

Developing the Next Suite of Tools for Setting Quantifiable Objectives for Habitat Management: Advancing our capabilities to estimate ecosystem service values for salt marsh and seagrass habitat

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January 2016



Grant acknowledgement

This report was prepared by The Nature Conservancy using Federal funds under award NA15NMF4690242 from the National Oceanic and Atmospheric Administration, U.S. Department of Commerce. The statements, findings, conclusions, and recommendations are those of the author(s) and do not necessarily reflect the views of the National Oceanic and Atmospheric Administration or the U.S. Department of Commerce.

This work should be cited as

DeAngelis, B., zu Ermgassen, P., Drake, C., Hancock, B., Kang, S., Landis, E., Piehler, M., Shepard, C., Spalding, M., zu Ermgassen, S., 2016. Developing the next suite of tools for setting quantifiable objectives for habitat management: Advancing our capabilities to estimate ecosystem service values for salt marsh and seagrass habitat. www.nature.org/habitat-objectives

Executive Summary

Coastal marine habitats provide a diverse array of ecosystem services, such as providing habitat for nursery and foraging fish, sequestering carbon, stabilizing shorelines and reducing erosion, and removing excess nitrogen. Efforts to integrate ecosystem services benefits into decision-making require a more detailed, targeted approach focusing on socio-economic drivers for sustainable use, protection and restoration of ecosystems. Central to this approach is locally accurate, spatially explicit quantification of ecosystem services using metrics that can be understood, utilized and provided at scales relevant to decision-makers. Detailed, evidence-based and spatially explicit values for ecosystem benefits produced and delivered in a clear and useful way, will lead to major changes in how ecosystems are viewed and utilized by multiple sectors.

This document is intended to describe the ‘state of the science’ for developing the applications for quantifying various ecosystem services derived from salt marsh and seagrass habitats in the U.S. and Caribbean region, that can be applied to relatively fine (bay or estuary) spatial scales. Ecosystem services discussed include fisheries enhancement from the nursery function of these habitats, habitat enhanced denitrification, carbon sequestration and coastal protection. A methodological approach is described for estimating regionally specific fisheries production from structured nursery habitats. A comprehensive review of empirical studies that can be incorporated into this fisheries production model from seagrass and salt marsh habitats is presented. This review of eligible empirical studies serves two purposes: First, it serves as an analytical tool to compare and understand the data availability and data needs of sub-regions of the U.S. and Caribbean, for each of the two habitat types. Secondly it is the initial step in producing the fisheries production models and quantification estimates, where data availability permits.

For each of the remaining three ecosystem services; denitrification, carbon sequestration, and coastal protection, the document presents a review of empirical studies. The results of the review are used to address common questions such as: Is there enough existing scientific information to build similar applications as to the one being proposed for fish production? Where does the empirical data exist by geography and habitat type? Which ecosystem services show promise for cooperatively tackling in the short-term, or where does the science need to be further developed? These are the types of analysis required to inform government, non-governmental agencies, and academics as to what our collective priorities and next steps need to be in order to significantly advance our ability to produce spatially-explicit, quantitative ecosystem service estimates. These estimates can then be applied to serve in various applications such as habitat restoration goal-setting, or applying ecosystem service credit for conservation actions.

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Chapter 1 Introduction

Coastal marine habitats are among the most valuable on earth (Costanza et al., 2014). They provide a diverse array and disproportionately high levels of ecosystem services, such as providing habitat for nursery and foraging fish, sequestering carbon, stabilizing shorelines and reducing erosion, and removing excess nitrogen (Costanza et al., 1997, Costanza et al., 2008, Newell et al., 2002, zu Ermgassen et al., 2015a, Grabowski et al., 2012, Piehler and Smyth, 2011, Barbier et al., 2011, Piazza et al., 2005, Thayer et al., 1978, Coen et al., 1998, Shepard et al., 2011, Rodriguez et al., 2014, Gittman et al., 2014). Moreover, these habitats and the fisheries they support have long formed the basis on which coastal human societies have been built (Beck et al., 2001, Barbier et al., 2011, Jackson et al., 2001). Coastal habitats such as wetlands are multiple-value systems, in that they do not just do one thing, but rather perform many of these processes simultaneously, and therefore provide a suite of values to humans (Mitsch and Gosselink, 2000). Yet, many of these services are at risk as coastal ecosystems are threatened globally through impacts such as overfishing, habitat loss, and pollution. Oyster reefs, coral reefs, seagrass beds, salt marshes, and mangroves all have experienced significant global losses (Lotze et al., 2006, Arioldi and Beck, 2007, Halpern et al., 2008, Waycott et al., 2009, Beck et al., 2011, zu Ermgassen et al., 2012). These impacts affect the many benefits coastal habitats provide to humans, putting people and communities at risk of significant economic and social loss (Costanza et al., 2014, United States Government Interagency Working Group on Social Cost of Carbon, 2015).

The impact and loss of these critical coastal ecosystems has not been ignored or overlooked. Restoring and maintaining the health of coastal ecosystems for present and future generations is now a preeminent global environmental and societal priority (Millennium Ecosystem Assessment, 2005). In the U.S. alone, hundreds of millions of public and private dollars have been invested to restore and protect coastal marine habitats. Evidence suggests the investment in restored habitat continues to increase annually (e.g. NOAA, 2015). These public and private investments are meant to recover and/or conserve the valuable ecosystem services these habitats provide. A large and growing array of ecosystem science confirms that coastal habitats are critically important and exceedingly valuable, yet this science is rarely translated into the language that could drive changes in the way we evaluate and manage nature for our many needs. Efforts to integrate ecosystem services benefits into decision-making require a more detailed, targeted approach focusing on socio-economic drivers for sustainable use, protection and restoration of ecosystems (Spalding, 2014). This approach to describe, in quantitative terms and representing spatial variability in all that the ocean does for us today, has been coined “mapping ocean wealth” by The Nature Conservancy (www.oceanwealth.org). Mapping ocean wealth will allow us to make smarter investments and decisions concerning the marine environment

by allowing us to account for their value and the distribution of those values across an array of spatial scales.

Central to this approach is locally accurate, spatially explicit quantification of ecosystem services using metrics that can be understood and utilized by decision-makers at different scales and in different socio-economic settings and assimilated into existing and new coastal and ocean management (Spalding, 2014). As described by Turner and Daily (2008), to make an ecosystem services framework operational, information has to be provided at scales relevant to decision-makers; involve practical know-how in the process of institutional design and implementation; and compelling models of success must exist in which economic incentives are aligned with conservation. The theory of change proposed through The Nature Conservancy's Mapping Ocean Wealth initiative is that detailed, evidence-based and spatially explicit values for ecosystem benefits (e.g. fish production) produced and delivered in a clear and useful way, will lead to major changes in how ecosystems are viewed and utilized by multiple sectors. This in turn will create: policy shifts and greater public/private investment in protecting and restoring valuable marine and coastal habitats; increased utilization of integrated ocean management approaches, with an emphasis on securing long-term delivery of ecosystem benefits; and a culture of stewardship and sustainable practices based on risk assessment decision-making (Spalding, 2014).

Applying the Science and Expected Outcomes

The true value in advancing the science behind ecosystem service quantification is “mechanizing” it into science-based support tools for decision-making, which can be integrated into natural resource management. By mechanizing the science, natural resource managers, communities, and other stakeholders will have the ability to manage habitats for the suite of services they provide. For example, The Nature Conservancy has been leading a project to quantify both the water filtration rate and the average production of finfish and crabs gained from area of oyster reef habitat (<http://oceanwealth.org/our-work/ecosystems/shellfish-reefs/>). Traditionally, oyster reef habitat is managed for a single ecosystem service; extraction or harvest. By developing the ‘production functions’ for water filtration and fish production from oyster habitat; decision makers can manage for maximizing or balancing multiple ecosystem services; which in turn provides habitat benefits to a wider array of people.

Changing the way people credit the value of services provided by a particular habitat is a complex process that involves well-developed science, application, and engagement strategies. Firstly, any products (e.g. scientific publications, on-line web tools, mapping portals, user-guides, policy briefings) used to influence decision-making need to be based on a robust foundation of science, and

that science should ideally be developed through a multi-expert-input scientific process. Secondly, efforts need to be made to identify the audience and understand the user-groups – i.e. their realities, needs, and limitations. Developing effective communications strategies for each stakeholder group is imperative, as those strategies may change from audience to audience. Lastly, products, deliverables and outputs need to be developed with the various audiences and user-groups in mind. These may range from highly technical products designed for resource managers and other scientists; to products with a greater focus on messaging the suite of ecosystem service values provided by a habitat or group of habitats and value of those services to people and nature. Regardless of the tone, each of the applied products needs to be based on that foundation of science noted above.

Objective of this Document

This document is intended to describe the ‘state of the science’ for developing the applications for quantifying various ecosystem services derived from salt marsh and seagrass habitats in the U.S. and Caribbean region, that can be applied to relatively fine (bay or estuary) spatial scales. Ecosystem services discussed include fisheries enhancement from the nursery function of these habitats, habitat enhanced denitrification, carbon, and coastal protection. We describe in detail a methodological approach for estimating regionally specific fisheries production from structured nursery habitats. This methodology was recently applied to oyster reef habitat (zu Ermgassen et al., 2015a), but could be applied to salt marsh and seagrass habitats where the data permit. To this end, we then present a comprehensive review of empirical studies that can be incorporated into this fisheries production model from seagrass and salt marsh habitats. This review of eligible empirical studies serves two purposes: First, it serves as an analytical tool to compare and understand the data availability and data needs of sub-regions of the U.S. and Caribbean, for each of the two habitat types. Secondly it is the initial step in producing the fisheries production models and quantification estimates (see methods below), where data availability permits.

For each of the remaining three ecosystem services; denitrification, carbon sequestration, and coastal protection, we present a review of empirical studies. We use the results to address common questions such as: Is there enough existing scientific information to build similar applications as to the one being proposed for fish production? Where does the empirical data exist by geography and habitat type? Which ecosystem services show promise for cooperatively tackling in the short-term, or where does the science need to be further developed? These are the types of analysis required to inform government, non-governmental agencies, and academics as to what our collective priorities and next steps need to be in order to significantly advance our ability to produce spatially-explicit, quantitative ecosystem service estimates. These estimates can then be applied to serve in various applications such as habitat restoration goal-setting, or applying ecosystem service credit for conservation actions.

Salt Marsh and Seagrasses

Coastal wetlands describes a diverse array of habitats that can include salt marshes, mangrove swamps, freshwater forested swamps, flat-woods, freshwater marshes, shrub depressions and wetlands adjacent to tidal rivers salt marshes, bottomland hardwood swamps, fresh marshes, mangrove swamps, and shrubby depressions (Dahl and Stedman, 2013). In the U.S., salt marsh and seagrass habitats, specifically, have received particular attention by the conservation and restoration community, and both are identified as priority habitats for restoration focus by the U.S. government (<http://www.habitat.noaa.gov/restoration>).

Seagrasses are submerged flowering plants that can form dense communities growing in bays, estuaries and shallow coastal waters. Globally, there are about 60 species of seagrasses grouped into 13 genera and 5 families (Short et al., 2001). At least 13 species are recognized to occur in U.S. waters (Fonseca et al., 1998). Seagrasses anchor themselves to the seafloor with their root systems. A strong root structure allows seagrasses to withstand strong currents and waves, especially during storm events. Seagrasses beds can be either monospecific or mixed, where more than one species coexist. In temperate areas usually one or a few species dominate, such as *Zostera marina* in the North Atlantic, whereas tropical beds usually are more diverse. Higher density seagrass meadows are typically associated with lower energy environments, softer sediments, and higher nutrient availability, although seagrasses can be found in higher-energy environments with courser sediments as well. Seagrasses have a wide distribution globally, and across the U.S. (Short et al., 2001). Physical controls on seagrass distribution include light availability (a combination of water clarity and depth), tide and water movement, salinity, temperature, anthropogenic influences and climate change (Short et al., 2001).

Tidal marshes are wetland habitats often associated with protected or lower-energy environments. Tidal marshes serve as the interface between marine and terrestrial habitats, and thus are effected by fresh-water (e.g. upland source ground and stream water), and salt water (tidal inundation). The inundation frequency of salt water is dictated by tidal fluctuations. The term salt marsh describes a subset of the broader term tidal marsh, in that the flooding waters are more saline than fresh. The halophytic plants associated with salt marshes form dense emergent structure. Plant zonation results from species-specific adaptations to physical and chemical conditions. The low marsh is located along the seaward edge of the salt marsh and is usually flooded at every tide and exposed during low tide. In the U.S., *Spartina alterniflora* (tall form) dominates the low marsh. The high marsh lies between the low marsh and the marsh's upland border. The low marsh typically occurs in relatively narrow bands fringing the seaward edge, while the high marsh can occupy relatively large swaths of area. The high

marsh is generally flooded only during higher than average high tides. Salt meadow cordgrass (*S. patens*) is the highly dominant species of the high marsh. Salt marsh formation and zonation is a complex and dynamic process that involves both environmental and biological factors, including climate (temperature and rainfall), hydrology (tidal inundation and wave energy), and physical factors (elevation and slope, sediment and soil composition, and surface water and soil salinity), as summarized by U.S. Fish and Wildlife Service, 1999. In the U.S. the majority of salt marshes exist along the east coast and Gulf of Mexico coastline. Salt marshes are less prevalent on the Pacific coast of the U.S. due to the lack of extensive coastal plain and steep topographic relief between land and sea (Dahl and Stedman, 2013).

Ecosystem Services of Seagrasses and Salt marshes

The roles that seagrasses and salt marshes serve in coastal ecosystems have been extensively documented (Thayer et al., 1975, Thayer et al., 1984, Zieman and Zieman, 1989, Vernberg, 1993) and the understanding of their importance in coastal ecosystems is widely accepted. The high degree of attention these two habitats have received is due, in part, both to the extensive degradation and disappearance of these habitats (Lotze et al., 2006, Orth et al., 2006, Waycott et al., 2009, Dahl and Stedman, 2013), as well as the critical services they provide to people and nature ((Boesch and Turner, 1984, Costanza et al., 1997, Bell, 1997, Beck et al., 2001, Heck Jr. et al., 2003a, Duarte et al., 2005, MacKenzie and Dionne, 2008, Mitsch and Gosselink, 2000, Barbier et al., 2011, Shepard et al., 2011, Pendleton et al., 2012, Ouyang and Lee, 2013, Seitz et al., 2013).

Seagrasses exert a major influence on the coastal ecosystem due to their high productivity and very fast growth rates. They serve as a primary food source as the photosynthetically fixed energy from the seagrasses may be grazed upon directly or utilized as detritus as the leaf material decays. The structure created by the seagrass beds serve as nursery grounds providing food and shelter, particularly for a variety of juveniles finfish and other crustaceans (Heck Jr. et al., 2003b). Seagrasses provide coastal protection services by attenuating waves and currents via above-ground shoots and stabilizing sediments by way of below-ground biomass of rhizomes and roots (Ward et al., 1984, Fonseca and Cahalan, 1992, Christianen et al., 2013). Bacteria in the seagrass rhizosphere and surrounding sediment have been shown to fix nitrogen (Miyajima et al., 2001, Welsh et al., 2000a), and seagrasses have been shown to take up nutrients from the sediments, releasing the nutrients into the water column through the leaching or decay, thus acting as a nutrient pump (Risgaard-Petersen et al., 1998, Hemminga et al., 1991).

Salt marshes also provide many critical services including having high rates of primary productivity and providing habitat for many marine species. Salt marshes protect upland areas, including valuable

residential and commercial property, by attenuating waves, storing floodwaters and stabilizing shorelines (Gedan et al., 2010, Shepard et al., 2011, Moeller et al., 1996). Salt marshes improve water quality by filtering pollutants (Valiela and Cole, 2002, White and Howes, 1994), and can influence the biogeochemical cycling of various materials, especially phosphorus, nitrogen, and carbon (Boynton et al., 2008). In addition, salt marshes are highly regarded for their recreational use by millions of people who utilize salt marshes for canoeing, kayaking, wildlife viewing and photography, recreational fishing and hunting.

More detail regarding the provision of ecosystem services from salt marsh and seagrass habitats is given in the following sections.

The Need for Spatial Habitat Data

As we develop a detailed understanding of the value of coastal wetlands there is a clear opportunity to use this information to support and influence management decisions. The value of habitats, however, varies considerably from place to place, so it is critical to know where and to what degree ecosystems provide benefits. Spatial data of habitat quality, extent and structure can be central both to the quantification of value and in the development of spatially relevant management decisions. With information about spatial variation in habitat structure, ecosystem service production function models can map variation in services provided by habitats for people across a landscape. Where ecosystem service models are combined with habitat maps it is also possible to develop alternate scenarios. This would allow the costs and benefits of different management interventions to be assessed, such as the future benefits from restoration or the losses that will be incurred if an ecosystem is lost. Therefore, maps of habitat are important in a single time step to understand spatial variation and through time to understand and forecast change in ecosystem services under alternative scenarios.

Despite the importance of spatial data, they are often unavailable to decision-makers at the scale or format required. At global scales indeed spatial data for these two critically important habitats is largely unavailable. However, the United States is better off than many other countries in terms of data availability. For example, salt marshes have been mapped across most states, and many larger areas of seagrass are also mapped (Dahl and Stedman, 2013, Commission for Environmental Cooperation, 2016, USFWS National Wetlands Inventory). Despite the apparent availability of spatial data, the science behind quantifying area-based ecosystem services is still developing. Different ecosystem services may rely on different spatial data needs. Thus, the availability of presence/absence data may not be sufficient, but rather, identifying characteristics that influence services may be equally critical. For example, preliminary investigation into modeling fish production from salt marsh habitat suggests that calculating area of the marsh edge – or most seaward line of

vegetation – will be the most critical attribute of salt marshes for fish production. However, to use maps to estimate wave attenuation or shoreline stabilization provided by area of salt marsh, the spatial data may have to provide additional marsh characteristics to differentiate mapped areas (e.g. grass density, marsh height, etc.). Thus, basic questions need to be considered prior to investing considerable effort into generating new maps to evaluate ecosystem services.

Furthermore, mapping ecosystem services at local scales requires very detailed understanding and modelling around ecological, social and economic variables. Ecosystem service-related habitat maps are often generated at the global or regional scale. While these maps have an important and useful function in communicating spatial variability of ecosystem services, or summarizing information across and within regions, they are insufficient for more localized decision making when evaluating ecosystem service provision of a given habitat. The approach of developing ecosystem service production functions discussed in this document assumes a relatively localized spatial resolution (i.e. bay and/or estuary level). Compiling and standardizing habitat maps at this spatial resolution requires complicated and potentially expensive investment.

Mapping of coastal habitats is generally undertaken using one of a few different approaches: measuring actual area of habitat extent, referred to as polygons, mapped using remote sensing; lengths of surveyed shoreline; or point data that is typically obtained through field observation, and may be as minimal as presence/absence. For the purposes of estimating ecosystem services delivered by area of a particular habitat, only polygon data is an applicable mapping technique. To obtain polygon-mapping data at a national-scale, two general approaches can be taken. The first would be to compile a “patchwork” compiled map based on existing spatial data. The advantages of this approach are that it does not require further physical mapping efforts as it relies on existing data and spatial data collected at finer scales is often of high quality. The disadvantages of this type of approach are that the different individual mapping efforts occur at different scales or resolutions and the compiled map is therefore difficult to update. Furthermore it relies on the data already being readily available and complete. The second approach would be to produce national-scale habitat maps from scratch, using remote imagery (i.e. orthophotography or satellites imagery) and a standardized methodology. Such an approach is costly, but would generate a consistent dataset, with a replicable approach enabling the quantification of trends over time. In addition to cost, this approach is challenged by the need for extensive field verification. Salt marshes have somewhat varied spectral signatures, and there are many adjacent wetland habitats which will be very difficult or impossible to disaggregate using entirely automated procedures. These challenges are even greater for submerged vegetation such as seagrass, where water clarity, surface reflectance, and depth further influence and hide spectral features, particularly of sparse communities (Ferguson et al., 1993, Mumby et al., 1999).

The hurdles and questions raised here need to be tackled in partnership. Habitat mapping is not new, and is being conducted at various degrees by many federal, state and non-governmental organizations – and as such extensive data already exists in various locations, particularly for salt marshes, and somewhat less so for seagrasses (Short et al., 2006). How existing mapping data could, or should, be used to estimate ecosystem services needs to be addressed. Different agencies and organizations compiling maps have different needs, interests, users, and areas of focus and expertise. Instead of these differences deterring working in partnership, however, collaboration should be encouraged. This is unlikely to happen unless a dedicated effort is made to centralize and standardize approaches to develop spatially-explicit habitat maps for evaluating ecosystem services.

Chapter 2 Estimating Fisheries Production from Salt Marsh and Seagrasses

The importance of coastal marine habitats serving as juvenile nurseries has been an accepted paradigm in fisheries science for well over a century (Beck et al., 2001). While investments in coastal habitat conservation and restoration have been undertaken to achieve various and multiple ecosystem services, the enhancement of fisheries production has remained a primary motivation in these investments. For example, the National Oceanic and Atmospheric Administration, National Marine Fisheries Service specifically identifies supporting commercially and recreationally important species as a programmatic mission achieved through coastal habitat conservation and restoration (www.habitat.noaa.gov). Unfortunately, despite being identified as a clear need (e.g. Peterson and Lipcius, 2003), the tools to quantify ecosystem services expected from conservation actions and/or restored habitat have not developed alongside the investments in habitat conservation and restoration, and fisheries production is no exception.

Quantifying fish production of natural habitat, such as salt marshes or seagrasses, involves complex, often expensive, dedicated studies. Fish production provided by a habitat may vary in regard to habitat size, location, and geographic distribution. Multiple studies are required to model the production values per unit area of a given habitat type. For many of these habitats, numerous individual studies have been published in the literature, and often many more exist in the grey literature. Using a meta-analysis approach, these individual studies can be combined to create models to predict the augmented fish production values provided by a given area of habitat (e.g. Peterson et al., 2003, zu Ermgassen et al., 2015a).

Here we describe a methodology originally developed by Peterson et al. (2003), and later revised by zu Ermgassen et al. (2015a) for estimating the fisheries production of oyster reef restoration in the south eastern United States, and the Gulf of Mexico and south and mid-Atlantic, respectively. A similar approach was used by Watson et al. (1993) to estimate the value of enhancement by seagrass to the penaeid shrimp fishery in northern Queensland, and by Blandon and zu Ermgassen (2014b, 2014a) to develop quantitative estimate of commercial fish enhancement by seagrass habitat in southern Australia. These methods combine quantitative abundance data of juveniles utilizing the nursery habitat, with established growth and mortality relationships to estimate the fish biomass enhancement for species over their lifetimes that can be attributed to the presence of the habitat. The method is based on the assumption that habitat can limit fish recruitment where nursery habitats have been severely reduced in extent.

Methods of Estimating Fish Production

To apply this methodology to other coastal habitats in United States, the initial step involves a review of the literature to identify studies that fulfill the following criteria: 1) conducted in the U.S. and Caribbean, 2) includes data on individual fish species and their density in both the habitat in question (seagrass or salt marsh) and an unvegetated control, and 3) uses sampling techniques that are strongly biased towards the sampling of young of year fish. From the literature available, data will be standardized to represent the mean number of individuals per m^2 . To determine which species show signs of enhancement by the habitat a series of criteria should be applied: 1) There must be life history information indicating the species benefits from structured habitat; 2) the weighted mean of the on, minus off, habitat densities must be positive; 3) the species must be more abundant on than off habitat in more than half of the independent sampling events; 4) the species must be represented by data from at least two geographically independent estuaries. Species meeting these criteria can be deemed enhanced by the habitat.

Production Calculations

The enhancement in production that can be attributed to the presence of a particular nursery habitat is determined by applying known growth and mortality relationships to the enhanced density of juveniles on the structured habitat, where the term “enhanced density” refers to the weighted mean of the density within habitat minus the density in the unstructured control. The number of surviving individuals at time t , $N(t)$, is calculated from $dN/dt = -M(t) N$, where $M(t)$ is the species-specific and size-dependent natural mortality. Size dependent mortality is computed as $M(t) = M (L_m/L(t))$, following Lorenzen (2000), where $L(t)$ is the length at time t and L_m is the length of recruitment to the fishery, or length at maturity if age or length of recruitment to the fishery is unavailable. Estimates of M found in the literature will be assumed to represent the natural mortality at size L_m . In cases where L_m was unknown, it can be calculated from L_{inf} (Froese and Binohlan, 2000).

Given $N(t)$, the rate of production is computed as $dP/dt = N(t) dW/dt$, where P is production, W is weight and t is time. Integrated over time, this formula gives an estimate of gross production (P_g) including both living individuals and individuals that died in the intervening time period. The growth rate, dW/dt , is computed using the von Bertalanffy growth equation to compute the mean length of individuals at a given age and applying published length-weight relationships to convert this to weight as a function of time. Gross production from a single recruitment event is computed by integrating this production rate from the age at which the species is sampled on the habitat (often c. 0.5 years) to the estimated maximum lifespan (t_{max}) for each species. This calculation is also equivalent to the annual production in a steady state, assuming annual recruitment.

Estimates of Uncertainty

The modelling approach allows uncertainty around the estimates to be calculated. This allows managers to visualize and account for the stochastic variability in recruitment that would be expected in the wild. The production enhancement attributable to habitat will vary spatially and the variability expressed as uncertainty in the production estimates may be used to account for intra-region variability. The estimated variability arises from differences in initial density of species between sites and sampling events. Managers seeking to use the predicted enhancement values can therefore assess the likely benefit on the basis of species presence and relative abundance at the site, with benefits likely to be lower where a species is rare relative to where it is abundant.

To compute the uncertainty around the calculations of the enhancement in fish production, the enhanced density is modeled as a normal distribution, modified such that if a negative value is drawn from the distribution, the density is set to zero. This results in a mixed probability distribution, with a continuous probability distribution for positive enhancements, plus a non-zero probability that the enhancement is the discrete value of zero. The parameters of the normal distribution are chosen such that the mean and standard deviation of the mixed distribution match the mean and standard error determined from the raw data on juvenile densities. The appropriate parameters for the normal distribution are found numerically using the Hybrid root finding algorithm. Negative enhancement values are truncated because the presence of habitat does not lead to a decrease in fish abundance, but not all fish are present at all sites and may therefore have zero abundance.

Estimates of enhanced productivity and uncertainty are calculated by drawing one hundred thousand samples independently from the modeled distribution of enhancements. Thus the mean, standard deviation and lower and upper quartiles of the distribution of productivity enhancements can be computed for each fish species, and for all species combined. Due to the lack of available scientific knowledge regarding variability in other life history parameters, all other life history parameters were assumed to be invariant.

Applying the Results of the Model

The proposed methodology for quantifying the fish production arising from the nursery function of structured coastal habitats provides us with an estimate of the biomass and production of fish arising from the enhancement of juveniles in the presence of the nursery habitat. It also provides us with estimates of the uncertainty or variance in these estimates. The results are presented in units of mass per area of habitat. As such, these estimates can be applied to situations where there is an interest in understanding the ecosystem service provision for a given area of habitat. In the case of oyster reefs, there was sufficient data for the results to be developed on a regional scale. This scale was chosen as the optimum scale for trading off accuracy (in that each region may be expected to support different

populations of similar species, may support a different community of species, or may be managed independently from a fisheries perspective), against data quantity. Where possible, estimates should be derived for regions independently, as regions often represent different communities and underlying levels of productivity (zu Ermgassen et al., 2015a, Spalding et al., 2007). When applying these estimates to a particular location within each region, however, minor adjustments should be made to the estimates to reflect the knowledge of the site. For example, a fish may be enhanced across the region, but be absent or rare within the site of interest. The overall estimates of enhancement should therefore be modified to reflect this local knowledge.

While the outputs of this model present quantitative estimates of fish production from the nursery value of structured coastal habitats, they are not without limitations. Firstly, as a modelled estimate, they should not replace the valuable role of field sampling in locations where the true value is required. Secondly, the values presented from a given analysis reflect only the data already available and included in the study at the time of its development. As applicable new studies become available, the methodology should be repeated in order to reflect the best current knowledge of any habitat. Thirdly, there are a number of important assumptions which must not be violated when applying the model results to real world problems. This includes the assumption of habitat limitation. Finally, this modelling approach considers fish production independently of all other ecosystem services, and provides an estimate for each habitat in isolation (i.e. does not account for a mosaic of habitats on a landscape scale). Including interactions with other habitats or ecosystem services is an important and necessary next step in applying this quantification methodology. The issues summarized here are revisited in more detail below. As the science and practice of quantifying and managing for ecosystem service provision develops, targeted conversations between experts and practitioners need to occur in tandem to develop consistent policies and practices for understanding and accounting for assumptions and limitations.

What is meant by limiting habitat?

The model relies on the assumption that habitat limits the recruitment of impacted fish species. In such a scenario the presence or addition of habitat increases the number of individuals recruiting to the population either as a result of enhanced settlement rates of larvae (Eckman, 1987) or lower post-settlement mortality of newly settled individuals (Heck Jr. et al., 2003b)). This

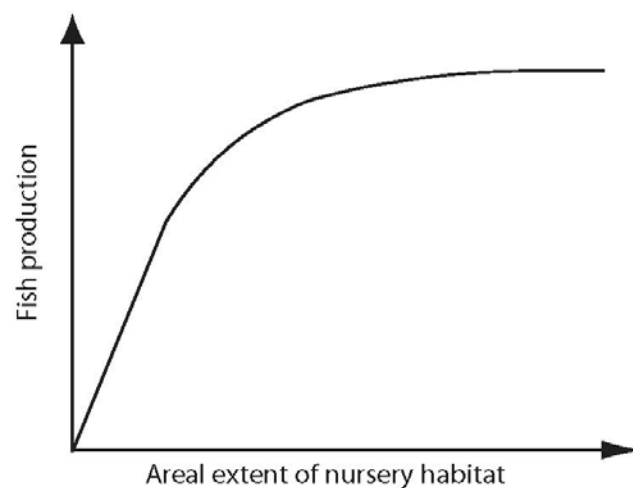


Figure 2-1. Theoretical relationship between habitat extent and fish production. Modified from zu Ermgassen et al. 2015

underlying assumption of habitat limitation critically underpins the representation of enhancement as a constant value per unit area (such as output by the model). While this may be a reasonable assumption where habitats are at a fraction of their historic extent, the exact area required for habitat to cease to be the limiting factor to juvenile recruitment and enhancement is unknown. The nature of the relationship between habitat and fish enhancement is also unknown, but is likely to take a form similar to that depicted in Figure 1 (zu Ermgassen et al., 2015a). At or nearing the point of asymptote, it would no longer be appropriate to apply our estimated values of enhancement. Further research is necessary to inform our understanding of the relationship between areal habitat extent and fish production, as well as how this relationship should be applied to current situations. Conversation with experts and practitioners needs to be undertaken to inform guidelines for managers to assess when it is appropriate to apply this methodology. Until such time, the application of these results to areas with extensive habitat remaining should be avoided, and care should be taken when applying this methodology to extensive restoration efforts. That said, the highly degraded nature of many coastal habitats in the USA strongly suggest that this methodology can currently be widely applied.

How do ecosystem services interact with each other's provision?

It is now widely illustrated that different ecosystem services may have different response curves with regard to habitat quality and extent (zu Ermgassen et al., 2015b). Even if the quantitative provision of services is closely matched, the perceived value of different services may differ greatly spatially as stakeholder opinion varies. Therefore, while this methodology only provides us with the means of quantifying a single ecosystem service from structured coastal habitats, we strongly urge decision makers to consider the suite of potential ecosystem services provided by a habitat in their decision making (Chan et al., 2011).

How do ecosystem services from different habitats interact?

The approach outlined here provides us with an estimate of the fish enhancement arising from the nursery function of each habitat independently. Coastal habitats, however, exist in a mosaic of different habitats across a landscape, rather than in isolation. It is therefore possible that there are locations where, for example, seagrasses may have declined and are rare, but other structured habitats are healthy or increased in area. In these situations, the degree to which species may utilize either habitat becomes important in assessing the ecosystem service value of either. The degree of redundancy (similarity in service provision) between coastal habitats is poorly elucidated (Heck Jr. et al., 2003b, Grabowski et al., 2005, Fodrie et al., 2015). Through our examination of multiple habitats using the outlined methodology we hope to elucidate this relationship to better inform the applicability of these models to practical, real world problems.

Literature Review

A structured review of published, peer-reviewed literature was undertaken to identify the regions and habitats for which sufficient data may currently be available to warrant applying the above described methodology for deriving fish and mobile crustacean enhancement. The structured review sought to identify studies sampling nekton and macrobenthos from seagrass or salt marsh habitats in the following regions of the U.S.: Southern and Mid Atlantic coast (defined as south of Cape Cod), Northern Atlantic Coast (north of Cape Cod), Pacific coast (inc. Alaska and Hawai'i), Gulf of Mexico, as well as the Caribbean. In addition, a review of studies sampling oyster reef habitat on the Pacific coast and in the Caribbean was undertaken. A complete list of search terms can be found in Table 1.

Studies were deemed appropriate if they fulfilled the criteria as in (zu Ermgassen et al., 2015a) outlined above. Additionally, in order to facilitate the assessment of species should the model be applied, information regarding the number of estuaries represented in the data set and the number of seasons sampled was also collated. Estuaries were defined by the NOAA CAF classification and seasons were defined as March - May (Spring), June - August (Summer), September - November (Autumn), and December - February (Winter). This information was combined to calculate the number of independent sampling events represented by each study, where an independent sampling event is defined as sampling within a season and/or estuary unit. Data for sampling events occurring in winter are excluded from our analysis as in (zu Ermgassen et al., 2015a).

Salt marsh habitats are critically important for fish, however, it is well illustrated in the literature that marsh edge is significantly more important and frequently used than inner marsh areas which are inundated for shorter periods (Baltz et al., 1993, Rozas, 1995, Minello and Rozas, 2002).

Furthermore, inner marsh habitat was rarely sampled and therefore poorly represented in the data ($n < 5$). We therefore determined that including inner marsh alongside marsh edge would only serve to increase the noise in the data rather than contribute to constraining our estimates in the future. For the purpose of this review, marsh edge is defined as the region 3m into the marsh from the marsh-water interface to the unvegetated habitat immediately adjacent to the marsh-water interface (Neahr et al., 2010)(Stunz et al. 2002). Data from marsh creeks as opposed to marsh edge were similarly excluded. Marsh creek width was rarely noted in the text and given that creeks represent a fundamentally different habitat type from the marsh edge (Baltz et al., 1993, Peterson and Turner, 1994), we once again determined that their inclusion was not conducive to improving estimates of a salt marsh fish production function. All seagrass versus control studies were included in this review.

Table 2-1. Search terms and combinations used in the literature review.

Fixed search terms	Habitat-specific search terms	Region-specific search terms
<p>Nekton</p> <p>Fish</p> <p>Habitat</p> <p>Community</p> <p>Density</p> <p>Abundance</p> <p>Unvegetated</p>	<p>Seagrass</p> <p>SAV</p> <p>Salt marsh</p> <p>Spartina</p> <p>Oyster reef</p>	<p>Caribbean</p> <p>Antigua</p> <p>Barbuda</p> <p>Cuba</p> <p>Dominica</p> <p>Dominican Republic</p> <p>Martinique</p> <p>Saint Barthelemy</p> <p>Saint Martin</p> <p>Grenada</p> <p>Haiti</p> <p>Jamaica</p> <p>Aruba</p> <p>Curacao</p> <p>Sint Maarten</p> <p>St Kitts (and Nevis)</p> <p>St Lucia</p> <p>St Vincent</p> <p>Grenadines</p> <p>Trinidad</p> <p>Tobago</p> <p>Anguilla</p> <p>British Virgin Islands</p> <p>Cayman Islands</p> <p>Montserrat</p> <p>Puerto Rico</p> <p>US Virgin Islands</p> <p>Bahamas</p> <p>Turks Islands</p> <p>Caicos Islands</p> <p>Atlantic</p> <p>Florida</p> <p>Georgia</p> <p>South Carolina</p> <p>North Carolina</p> <p>Virginia</p> <p>Maryland</p> <p>Delaware</p> <p>New Jersey</p> <p>New York</p> <p>Connecticut</p> <p>Rhode Island</p> <p>Massachusetts</p> <p>New Hampshire</p> <p>Maine</p> <p>Pacific</p> <p>California</p> <p>Oregon</p> <p>Washington</p> <p>Alaska</p> <p>Hawaii</p> <p>Gulf of Mexico</p> <p>Florida</p> <p>Mississippi</p> <p>Louisiana</p> <p>Alabama</p> <p>Texas</p>

For a number of regions which were particularly data deficient, most notably the Caribbean, we recorded studies that sampled using inappropriate sampling methodologies in order to thoroughly convey what data is currently available. For example, we identified no appropriate studies for Caribbean seagrasses, but recorded all passably relevant studies to provide an overview of what data is currently available (see Table 2).

The review was conducted from 6/20/14-8/20/14 and from 10/12/15 – 11/8/15 using Google Scholar. For each permutation of region and habitat type, multiple searches were conducted using different combinations of fixed and habitat-specific search terms. The search was terminated once five consecutive Scholar pages yielded no appropriate papers. A shorter Google search was also conducted for each region to identify appropriate grey literature. This yielded no extra results. A subset of search terms was also applied in PubMed and Web of Knowledge, but these were found to yield no additional studies. Relevant papers were read and any novel sources identified in the text were also obtained and included in the review.

Results

Our review identified a total of 64 appropriate studies of fish enhancement by salt marshes and seagrasses across all regions. The Gulf of Mexico was particularly well sampled for both salt marshes and seagrass habitats, as were seagrasses on the Southern and Mid Atlantic coast (see Table 1). Full details of the identified studies are given in Appendices I - III.

Several regions were identified as data deficient (Table 2), meaning that at this stage there is not sufficient data to warrant developing a fish production function for those region and habitat combinations. Sufficient data were, however, identified for seagrasses and salt marshes in the Gulf of Mexico, and seagrasses on the Southern and Mid Atlantic coast. For these habitats and regions, we found a minimum of 11 studies for each containing appropriate data, sampled from a minimum of eight estuaries / bays across the regional coastlines and representing a minimum of 54 independent sampling events each (see Table 2).

Salt Marsh

While salt marsh fish sampling is well represented in the literature, there is a strong regional bias. As such, we found that only one region, the Gulf of Mexico, is currently well enough represented to undertake a full meta-analysis and determine fish production functions. The spatial distribution of studies in the Gulf of Mexico is diverse, with 18 papers providing suitable data, representing samples from all five Gulf states and 78 independent sampling events. That said, Galveston Bay is heavily overrepresented relative to other estuaries on the Gulf coast, with Rozas et al. 2007's 11-year synoptic study representing 33 of the independent sampling events for Gulf salt marsh ((Rozas et al., 2007) see Appendix I). We do not, however, believe that this undermines the robustness of our analysis, as

Galveston Bay's salt marsh complex is considered highly representative of other estuaries across the Gulf coast.

All other regions were represented by too few studies to allow for a robust meta-analysis of enhancement. The Southern and Mid Atlantic coast was represented in only eight studies. This small number of studies nevertheless represents a large number of independent sampling events ($n=52$). The majority of these sampling events ($n=18$) are, however, from a single estuary, Delaware Bay (Able et al., 2007). A greater geographical spread and a greater number of studies on the Southern and Mid Atlantic coast is therefore required before we would be able to perform a robust enhancement analysis.

The Northern Atlantic and Pacific coasts, are even more data poor, with only three publications identified representing 18 independent sampling events from just four bays across both regions combined (Table 2). The geographic spread of studies was also limited, with both Pacific studies undertaken in California, and only Maine sampled on the Northern Atlantic coast (Appendix I). Both more and more geographically diverse data is required to perform analyses on these coastlines. No appropriate data were identified for the Caribbean, which is perhaps not surprising given the very limited extent of the habitat in this region.

Seagrass

Two regions were found to be represented by sufficient data to undertake a further meta-analysis and develop fish production models for; the Gulf of Mexico and the South and Mid Atlantic. Eighteen appropriate studies were identified for seagrass habitats in the Gulf of Mexico. These represent a good geographical spread, with no estuaries heavily overrepresented and every state apart from Mississippi represented. In the case of the South and Mid Atlantic we found 11 appropriate studies. Similarly these represented a good geographical spread, with data from seven Atlantic states and a relatively well balanced distribution of the sampling effort across the different states (see Appendix II). We identified six appropriate studies on seagrass macrofauna on the Northern Atlantic coast, representing 102 independent sampling events, and a further four Canadian studies not included in this U.S. summary. The very high number of independent sampling events is almost entirely driven by trawl data from Maine collected by Mark Lazzari from 1999-2009 ($N=97$) (Lazzari, 2002, Lazzari and Stone, 2006, Lazzari, 2013, Lazzari, 2015). In this case the shortage of appropriate studies undertaken at a diversity of locations prevents us from conducting a robust enhancement analysis on the region, as the current methodology requires each species to be represented in multiple studies to ensure robustness in the estimates. More studies representing greater geographical diversity are required before this analysis could be taken forward.

Only six papers were found containing relevant data on seagrass fish and macroinvertebrates on the Pacific coast of the U.S. Of these, four contained data that are likely to be incompatible with our proposed methodology. The geographical spread of this data is, on the other hand, appropriate, with only Alaska unrepresented out of the mainland Pacific coast states. This is not problematic as Alaska should likely be considered an independent region in these analysis in any case (Spalding et al., 2007). Finally, six relevant studies were identified for the Caribbean. It is likely, however, that all six studies used sampling methodologies incompatible with our analysis. The Bahamas are heavily overrepresented in this data.

Oyster Reef

The fish production function for oyster reefs has already completed been for the Atlantic and Gulf coasts (zu Ermgassen et al., 2015a). Here we therefore explored only data from the Pacific coast and the Caribbean. No appropriate studies from the Caribbean were identified, and four relevant studies were identified for the Pacific coast, although three of these have sampling methodologies that may be incompatible with our analysis (see Appendix III). As such, significant further scientific sampling of these habitats is required in these regions before the contribution of oyster reefs to fish production can be quantified.

Summary

Our literature review identified a promising wealth of available data on the densities of juvenile fish and mobile invertebrates in seagrasses and salt marshes in the U.S.. The spatial distribution of the data is, however, highly uneven. This has the positive impact that there are a handful of regions for which we believe there are sufficient data to develop region specific fish production functions, including seagrass and salt marshes in the Gulf of Mexico, and seagrass habitats in the southern and mid Atlantic. We have also identified a number of regions for which there are significant data needs before such models could be developed, in particular appropriate sampling of these coastal habitats is predominantly lacking on the Pacific coast and in the Caribbean. We therefore recommend and encourage further study of these habitats in these regions in order to support the future development of such models.

Finally, while not explicitly explored in this review, assessment of the available literature identified a number of missing attributes in the available literature, which may be useful in refining future iterations of such ecosystem service models. These focus primarily on attributes of the habitat, such as stem density, patch size and species composition. Little is currently known regarding how these factors might influence the fish production function of these habitats, and they therefore warrant further investigation.

Table 2-2. Summary of the number of sampling events and papers providing appropriate data for the different habitat types by region. Some papers have been categorized as possibly containing inappropriate data, with further analysis required to determine whether the sampling methodologies used in these papers are appropriate for our analyses. Where this is the case, the number of independent sampling events (n) has been given as a range, from a maximum of all of the studies being considered appropriate, to a minimum of none of the studies being included in the analysis.

Habitat Type	Region	Number of States sampled	Number of different bays / estuaries sampled	Number of papers	Number of those papers whose data may be inappropriate	Maximum n	Minimum n
Salt marsh	Northern Atlantic Coast	1	2	1	0	6	
	Southern and Mid Atlantic Coast	6	9	8	2	52	41
	Pacific Coast	1	2	2	2	11	0
	Gulf of Mexico	5	13	19	0	78	
	Caribbean	0	0	0	0	0	0
Seagrass	Northern Atlantic Coast	2	10	6	0	102	
	Southern and Mid Atlantic Coast	7	8	11	0	57	
	Pacific Coast	3	8	6	4	24	6
	Gulf of Mexico	4	14	18	0	54	
	Caribbean	5	na	6	6		0
Oyster Reef	Atlantic Coast			<i>analysis already completed</i>			
	Pacific Coast	3	6	4	3	15	3
	Gulf of Mexico			<i>analysis already completed</i>			
	Caribbean	0	0	0	0	0	0

Chapter 3 Enhancement of Denitrification by Salt Marsh and Seagrasses

Nitrogen availability is a critical feature of coastal ecosystem function in that it limits primary productivity in most systems worldwide. However, changes in human activities on land, particularly over the past half-century, have led to significant increases in the delivery of nitrogen to coastal systems (Vitousek et al., 1997). Concomitant with the increase in loading of nitrogen has come high rates of loss of the habitats recognized as sinks for nutrients (Orth et al., 2006, Gedan et al., 2009). Much of the nitrogen removed by habitats identified as sinks occurs through denitrification, a microbially-mediated process that converts bioavailable nitrate to inert nitrogen gas. Increased nutrient loading and habitat loss are critical drivers of the broad increase in the prevalence and severity of eutrophication in coastal systems worldwide (Bricker et al., 2007).

Salt marshes and seagrass beds occur in shallow subtidal and intertidal areas of coastal ecosystems, and therefore usually at the land-water interface. Their position in the landscape and the physical structure provided by their vegetation enhances the degree to which they are exposed to dissolved and particulate materials in the water column. They baffle flow, thus enhancing transport of materials from the water column to the sediments. Salt marsh and seagrass habitats therefore tend to have sediment with higher organic matter content than adjacent unstructured habitats. Enhanced sediment organic matter promotes both active microbial activity and the development of biogeochemical gradients (especially oxygen). The presence of oxic and anoxic sediments in close proximity and an active and diverse microbial community contribute to make these habitats areas of enhanced nitrogen transformations (Eyre et al., 2011).

Studies of nitrogen cycling in coastal habitats such as salt marshes and seagrasses have been ongoing for many decades. Over the last 30 years there has been an increased emphasis on quantifying nitrogen cycling in restored systems, in an effort to better understand the impacts of habitat loss and restoration on this critical coastal ecosystem service. In areas affected by increased concentrations of bioavailable nitrogen through human activities, the role of these coastal habitats in enhancing denitrification is well established. Methodological challenges associated with quantifying denitrification persist, complicating data syntheses. Groffman and colleagues (2006) described the myriad of methods and documented the numerous challenges associated with measuring the process.

Quantifying and parameterizing the role that coastal habitats can play in nitrogen removal has been a valuable contribution to understanding contemporary coastal ecosystem function. With the adoption of the concept of ecosystem services and the development of markets for these services, there is increasing interest in nitrogen removal through habitat restoration as a fungible commodity. Because society devotes significant resources to activities that decrease nitrogen loading to coastal waters, there is pronounced interest in improving our understanding of the role of seagrass and salt marshes in attenuating nitrogen loading.

Bioeconomic modeling combines understanding of ecosystem function with economic assessments of the value of natural processes. Grabowski and colleagues (2012) calculated and compared the values of oyster reef ecosystem services. Their model found denitrification to be a significant contributor to the total value computed. There is every reason to believe that denitrification would be a similarly important ecosystem service in salt marshes and seagrass. These habitats have been included in evaluations of coastal ecosystem services (Barbier et al., 2011), but the development of more comprehensive models of ecosystem services for salt marshes and seagrass should be pursued.

Here we explore our existing knowledge of denitrification in seagrass and salt marsh habitats. In particular we seek to present the current state of play of denitrification science and the denitrification rates currently reported in the scientific literature. We will use these to explore the potential to model and quantify this ecosystem service across time and space, and to identify current data gaps.

Review of Science Describing Denitrification Services

Literature searches were conducted between 09/30/2015-10/06/2015 in the Web of Science database, using keyword searches for “denitrification” plus each of the following terms: “salt marsh”, “seagrass”, “submerged aquatic vegetation”, and “SAV”. These four initial searches yielded a combined 486 results. Each scientific paper was examined to identify studies presenting habitat specific data on denitrification values. Eighty-three of the 486 papers were identified for further review on this basis. Ad hoc searches prompted by references within the identified papers produced an additional 10 results.

In total, 93 sources were identified as relevant; ten of these were reviews of published literature, without original measurements. Literature with original data relevant to salt marsh and seagrass habitats comprised 61 and 27 papers, respectively, with five sources including studies of both seagrass and salt marsh habitats.

Denitrification rates explicitly stated in the literature were extracted and compiled for analysis. All rates were converted to $\mu\text{mol N m}^{-2} \text{h}^{-1}$. Conversion from a rate given per sediment volume to an areal rate utilized sediment water content or sediment density, and integration along core length was undertaken as outlined in Greene 2005. These values were drawn from each study, or if not provided, a bulk density of 1.4 g cm^{-3} and 10 cm core length were assumed (Seitzinger, 1988, Greene, 2005). If multiple measurements were reported for a single sample date and site, they were averaged such that each denitrification rate included in the meta-analysis presented represented a discreet sample site and measurement event. If a range of values was the only datum provided in the text, the maximum value was selected.

For comparison of extracted values, rates were categorized as ‘vegetated’ or ‘control’ (control values were taken only from studies that also included vegetated measurements), by season (or as ‘annual’ if the source reported a rate reflecting multiple seasons), and by measurement technique. Unless otherwise specified, all numbers presented in the Results section are derived from ‘ambient’ denitrification rates in the literature, meaning the values included in calculations reflect *in situ* conditions (see further discussion in Results section, “Variability in techniques applied for quantifying denitrification”).

Results

Salt Marshes

Salt marshes enhance denitrification relative to unstructured habitats

Control sediments, such as creek bottoms or neighboring mudflats, exhibit lower denitrification rates than vegetated counterparts; the mean annual denitrification rate in unvegetated sediments was found to be $36 \pm 10 \mu\text{mol N m}^{-2} \text{h}^{-1}$, roughly one third the vegetated average, $116 \pm 25 \mu\text{mol N m}^{-2} \text{h}^{-1}$. While this enhancement is largely confirmed throughout the literature, individual studies have found control sediment to have higher or equal rates compared to vegetated counterparts (e.g. Abd. Aziz and Nedwell, 1986, Anderson et al., 1997, Kaplan et al., 1979).

Variability in techniques applied for quantifying denitrification

Denitrification can be measured using a wide variety of techniques, and salt marsh habitats in particular have been sampled using an exceptionally wide range of methodologies (Table 1). The resulting measurements of denitrification are highly influenced by the methodology used. Each method carries

specialized consequences of over- or under-estimating denitrification, making direct comparisons of rates across the body of literature difficult (Groffman et al., 2006, Cornwell et al., 1999).

Measurements can, however, be broadly grouped as ‘ambient’ or ‘potential’, as determined by methodology and experimental procedure. Ambient values are from experimentally unamended samples and represent *in situ* conditions. Potential values result from the experimental addition of dissolved nitrate, and thus reflect an artificially elevated denitrification capacity. Though potential rates are useful in understanding the denitrification capability given favorable conditions, they cannot be considered true *in situ* results, and are not comparable to ambient rates. To illustrate the significant influence of methodology on reported values, the averages of marsh measurements using the acetylene block technique for ambient and potential rates are $54 \pm 16 \mu\text{mol N m}^{-2} \text{h}^{-1}$ and $7239 \pm 2127 \mu\text{mol N m}^{-2} \text{h}^{-1}$, respectively.

The acetylene block technique is the most frequently employed, but its major limitation of inhibiting coupled nitrification-denitrification has led to advances in new techniques. Measurement of N_2 based on its ratio to argon is a common alternative (e.g. Smyth et al., 2015). Recent combinations of $\text{N}_2:\text{Ar}$ and isotope pairing methods have added to denitrification studies by measuring denitrification components: water column denitrification and sediment nitrification-denitrification (e.g. Koop-Jakobsen and Giblin, 2010).

Regional distribution of denitrification studies

The diversity of methodologies used and the small number of studies from some regions precluded a numerical analysis of differences in denitrification rates between regions. It is known that background rates of denitrifications vary across both small and large spatial scales (Seitzinger et al., 2006). As such, the geographic distribution of studies is of interest when assessing data gaps and next steps. Only one study examined locations within two regions (sites in Georgia and Louisiana) (Baas et al., 2014). Although they found the average denitrification rates to be comparable at both sites, further examination of large-scale variability is warranted.

The literature is dominated by studies undertaken in the U.S. (Table 1). Within the U.S. there is a strong bias towards studies undertaken on the Atlantic coast (34 of 46 studies). The Gulf of Mexico and Pacific coasts therefore appear to be under represented in the literature as regards measures of denitrification, despite the dominance of salt marsh as a threatened habitat type in the Gulf of Mexico in particular. That

said, while the Atlantic coast seems to be represented by a large number of studies, very few of them are comparable due to differences in methodology (Table 1).

Table 3-1. Methods used in assessing salt marsh denitrification, and occurrences by region. Table does not include references listed as ‘Control Only’ in Appendix IV. Data repeated in numerous references are included only once. References may appear more than once if multiple methods employed.

Method	Number of studies					
	North America			Europe	Asia	Oceania
	<i>Atlantic Coast</i>	<i>Gulf Coast</i>	<i>Pacific Coast</i>			
Acetylene block	10	5	3	3	1	1
N ₂ :Ar	8	-	1	-	-	-
N ₂ flux	4	-	-	1	-	-
¹⁵ N tracer	2	1	1	1	-	-
N ₂ O reductase	3	-	-	-	-	-
Isotope pairing + N ₂ :Ar	2	-	-	-	-	-
Isotope pairing + N ₂ :Ar + push-pull	2	-	-	-	-	-
Mass balance	2	1	-	1	-	-
Isotope pairing	1	-	-	1	-	-
N ₂ O isotope pool dilution	1	-	-	-	-	-
N ₂ :Ar + isotope pool calculation	1	-	-	-	-	-
Total	34	7	5	7	1	1

Small scale variability in denitrification by salt marshes

Denitrification rates are likely to vary by location due to a number of external factors, such as nutrient availability, sediment load, salinity, temperature, flow rates and differences in the underlying microbial community between locations (Fennel et al., 2009). One source of such variability which has received some attention, is the difference in denitrification activity along a salt marsh gradient. Greater denitrification in low marsh zones than in high marsh zones have been reported (Addy et al., 2005, Wigand et al., 2004, Valiela and Teal, 1979, Kaplan et al., 1979). In some cases it was possible to differentiate by vegetation species to explore variability in denitrification throughout the marsh. Higher denitrification rates have been found in tall-form *S. alterniflora* stands than in the short form of the species, the latter which tends to grow in higher areas of the marsh. Kaplan et al. (1979) reported tall and short form *S. alterniflora* denitrification rates of $97 \mu\text{mol N m}^{-2} \text{h}^{-1}$ and $24 \mu\text{mol N m}^{-2} \text{h}^{-1}$, respectively, while Dollhopf et al. (2005) noted an order of magnitude greater denitrification in the tall relative to short form. O'Meara et al. (2015) found significantly higher denitrification rates in *S. alterniflora* marshes compared to marshes dominated by *S. cynosuroides*.

Temporal variability in denitrification measurements

While the published data are extremely diverse, they show denitrification roughly peaks in summer and fall at 1.5 and 1.4 times the calculated annual average of $83 \pm 24 \mu\text{mol N m}^{-2} \text{h}^{-1}$ respectively (Fig. 1). Denitrification declines in spring to a third of the annual average. Many year-round studies notably find denitrification to be greatest in summer, late summer, and fall (e.g. Wang et al., 2007, Hamersley and Howes, 2005), yet there is some evidence for winter or spring maxima (Koch et al., 1992, Thompson et al., 1995).

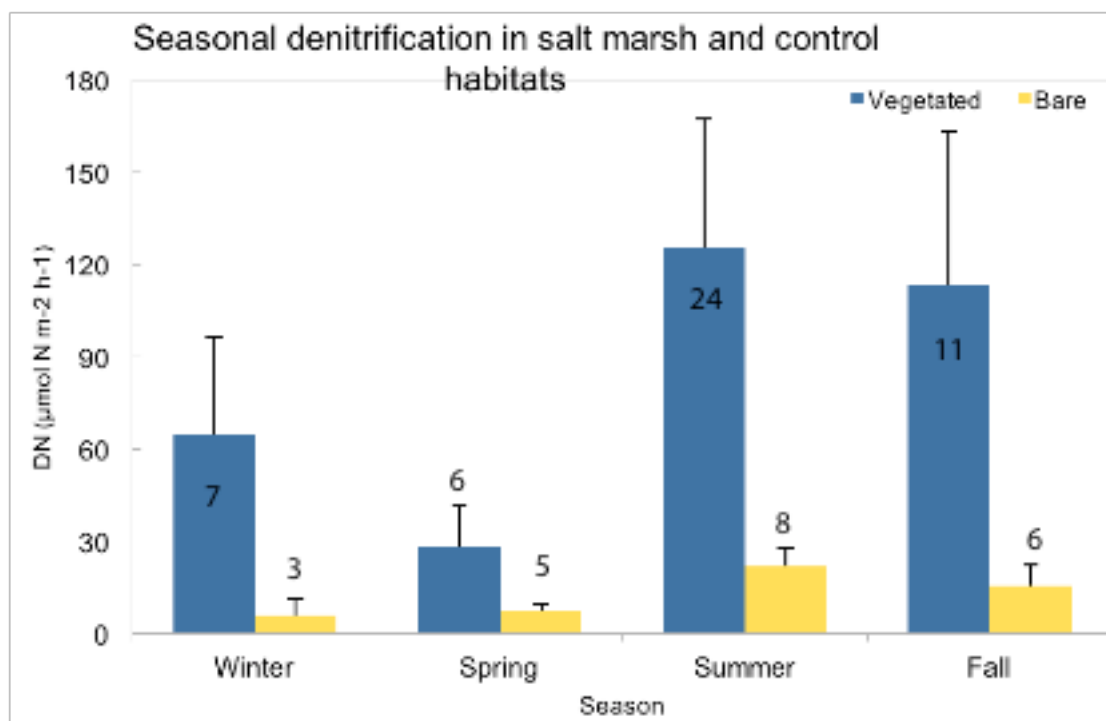


Figure 3-1. Average ambient denitrification rates by season in salt marsh vegetated (blue) and bare (yellow) sediment. Error bars are standard error and numbers indicate the number of measurements included.

Seagrass

Seagrasses enhance denitrification relative to unstructured control

Our analysis indicates an increase in the denitrification rate in vegetated sediments relative to bare sediment, with denitrification measured as $87 \pm 13 \mu\text{mol N m}^{-2} \text{h}^{-1}$ and $51 \pm 15 \mu\text{mol N m}^{-2} \text{h}^{-1}$ respectively. A consensus in the literature has, however, not been established (McGlathery et al., 2007). Studies finding depressed denitrification in vegetated sediments (e.g. Kaspar, 1983, Risgaard-Petersen et al., 1998) underscore the need for further research to confirm the importance of seagrasses in nitrogen removal.

Variability in techniques applied for quantifying denitrification

Like salt marshes, seagrass denitrification studies exhibit variability in methodologies employed and the associated difficulty in cross-methodology comparisons. In recent studies, newer methods of isotope pairing (e.g. Welsh et al., 2001), $\text{N}_2:\text{Ar}$ ratios (e.g. Smyth et al., 2015), and a combination of the two (e.g. An and Gardner, 2002) are favored over the once-common acetylene block technique (e.g. Caffrey and Kemp, 1990). There is some question if typically low rates measured with isotope pairing (average of measurements, $6 \pm 2 \mu\text{mol N m}^{-2} \text{h}^{-1}$) compared to $\text{N}_2:\text{Ar}$ ($118 \pm 18 \mu\text{mol N m}^{-2} \text{h}^{-1}$) are methodological, or related to external variables such as region or species biogeochemistry (Eyre et al., 2013).

Table 3-2. Methods used in assessing seagrass denitrification, and occurrences by region. Table does not include references listed as ‘Control Only’ in Appendix IV. Data repeated in numerous references are included only once. References may appear more than once if multiple methods employed.

Method	Number of studies			
	US & Caribbean	Europe	Asia	Oceania
N ₂ :Ar	4	-	-	5
Acetylene block	2	1	2	1
Isotope pairing + N ₂ :Ar	2	-	-	-
¹⁵ N tracer	1	-	-	-
Isotope pairing	-	5	-	-
Isotope pairing + ¹⁵ N perfusion	-	1	-	-
N ₂ flux	-	-	1	-
C:N Stoichiometry	-	-	-	1
Total	9	7	3	7

Regional distribution of denitrification studies

The diversity of methodologies used and the small number of studies from some regions precluded a numerical analysis of differences in denitrification rates between regions. In the case of seagrass we identified no studies that examined differences in denitrification rates between regions and therefore are unable to draw any conclusions regarding the transferability of studies across or within regions. As such, the geographic distribution of studies is of interest when assessing data gaps and next steps.

The global distribution of studies of denitrification by seagrass habitats is relatively well balanced (Table 2). Seagrass habitats are, however, much less well studied than salt marsh habitats, in particular within the U.S. (Table 1 and 2). Within the U.S., research has focused on the Atlantic Coast (4 of 9 studies) and the Gulf Coast (3 of 9 studies), in particular in Florida Bay, where seagrass dieback has been a motivating factor in undertaking studies there (Gardner and McCarthy, 2009). With only one additional study in each

of the Caribbean (Jamaica; Blackburn et al., 1994) and the Pacific (Alaska; Iizumi et al., 1980), far more work is necessary to achieve complete coverage across the US & Caribbean region.

Small scale variability in denitrification by seagrasses

Differences in denitrification rates between species have been observed, although there are few direct comparisons. Eyre et al. (2011) found *Zostera* seagrass colonies support greater denitrification than *Halophila* communities ($412 \mu\text{mol N m}^{-2} \text{h}^{-1}$ compared to $77 \mu\text{mol N m}^{-2} \text{h}^{-1}$, respectively), while Eyre et al. (2013) showed *Zostera*, *Halophila*, and *Ruppia* species all exhibit greater denitrification than *Posidonia* species.

Temporal variability in denitrification measurements

Seasonally, seagrass denitrification exhibits little variability throughout the year, with a drop in winter to half the calculated annual average of $74 \pm 11 \mu\text{mol N m}^{-2} \text{h}^{-1}$, and a spring maximum of 1.25 times the annual average (see Fig. 2). Several year-round studies found elevated rates in the spring up to twice the annual rate (Risgaard-Petersen and Ottosen, 2000, Eyre et al., 2013, Caffrey and Kemp, 1990), while others found winter peaks (Risgaard et al., 1996) or no seasonality (Welsh et al., 2000b).

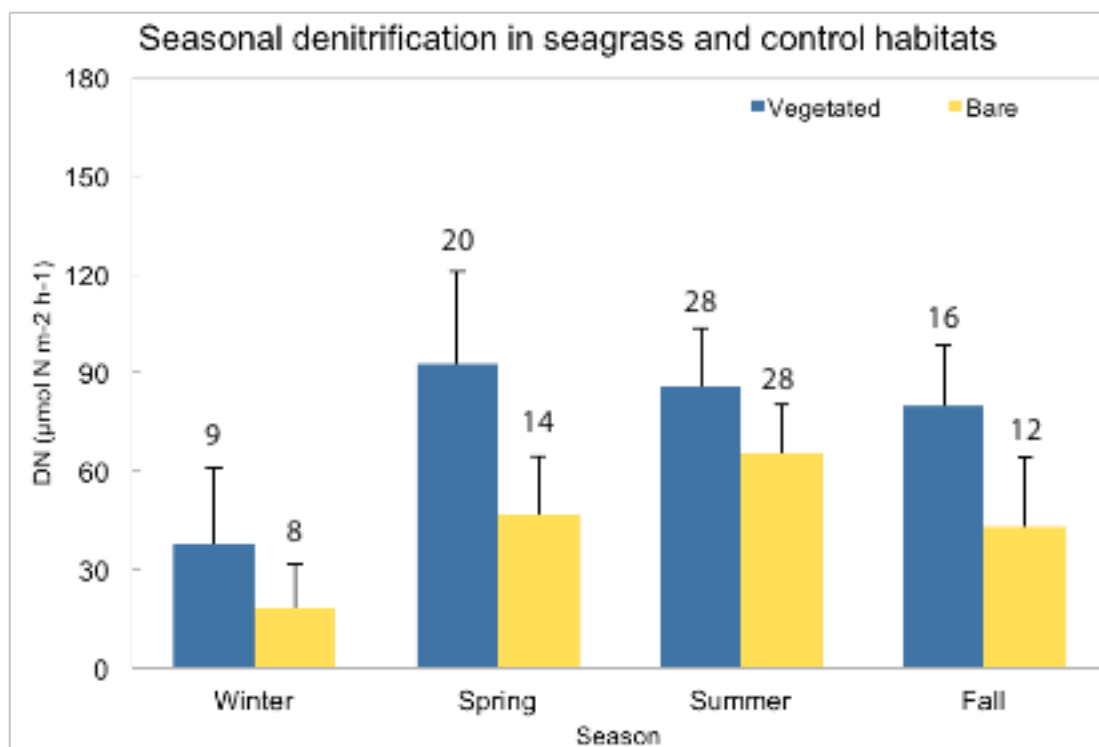


Figure 3-2. Average ambient denitrification rates by season in seagrass vegetated (blue) and bare (yellow) sediment. Error bars are standard error and numbers indicate the number of measurements included.

Recommendations for Next Steps and Developing the Science

Information resulting from this review of seagrass and salt marsh denitrification underscores conventional wisdom that these habitats are important sinks for nitrogen. Efforts to conserve these coastal habitats should therefore consider this ecosystem function and its resulting services. We found sufficient data to broadly support the concept that these habitats are important sinks for nitrogen.

As with all quantifications of ecosystem function that will be used in assessments of ecosystem services, denitrification measurements should be made using methods that will be best adapted into bioeconomic models. Optimally, measurements should be direct quantifications of the process, made seasonally and should be made in a manner that yields a rate per area. Fortunately, most of the recent assessments that have been made meet these criteria.

Measurement of denitrification has been identified as a major methodological challenge (Groffman et al., 2006) and only in the past 20 years have direct measurements of the process been made in salt marshes and seagrass beds. While many studies have focused on denitrification in these coastal habitats, there still remains a need for additional data to improve extrapolations of nitrogen removal by seagrass and salt marshes. Our literature search revealed some regions are better studied than others and that no single method has been used in all systems. Resolving the degree to which multiple methods are comparable is an ongoing challenge.

There is increasing evidence that the landscape context of habitats is very important in determining a range of functions from fish production (Grabowski et al., 2005) to nutrient removal (Smyth et al., 2015). The rates we report here are from a range of coastal systems and do not account for factors that may significantly affect the rates and values of denitrification, such as quantity of nutrient delivery from rivers and streams and adjacent land use. While it is unlikely that a fully transferable mechanistic model of denitrification in salt marshes and seagrass beds will be developed in the near term, the more information we have about the factors that affect the process, the more accurate extrapolations to multiple systems will be.

Future research should explore biological indicators to predict changes in denitrification. Analogous work on oyster reefs has found a habitat attribute such as oyster density may be a good indicator of denitrification (Smyth et al., 2015, Kellogg et al., 2014). Relationships between stem density, percent cover and primary productivity in salt marshes and seagrass could be similarly effective indicators of denitrification. Given the dynamic nature of coastal regions, the ability to predict changes in nitrogen

removal by these habitats as their condition changes would be invaluable in the development of spatially explicit models of denitrification value.

Further synthesis of denitrification measurements and the factors affecting the rates would be invaluable in improving nutrient removal attributes in ecosystem assessment tools widely applied in marine spatial planning. This requires further development of the understanding of the magnitude of spatial variability in denitrification on multiple scales. For example, we assessed the state of knowledge in coastal systems. An expanded analysis of marsh and seagrass bed nitrogen cycling in lower salinity and tidal freshwater regions of estuaries would provide additional value in understanding and quantifying the importance of denitrification by coastal habitats.

While we found a significant quantity of existing data which could be used to begin to inform the development of a model to predict or estimate the rate of denitrification in salt marshes and seagrasses within the U.S., a concerted effort to improve data coverage in a number of geographic regions was noted, as well as the need to elucidate further the predictive drivers of variability in denitrification by these habitats.

Chapter 4 Carbon Sequestration of Salt Marsh and Seagrasses

It is widely acknowledged by the scientific community that the overall global temperature is increasing due to greenhouse gases (GHG) being emitted at unsustainable levels due to human activities. Increases in GHGs threaten our planet and are already affecting weather patterns, biodiversity, food security and livelihoods (Intergovernmental Panel on Climate Change, 2014). The U.S. has committed to reducing its GHG emissions by ‘26-28 percent below its 2005 level in 2025 (UNFCCC, 2015)’. In order to reach this target, the mitigation solution must be complex and multifaceted.

Scientists and policy makers have increasingly recognized the role of natural ecosystems in addressing climate change mitigation. Losses and degradation of natural ecosystems comprise at least 20-30% of our total emissions (Nellemann et al., 2009). While tropical, temperate and boreal forest systems sequester and store a large amount of carbon (Pan et al., 2011, Phillips and Lewis, 2014) and have traditionally formed the basis of habitat based climate mitigation strategies, studies have now demonstrated that on a per area basis, coastal ecosystems are much more efficient carbon sinks. In particular, intertidal salt marshes, seagrass meadows and mangroves play a significant role in the sequestration and storage of carbon, accounting for at least 50% of the carbon stored in ocean sediments globally (Nellemann et al., 2009). These three ecosystems are often referred to as ‘blue carbon’ or ‘coastal carbon’.

Climate mitigation is an often undervalued ecosystem service as a result of its low market value, yet the social cost of carbon is significantly higher. The U.S. government developed estimates of the social cost of carbon (SCC) to support federal agencies in their regulatory decision-making. The social cost of CO₂ “represents the present value of the future [global] damages that would arise from an incremental unit of CO₂ being emitted in a given year” (United States Environmental Protection Agency, 2010). The most recent estimates of the SCC suggest damages would range from \$12 to \$109 per metric ton of CO₂ emitted to the atmosphere in 2015 (United States Government Interagency Working Group on Social Cost of Carbon, 2013). Given the high costs, it makes sense to invest in natural low-cost solutions like coastal wetlands restoration and conservation for climate mitigation.

Habitat protection has a significant role in blue carbon; the emission rates of salt marshes, based on annual global loss rates are estimated to be between 20 and 240 million tons of CO₂ per year with a median value of 60 million tons of CO₂ per year (Pendleton et al., 2012). What makes coastal carbon

ecosystems even more desirable as a climate mitigation tool is the additional benefits they provide to people. Coastal carbon habitats also provide other ecosystem services, such as coastal protection from storm surges, fisheries, water purification and local livelihoods from tourism. The combination of value from these services and mitigating the social cost of carbon could justify the financial cost of protection for climate mitigation.

The U.S. has a viable opportunity to protect and support longer-term restoration for coastal wetlands carbon benefits. In the United States 2013 National Ocean Policy (NOP) Implementation Plan there is an action item that directs federal agencies to ‘*develop a protocol for carbon sequestration as an ecosystem service that can be incorporated into existing Federal policies*’ (National Ocean Council, 2012). To implement the actions, agencies will need to review existing policies, possibly develop additional protocols for incorporation of coastal carbon services into federal policies, and understand the implications of including these services in federal decision-making.

This chapter serves to describe the “state of the science” of blue carbon for salt marsh and seagrass habitats, particularly in the U.S.. Understanding the state of the science is necessary to make informed decisions regarding the prioritizing of research that would allow blue carbon to be better integrated into everyday management of habitat. The following sections provide an overview of the current science available on the role of salt marshes and seagrasses in sequestration and storage of carbon. Mangroves, while not considered in this paper, are also a significant carbon-influencing ecosystem. A similar review of mangrove carbon storage and sequestration rates is warranted.

The Role of Salt marsh and Seagrass in Carbon Cycling

Coastal wetlands store large pools of carbon in biomass and especially soils (Table 1). Soil carbon originates largely in situ, from root biomass and litter, and can result in significant stocks, especially when compared with terrestrial forests (Intergovernmental Panel on Climate Change, 2014). Over time, coastal wetland soils accumulate vertically, keeping pace with sea level rise, making it a continuous sink (Mudd et al., 2009). The saline waters and anaerobic nature of these sediments means the burial of organic matter into high carbon soils occurs with limited methane emissions (Livesley and Andrusiak, 2012) and can be stored for millennia (McLeod et al., 2011). These systems also store external carbon as coastal ecosystems act as sediment traps for runoff from terrestrial systems and other suspended solids. Human-driven changes to coastal carbon ecosystems – such as conversion for aquaculture, coastal development and numerous other land uses – can result in significant carbon emissions into the ocean and atmosphere.

Table 4-1. Global estimates of blue carbon by habitat. [1] (Duarte et al., 2013b); [2] (Pendleton et al., 2012)

	Carbon sequestration rate (Tg C yr ⁻¹) [1]	Average carbon storage (Mg C ha ⁻¹ yr ⁻¹) [2]		Average carbon emissions from conversion [2] (Mg CO ₂ yr ⁻¹)
		Top Meter of Soil	Above-ground Biomass	
Salt marshes	4.8-87.3	156.2	5.4	60 million
Seagrasses	48-112	81.9	16.7	150 million

Salt Marsh Carbon

In salt marshes salinity is one of the driving factors determining whether a marsh acts as a source or a net sink of greenhouse gases (Poffenbarger et al., 2011, Chmura et al., 2011). Generally marshes with salinity above 18ppt emit negligible amounts of methane, whilst those with salinity under 18ppt emit enough methane to offset the carbon stored in sediments (Commission for Environmental Cooperation, 2013). Therefore, salt marshes are defined as marshes with salinity above 18ppt in this review.

The average carbon sequestration rate for salt marshes globally is 2.18 Mg C ha⁻¹ yr⁻¹ (McLeod et al., 2011) with the caveat that it is highly variable. Carbon is stored in above-ground biomass of salt marshes but the plants are small and the carbon stored is significantly less compared to other systems such as forests. Salt marshes gain their importance based on the storage of carbon in the soils. Salt marsh ecosystems continue to build organic-rich soils by accreting both sediments and organic material, giving them an almost unlimited capacity to store carbon for very long time periods. Understanding that the organic soil may extend several meters, a conservative global average for carbon stored in the top meter of soil and vegetation biomass is estimated to be 64.6 - 258 Mg C ha⁻¹ (Yu and Chmura, 2009, Poffenbarger et al., 2011, FitzGerald et al., 2008).

Although the exact historic and current extent is difficult to determine, it is estimated that we have already lost at least 25% of the global salt marsh area since 1800, and the current global rate of loss averages between 1-2% each year (McLeod et al., 2011). The emission rates of salt marshes, based on annual global loss rates, are estimated to be between 20 and 240 million metric tons of CO₂ per year with a median value of 60 million metric tons of CO₂ per year or about 13% of the blue carbon emissions globally per year (Pendleton et al., 2012). Salt marshes are primarily threatened by land use change or pollution,

although accelerated sea level rise due to climate change may pose an even more pressing challenge to some areas (FitzGerald et al., 2008). Increases in the rates of sea level rise over the 20th century and into the 21st may lead to the destruction of marsh areas that cannot keep pace with the rising water levels and therefore end up drowning (Chmura et al., 2011, Kirwan et al., 2010). Habitat protection therefore has an important role to play in managing carbon stocks, continuing sequestration, and reducing emissions from salt marsh habitats.

Seagrass Carbon

Studies on the global seagrass distribution are limited but seagrass meadows have been reported on every continent except for Antarctica. Seagrass habitats primarily sequester carbon through normal plant photosynthesis and transfer of carbon into the sediment. They also trap nutrients and sediments from the water column, supporting additional carbon loading into the ocean floor. It is estimated that 50% of carbon found in seagrass sediments originate elsewhere- also known as allochthonous carbon (Kennedy et al., 2010). The average global carbon sequestration rates for seagrass are $1.38 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (McLeod et al., 2011). Though seagrass take up only a small fraction of the ocean floor, they are responsible for up to 20% of global marine carbon burial (Duarte et al., 2013a). Seagrass ecosystems require high light levels for productivity (close to 25% of incident radiation in some species) and are therefore sensitive to environmental changes affecting water clarity (Orth et al., 2006). This means seagrass carbon sequestration rates and carbon stocks are vulnerable to small habitat changes whether human induced or natural.

Though carbon storage can vary by species, the global average for seagrass carbon storage in the first meter of soil is $512 \text{ Mg CO}_2\text{e ha}^{-1}$, and carbon buried can remain locked for centuries if not disturbed (Pendleton et al., 2012). However, an estimated 150 million tons of CO_2 are emitted from seagrass meadow degradation every year. Loss of seagrass habitats is mainly the result of reduced water quality due to sediment and nutrient runoff from terrestrial sources, and from direct impacts such as dredging and trawling (Pendleton et al., 2012). A study by Fourqurean et al. (2012) estimates that globally seagrass ecosystems store up to 19.9 Pg organic carbon. Their more conservative estimate for global seagrass carbon storage ranges from 4.2 to 8.4 Pg carbon, a significant amount considering these values are for the first meter of soil only.

Common terminology used when discussing coastal blue carbon and climate mitigation. These terms are often misused or not well understood.

<p>Natural Carbon Sinks</p> <p>A natural carbon sink results from processes that removes GHGs from the atmosphere (such as photosynthesis or dissolution in the ocean) and stores that carbon in mechanism such as in plants, soils, or in the ocean.</p> <p>Degradation and destruction of natural carbon sinks can lead to the release of GHGs, turning a sink into a source.</p>	<p>Natural Carbon Sources</p> <p>A carbon source is any process, activity, or mechanism that results in release of GHGs to the atmosphere; natural carbon source is decomposing organic material and respiration.</p> <p>Natural areas, such as forests or wetlands, can become human-caused sources when human activities result in the emissions of more GHGs than would have resulted from natural processes.</p>
<p>Carbon Sequestration (also called carbon capture or carbon burial)</p> <p>Carbon sequestration is the physical process of removing carbon dioxide from the atmosphere or ocean and occurs via photosynthesis or dissolution in the ocean.</p> <p>Carbon Accumulation Rate (CAR)</p> <p>CAR is calculated by the sediment accretion rate and average carbon density of the soil. It does not take into account store carbon in the above-ground biomass from photosynthesis.</p>	<p>Carbon Storage</p> <p>Carbon storage is the long-term repository of carbon that has been taken up via sequestration and occurs in long-lived plants, soils, or the ocean. Carbon is stored long-term if it remains in the ecosystem for periods of decades to thousands of years.</p>
<p>Above-ground biomass (AGB)</p> <p>AGB consists of 1) All living biomass including foliage, branches, stems, stump, bark, and seeds above the soil and 2) dead above-ground biomass including mostly leaf detritus, wood, and other organic debris such as macro-algae.</p>	<p>Below-ground carbon pools</p> <p>Below-ground carbon pools biomass consists of 1) all living biomass below in the soil such as roots and rhizomes 2)the below-ground carbon comprised of dead plant tissues and soil organic matter</p>

Methods for Quantifying Coastal Carbon

A major barrier to incorporating blue carbon into decision making coastal carbon habitats thus far has been the lack of standardization in carbon stocks accounting and the fluxes in GHGs emissions. This issue has, however, been addressed in a recent review on methodologies, *The Coastal Blue Carbon Manual* (Howard et al., 2014). Howard et al. (2014) describe and recommend specific measuring and monitoring procedures. Adoption of standardized methods and reporting will make it easier for blue carbon conservation and restoration to be supported through various management and policy approaches, regulatory frameworks, and participation in voluntary carbon markets (Howard et al., 2014).

Review of Science Describing Blue Carbon Services

Using Google Scholar, a search of the most recent literature reviews of carbon in seagrass and salt marshes was conducted between 10/01/2015-11/15/2015 using key words of ‘carbon’, ‘seagrass’, ‘salt marshes’, ‘blue carbon’ and ‘coastal wetlands’. The top studies identified were (Craft, 2007, Sifleet et al., 2011, DeLaune and White, 2011, Commission for Environmental Cooperation, 2016, Ouyang and Lee, 2014, Fourqurean et al., 2012, Duarte et al., 2010). These studies were determined to be the most appropriate for review here, based on the number of times cited, relevance to the U.S., and availability of the observation datasets the papers used in the analysis. It should be noted that many of the studies included in these reviews were not primarily conducted with the intent to measure carbon solely, but rather may be studies focused on other ecological questions and include more indirect carbon measurements.

For salt marshes, we combined the observations and eliminated duplicates from the identified datasets (Sifleet et al., 2011, DeLaune and White, 2011, Ouyang and Lee, 2014, Commission for Environmental Cooperation, 2016, Craft, 2007). After removing data outside the U.S. we were left with 116 case studies from the U.S.. For seagrasses, blue carbon datasets were extracted from Duarte et al. (2010) and Fourqurean et al. (2012).

Results

Carbon in North American Salt Marshes

We identified 116 studies from the U.S. that contained measurements for salt marsh carbon. Coastal wetland carbon-related data, including biomass (above- and below-ground), sediment organic carbon content, sediment organic carbon density and sediment carbon accumulation rate, were variously

recorded. Forty-eight observations were from Louisiana, 23 from New England, 22 from the Pacific coast, 14 from the Chesapeake Bay region, and 12 from the mid-Atlantic region (excluding New England and the Chesapeake). The datasets are not all directly comparable, with some studies measuring only above-ground biomass and others only calculating soil carbon stock.

As discussed by Craft (2007) and Ouyang and Lee et al. (2014), sediment carbon accumulation rate (CAR) for salt marshes can be either measured directly or calculated indirectly from sediment accretion rate (SAR) and average carbon density of soil. Case studies recorded CAR in different ways, for instance, in terms of sequestered CO₂ (gas exchange techniques), or calculated and/ or estimated from the accumulation rate of organic matter. Long-term isotopic profiling (Cs-137, Pb-210) and short-term marker horizon were commonly applied for measuring SAR. Differences in isotopic profile and marker horizon result in increased variability of estimated CAR, and raises questions in the comparability of CAR data across case studies. These differences in the methodologies applied in measurement and/or calculation of CAR can generate biases.

Extracting the U.S. observations from Ouyang and Lee et al. (2014), salt marsh soil carbon accumulation rates for the U.S. were estimated to be 207.6 g C m⁻² y⁻¹ (standard deviation 246.9). This is based on 73 observations. There was a strong geographic bias in the available measurements, with over half of the observations being from Louisiana (n=24) and Connecticut (n=17) (Figure 1; Table 2). The carbon measurements were extremely variable, ranging from 1713 g C m⁻² y⁻¹ to just 18 g C m⁻² y⁻¹. It was also noted that there were biases caused by conversion to create a uniform dataset for analyses. Most (56) of the studies used radionuclide (i.e., 137Cs, 14Cs, 210Pb markers) to measure carbon accumulation rates, while a smaller portion (14) used marker horizons. Three studies failed to report their methods.

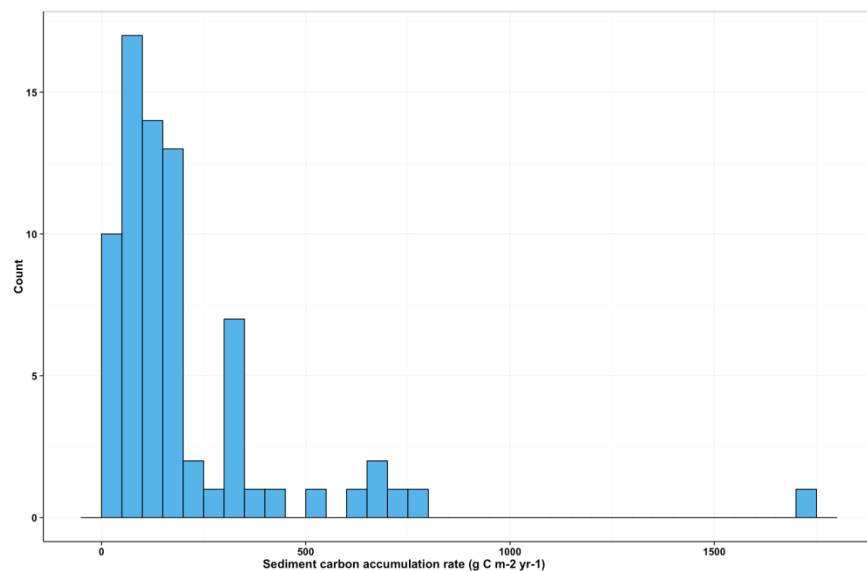


Figure 4-1. Distribution of annual sediment carbon accumulation rates in salt marsh in the U.S. Data obtained from Ouyang and Lee (2014)

Table 4-2. Annual sediment carbon accumulation rate data for salt marsh in the U.S.. Data extracted from Ouyang and Lee (2014).

State	Number of case studies	CAR range (g C m ⁻² y ⁻¹)	Average CAR (g C m ⁻² y ⁻¹)
Louisiana	24	18-1713	358.65
Connecticut	17	70-204	125.14
California	8	43-385	173.60
North Carolina	5	21-146	80.6
Texas	3	95-203	158.67
Maryland	3	279.5-340	310.23
Massachusetts	3	88.8-155	116.27
Georgia	3	26.5-48.2	39.20
Delaware	2	119-154	136.50
Maine	2	40-78.3	59.15
Mississippi	1	-	153
Rhode Island	1	-	165
Florida	1	-	44
Total	73	18-1713	207.58

The Ouyang and Lee (2014) study, which used a global data set, showed that for salt marshes, carbon accumulation rate was influenced by changes with latitude, tidal range, halophyte genera and habitat elevation. Ouyang's team recommend the following based on data gaps: studies to assess the relationship between halophytes and CAR rate, and case studies and experiments to further explain the relationship between marsh elevation and CAR rates. Such insights into the drivers of variability in CAR are critically important for the development of spatially explicit predictive models.

Using the U.S. observations extracted from Ouyang and Lee (2014) as described above, we examined the factors considered significant in the global data to see if they were significant in the U.S.. However, since the U.S. observations are largely skewed, we only applied statistical analyses to variables that have adequate sample sizes (Table 3). Data on tidal ranges and habitat elevation were not documented in the datasets and further research is needed to determine if it shows a statistically significant relationship. From our analyses, we found no statistically significant relationships as seen in the global dataset. This could be due to a small dataset or there may not be a relationship. Further analyses and data inclusion are warranted to draw any conclusions.

Table 4-3. Relationship tests conducted on U.S. salt marsh observations to determine relationship with CAR.

Relationship	Observations	Results
CAR and species	Compared <i>S. alterniflora</i> (n=25) and <i>S. patens</i> (n=20)	t=1.139, df=35.24, p-value=0.2625
CAR among latitude	73 out of 73 cases	chi-squared = 5.1859, df = 4, p-value = 0.2687
CAR among states with adequate data	Compared CAR from Louisiana (n=24), Connecticut (n=17) and California (n=8)	chi-squared=4.5562, df=2, p-value=0.1025

Another extensive review of salt marshes in North America comes from The Commission for Environmental Cooperation (2013, 2016). They assessed soil carbon density from a dataset of 159 observations in North America (the U.S. and Canada) primarily from the Atlantic Coast and the Gulf of Mexico. That study found that the total carbon stored in the top meter of soil ranged from 173 to 8,085 tonnes CO₂e ha⁻¹ with a mean of 1,562 CO₂e ha⁻¹ (SD = 1197) and a median of 1,210 CO₂e ha⁻¹ (Figure 2). It should be noted that these values do not account for the entire depth of soil, just the first meter of

soil sampled. Sifleet et al. (2011) used 15 studies that measured the full extent of soil in salt marshes. The measurements showed the depth of salt marshes range between 0.41 to 4.57 m, with a mean of 0.85 m (SD =1.14) and a median of 1.37 m (Commission for Environmental Cooperation, 2013). Therefore assuming that salt marsh soils always reach a depth of one meter and never extend further below will result in either under or over estimation of carbon stocks in specific locations.

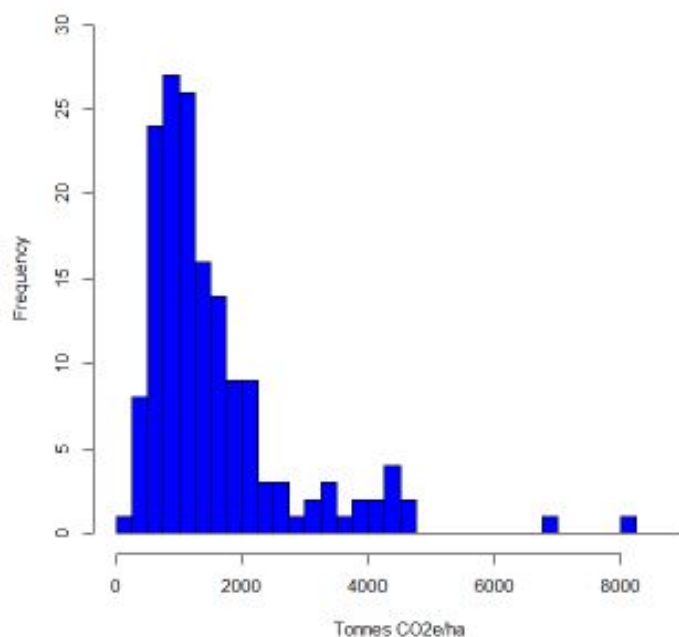


Figure 4-2. Distribution of estimates of carbon storage in the top meter of salt marsh in North America. Graph from Commission for Environmental Cooperation (2013).

Carbon in North American Seagrass

Our review identified a series of reviews of seagrass carbon (Commission for Environmental Cooperation, 2013, Sifleet et al., 2011, Fourqurean et al., 2012, Cebrian, 2002, Duarte et al., 2010). Despite the large number of observations captured by these reviews, many studies could not be compared as they did not follow the same methodologies. We therefore focused the following assessment of the current status of knowledge on the two most complete and coherent, non-overlapping datasets, Duarte et al (2010) and Fourqurean et al (2012). Data derived from Duarte et al. (2010) gave 195 U.S. based observations of net primary productivity, which they equated to the rate of CO₂ sequestered in seagrass meadows. Fourqurean et al. (2012) focused on sediment organic carbon content, some of which can further be used to calculate carbon accumulation rate. The annual carbon accumulation rate calculated from the latter is different from the sequestration rate obtained from Duarte et al. (2010) in both definition and methodology, and therefore should not be compared.

We summarized by location the U.S. based observations on carbon sequestration rate for seagrass meadows from Sifleet et al. (2011) to provide a sense of the spatial variability in carbon sequestration by seagrass meadows (Table 4). The existing variability in measurements highlights that transferring measurements from one location to another is not a valid approach to estimate carbon sequestration rate. If such variability by location can, however, be predicted by commonly measured drivers or metrics, such as salinity, temperature and latitude, then there is the potential to develop predictive models to estimate rates. It is important to note the large range in the estimates of annual carbon sequestration rates, even within the same location, illustrating the possible limitations to developing large-scale predictive models.

Table 4-4. Summary of annual carbon sequestration rates in seagrass meadows by state. Data from Sifleet et al. (2011)
Note: Minus values represent when seagrass meadows function as carbon sources instead of sinks.

Location	Number of sites	Range Mg CO₂e/(ha*y)	Average Mg CO₂e/ (ha*y)
Laguna Madre, Texas	13	-11.05-62.78	10.61
Redfish Bay, Texas	36	-46.96-26.62	-6.77
Alabama	13	-1.39-53.54	25.8
Northwest Florida	29	-9.97-16.97	1.94
Florida Keys	84	-9.4-50.22	2.83
Beaufort, North Carolina	3	0.38-2.4	1.24
Chesapeake Bay	19	-12.33-62.13	13.81
New England (NH, MA)	3	-1-1.51	0
Padilla Bay, Washington	1		-2.01
Total	201		

Rates of carbon sequestration are known to differ by seagrass species (Lavery et al., 2013). Preliminary investigations using the dataset from Duarte et al. (2010) suggest that U.S. species are no exception. The same dataset also revealed a strong effect of location on the rate of carbon sequestration (Figure 3), although this trend should be viewed with caution as there were also strong biases in sampling effort between regions. There was a significant geographic bias towards Florida, while the Northeast and the West coast were both underrepresented (see table 4).

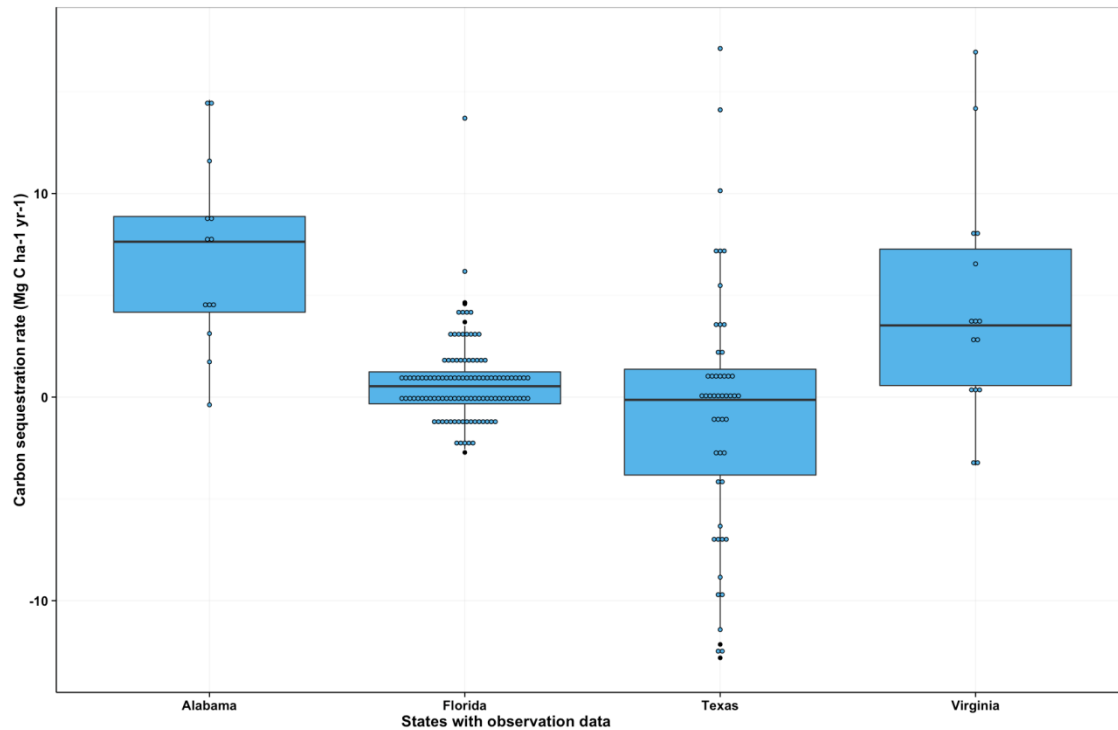


Figure 4-3. Boxplot of relationship between carbon sequestration rate and U.S. states from observations obtained in Duarte et al. (2010).

Fourqurean and colleagues' (2012) dataset records dry bulk density, sediment organic content (%), and sediment depth. We extracted all observations from the U.S. (n=106). After excluding those that only recorded sediment organic carbon content, 76 observations remained. These data represented either vegetative biomass (above + below-ground, in terms of carbon stock), sediment carbon stock, or both. We were, however, unable to generalize the sediment carbon stock in the top meter range, because Fourqurean et al. (2012) found that organic carbon percentage and bulk density of seagrass sediments are affected by depth. Specifically, the percent organic carbon decreased with depth and bulk density increased with depth. This means using estimates using carbon density values from shallow core samples may be inaccurate when extrapolated to the top meter (values are often derived from cores as small as one centimeter, from shallow depths and extrapolated to one meter's depth). We therefore recommend that, in light of Fourqurean et al.'s findings, greater effort be directed toward gathering data on soil stock below 5 cm (Figure 4). This will allow a more accurate assessment of soil carbon.

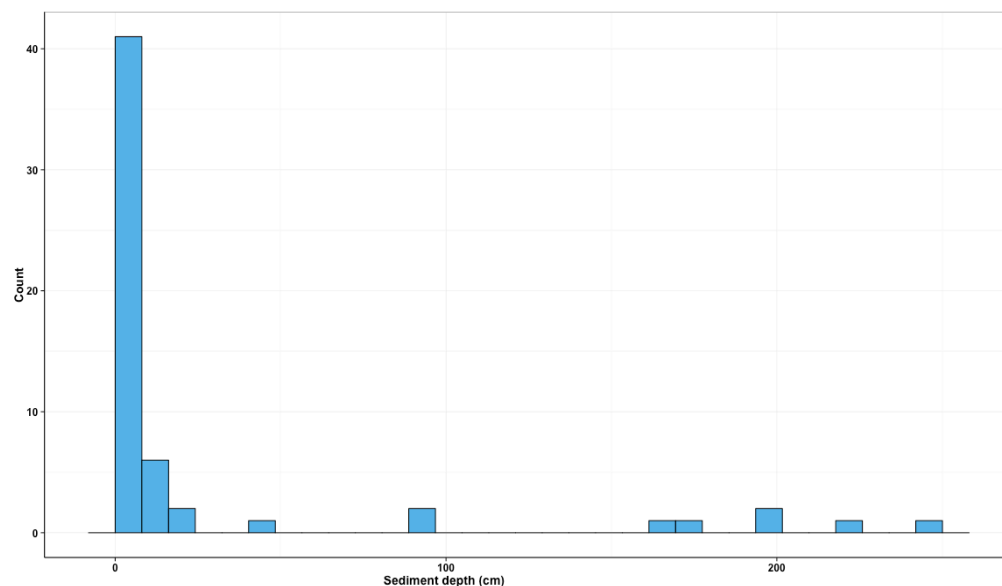


Figure 4-4: Distribution of sediment depth data from observations obtained in Fourqurean et al. (2012)

Sixty-nine of the 76 case studies recorded by Fourqurean et al. (2012) gave exact data of the above- and below- ground carbon stock in seagrasses across the U.S., which we used to compare the distribution of above- and below-ground C stock estimates. We found that carbon stock is significantly higher than that of above-ground C stock (paired t-test on log transformed values, $t=-8.81$, $p\text{-value}=7.32 \times 10^{-13}$). This is consistent with the academic community's consensus that more carbon is stored below-ground in seagrass communities globally.

Fourqurean et al.'s dataset of vegetative carbon stock (above- and below-ground biomass) showed an uneven spatial and species distribution. Studies were heavily biased towards *T. testudinum* as the dominant species ($n=37$, $>50\%$ of studies), followed by *H. wrightii* ($n=13$) and *Z. marina* ($n=12$). The imbalance in the species represented is partly a reflection of the bias in observations by State: 39 records were from Florida, 18 from North Carolina, seven from Virginia and five from Oregon. Analyses of these data illustrate that the interspecies differences and latitudinal differences described in the global literature also appear to hold for the U.S. (Table 5), thus these factors should be included in future blue carbon model development for seagrasses. The extent of the interaction between these two effects was not investigated here, but should be considered in future model development.

Table 4-5. Above-ground and below-ground carbon stock and interaction with seagrass species and location. Data extracted from Fourqurean et al. (2012), n=69.

Relationship	Statistical results	Mean Vegetative C stock (g C m ⁻²)
Vegetative carbon stock and dominant species	Compared <i>T. testudinum</i> (n=37), <i>H. wrightii</i> (n=13) and <i>Z. marina</i> (n=12) by ANOVA F=8.56, p-value=0.0005	<i>T. testudinum</i> : 75.239 <i>H. wrightii</i> : 140.996 <i>Z. marina</i> : 130.258
Vegetative carbon stock and states	Compared Florida (n=39) and North Carolina (n=18) by Welch's t-test t=-2.22, df=20.9, p-value=0.038	Florida: 79.427 North Carolina: 124.386

Recommendations for Next Steps and Developing the Science

Conduct more site-level data

Interest in coastal blue carbon is gaining momentum, with 110 papers on the topic published in 2012 compared with just 30 studies in 2005 (Duarte et al., 2013b). Nevertheless, as blue carbon is a recent area of research, published studies of blue carbon measurements are limited and geographically biased (as demonstrated in this review). Existing studies illustrate the large variability in reported carbon storage and sequestration rates, and many of the factors that may drive that variability. Therefore a significant need exists for more observations to improve our understanding of the dynamics affecting carbon sequestration and storage in coastal wetlands across the U.S. It was especially noted that, while the Southeast U.S. is well represented, more studies are needed in the Northeast and Northwest to understand differences between temperate and tropical seagrass and salt marshes. In particular future studies should seek to report quantitatively possible explanatory variables, such as species composition, water depth, flow rate and salinity (Lavery et al., 2013).

Data needs to develop predictive coastal carbon models

To integrate 'blue carbon' into standard natural resource decision-making processes, we need to understand and predict the carbon storage and sequestration benefits that are provided when conservation and/or restoration actions are made. In order to do so, it would be useful to develop a model which accounts for the impact of location, as well as factors which might be impacted by management, such as habitat quality, freshwater flows and species composition.

While there is agreement in the global literature regarding the many of the possible drivers (Ouyang and Lee, 2014, Duarte et al., 2010), the quantitative influence of those drivers within the U.S. needs to be

better elucidated. There is already a substantial body of literature that could be used to explore these drivers, as illustrated in our review, however, the lack of uniformity across datasets means that further analysis is required before it can be ascertained whether the existing literature is sufficient. We therefore recommend that further studies examining the factors affecting carbon sequestration, accumulation rates, and storage for both ecosystems in the U.S. be undertaken in order to support the development of a national or regional model of carbon sequestration.

Standardization of measurements

A significant issue affecting these analyses is the lack of uniformity in assessing sequestration, storage and emissions. For example, the term ‘sequestration rate’ is used frequently but the methods used to determine that rate differ and hence support different definitions of the term. Some consider sequestration rate as a measure of primary productivity while others measure it using accumulation rates in soils. In some sites above-ground biomass has been completely excluded and vegetated species are not identified. A standard methodology has been proposed by Howard et al. (2014), and those involved in measuring blue carbon should encourage the use of such standardized approaches.

A further methodological issue that needs to be addressed is the general assumption that blue carbon soils average one meter’s depth with a constant soil carbon density. There is substantial evidence to the contrary, which calls to question the use of this assumption when comparing carbon between locations. Indeed, in seagrass soils it is clear that organic carbon and bulk density are not uniform with depth (Fourqurean et al., 2012). It is possible that this could also be the case with salt marshes, although it has yet to be researched.

Case Studies for science, markets and policy

While it is important to have datasets of current carbon stocks, we also need long-term monitoring at coastal wetlands sites to show how ecological and man-made factors can effect carbon sequestration and stocks. This includes long-term monitoring of sea level rise and its effects, comparison of restoration methods and over what time frame restored sites develop stocks comparable to undisturbed ecosystem, as well as natural seasonal fluxes in temperate coastal ecosystems.

Coastal wetlands restoration and conservation are and will be important opportunities to mitigate carbon emissions. Because most restoration projects do not have long-term monitoring, most of our understanding of carbon wetland restoration is only the immediate effect of sequestration increases and stock accumulation rather than the full potential over a long period of time. It is therefore critical for

government and non-governmental agencies to partner to establish geographically diverse conservation and restoration sites for long-term monitoring. This will also offer the opportunity to monitor specific interactions with ecological stressors at a granular level.

Chapter 5 Coastal Protection Services Provided by Salt Marsh and Seagrass

One of the most important ecosystem services provided by salt marshes and seagrasses is their role as buffers in protecting coastlines. Our coasts face a variety of natural hazards including storms, hurricanes, and tsunamis. These hazards are natural processes that have always affected the coastal zone, however, the impacts and associated costs of these hazards to humans have increased as the amount and value of coastal infrastructure have grown and continue to grow. The effects of climate change will further amplify these impacts and costs. Sea level rise and ocean warming will increase the frequency and magnitude of many coastal hazards (Donat et al., 2011, Donnelly et al., 2004, Young et al., 2011) while at the same time threatening coastal ecosystems such as seagrasses and salt marshes that humans are dependent upon.

Historically, coastal protection plans have relied on hardened infrastructure solutions such as sea walls, jetties and groins while ignoring or even destroying coastal habitats that could provide protective benefit. However, interest in natural or ecosystem-based coastal protection strongly increased after several recent natural disasters: the Indian Ocean tsunami, hurricane Katrina and superstorm Sandy. Whereas the tsunami generated a great deal of inquiry into the protective role of mangroves (i.e. Dahdouh-Guebas et al., 2005, Das and Vincent, 2009), hurricane Katrina focused attention on the role of salt marshes in coastal protection (Bohannon and Enserink, 2005, Day et al., 2007, Fischetti, 2005). After Katrina both the popular press and academic community quickly touted the importance of marshes for reducing storm surge waves and cited marsh loss as one culprit in the disaster. Many of the post-Katrina articles suggesting a link between salt marshes and surge reduction pointed to a 1963 U.S. Army Corp of Engineers report that correlated storm surge elevations with over-marsh distance inland for seven storms crossing Louisiana between 1909 and 1957. While the frequently cited report does suggest that marshes can attenuate storm surge waves under some circumstances, nearly fifty years later we are only beginning to understand the role that wetlands play in wave attenuation and more broadly in coastal protection.

Here we focus on the capacity of salt marshes and seagrass beds to provide three specific ecosystem services associated with coastal protection: wave attenuation, shoreline stabilization, and floodwater attenuation, and comment on the current ability for resource managers and other decision makers to be able to set quantitative area-based estimates of these services.

Wave attenuation is the reduction in wave energy or wave height that occurs when a wave passes through submerged or emergent vegetation. The energy of waves, tides, and currents is attenuated via frictional

drag introduced by vegetation and by bottom friction in shallow water areas maintained by seagrasses and marshes (Boesch et al., 2006, Leonard et al., 2006, Tsihrintzis and Madiedo, 2000).

Shoreline stabilization describes the processes by which salt marsh and seagrass vegetation promotes sediment deposition, increases elevations through below-ground production and stabilizes sediments. The seaward salt marsh edge is linked to marsh elevation as a minimum elevation must be maintained to prevent marsh plant drowning and subsequent marsh edge loss. As a result, processes that maintain marsh elevation can also help maintain marsh shorelines and reduce erosion. Sediment deposition within marshes accounts for a large portion of elevation gains on the marsh surface along with small contributions from below-ground processes such as root production (Cahoon et al., 1999, Reed, 1995). Subsidence and compaction can also affect the elevation of the marsh surface, particularly in rapidly subsiding marshes (Penland and Ramsey, 1990). Below-ground biomass, including roots and rhizomes, has been shown to reinforce the substrate and increase the shear strength of the soil potentially reducing erosion (Waldron, 1977, van Eerd, 1985). Seagrass blades reduce hydrodynamic energy which can lead to sediment accumulation which can reduce water heights. Such sediment accretion also contributes to coastal protection, because wave attenuation increases with decreasing relative water depth (Christianen et al., 2013). The bathymetric wave-attenuating effect of vegetation-induced sediment accretion is especially important for seagrasses because they have a relatively small direct wave attenuating effect via their above-ground biomass.

Floodwater attenuation describes the capacity of salt marshes to reduce flood peaks or durations through storage and drainage of floodwaters. It is well known that marshes have a significant influence on the hydrological cycle both in terms of water quality and water quantity. However, the majority of this understanding lies in riparian or inland systems (Bullock and Acreman, 2003). While the floodwater attenuation capacity of wetlands along a river makes intuitive sense, the flood attenuation capacity of complex coastal marshes is likely not as straightforward. According to the United States Environmental Protection Agency (EPA), a one-acre wetland can on average store about three-acre feet of water, or one million gallons (U.S. EPA, 2006). Although this value is a general value for a nondescript 'wetland', it reflects the likelihood that the storage capacity of coastal marshes may have the potential to reduce flood water heights and lessen flood related damages in the coastal zone.

Review of Science Describing Coastal Protection Services

In 2011, Shepard et al. published a synthesis of the protective benefits of salt marshes. The review addressed three specific ecosystem services associated with coastal protection: wave attenuation, shoreline stabilization, and floodwater attenuation. For each service they performed an extensive search of the literature to identify primary research studies assessing the capacity for salt marshes to perform the service(s). They also quantified service provision and recorded marsh vegetation characteristics and environmental factors that were associated with service provision. For services with sufficient studies (wave attenuation and shoreline stabilization), the authors conducted meta-analyses to assess the overall degree to which salt marshes perform each service, and where possible did sub-analyses to examine how subgroups of studies performed differently. When meta-analysis was not possible, they quantified the frequencies of service provision across a range of salt marsh types and geographies to quantitatively summarize the evidence.

Here, we summarize the results from the Shepard et al. (2011) synthesis by ecosystem service type. Because Shepard et al. was published in 2011 and did not address seagrasses, we also conducted a review of the available literature published in the past five years that estimates service provision for wave attenuation, shoreline stabilization, and floodwater attenuation on salt marshes and/or seagrass habitat.

For the new literature search, papers were identified using google scholar between the dates of October 1, 2015 to December 15, 2015. Search terms included (marsh or seagrass) AND (wave attenuation, erosion or flood). Results were limited to manuscripts published between 2010 and 2015 and only those publications that clearly focused on quantifying these ecosystem services at the site scale were evaluated further.

Results

Salt Marsh and Seagrass New Science Review 2011 - present

The new literature search identified 17 relevant studies published from 2011 to 2016 (Table 1). Each study focused on field measurements and new models of wave attenuation, while some additionally focused on erosion reduction and floodwater attenuation. Though the overall body of literature on the coastal protection benefits of seagrass is significantly less than that of salt marshes (beyond just the past five years), it appears to be increasing over the past few years (Ondiviela et al., 2014). Very limited new information exists regarding erosion reduction and floodwater attenuation for either habitat type.

Table 5-1. Results of seagrass and salt marsh literature search pertaining to coastal protection services from 2011 to 2015.

Service	Geography	Habitat	Methods	Reference
Wave attenuation (storm surge)	Gulf of Mexico	Marsh	Review of few available storm surge attenuation estimates	(Engle, 2011)
Wave attenuation	Essex, UK and Galveston, TX	Marsh	Provides field-based measurements of marsh characteristics	(Feagin et al., 2011, Gedan et al., 2010)
Wave attenuation	Multiple	Marsh	Review of few available storm surge attenuation estimates	(Gedan et al., 2010)
Wave attenuation	United Kingdom	Seagrass	Minimum density required for wave attenuation	(Paul and Amos, 2011)
Wave attenuation	Flume	Seagrass (mimics)	wave attenuation is positively correlated with blade stiffness and dependent on a combination of shoot density and leaf length	(Paul et al., 2012)
Wave attenuation	Yangtze Estuary, China	Marsh	Field measurements of wave attenuation compared between two species	(Ysebaert et al., 2011)
Wave attenuation	Mediterranean	Seagrass	Wave attenuation measured in low energy environment (50% attenuation)	(Infantes et al., 2012)
Wave attenuation	Louisiana	Marsh	Field measurements of wave attenuation during a tropical storm (4% to 1.5%/meter)	(Jadhav et al., 2013)
Wave attenuation	Yangtze Estuary, China	Marsh	Field measurements of wave attenuation under medium energy conditions	(Yang et al., 2012)
Wave attenuation (storm surge), floodwater attenuation	Louisiana	Marsh	Simulated four storms to show effect of vegetation roughness and continuity on storm surge levels and damage	(Barbier et al., 2013)
Wave attenuation, erosion reduction	Indonesia	Seagrass	Field study to show that low biomass seagrass can reduce wave-induced erosion	(Christianen et al., 2013)
Wave attenuation	Multiple	Marsh, Seagrass	Re-analyzed existing field data to show importance of drag coefficient	(Pinsky et al., 2013)
Wave attenuation	Flume (UK)	Marsh	Measured wave attenuation under storm conditions	(Moller et al., 2014)
Wave attenuation, erosion reduction	Model	Seagrass	Integrated model that accounts for both wave attenuation and erosion reduction	(Guannel et al., 2015)
Wave attenuation, erosion reduction	N/A	Seagrass	Review paper highlighting factors influencing coastal protection provided by seagrass (qualitative only). Concludes that few available field studies hamper creation of generalized model that can apply to site scale.	(Ondiviela et al., 2014)
Wave attenuation	Model	Seagrass	Model simulation of wave damping incorporating vegetation characteristics into the model	(Karambas et al., 2016)
Wave attenuation, floodwater attenuation	Model Freeport, Texas	Marsh	Modeled wave attenuation of marshes using InVest	(Reddy et al., 2015)

Summary of Shepard et al. 2011

Wave attenuation

Fourteen studies provided quantitative wave attenuation estimates that were sufficient for analysis. Eleven studies were field based and three measured wave attenuation within a flume. The majority of the studies took place in the United Kingdom, U.S. and China. Ten studies examined wave attenuation rates per unit distance in both mud flats and adjacent salt marsh vegetation, while the remaining four studies provided wave attenuation estimates only within marsh vegetation. All ten studies comparing vegetated and unvegetated areas concluded that wave attenuation is greater across marsh vegetation than intertidal mudflat. A meta-analysis conducted on a subset of these found a significant positive effect of vegetation on wave attenuation. Wave attenuation rates generally increased with marsh transect length, and while attenuation rates for shorter transects (<10 m) were highly variable, the results showed that significant attenuation can occur even within the marsh edge.

Marsh width and vegetation height showed a consistent positive effect on wave attenuation which supports the theory that bigger, taller marshes attenuate more waves. Though vegetation characteristics such as vegetation density, vegetation stiffness and marsh width were frequently identified as being important determinants of wave attenuation within salt marshes, the relationships between each characteristic and wave attenuation have not been adequately modeled and tested in the field. This limits our ability to predict wave attenuation on a per area basis even when we have measured these marsh characteristics. Hydrodynamic factors also influence wave attenuation. Although authors have noted these relationships (i.e. increasing wave energy decreases attenuation), the range of favorable conditions has not been thoroughly documented. Thus, it is not possible to quantify the level of wave attenuation expected even if you have detailed information about hydrodynamic conditions and forcing.

Shoreline stabilization

Shepard et al. (2011) identified 57 relevant publications for inclusion in the review of shoreline stabilization provided by marshes. The majority of the experiments were conducted in the field (n = 53) with most studies taking place in North America, Europe and China. Thirty-three studies compared vegetated and unvegetated areas, yielding 36 independent comparisons of the effect of vegetation on one of the three measures of shoreline stabilization. Accretion was the most frequently evaluated response (64% of studies), followed by erosion (22%) and elevation change (14%). Across all studies, a positive effect of marsh vegetation (increased accretion/surface elevation or reduced erosion) was reported in 58% of studies. Of the 33 studies comparing vegetated and unvegetated areas, 18 studies and 38 independent

measures of accretion, erosion, or surface elevation change had sufficient quantitative information for inclusion in a meta-analysis. The overall effect of vegetation on shoreline stabilization was positive.

Though the overall effect of vegetation on stabilization was positive, vegetation characteristics such as species identity, vegetation density, vegetation height, and biomass production all influence stabilization. More importantly, local site characteristics such as the level of wave energy, hydroperiod (length of tidal inundation) and distance to a sediment supply such as a river or creek significantly influence the ability of marsh vegetation to stabilize shorelines. Although these factors are known to influence shoreline stabilization, there is currently insufficient data to confidently develop a model which would allow the prediction of shoreline stabilization per unit area.

Floodwater attenuation

The Shepard et al. review highlighted the lack of quantitative data (at the time) related to the floodwater attenuation benefits of salt marshes. No field studies evaluated floodwater attenuation services with paired experiments within and outside of salt marsh vegetation. Four studies were identified that evaluated the effects of marsh alteration on flooding at scales ranging from individual marsh areas to coastal watersheds, but the lack of control data made it difficult to attribute the role of the marsh vegetation. Therefore the data do not allow for the prediction of floodwater attenuation by areas of salt marsh habitat.

Recommendations for Next Steps and Developing the Science

Our review of the current literature provides strong evidence that coastal vegetation can provide coastal protection benefits. However, the very limited number of field studies and lack of consistent reporting make it difficult to generalize and estimate service delivery for a given area of marsh or seagrass.

Most scientific studies of salt marshes (and to a lesser extent seagrasses) have focused on wave attenuation, and to date, this ecosystem service has the greatest potential to be modeled under certain conditions. However, before that is possible, there is a need to better understand what the upper bounds are on service delivery, based on both vegetation characteristics, forcing and bathymetric conditions. Additional field measurements of wave attenuation through salt marshes under a variety of circumstances are critical for defining these boundaries and fitting models to the observed decreases in wave height. The review identified a substantial need for large-scale, field-based studies evaluating attenuation of large

waves (>1 m) and storm surge. With additional field measurements of wave attenuation in storm conditions, it would be possible to estimate a range of potential wave attenuation under various levels of wave exposure.

Though several different models of wave attenuation have been proposed in the literature, C_d (drag coefficient) values for vegetation, a critical component of these models, are highly dependent on the context in which they were developed or measured and therefore cannot be applied universally (Guannel et al., 2015). Other vegetation parameters, including biophysical measurements such as stem densities and stem heights, are not well understood and need to be measured at a variety of locations throughout the U.S. to generate a database of vegetation parameters (e.g. by region) to allow more accurate modeling of the protective benefits of vegetation (Feagin et al., 2011). We recommend a thorough review and analysis of vegetation parameters and drag coefficient values applied in published studies for marshes and seagrasses (both model and field-based) with complementary field research to verify and fill gaps. This will result in recommended vegetation parameter values (min, max and recommended values) for use in modelling the coastal protection benefits of coastal vegetation.

The complementary field measurements would provide an opportunity to test and validate some of the published models of wave attenuation. The goal of this recommended work is to identify which existing models provide the best fit with observed data using the fewest parameters. Many of the recently published models have not been field-validated and this is a critical gap restricting our ability to predict wave attenuation under a variety of hydrodynamic conditions.

Large gaps remain in our scientific understanding of the shoreline stabilization services provided by coastal vegetation, which, at this time make it impossible to predict, even at relatively large scales (i.e. coastal regions) service provision based on habitat characteristics. Variation in provisioning of this service is likely dependent upon local hydrodynamic conditions. In some circumstances, such as high energy environments, coastal vegetation alone is unlikely to be helpful for shoreline stabilization. Additional studies (such as correlating marsh edge loss with wave exposure) are necessary to delineate what type of environments this benefit is anticipated, and where shoreline stabilization is expected to be lower. Field manipulation of seagrasses and marshes to quantify how the loss (or gain) of vegetation affects erosion is also recommended to better understand and predict this ecosystem service. These experiments should be developed for seagrass and marsh habitats, both separately and in locations where multi-habitat complexes exist to better understand synergistic effects.

Floodwater attenuation has the least number of peer reviewed articles attempting to quantify this service. There is no standardized methodology for estimating reductions in floodwater elevations or extents attributable to coastal habitats. In a few studies hydrodynamic modelling of flooding has been applied to calculate the water level heights with and without the vegetation. However, many coastal projects do not have sufficient funding for this approach and there is a significant need for guidance on approximating post-restoration flooding levels so that “avoided damages” of a potential project can be estimated.

It is important to note that we have only reviewed publications focused on quantifying the three ecosystem services of wave attenuation, shoreline stabilization and flood attenuation for salt marshes and seagrasses. This review does not review the science necessary to convert these values into monetary terms such as damages avoided. While there are a few estimates of damages avoided (Barbier et al., 2013, Reddy et al., 2015), there is not a standard methodology for quantifying damages avoided from acute (i.e. hurricane) and/or chronic events (i.e. erosion). To quantify the coastal protection of a habitat in terms of avoided economic damages, you need to calculate damages both with and without the habitat or restoration project. The difference of these dollar values is the “damages avoided” due to the project.

Damages are calculated using damage curves that plot the relationship between water level and property damage for a variety of structures. A critical decision point is reached when estimating the water levels both with and without a coastal restoration project. Historical or modeled water levels can be used to calculate damages for the “without project scenario”. However, the ‘theoretical’ water level depends very much on the floodwater attenuation benefits of a habitat restoration project. Policy and decision makers often demand economic information such as potential avoided damages. It is critical to note that our ability to provide this information is highly dependent on our ability to estimate the coastal protection services provided by coastal habitats, particularly floodwater attenuation.

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Appendix I: Details of the studies identified through our literature review applying to fish enhancement by salt marshes by region

Salt Marsh in the United States										
Region	State	Bay	Coastal vs Estuarine	Reference	Appropriate methodology and presentation of data	Number of seasons sampled	Season	Year	n (independent sampling events or bays)	Sampling technique
Northern Atlantic Coast	Maine	Wells Harbour, Waquoit Bay	Estuarine	Ayvazian et al., 1992	Yes	8	All	1988-1989	6	seine and trawls
Southern and Mid Atlantic coast	Virginia	Chesapeake Bay	Estuarine	Cicchetti and Diaz 2000	Yes	2	Summer - Autumn	1996	2	drop ring
	New Jersey	Delaware Bay	Estuarine	Able et al., 2007	Yes	18	Spring - Fall	1998-2004	18	otter trawl
	New Jersey	Great Bay	Estuarine	Sogard and Able 1991	Use of marsh creeks	3	Spring - Fall	1989	3	throw trap
	Rhode Island	Narragansett Bay	Coastal	Meng et al., 2004	Yes	4	Summer - Fall	1999 - 2000	4	drop ring
	Florida	Northern Indian River Lagoon Estuary	Estuarine	Stolen et al., 2009	Use of impounded marsh	4	All	2001 - 2002	3	throw trap
	Florida	Sister's Creek/Deep Creek	Estuarine	Panciello 2003	Yes	2	Summer - Fall	2000	2	throw trap
	Massachusetts	Waquoit Bay	Estuarine	Ayvazian et al., 1992	Yes	8	All	1988-1989	6	seine and trawls
	New Jersey	Little egg harbour	Estuarine	Wilson et al., 1990	Poorly paired controls	9	All	1986-1988	7	suction pump
Pacific coast	California	Malibu Lagoon	Estuarine	Ambrose and Meffert 1999	Possibly	5	All	1993-4	5	Seines, fish traps
	California	San Francisco	Estuarine	Grimaldo et al., 2012	Possibly	6	All	1998-9	6	beach seines

Gulf of Mexico	Louisiana	Atchafalaya Bay	Estuarine	Castellanos and Rozas 2001	Yes	1	Spring	1995	1	throw trap
	Alabama	Mobile	Estuarine	Howe et al., 1999	Yes	5	5 incl. 1 winter	1989-1990	4	drop trap
	Texas	Galveston	Estuarine	Minello et al., 1991	Yes	1	Spring	1990	1	drop trap
	Texas	Aransas and Corpus Christi	Estuarine	Neahr et al., 2010	Yes	2	Summer - Fall	2005	4	epibenthic sled - 0.6x0.75 dragged for 10m
	Texas	Sabine Lake	Estuarine	Nevins et al., 2014	Yes	4	Fall, Spring	2011-2013	4	epibenthic sled - 0.6x0.75 dragged for 17m - covering 10m2
	Texas	Galveston	Estuarine	Petrik et al., 1999	Yes	1	Autumn	1996	1	epibenthic sled sampling 10m2
	Mississippi	Mississippi sound	Estuarine	Rakocinski and McCall 2005	Yes	2	Summer - Autumn	1999	2	suction within 1.77m2 drop net
	Texas	San Antonio Bay	Coastal	Rozas and Minello 1998	Yes	2	Autumn, Spring	1993 - 1994	2	drop trap
	Louisiana	Barataria	Estuarine	Rozas and Minello 2006	Yes	2	Autumn, Spring	2003 - 2004	2	drop sampling
	Louisiana	Breton Sound	Estuarine	Rozas et al., 2005	Yes	1	Spring	2001	1	drop sampling
	Texas	Galveston	Estuarine	Rozas et al., 2007	Yes	44	All	1982-1992	33	Drop sampling
	Florida	St Andrew Sound	Coastal	Rozas et al., 2012	Yes	2	Summer - Autumn	2006	2	drop sampling
	Mississippi	Grand Bay, Crooked Bayou and Bayou Heron	Estuarine	Shervette et al., 2011	Yes	3	Autumn, Spring - Summer	2003 - 2004	3	drop trap
	Texas	Galveston	Estuarine	Stunz et al., 2010	Yes	4	All	2000-2001	3	drop trap
	Texas	Galveston	Estuarine	Stunz et al., 2002	Yes	1	Autumn	1997	1	epibenthic trawl covering 10m2
	Texas	Galveston	Estuarine	Thomas et al., 1990	Yes	4	Summer - Autumn, Spring - Summer	1984 - 1985	4	drop trap
	Texas	Lavaca	Estuarine / Coastal	Zimmerman et al., 1990	Yes	2	Autumn, Spring	1985 - 1986	2	drop trap
	Louisiana	Sabine Lake	Estuarine	Bush Thom et al., 2004	Yer	3	Winter, Spring, Fall	2001-2002	2	drop trap and seines
	Louisiana	Barataria	Estuarine	Rozas and Minello 2015	Yes	6	Spring, Autumn	2002, 2005 - 2006	6	drop trap
Caribbean										0

Appendix II: Details of the studies identified through our literature review applying to fish enhancement by seagrass by region

Seagrass in the United States											
Region	State	NOAA CAF Bay Classification	Bay	Coastal vs Estuarine	Reference	Appropriate methodology and presentation of data	Number of seasons sampled	Season	Year	n (independent sampling events or bays)	Sampling technique
Northern Atlantic Coast	Massachusetts	Cape Cod Bay	Cape Cod Bay	Estuarine	Heck et al., 1989	Yes	5	Summer - Summer	1985- 1986	4	Otter Trawl
	Maine	Casco Bay, Penobscot Bay	Casco Bay, Weskeag River	Coastal	Lazzari, 2002	Yes	2	Summer- Fall	1999	4	Throw trap
	Maine	Damariscotta River	Damariscotta River	Estuarine	Matilla et al., 1999	Yes	1	Fall	1999	1	Haul seine
	Maine	Penobscot bay	Penobscot bay	Estuarine	Lazzari 2015	Yes	4	All	2003 - 2004	6	Drop net
	Maine	Casco Bay, Penobscot Bay, Muscongus Bay	3 bays	Estuarine	Lazzari 2013	Yes	15	Spring - Fall	2005-2009	45	Beam trawl
	Maine	Piscataqua- Salmon Falls, Saco Bay, na (Goose Rocks), Casco Bay, Kennebec River, Muscongus Bay, Penobscot Bay, Penobscot Bay, Narraguagus Bay	25 Maine estuaries	Estuarine	Lazzari and Stone 2006	Yes	6	Spring - Fall	2000-2004	42	Beam trawl
Southern and Mid Atlantic Coast	Connecticut, New Jersey	Long Island Sound, Raritan Bay, New Jersey Inland Bays	3 bays	Estuarine	Goldberg et al., 2002	Yes	6	Spring - Fall	1995 - 1996	18	Beam Trawl
	Virginia	Cheasapeake Bay	Cheasapeake Bay	Estuarine	Heck & Orth, 1980	Yes	4	All	1977	3	Otter Trawl
	Maryland, Virginia	Cheasapeake Bay	Parson's island, York River	Estuarine	Heck & Thoman, 1984	Yes	7	Fall, Spring - Fall	1978 - 1980	7	Otter Trawl
	Virginia	Cheasapeake Bay	Lower Cheasapeake Bay	Estuarine	Orth & Heck, 1980	Yes	1	Spring - Fall	1977	3	Otter Trawl

Pacific Coast	New York	Great South Bay	Fire Island National Seashore	Coastal	Raposa & Oviatt, 2000	Yes	1	Summer	1995	1	Throw trap
	New Jersey	New Jersey Inland Bays	2 Islands in Great Bay	Estuarine	Sogard & Able 1991	Yes	3	Spring-Fall	1988, 1989	6	Throw trap
	North Carolina	Bogue Sound	Back Sound, Carteret County	Coastal	Summerson & Peterson, 1984	Yes	2	Summer-Winter	1977	2	Seine hauls
	New Jersey	New Jersey Inland Bays	Little Egg Harbour	Coastal	Wilson et al., 1990	Yes	9	Summer - Fall, Spring - Fall, Spring	1986 - 1988	6	Suction sampler
	Massachusetts	Buzzards Bay, Chesapeake Bay	Buzzards Bay	Estuarine	Wyda et al., 2002	Yes	1	Summer	1995 - 1996	2	Otter trawl
	Virginia	Chesapeake Bay	Chesapeake Bay	Estuarine	Sobocinski et al., 2013	Yes	6	Summer, All four, Summer	2009-2011	5	Otter trawl
	Virginia	Chesapeake Bay	Chesapeake Bay	Estuarine	Olney and Boehlert 1988	Possibly	5	Spring - Spring	1979 - 1980	4	Pushnet
	Washington		Willapa Bay	estuarine	Hosack et al., 2006	Possibly	2	Spring, summer	2001	2	fyke nets
	Washington		Willapa Bay	estuarine	Dumbauld et al., 2015	Yes	3	Summer, autumn, spring	2002-2003	3	modified trawl
	California		San Francisco	estuarine	Grimaldo et al., 2012	Possibly	6	All	1998-9	6	beach seines
	California		Elkhorn Slough	estuarine	Grant 2009	Yes	4	All	2008	3	drop net
	Washington / Oregon		4 bays	estuarine	Ramsay 2012	Possibly		Summer	2011	1	quadrats
	California		Humboldt	estuarine	Pinnix et al., 2005	Possibly	9	All	2003-2005	9	fyke nets, shrimp trawls
Caribbean	British Virgin Islands		3 lagoons on Tortola	coastal	Gratwicke and Speight 2005	Possibly		Summer-Autumn	2001	6	Quadrat, counting
	British Virgin Islands		3 lagoons on Tortola	coastal	Gratwicke et al., 2006	Possibly		Summer-Autumn	2001	6	Quadrat, counting
	Bahamas		Numerous bays on Andros Island	estuarine	Layman et al., 2004	No		Summer	2001/2002	6	Underwater Visual Census

											et al., 1984)
	Louisiana	Breton Sound	Breton Sound	Estuarine	Rozas et al., 2005	Yes	1	Spring	2001	1	Drop sampler 1m ²
	Texas	Galveston Bay	Galveston Bay	Estuarine	Scott et al., 1998	Yes	4	Fall, Spring - Fall	1993 - 1994	4	Throw trap, 1 m ² (Kushlan, 1981)
	Florida	North Ten Thousand Islands	Rookery Bay	Estuarine	Sheridan 1992	Yes	3	Summer, Fall, Spring	1988 - 1989	3	Drop sampler (Zimmerman et al., 1984)
	Texas	Galveston Bay	Galveston Bay	Estuarine	Sheridan 2003a	Yes	6	Spring - Fall	1994 - 1995	6	Throw trap, 1 m ² (Kushlan, 1981)
	Texas	Laguna Madre	Laguna Madre	Estuarine	Sheridan and Minello 2003	Yes	4	Spring, Autumn	1996 - 1997	4	Drop sampler, 1m ² (Zimmerman et al., 1984)
	Florida	Florida bay	Florida bay	Estuarine	Sheridan et al., 1997	Yes	3	Summer, Fall 1990, Spring 1991	1990-1991	3	drop sample 2.6 m ²
	Texas	Galveston Bay	Galveston Bay	Estuarine	Stunz 2002	Yes	1	Fall	1997	1	Epibenthic sled 0.6 m x 0.75 m, 1 mm mesh, Holt et al., 1983
	Texas	Galveston Bay	Galveston Bay	Estuarine	Thomas 1990	Yes	5	1984 - All, 1985 Summer	1984 - 1985	4	Cylindrical drop trap, 1.8 m ² diameter (Zimmerman et al., 1984)
	Alabama	na	Bayou Saint John	Estuarine	Williams 1990	Yes	5	Summer - Summer	1987 - 1988	4	Suction sampler (Orth & Van Montfrans, 1987), 0.91 m diameter, 0.66 m ² substratum surface area

Note: Caribbean studies in italics use the same data as the previous paper in the table.

Appendix III: Details of the studies identified through our literature review applying to fish enhancement by oyster reefs by region

Oyster Reef in the United States										
Region	State	Bay	Coastal vs Estuarine	Reference	Appropriate methodology and presentation of data	Number of seasons sampled	Season	Year	n (independent sampling events or bays)	Sampling technique
Atlantic Coast	<i>analysis already completed</i>									
Pacific Coast	Washington	Willapa Bay	estuarine	Dumbauld et al., 2015	Yes	3	Summer, autumn, spring	2002-2003	3	modified trawl
	Washington	Willapa Bay	estuarine	Hosack et al., 2006	Poorly paired controls	2	Spring, summer	2001	2	fyke nets
	Washington / Oregon	4 bays	estuarine	Ramsay 2012	Possibly	1	Summer	2011	1	quadrats
	California	Humboldt	estuarine	Pinnix et al., 2005	Possibly	9	All 4	2003-5	9	fyke nets, shrimp trawls
Caribbean										
Gulf of Mexico	<i>analysis already completed</i>									

Appendix IV: Details of the studies identified through our literature review applying to denitrification by region

SALT MARSH

Citation	Habitats Sampled	Method	Season	Species	Control present
US					
Atlantic Coast					
Baas et al. 2014†	Marsh	Acetylene block; potential	Spring Fall	<i>Spartina alterniflora</i>	Y
O'Meara et al. 2015	Mid-marsh	N ₂ :Ar	Spring Summer Fall Winter Annual	<i>Spartina cynosuroides</i> <i>Juncus roemerianus</i> <i>S. alterniflora</i> <i>Salicornia</i> spp. <i>Phragmites australis</i>	Y
Smyth et al. 2015*	Marsh Mudflat	N ₂ :Ar; ambient & potential	Summer	-	Y
Porubsky et al. 2014	Creekbank	Acetylene block; potential	Spring/ Summer	<i>S. alterniflora</i> <i>Salicornia</i> spp <i>Juncus</i> spp (adjacent)	Control only
Smyth et al. 2013*	Marsh Intertidal flat Subtidal flat	N ₂ :Ar	Spring Summer Fall Winter Annual	-	Y
Deegan et al. 2012	Low marsh	Acetylene block; potential	-	<i>S. alterniflora</i>	N
Piehlér & Smyth 2011*	Marsh Intertidal flat Subtidal flat	N ₂ :Ar	Spring Summer Fall Winter Annual	-	Y

Aelion & Engle 2010	Tidal creek	Acetylene block; potential	-	-	Control only
Koop-Jakobsen & Giblin 2010	High marsh Creek bottom	Isotope pairing + N ₂ :Ar; potential & ambient Isotope pairing + N ₂ :Ar + push pull ¹⁵ N tracer; potential	Summer	<i>Spartina patens</i>	Y
Koop-Jakobsen & Giblin 2009a	Oligohaline Transition High marsh Low marsh	¹⁵ N tracer; potential	Summer	<i>S. patens</i> <i>S. alterniflora</i> <i>P. australis</i> <i>T. angustifolia</i>	Y
Koop-Jakobsen & Giblin 2009b	Oligohaline High marsh Mid-marsh Low marsh	Isotope pairing + N ₂ :Ar + push pull	Summer	<i>S. patens</i> <i>S. alterniflora</i> <i>Distichlis. spicata</i> <i>T. angustifolia</i>	N
Porubsky et al. 2009	Tidal creek	Isotope pairing + N ₂ :Ar	Spring Winter	<i>S. alterniflora</i> (adjacent)	Control only
Boynton et al. 2008	Oligohaline Mesohaline	N ₂ :Ar	Annual	-	Y
Craft et al. 2009	Salt marsh Brackish marsh Freshwater marsh	Acetylene block; potential	Spring	<i>S. alterniflora</i> <i>J. roemerianus</i> <i>Zizaniopsis mileacea</i>	N
Caffrey et al. 2007	High marsh	N ₂ :Ar	Summer	<i>S. patens</i>	N
Addy et al. 2005	Transition High marsh Low marsh	¹⁵ N tracer + push pull; potential	Spring Summer Fall	<i>Iva frutescens</i> <i>Limonium nashii</i> <i>Solidago sempervirens</i> <i>S. alterniflora</i>	N
Dollhopf et al. 2005	Marsh Creek bank	Acetylene block; potential	Summer Winter	<i>S. alterniflora</i>	Y

Hamersley & Howes 2005	Marsh	^{15}N retention; mass balance	Spring Summer Fall Winter Annual	<i>S. alterniflora</i>	N
Ma & Aelion 2005	Streambed	Acetylene block; ambient + potential	Summer Fall Winter	<i>Spartina</i> spp.	Control only
Davis et al. 2004	High marsh	N_2 flux	Summer	<i>S. patens</i> <i>D. spicata</i> <i>Schoenoplectus pungens</i>	Y
Wigand et al. 2004	High marsh Low marsh	Acetylene block; potential	Spring Fall	<i>S. patens</i> <i>S. alterniflora</i>	N
Hamersley & Howes 2003	Mud flat Sand flat	N_2 flux Nitrate uptake	Spring Summer Fall Winter Annual	-	Control only
Tobias et al. 2001a	Marsh	Acetylene block; potential	Spring Fall	<i>S. cynosuroides</i> <i>S. alterniflora</i>	N
Tobias et al. 2001a	Marsh	^{15}N tracer + N_2 :Ar + isotope pool calculations	-	<i>S. cynosuroides</i> <i>S. alterniflora</i>	N
Nowicki et al. 1999	Estuary sediment	N_2 flux	Spring Summer Fall Winter Annual	-	Control only
Anderson et al. 1997	Marsh Creek bank	$^{15}\text{N}_2\text{O}$ isotope pool dilution	Spring Summer Fall Winter Annual	<i>S. alterniflora</i>	Y
Curran et al. 1996	Marsh	Acetylene block; ambient & potential	Summer	<i>S. alterniflora</i>	N

DeSouza & Yoch 1996	Low marsh	Acetylene block; potential	Late Summer	<i>S. alterniflora</i>	N
Thompson et al. 1995	Marsh	Acetylene block; potential	Spring Summer Fall Winter	<i>S. alterniflora</i>	N
Johnson et al. 1994	Marsh	N ₂ flux	Summer	<i>S. alterniflora</i>	N
White & Howes 1994	Marsh	¹⁵ N retention; mass balance	Summer	<i>S. alterniflora</i>	N
Slater & Capone 1989	Low marsh	Acetylene block; ambient & potential N ₂ O reductase; potential	-	<i>S. alterniflora</i>	N
Sherr & Payne 1981	Marsh	N ₂ O reductase; potential	Fall	<i>S. alterniflora</i>	N
Kaplan et al. 1979	High marsh Low marsh Panne Creek bottom	N ₂ :Ar N ₂ flux; gas partitioning	Spring Summer Fall Winter Annual	<i>S. alterniflora</i> <i>S. patens</i> <i>D. spicata</i>	Y
Valiela & Teal 1979	High marsh Low marsh Panne Creek bottom	N ₂ :Ar N ₂ flux; gas partitioning	Spring Summer Fall Winter	<i>S. patens</i> <i>D. spicata</i> <i>S. alterniflora</i>	Y
Sherr & Payne 1978	Marsh	N ₂ O reductase; potential	Spring Summer Fall Winter	<i>S. alterniflora</i>	N
Kaplan et al. 1977	Tidal creek	N ₂ flux; gas partitioning	Spring Summer Fall Winter	-	Control only
Gulf Coast					

Baas et al. 2014†	Marsh	Acetylene block; potential	Spring Fall	<i>S. alterniflora</i>	Y
Pietroski et al. 2015a	Marsh	Acetylene block; potential	Spring	<i>S. alterniflora</i>	N
Pietroski et al. 2015b	Marsh	Acetylene block; potential	Spring	<i>S. alterniflora</i>	N
Horel et al. 2014	Marsh	Acetylene block; potential	Spring Fall Winter	<i>J. roemerianus</i>	N
Shi & Yu 2014	Marsh	Acetylene block; potential	-	<i>S. alterniflora</i> <i>S. patens</i>	N
Lindau & DeLaune 1991	Marsh	¹⁵ N tracer; N ₂ flux	Fall	<i>S. alterniflora</i>	N
DeLaune & Patrick 1990	Brackish marsh	Mass balance	Annual	<i>S. patens</i>	N
Pacific Coast					
Yang et al. 2015	High marsh	¹⁵ N tracer; N ₂ O flux Acetylene block	Summer	<i>Salicornia virginica</i> <i>D. spicata</i> <i>Grindelia stricta</i> <i>Jaumea carnosa</i> <i>Limonium californicum</i> <i>Triglochin concinna</i>	N
Caffrey et al. 2010	Low marsh Tidal Pond	N ₂ :Ar.	Summer	-	N
Joye & Paerl 1994	Marsh Mudflat	Acetylene block; ambient & potential	Spring Summer Fall	<i>Salicornia</i> spp	Y
Joye & Paerl 1993	Marsh Mudflat	Acetylene block; potential	Spring	<i>Salicornia</i> spp	Y
Canada, Atlantic					

Poulin et al 2007	Low marsh	Isotope pairing	Summer Fall Winter	<i>S. alterniflora</i>	N
Europe					
UK					
Olsen et al. 2011	High marsh	Acetylene block; ambient & potential	Summer	<i>Elymus repens</i> <i>Festuca rubra</i> <i>Triglochin maritima</i> <i>Sonchus arvensis</i>	N
Blackwell et al. 2010	Marsh	Acetylene block; ambient & potential	Winter	<i>Agrostis stolonifera</i> <i>Juncus effusus</i> <i>Puccinellia maritima</i> <i>Aster tripolium</i> <i>Glaux maritima</i> <i>Spartina anglica</i>	N
Koch et al. 1992	Marsh Mudflats	Acetylene block	Spring Summer Fall Winter	<i>Halimione portulacoides</i>	Y
Abd. Aziz & Nedwell 1986	High marsh Drainage creek Salt pan	¹⁵ N tracer	Summer	<i>P. maritima</i> <i>H. portulacoides</i> <i>Spartina townsendii</i>	Y
King & Nedwell 1985	Drainage creek	Acetylene block; potential	-	-	Control only
Nedwell 1982	Creek	Mass balance; ambient & potential	-	-	Control only
Portugal					
Cartaxana & Lloyd 1999	Low marsh	N ₂ and N ₂ O flux; ambient & amended	Winter	<i>S. maritima</i>	N
Lillebø et al. 1999	Marsh	Mass balance	-	<i>S. maritima</i>	Y
Mediterranean					

Eriksson et al. 2003	Marsh Tidal creek	Isotope pairing	Spring Summer Fall	<i>Limonium serotinum</i> <i>Juncus maritimus</i> <i>H. porulacoides</i>	Y
Asia					
Wang et al. 2007a	Mid marsh Bare sediment	Acetylene block	Spring Summer Fall Winter Annual	<i>Scirpus mariqueter</i> <i>Schoenoplectus triqueter</i>	Y
Wang et al. 2007b	Mid marsh Bare sediment	Acetylene block	Summer	<i>S. mariqueter</i>	Y
Oceania					
Kaspar 1983*	High marsh	Acetylene block; ambient & potential	Fall	<i>J. maritimus</i>	See Kaspar 1982
Kaspar 1982*	Mudflat	Acetylene block; ambient & potential	Fall	-	Control only

Marsh: If habitat not specified as high, low, etc., in literature, listed here as “marsh”.

Seagrass: If habitat not specified as intertidal or subtidal in literature, listed here as “bed”.

*Reference includes both marsh and seagrass sites and is listed once in each table.

†Reference includes sites in multiple regions and is listed once in each applicable region.