Heck Jr., K. L., J. R. Pennock, J. F. Valentine, L. D. Coen, and S. A. Sklenar. 2000. Effects of nutrient enrichment and small predator density on seagrass ecosystems: an experimental assessment. *Limnology and Oceanography*, 45:1041–1057.

Herzka, S., and K. Dunton. 1998. Light and carbon balance in the seagrass *Thalassia testudinum*: evaluation of current production models. *Marine Biology*, 132:711-721.

Herzka, S. Z., and K. H. Dunton. 1997. Seasonal photosynthetic patterns of the seagrass Thalassia testudinum in the western Gulf of Mexico. *Marine Ecology Progress Series*, 152:103–117.

Holst, L., R. Rozsa, L. Benoit, S. Jacobson, and C. L. Rilling. 2003. Long Island Sound Habitat Restoration Initiative: Technical Support for Coastal Habitat Restoration, Section 3: Submerged Aquatic Vegetation.

Hoskin, C. 1983. Sediment in seagrasses near Link Port, Indian River, Florida. *Florida Scientist*, 46:153-161.

Huettel, M., and I. Webster. I. 2001. “Porewater flow in permeable sediments” in the Benthic Boundary Layer: Transport processes and biogeochemistry. Eds, Bernard P. Boudreau and Bo Barker Jorgensen, pp, 144-154. Oxford University Press.

Huettel, M., P. Berg, and J. Kostka. 2014. Benthic exchange and biogeochemical cycling in permeable sediments. *Annual Reviews of Marine Science*, 6:23-51.

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

Idso, S., and R. Gilbert. 1974. On the universality of the Poole and Atkins secchi-disk-light extinction equation. *Journal of Applied Ecology*, 11:399-401.

IPCC (Intergovernmental Panel of Climate Change). 2013. In Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Pp. 1029-1136. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Iverson, R. L., and H. F. Bittaker. 1986. Seagrass distribution and abundance in Eastern Gulf of Mexico coastal waters. *Estuarine, Coastal and Shelf Science*, 22(5), 577-602. http://doi.org/10.1016/0272-7714 (86)90015-6

James, W., J. Barko, and M. Butler. 2004. Shear stress and sediment resuspension in relation to submersed macrophyte biomass. *Hydrobiologia*, 515:181-191.

Kahn, A., and M. Durako. 2006. *Thalassia testudinum* seedling responses to changes in salinity and nitrogen levels. *Journal of Experimental Marine Biology and Ecology*, 335:1–12.

Kahn, A., and M. Durako. 2008. Photophysiological responses of *Halophila johnsonii* to experimental hyposaline and hyper-CDOM conditions. *J Exp Mar Biol Ecol.*, 367: 230–235.

Kaldy, J., and D. Shafer. 2012. Effects of salinity on survival of the exotic seagrass Zostera japonica subjected to extreme high temperature stress. *Botanica Marina*, 56:75-82. https://doi.org/10.1515/bot-2012-0144

Kaldy, J., and J. Dunton. 2000. Above- and belowground production, biomass and reproductive ecology in a subtropical coastal lagoon. *Marine Ecology Progress Series*, 193:271-283.

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

Kelly, N., M. Fonseca, and P. Whitfield. 2001. Predictive mapping for management of seagrass beds. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 11:437-451.

Kemp, W., R. Bartleson, and L. Murray. 2000. Epiphyte contributions to light attenuation at the leaf surface, p. 55- 70. In R. Batiuk, R. Orth, K. Moore, J. C. Stevenson, W. Dennison, L. Staver, V. Carter, N. Rybicki, R. Hickman, S. Kollar, and S. Bieber (eds.), Chesapeake Bay Submerged Aquatic Vegetation Water Quality and Habitat-Based Requirements and Restoration Targets: A Second Technical Synthesis. CBP/ TRS 245/00. EPA 903-R-00-014. US EPA, Chesapeake Bay Program, Annapolis, Maryland.

Kemp, W., R. Batiuk, R. Bartleson, P. Bergstrom, V. Carter, C. Gallegos, W. Hunley, L. Karrh, M. Naylor, N. Rybicki, J. Stevenson, and D. Wilcox. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water quality, light regime, and physical-chemical factors. *Estuaries*, 27(3):363-377.

Kemp, W, W. Boynton, R. Twilley, J. Stevenson, and L. Ward. 1984. Influences of submersed vascular plants on ecological processes in the upper Chesapeake Bay, p. 367-394. In V. S. Kennedy (ed.), The Estuary as a Filter. Academy Press, New York.

Kendrick, G., and J. Burt. 1997. Seasonal changes in epiphytic macroalgae assemblages between offshore exposed and inshore protected *Posidonia sinuosa* Cambridge et. Kuo seagrass meadow. Western Australia. *Botanica Marina*, 40:77-85.

Kenworthy, W. 1997. An updated biological status review and the summary of the proceedings of a workshop to review the biological status of the seagrass, *Halophila johnsonii* Eiseman. Office of protected resources NMFS, NOAA. 15 Oct. 1997.

Kenworthy, W., and M. Fonseca. 1996. Light requirements of seagrasses Halodule wrightii and Syringodium filiforme derived from the relationship between diffuse light attenuation and maximum depth distribution. *Estuaries,* 19:740-750.

Kirwan, M. L., and J. P. Megonigal. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature*, 504:53-60.

Koch, E. 1994. Hydrodynamics, diffusion-boundary layers and photosynthesis of the seagrasses *Thassassia testudinum* and *Cymodocea nodosa*. *Marine Biology*, 118:767-776.

Koch, E. 2001. Beyond Light: Physical, geological, and geochemical parameters as possible submersed aquatic Vegetation habitat requirements. *Coastal and Estuarine Research Federation*, 24(1):1-17.

Koch, E., J. Ackerman, M. van Keulen, and J. Verduin. 2006a. Fluid dynamics in seagrass ecology: from molecules to ecosystems. In Seagrasses: biology, ecology and conservation. Editors; Larkum A., Orth R., Duarte, C. Springer Verlag, 193-225.

Koch, E., 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., L. Sanford, S. Chen, D. Shafer, and J. Smith. 2006b. Waves in seagrass systems: review and technical recommendations. ERDC TR-06-15. Vicksburg, MS: USACE Engineer Research and Development Center.

Koch, E., and S. Beer. 1996. Tides, light and the distribution of Zostera Marina in Long Island Sound, USA. *Aquatic Botany*, 53:97-107.

Koch, M., G. Bowes, C. Ross, and X. Zhang. 2013. Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Global Climate Change*, 19(1):103-132.

Koch, M., and S. Schopmeyer, O. Nielson, C. Kyhn-Hansen, and C. Madden. 2007. Conceptual model of seagrass die-off in Florida Bay: Links to biogeochemical processes. *Journal of Experimental Marine Biology and Ecology*, 350:73-88.

Krause-Jensen, D., J. Carstensen, S. Nielsen, T. Dalsgaard, P. Christensen, H. Fossing, and M. Rasmussen. 2011. Sea bottom characteristics affect depth limits of eelgrass Zostera marina L. *Marine Ecology Progress Series*, 425:91–102.

Kreiling, R., Y. Yin, and T. Gerber. 2007. Abiotic influences on the biomass of Vallisneria americana Michx. in the Upper Mississippi River. *River Research and Applications*, 23(3):343-349.

Lamers, L., L. Govers, I. Janssen, J. Geurts, M. Van der Welle, M. Katwijk, T. Van der Heide, J. Roelofs, and A. Smolders. 2013. Sulfide as a soil phytotoxin-a review. Frontiers in Plant Science. 4:268. http://doi.org/10.3389/fpls.2013.00268.

Lee, K., and K. 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, K., and K. Dunton. 1997. Effects of in situ light reduction on the maintenance, growth and partitioning of carbon resources in *Thalassia testudinum* Banks ex Konig. *Journal of Experimental Marine Biology and Ecology*, 210:53-73.

Lee, K., and K. Dunton. 2000. Diurnal changes in pore- water sulfide concentration in the seagrass Thalassia testudinum beds: The effects of seagrasses on sulfide dynamics. *Journal of Experimental Marine Biology and Ecology*, 225:201-214.

Lee, K., S. Park, and J. Kim. 2005. Production dynamics of the eel grass, Zostera marina in two bay systems on the south coast of the Korean peninsula. *Marine Biology*, 147:1091-1108.

Lee, K., S. Park, and Y. Kim. 2007. Effects of radiance, temperature, and nutrients on growth dynamics of seagrass: A review. *Journal of Experimental Marine Biology and Ecology*, 350:144-175.

Lee, R. 1999. Oxidation of sulfide by Spartina alternifori roots. *Limnology and Oceanography*, 44(4):1155-1159.

Lefcheck, J., R. Orth, W. Dennison, D. Wilcox, R. Murphy, and J. Keisman, plus 8 others. 2018. Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. In *Proceedings of the National Academy of Science* 115:3658-3662.

Lelong, M. G. 1988, Noteworthy monocots of Mobile and Baldwin Counties, Alabama: SIDA, v. 13, no. 1, p. 101–113.

Leonardi, N., Z. Defne, N. Ganju, and S. Fagherazzi. 2016. Salt marsh erosion rates and boundary features in a shallow bay. *Journal of Geophysical Research: Earth Surface*, 121:1-15.

Leschen, A., K. Ford, and N. Evans. 2010. Successful Eelgrass (Zostera marina) Restoration in a Formerly Eutrophic Estuary (Boston Harbor) Supports the Use of a Multifaceted Watershed Approach to Mitigating Eelgrass Loss. *Estuaries and Coasts*, 33(6):1340-1354.

Li, Z., L. Kong, L. Yang, M. Zhang, T. Cao, J. Xu, Z. Wang, and Y. Lei. 2012. Effect of substrate grain size on the growth and morphology of the submerged macrophyte *Vallisneria natans* L. Limnologica: Ecology and Management of Inland Waters. 42(1): 81-85.

Liphschitz, N., and Y. Waisel. 1974. Existence of salt glands in various genera of the graminae. *New Phytologist*, 73:507-513.

Lirman, D., and W. P. Cropper. 2003. The influence of salinity on seagrass growth, survivorship, and distribution within Biscayne Bay, Florida: field, experimental, and modeling studies. *Estuaries*, *26*(1), pp.131-141.

LISHRI 2015. Long Island Sound Habitat Restoration Initiative, submerged aquatic vegetation. http://www.longislandsoundstudy.net/wp-content/uploads/2004/12/sav-with-cover1.pdf.

Livingston, R., S. 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.

Long, B., A. Aucoin, R. Montreuil, V. Robintaille, and R. Xharde. 2010. Airborne LiDAR Bathymetry applied to coastal hydrodynamic processes. Coastal Engineering. Report G1K9A9.

Mackey, K. M., J. Morris, F. Morel, and S. Kranz. 2015. Response of photosynthesis to ocean acidification. *Oceanography*, 28:74-91.

Madsen, J., P. Chambers, W. James, E. Koch, and D. Westlake. 2001. The interaction between water movement, sediment dynamics, and submersed macrophytes. *Hydrobiologia*, 444:71-84.

Mahajan, S., and N. Tuteja. 2005. Cold, salinity and drought stresses: An overview. *Archives of Biochemistry and Biophysics*, 444:139-158. doi:10.1016/j.abb.2005.10.018

Marba, N., and C. Duarte. 1997. Interannual changes in seagrass (*Posidonia oceanica*) growth and environmental change in the Spanish Mediterranean littoral zone. 42:800-810.

Marba, N., and C. Duarte. 2010. Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. *Global Change Biology*, 16:2366-2375.

Marchand, C., E. Baltzer, E. Lallier-erges, and P. Alberic. 2006. Pore-water chemistry in mangrove sediments: relationship with species composition and developmental stages (French Guiana). *Geochimica et Cosmochimica Acta*. 69:131-142.

Marsh Jr., J., W. Dennison, and R. Alberte. 1986. Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). *Journal of Experimental Marine Biology and Ecology*, 101:257-267.

Marshall, N., and K. Lukas. 1970. Preliminary observations on the properties of bottom sediments with and without eelgrass, *Zostera marina*, cover. In *Proceedings of the National Shellfish Association* 60:107-111.

Matthews, M. 2011. A current review of empirical procedures of remote sensing in inland and near-coastal transitional waters. *International Journal of Remote Sensing*, 32:6855-6899. Doi:10.1080/01431161.2010.512947

Mattson, R., T. Frazer, J. Hale, S. Blitch, and L. Ahijevych. 2007. Florida Big Bend *In* Handley, L., Altsman, D., and DeMay, R., eds., 2007, Seagrass Status and Trends in the Northern Gulf of Mexico: 1940–2002: US Geological Survey Scientific Investigations Report 2006–5287, 267 p. https://pubs.usgs.gov/sir/2006/5287/pdf/FloridaBigBend.pdf.

McMahan, C. 1968. Biomass and salinity tolerance of shoal grass and manatee grass in Lower Laguna Madre. *Journal of Wildlife Management*, 32:501-506.

McMillian, C., and F. Moseley. 1967. Salinity tolerance of five marine spermatophytes of Redfish Bay, Texas. *Ecology,* 48:503-506.

McRoy, C. 1969. Eelgrass under the Arctic winter ice. *Nature,* (224):818–819.

Merino, J. H., J. Carter, and S. L. Merino. 2009. Mesohaline submerged aquatic vegetation survey along the US Gulf of Mexico Coast, 2001 and 2002: a salinity gradient approach. *Gulf of Mexico Science*, 27:1-12.

Michot, T., J. Burch, A. Arrivillage, P. Rafferty, T. Doyle, and R. Kemmerer. 2002. Impacts of Hurricane Mitch on seagrass beds and associated shallow reef communities along the Caribbean Coast of Honduras and Guatemala: USGS Open file Report 03-181, pp 65.

Mitchell, S., J. Thayer, and M. Hayman. 2010. Polarization LiDAR for shallow water depth measurement. *Applied Optics*, 49:6995-7000. doi:10.1364/AO.006995

Moncreiff, C. 2007. Mississippi Sound and the Gulf Islands. In: L Handley, D. Altsman and R. DeMay, eds. *Seagrass status and trends in the Northern Gulf of Mexico: 1940-2002*. US Geological Survey Scientific Investigations Report 2006-5287, 77-86.

Moncreiff, C., T. Randall, and J. Caldwell. 1998. Mapping of seagrass resources in Mississippi Sound. Ocean Springs, Mississippi, USA: The University of Southern Mississippi, Gulf Coast Research Laboratory, 33.

Moore, K. A., D. J. Wilcox, and R. J. Orth. 2000. Analysis of the abundance of submersed aquatic vegetation communities in the Chesapeake Bay. *Estuaries,* 23:1, 115-127.

Moore, K. A., and F. T. Short. 2006. Zostera: biology, ecology, and management. In T. Larkum, R. Orth and C. Duarte (eds.). SEAGRASSES: BIOLOGY, ECOLOGYAND CONSERVATION (pp. 361-386). Springer, Dordrecht.

Moore, K., E. Shields, and J. Jarvis. 2010. The role of habitat and herbivory on the restoration of tidal freshwater submerged aquatic vegetation populations. *Restoration Ecology*, 18:596-604.

Moore, K., H. Neckles, and R. 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. doi:10.3354/meps142247

Murphey, P., and M. Fonseca. 1995. Role of high and low energy seagrass beds as nursery areas for *Penaeus duorarum* in North Carolina. *Marine Ecology Progress Series*, 121:91-98.

Nielson, S., 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.

Nikora, V., D. Goring, and B. Biggs. 2002. Some observations of the effect micro-organisms growing on the bed of an open channel on the on the turbulence properties. *Journal of Fluid Mechanics*, 450:317-341.

Orth, R. J. 1977. The importance of sediment stability in sea- grass communities, p. 281-300. In B. C. Coull (ed.), Ecology of Marine Benthos, University of South Carolina Press, Columbia, South Carolina.

Orth, R. J., and K. A. Moore. 1983, Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. *Science*, (222):51–53.

Orth, R., J. Wilcox, A. Nagey, J. Owens, J. Whiting, and A. Serio. 2004. 2003 distribution of submerged aquatic vegetation in Chesapeake Bay and coastal bays. EPA Chesapeake Bay Program Report. http://web.vims.edu/bio/sav/sav03/index.html.

Orth, R., T. Carruthers, W. Dennison, C. Duarte, J. Fourqurean, K. Heck, Jr., A. Huges, G. Kendrick, W. Kenworthy, S. Olyarnik, F. Short, M. Waycott, and S. Williams. 2006. A global crisis for seagrass ecosystems. *Bioscience,* 56:987-996. Doi:10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Oviatt, C. 2004. The changing ecology of temperate coastal waters during a warming trend. *Estuaries,* 27:895-904.

Palacios, S., and R. Zimmerman. 2007. Response of eelgrass *Zostera marina* to CO_2 enrichment: possible impacts of climate change and potential for remediation of coastal habitats. *Marine Ecology Progress Series*, 344:1-13.

Penhale, P. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (Zostera marina L. community. *Journal of Experimental Marine Biology and Ecology*, 26:211-224.

Pezeshki, S., and R. DeLaune. 2012. Soil oxidation-reduction in wetlands and its impact on plant functioning. *Biology*, 1L196-221. doi:10.3390/biology1020196.

Pham, L. T., P. D. Biber, and G. A. Carter. 2014. Seagrasses in the Mississippi and Chandeleur Sounds and problems associated with decadal-scale change detection. *Gulf of Mexico Science*, 32, 24-43.

Phillips, R. C., 1960. Observations on the ecology and distribution of the Florida seagrasses. Prof. Paper Florida State Board of Conservation., 2:1-72.

Phillips, R. C. 1984 Ecology of eelgrass meadows in the Pacific Northwest: a community profile. United States.

Pilkey, O., J. Cooper, and D. Lewis. 2009. Global distribution and geomorphology of fetch-limited barrier island. *Journal of Coastal Research*, 4:819-837. doi:10.2112/08-1023.1

Poirrier, M. A., and L. A. Handley. 2007. Chandeleur Islands in Seagrass Status and Trends in the Northern Gulf of Mexico: 1940-2002. US Geologic Survey Scientific Investigations Report 2006-5287.

Pollard, P., and D. Moriarty. 1991. Organic carbon decomposition, primary and bacterial productivity, and sulphate reduction, in tropical seagrass beds of the Gulf of Carpentaria, Australia. *Marine Ecology Progress Series*, 69:149-159.

Pollman, C., E. Swain, D. Bael, A. Myrbo, P. Monson, and M. Shore. 2017. The evolution of sulfide in shallow aquatic ecosystem sediments: An analysis of the roles of sulfate, organic carbon, and iron and feedback constraints using structural equation modeling. *Journal of Geophysical Research: Biogeosciences*, 122:2719-2735.

Poole, H., and W. Atkins. 1929. Photo-electric measurements of the penetration of light into sea water. *Journal of the Marine Biological Association of the United Kingdom*, 16:297-270.

Portner, H., D. Karl, P. Boyd, W. Cheung, S. Lluch-Cota, Y. Nojiri, D. Schmidt, and P. Zavialov. 2014. Ocean Systems. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the International Panel of Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 411-484.

Potouroglu, M., J. Bull, K. Krauss, H. Kennedy, M. Fusi, D. Daffonchio, M. Mangora, M. Githaiga, K. Diele, and M. Huxham. 2017. Measuring the role of seagrasses in regulating sediment surface elevation. *Scientific Reports*, 7:11917

Preen, A., W. Long, and R. Coles. 1995. Flood and cyclone related loss, and partial recovery of more than 1,000 km^2 of seagrass in Hervey Bay, Queensland, Australia. *Aquatic Botany*, 52:3-17.

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

Pulich, W., and C. Onuf. 2007. Statewide Summary for Texas in Seagrass Status and Trends in the Norther Gulf of Mexico: 1940-2002. US Geological Survey Scientific Investigations Report 2006-5287, 267 p.

Pulich, W., and W. White. 1991. Decline of submerged vegetation in the Galveston Bay system: chronology and relationships to physical processes. *Journal of Coastal Research*, 7:1125–1138.

Ralph, P. 1998 Photosynthetic response of laboratory-cultured *Halophila ovalis* to thermal stress. *Marine Ecology Progress Series*, 171:123-130.

Rasheed, M. 2004. Recovery and succession in a multi-species tropical seagrass meadow following experimental disturbance: the role of sexual and asexual reproduction. *Journal of Experimental Marine Biology and Ecology*, 310:13-45.

Rasmussen, E. 1977. The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. In: McRoy, C.P., Helfferich, C. (Eds.), Seagrass Ecosystems, Marcel Dekker, New York, pp. 1–51.

Reif, M., C. Piercy, J. Jarvis, B. Sabol, C. Macon, R. Loyd, P. Colarusso, H. Dierssen, and J. Aitken. 2011. Ground truth sampling to support remote sensing research and development: Submersed aquatic vegetation species discrimination using an airborne hyperspectral/LiDAR system. DOER Technical Notes Collection. ERDC TN-DOER-E30 Vicksburg, MS: US Army Engineer Research and Development Center.

Repolho, T., B. Duarte, G. Dionisio, J. Paula, A. Lopes, I. Rosa, T. Grilo, I. Cacador, R. Calado, and R. Rosa. 2017. Seagrass ecophysiological performance under ocean warming and acidification. Scientific Reports 7: Article number 41443. doi:10.1038/srep41443

Robbins, B., and S. Bell. 2000 Dynamics of a subtidal seagrass landscape: Seasonal and annual changes in relation to water depth. *Ecology,* 81:1193-1205.

Rui, Y., D. Murphy, X. Wang, and F. Hoyle. 2016. Microbial respiration, but no biomass, responded linearly to increasing light fraction organic matter input: Consequences for carbon sequestration. Scientific Reports: 6:35496. http://doi.org/10.1038/srep35496.

Rybicki, N., H. Jenter, V. Carter, R. Baltzer, and M. Turtora. 1997. Observations of tidal flux between a submersed aquatic plant sand and the adjacent channel in the Potomac River near Washington, DC. *Limnology and Oceanography*, 42:307-317.

Salo, T., M. Pedersen, and C. Bostrom. 2014. Population specific salinity tolerance in eelgrass (Zostera marina). *Journal of Experimental Marina Biology and Ecology*, 461:425-429. https://doi.org/10.1016/j.jembe.2014.09.010

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.

Shafer, D. J., T. M. Swannack, C. Saltus, J. E. Kaldy, and A. Davis. 2016. Development and validation of a habitat suitability model for the non-indigenous seagrass Zostera japonica in North America. *Management*, 7(2), pp.141-155.

Shivers, S. 2010. The impact of submerged aquatic vegetation on nutrient dynamics and bacterial metabolism in a southeastern reservoir. Master of Science Thesis, University of Georgia.

Short, F., and A. Neckles. 1999. The effects of global climate change on seagrasses. *Aquatic Botany*, 63:169-196. Doi:10.1016/S0304-3770(98)00117-X

Short, F, D. Burdick, J. Wolf, and G. Jones. 1993. Eelgrass in Estuarine Research Reserves along the East Coast, USA, Part I: Declines from Pollution and Disease; Part II: Management of Eelgrass Meadows. National Oceanic and Atmospheric Administration Coastal Ocean Program Publication. Durham, New Hampshire.

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. Carruthers, W. Dennison, and M. Waycott. 2007. Global seagrass distribution and diversity: a bioregional model. *Journal of Experimental Marine Biology and Ecology*, 350:3-20. doi:10.1016/j.jembe.2007.06.012

Smith, R., A. Pregnall, and R. Alberte. 1988. Effects of anaerobiosis on root metabolism of Zostera marina (eel- grass); Implications for survival in reducing sediments. *Marine Biology*, 98:131-141.

Strazisar, T., M. S. Koch, C. J. Madden, J. Filina, P. U. Lara, et al. 2013. Salinity effects on *Ruppia maritima* L. seed germination and seedling survival at the Everglades-Florida Bay ecotone. *J Exp Mar Biol Ecol.*, 445: 129–139.

Steward, J., R. Virnstein, L. Morris, and E. Lowe. 2005. Setting seagrass depth, coverage, and light targets for the Indian River Lagoon System, Florida. *Estuaries,* 28:923-935.

Stout, J. P., and M. G. Lelong. 1981, Wetland habitats of the Alabama coastal zone, part 2: an inventory of wetland habitats south of the Battleship Parkway, technical publication no. 81-01, Dauphin Island: Daphne, Alabama Coastal Area Board, 47 p.

Texas Parks and Wildlife. 1999. Seagrass conservation plan for Texas. Final Report. 84pp.

Thayer, G. W., W. J. Kenworthy, and M. S. Fonseca. 1984. Ecology of eelgrass meadows of the Atlantic Coast: a community profile. Fish and Wildlife Service, US Department of the Interior, 1984.

Tinoco, A., B. Furman, K. Darnell, and B. Peterson. 2017. Submerged aquatic vegetation, topography, and flow characteristics in the upper, tidal Hudson River: Progress toward a predictive habitat model. *Aquatic Botany*, 142:53-60.

Tomasko, D., and M. Hall. 1999. Productivity and biomass of the seagrass *Thallassia testudinum* along a gradient of freshwater influence in Charlotte Harbor, Florida. *Estuaries,* 22:592-602.

Torquemada, Y., and J. Lizaso. 2011. Responses of two Mediterranean seagrasses to experimental changes in salinity. *Hydrobiologia,* 669: 21–33.

Torquemada, Y., M. Durako, and J. Lizaso. 2005. Effects of salinity and possible interactions with temperatutre and pH on growth and photosynthesis of *Halophila johnsonii* Eiseman. *Marine Biology*, 148:251-260.

Touchette, B. 2007. Seagrass-salinity interactions: Physiological mechanisms used by submersed marine angiosperms for a life at sea. *Journal of Experimental Marine Biology and Ecology*, 350:194-215. doi:10.1016/j.jembe.2007.05.037

Twilley, R., M. Kemp, K. Staver, J. Stevenson, and W. 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.

US Army Corps of Engineers (USACE). 2014a. Mississippi Coastal Improvements Program (MsCIP) – Comprehensive Barrier Island Restoration Plan Ship Island, MS. Hancock, Harrison and Jackson Counties, Mississippi.

US Army Corps of Engineers (USACE). 2014b. Mississippi Coastal Improvements Program Comprehensive Barrier Island Restoration Draft Supplemental Environmental Impact Statement. Mobile District.

US Army Corps of Engineers (USACE). 2014c. Bonnet Carré Spillway Booklet. https://www.mvn.usace.army.mil/Portals/56/docs/PAO/Brochures/BCspillwaybooklet.pdf.

US Army Corps of Engineers (USACE). 2020. Spillway Operation Information website. Accessed 09 June 2020. https://www.mvn.usace.army.mil/Missions/Mississippi-River-Flood-Control/Bonnet-Carre-Spillway-Overview/Spillway-Operation-Information/.

US Geological Survey (USGS). 2017. Measuring land subsidence. https://ca.water.usgs.gov/land_subsidence/california-subsidence-measuring.html.

Verduin, J., and J. Backhaus. 2000. Dynamics of plant-flow interactions for the seagrass *Amphibolis antarctica*: Field observations and model simulations. *Estuarine, Coastal and Shelf Science*, 50:185-204. doi:10.1006/ecss.1999.0567

Vermaat, J., and R. De Bruyne. 1993. Factors limiting the distribution of submerged waterplants in a lowland River Vecht (The Netherlands). *Freshwater Biology*, 30:147-157.

Visser, F., K. Buis, Z. Verschoren, and P. Meire. 2015. Depth estimation of submerged aquatic vegetation in clear water streams using low altitude optical remote sensing. *Sensors*, 15(10):25287-25312.

Ward, L, W. Kemp, and W. Boynton. 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Marine Geology*, 59:85- 103.

Wetzel, R., and P. Penhale. 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. *Marine Technology Society Journal*, 17:22-31.

Wood, E., W. Odum, and J. Zieman. 1969. Influences of seagrasses on the productivity of coastal lagoons, p. 495-502. In A. A. Castanares and F. B. Pflueger (eds.), Coastal Lagoons, Universidad Autonoma de Mexico, Ciudad Universitaria, Mexico.

Wright, A., and K. Reddy. 2009. Reactivity and mobility of metals in wetlands. Department of Soil and Water Sciences, UF/IFAS Extension. SL 297.

Wyllie-Echeverria, S., and J. D. Ackermann. 2003. The seagrasses of the Pacific Coast of North Merica. In: Green, E.P., and Short, F.T. (eds) World Atlas of Seagrasses, pp 199-206. University of California Press, Berkeley. 44.

Xue Z., A. Feng, P. Yin, and D. Xia. 2009. Coastal erosion induced by human activities: A Northwest Bohai Sea Case Study. *Journal of Coastal Research*, 25(3):723-733.

Yates, K., G. Morrison, and H. Greening. 2011. Seagrasses: Integrating Science and Resources Management in Tampa Bay, Florida. 63-104. http://pubs.usgs.gov,circ/1348/

York, P., R. Gruber, R. Hill, P. Ralph, D. Booth, and P. Macreadie. 2013. physiological and morphological responses of the temperate seagrass *Zostera muelleri* to multiple stressors: Investigating the interactive effects of light and temperature. PLOSONE 8:e76377

Zieman, J. 1975. Seasonal variation of turtle grass, *Thalassia testudinum* Konig, with reference to temperature and salinity effects. *Aquatic Botany*, 1:107-123.

Zieman, J. 1982. The ecology of the seagrasses of south Florida: A community profile. USFWS, Office of Biological Services, Washington, D.C. FWS/OBS-82 (reprinted September 1985).

Zimmerman, R., D. Kohrs, D. Steller, and R. Alberte. 1995. Carbon partitioning in eelgrass: regulation by photosynthesis and the response to daily light-dark cycles. *Plant Physiology*, 108:1665-1671.

Zimmerman, R., D. Kohrs, D. Steller, and R. Alberte. 1997. Impacts of CO_2 enrichment on productivity and light requirements of eelgrass. *Plant Physiology*, 115:599-607.

Zobeck, T. 2004. Rapid particle size analysis using laser diffraction. Transaction of the American Society of Agricultural Engineers. 20:633-663.

Abbreviations and Acronyms

Term	Definition
ALB	Airborne LiDAR Bathymetry
AVS	Acid Volatile Sulfides
CHL	Coastal Hydraulics Laboratory
EL	Environmental Laboratory
EMRRP	Ecosystem Management and Restoration Research Program
ERDC	Engineer Research and Development Center
ICP-MS	Inductively-Coupled Plasma Mass Spectrometry
InSAR	Interferometric Synthetic Aperature Radar
LiDAR	Light Detection and Ranging
LISHRI	Long Island Sound Habitat Restoration Initiative
LISST	Laser In-Situ Scattering Transmissometer
MDR	Mixed-Diamine Reagent
NTU	Nephelometric Turbidity Units
O/AES	Optical or Atomic Emission Spectroscopy
PLL	Percent Light at the Leaf
PLW	Percent Light through the Water

PPT	Parts Per Thousand
RGB	Red Green and Blue (aerial imagery)
SAV	Submerged Aquatic Vegetation
SEM	Simultaneously Extracted Metals
TC	Total Carbon
TIC	Total Inorganic Carbon
TOC	Total Organic Carbon
TSS	Total Suspended Solids
USGS	United States Geologic Survey

REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

1. REPORT DATE *(DD-MM-YYYY)* September 2021	**2. REPORT TYPE** Special Report	**3. DATES COVERED *(From - To)***

4. TITLE AND SUBTITLE Environmental Factors Affecting Coastal and Estuarine Submerged Aquatic Vegetation (SAV)	**5a. CONTRACT NUMBER** **5b. GRANT NUMBER** **5c. PROGRAM ELEMENT NUMBER**
6. AUTHOR(S) Eve Eisemann, Catherine Thomas, Matthew Balazik, Damarys Acevedo-Mackey, and Safra Altman	**5d. PROJECT NUMBER** **5e. TASK NUMBER** **5f. WORK UNIT NUMBER**
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Environmental Laboratory US Army Engineer Research and Development Center 3909 Halls Ferry Road Vicksburg, MS 39180--6133	**8. PERFORMING ORGANIZATION REPORT NUMBER** ERDC/EL SR-21-6
9. SPONSORING / MONITORING AGENCY NAME(S) AND ADDRESS(ES) Ecosystem Management and Restoration Research Program 3909 Halls Ferry Road Vicksburg, MS 39180-6199	**10. SPONSOR/MONITOR'S ACRONYM(S)** EMRRP **11. SPONSOR/MONITOR'S REPORT NUMBER(S)**

12. DISTRIBUTION / AVAILABILITY STATEMENT

Approved for public release; distribution is unlimited.

13. SUPPLEMENTARY NOTES

Funding Account Code U4368952, AMSCO Code 031342

14. ABSTRACT

Submerged aquatic vegetation (SAV) growing in estuarine and coastal marine systems provides crucial ecosystem functions ranging from sediment stabilization to habitat and food for specific species. SAV systems, however, are sensitive to a number of environmental factors, both anthropogenic and natural. The most common limiting factors are light limitation, water quality, and salinity, as reported widely across the literature. These factors are controlled by a number of complex processes, however, varying greatly between systems and SAV populations. This report seeks to conduct an exhaustive examination of factors influencing estuarine and coastal marine SAV habitats and find the common threads that tie these ecosystems together. Studies relating SAV habitats in the United States to a variety of factors are reviewed here, including geomorphological and bathymetric characteristics, sediment dynamics, sedimentological characteristics, and water quality, as well as hydrologic regime and weather. Tools and methods used to assess each of these important factors are also reviewed. A better understanding of fundamental environmental factors that control SAV growth will provide crucial information for coastal restoration and engineering project planning in areas populated by SAVs.

15. SUBJECT TERMS

Aquatic plants Ecosystem management Marine ecology -- Data processing Coastal ecology
Vegetation dynamics -- Data processing Restoration ecology Geomorphology Sedimentology

16. SECURITY CLASSIFICATION OF:			**17. LIMITATION OF ABSTRACT**	**18. NUMBER OF PAGES**	**19a. NAME OF RESPONSIBLE PERSON**
a. REPORT Unclassified	**b. ABSTRACT** Unclassified	**c. THIS PAGE** Unclassified	SAR	77	**19b. TELEPHONE NUMBER *(include area code)***

Standard Form 298 (Rev. 8-98)
Prescribed by ANSI Std. 239.18