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Geographic variation in salt marsh structure and function for nekton: a guide to finding commonality across multiple scales --Manuscript Draft--

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Abstract:	<p>Coastal salt marshes are distributed widely across the globe and are considered essential habitat for many fish and crustacean species. Yet the literature on fishery support by salt marshes has largely been based on a few geographically distinct model systems, and as a result, inadequately captures the hierarchical nature of salt marsh pattern, process, and variation across space and time. A better understanding of geographic variation and drivers of commonalities and differences across salt marsh systems is essential to informing future management practices. Here, we address the key drivers of geographic variation in salt marshes: hydroperiod, seascape configuration, geomorphology, climatic region, sediment supply and riverine input, salinity, vegetation composition, and human activities. Future efforts to manage, conserve, and restore these habitats will require consideration of how environmental drivers within marshes affect the overall structure and subsequent function for fisheries species. We propose a future research agenda that provides both the consistent collection and reporting of sources of variation in small-scale studies and collaborative networks running parallel studies across large scales and geographically distinct locations to provide analogous information for data poor locations. These comparisons are needed to identify and prioritize restoration or conservation efforts, identify sources of variation among regions, and best manage fisheries and food resources across the globe.</p>	

**Geographic variation in salt marsh structure and function for nekton: a guide to finding
commonality across multiple scales**

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Abstract

Coastal salt marshes are distributed widely across the globe and are considered essential habitat for many fish and crustacean species. Yet the literature on fishery support by salt marshes has largely been based on a few geographically distinct model systems, and as a result, inadequately captures the hierarchical nature of salt marsh pattern, process, and variation across space and time. A better understanding of geographic variation and drivers of commonalities and differences across salt marsh systems is essential to informing future management practices. Here, we address the key drivers of geographic variation in salt marshes: hydroperiod, seascape configuration, geomorphology, climatic region, sediment supply and riverine input, salinity, vegetation composition, and human activities. Future efforts to manage, conserve, and restore these habitats will require consideration of how environmental drivers within marshes affect the overall structure and subsequent function for fisheries species. We propose a future research agenda that provides both the consistent collection and reporting of sources of variation in small-scale studies and collaborative networks running parallel studies across large scales and geographically distinct locations to provide analogous information for data poor locations. These comparisons are needed to identify and prioritize restoration or conservation efforts, identify sources of variation among regions, and best manage fisheries and food resources across the globe.

Keywords: salt marshes, spatial scales, environmental drivers, global networks, open science

Introduction

Understanding the drivers of geographic variation in the condition and composition of habitats is crucial to our capacity to generalize management plans across space and time, and to clarify and perhaps challenge assumptions of functional equivalence among sites. Broadly defined wetland types such as salt marshes are often assumed to provide similar functions throughout their global range, such as providing nursery habitat for fishery species. However, a growing body of evidence suggests substantial geographic variation in the functioning of salt marsh and other coastal ecosystems (Bradley et al. 2020; Whalen et al. 2020). Variation in ecological patterns and processes within habitat types can alter community structure and dynamics. Local scale patterns and processes (e.g., patch [10s of meters], local [100s of meters]) can be influenced by processes that occur at larger spatial scales (e.g., regional [kms], global), thereby causing geographic differences in the function and ecosystem service delivery of a given habitat type.

Salt marshes (which include vegetated platform, interconnected tidal creeks, fringing mudflats, ponds, and pools) are widely distributed (Figure 1), and function as valuable nursery habitats by providing key resources for many estuarine species that transition to marine and terrestrial habitats as adults (Beck et al. 2001, Minello et al. 2003, Sheaves et al. 2015). However, factors that underlie variability in the delivery of ecological functions are still inadequately understood. Previous studies have explored geographic variation in the function of salt marshes for fish and mobile crustaceans ('nekton'; e.g., Minello et al. 2012, Baker et al. 2013). However, field studies that compare multiple sites across a geographical gradient are typically limited in duration and scale. In addition, the explanatory variables (e.g., elevation,

flooding duration, plant structure) collected by smaller-scale studies are often inconsistent and therefore limit generalizations across sites.

The absence of evidence on how marshes are structured and function in specific areas results in management decisions based on knowledge from other locations without a clear understanding of the limitations, drivers of variability in function, or equivalence between locations. This limits the confidence in these extrapolations (Bradley et al. 2020). In many cases, equivalence in salt marsh function is inappropriately assumed, even at small scales, such as along salinity gradients within a single estuary (Duffy et al. 2015a), and at larger regional scales (Ziegler et al. 2020). These differences in function has significant implications for identifying and prioritizing restoration or conservation efforts, identifying sources of variation among locations, and incorporating habitat and environmental drivers into stock assessments and ecosystem-based fisheries management.

In this perspective, we aim to guide salt marsh research toward a standardized data collection process that will facilitate the identification of geographic variation in structure and function relevant to fisheries management decisions. We propose a framework that includes reporting key variables of ecological drivers that can be used for comparison (Rozas 1995, Connolly 1999) to better determine equivalence among geographically distinct locations. We encourage the creation of collaborative research consortiums (e.g., Duffy et al. 2015b), and the use of data syntheses and meta-analysis approaches (e.g., Ziegler et al. 2019, Kimball et al. this issue) to better assess marsh structure and function and to disentangle overarching global patterns of marsh function (e.g., trophic transfer, global consumption rates).

Large-scale patterns of geographic variation observed across ecological systems, such as salt marshes, are governed by latitudinal gradients (Schemske et al. 2009) and range limits (e.g.,

Sagarin and Gaines 2002), shaping the overall species pool. We view patterns in geographic variation as hierarchical, whereby small-scale heterogeneities (temporal, spatial, abiotic, biotic) are nested within larger-scale patterns that collectively shape salt marsh communities. Here, we identify eight key drivers of variation in salt marsh structure and function: hydroperiod, seascape configuration, geomorphology, climatic region, sediment supply and riverine input, salinity, vegetation composition, and human activities (Table 1). Although we have identified human activities as a key driver of variation for marsh structure and function, this topic is synthesized in depth by Gilby and colleagues (this issue); therefore, we focus on the seven other environmental drivers of variation in salt marsh function. We discuss how each driver affects marsh structure and function for nekton and highlight important sources of variation. We recommend that future studies focus on collecting and reporting data on these environmental drivers and their sources of variation (including human activities) to identify commonality in salt marshes across local, regional, and global scales (Table 1). In addition, we propose the creation of a collaborative salt marsh research network rooted in open science principles that implements simple, standardized experiments at local sites to aid comparisons across regional and global scales. The combination of unified data collection and reporting, open science, and regional- or global-scale synthesis can help provide a clearer understanding of how marshes support nekton communities, and how marsh function varies among regions and through time. Our overarching goal is to ensure that the evidence used to inform conservation, restoration, and management practices, especially in data deficient locations, comes from systems for which comparable information is available.

Environmental Drivers of Geographic Variation

Hydroperiod. Hydroperiod, defined as the duration, frequency, and depth of flooding of the intertidal salt marsh surface (Rozas 1995; Table 1), directly mediates access to intertidal areas within the salt marsh complex by nekton. Hydroperiod also indirectly influences salt marsh habitat use through its effects on vegetation structure (Mitsch and Gosselink 1986) and the distribution of prey resources (Kneib 1984). Salt marsh habitats have long been considered to support enhanced growth and survival for nekton compared to unstructured habitat (Boesch and Turner 1984). While empirical data demonstrating the mechanisms are challenging to obtain (Lefcheck et al. 2019), it is clear that the benefits nekton gain from accessing shallow intertidal parts of the salt marsh are regulated by hydroperiod (Rozas 1995, Nelson et al. 2015).

The hydroperiod of salt marshes and other intertidal wetlands varies at multiple spatial and temporal scales (e.g., Minello et al. 2012; see types in Figure 1), and evidence is growing that these differences in hydroperiod drive variation in ecosystem function (Igulu et al. 2014, Bradley et al. 2020). Patterns of flooding determine opportunities for fish foraging on the salt marsh surface (Hollingsworth and Connolly 2006) or in adjacent intertidal creeks and may control the flow of salt marsh production to aquatic food webs (Baker et al. 2013). Nekton foraging within the salt marsh transfer production to aquatic food webs via trophic relay (Kneib 1997), and hydroperiod may be a key driver of spatial variation in predator-prey dynamics by controlling the patterns of exposure of small nekton to predators in open waters adjacent to the salt marsh (Ziegler et al. 2019).

The key sources of variation in marsh hydroperiod are tidal regime, including astronomical tides or meteorological forcing (e.g., wind, rainfall and river flows), flooding frequency, duration, and depth (directly influenced by marsh surface elevation), and the overall coastal geomorphology (Rozas 1995; Table 1). The relative importance and interactions among

these sources vary substantially among locations. Tidal amplitude and freshwater discharge combine to regulate hydroperiod (Rozas 1995), and these drivers show complex variation at a global scale. Weather fronts and the associated winds have greater influence on salt marsh hydroperiod in microtidal regions than in macrotidal ones (Rozas 1995, Minello et al. 2012; Tweedley et al. 2016), and can drive variations in salt marsh flooding in different parts of individual estuaries (Ward 1980). These key sources of variation in hydroperiod are being modified by global climate change across multiple scales (see Able this issue; Colombano et al. this issue).

Seascape configuration. The location, shape, and positioning of salt marshes within seascape mosaics can also impact the structure and complexity of marshes, and the number and diversity of animals that inhabit them (Gilby et al. this issue, James et al. this issue). This seascape context can have subsequent influence on the rate and distribution of key ecological functions and services throughout the broader seascape (Boström et al. 2011). Local-scale (e.g., amount of edge, area, and shape) to patch-scale (e.g., salt pools, ponds or channels) features of salt marshes may be responsible for changes in the abundance of fauna at a given site (Meyer and Posey 2014: Table 1). As with other vegetated habitats in terrestrial and aquatic ecosystems, edge effects in salt marshes appear particularly important by enhancing material exchange, secondary production, and trophic relays (Minello et al. 2008, Weinstein et al. 2014). In addition, high marsh-to-open-water-ratio provides valuable foraging (Hammock et al. 2019) and nursery habitats for both resident and transient fishes (Colombano et al. 2020).

The landscape context and connections between salt marshes and adjacent habitats (connectivity) varies greatly across the globe. Depending on the location, salt marshes may be found in seascapes that include shallow mud- and sand-flats, seagrass, shellfish reefs,

mangroves, and rocky or coral reefs or terrestrial landscapes with relatively flat coastal plains, upland forests, or mountains (see examples in Figure 1). Connectivity with adjacent habitats affects the faunal species inhabiting or using the salt marshes. For instance, seascapes with highly connected seagrass and salt marsh exhibit higher nekton diversity and density, and higher catch rates of fishery species, than seascapes composed of seagrass habitat alone (Baillie et al. 2014). Movement of fauna between habitat patches influences nutrient fluxes, trophic transfer, fishery production, and ultimately patterns of species diversity within estuaries (Duffy 2006).

Although ecologists have often hypothesized the spatial variables that most determine the value of salt marsh habitat for nekton species, and tested for some of these effects in isolation, we often lack empirical evidence regarding the relative importance of interactions across the full suite of structure and spatial components that influence the value of salt marshes for coastal species (Boström et al. 2011). Similarly, the influence of variation in the structure of seascapes at continental scales on the consistency of patterns in salt marsh structure and function remains unclear.

Geomorphology. Studies of salt marsh ecosystems have provided unique insight into the role of geomorphology in shaping habitat distribution and influencing energy flow across the landscape (Table 1). Geomorphology can control food web dynamics by regulating predator access to specific habitats (Nelson et al. 2019a) and potentially change the magnitude of top-down control on local prey communities (Power et al. 1996). In turn, if geomorphology limits predator access, then the magnitudes of top-down and bottom-up forcing will vary as a function of the duration of access and the intensity of predation (Power et al. 1996).

Local geomorphology (positioning) is known to have a substantial influence on salt marsh species distributions, access to foraging areas, subsequent species interactions, production,

and energy flow to adjacent habitats (Allen et al. 2007, Christian and Allen 2014, Nelson et al. 2019a; Table 1). The periodicity of tidal pumping is a strong control on the connectivity of salt marsh habitats across geomorphic boundaries. Most often, tidally controlled connectivity in salt marshes is characterized by a unidirectional flow of energy from areas only flooded during high tide to the aquatic environment determined by marsh surface elevation, edge morphology or slope, and the degree of channelization (Power et al. 1996, Sheaves 2009). This unequal energy flow can result in intermittently flooded habitats that link and subsidize food webs (Nelson et al. 2019a). Therefore, changes in habitat structure or configuration (ratio of vegetated to non-vegetated habitat and number of open water pools or ponds) can disrupt ecosystem-level energy flows by altering the ability of mobile consumers to access critical resources and move energy across the landscape (Sheaves 2009; Table 1).

At larger scales, the local effects of geomorphology can compound to create spatial habitat mosaics that alter ecosystem function (Kennedy et al. 2016). In areas where local geomorphologies facilitate movement and food web connectivity, regional “hotspots” can occur where consumers and prey are brought together by geomorphic characteristics that facilitate the transfer of energy (Kneib 2000, Kennedy et al. 2016). Alternatively, geomorphic discontinuities can result in barriers to energy flow and alter animal movement by creating boundaries or divisions in productivity regimes that can redistribute top down pressure (Wilcove and Wikelski 2008). With increasing geomorphic scale, boundaries between systems facilitate ecotonal transition areas that can develop their own pattern of energy flow and habitat distribution (Poole 2002). As a result, geomorphology drives hierarchically structured variation in salt marshes, with small-scale variations in surface topography creating variable microhabitats nested within large-

scale variation in landscape structure. Such geomorphic structures and processes also strongly mediate the capacity of salt marshes to persist under sea-level rise (Colombano et al. this issue).

Climatic region. Climatic sources of variation (primarily temperature, precipitation, and disturbance regimes) greatly influence the structure and functioning of ecosystems across the globe (Jobbágy and Jackson 2000; Table 1). Variation between climatic regions and associated disturbances are superimposed and interact to produce a mosaic of climatic conditions that may vary at quite small scales (e.g., Sheaves and Johnston 2009). Climatic variability is more pronounced in some regions, such as poleward regions with freezing winters, as well as regions with strong seasonal periodicity in precipitation (e.g., Mediterranean climates with wet winters and dry summers; examples in Figure 1). The latter are often combined with inter-annual variation in ocean conditions (e.g., El Niño-La-Niña cycles). Such temporal shifts in hydroclimate may determine community composition in salt marshes that are subject to both marine and freshwater processes (Davis et al. 2012).

The major disturbances affecting salt marshes include winter ice (Hardwick-Whitman 1985, 1986), monsoons (Jin et al. 2007, Davis et al. 2012), floods and droughts (Angelini et al. 2016), and tropical cyclones (see Cahoon 2006, Wang et al. 2016; Table 1). Globally, the magnitude, frequency, and duration of these disturbances and their influences of plant and faunal communities vary considerably (Figure 1). While nekton communities are generally resilient to these large, anomalous disturbances (Oakley and Guillen 2020), some time-assisted restoration may be needed to recover to pre-disturbance states (Waltham et al. this issue). We recognize that disturbances may also directly affect other key environmental drivers (e.g., geomorphology, sediment supply, etc.) across multiple temporal and spatial scales, and thus induce cascading effects on nekton communities. Therefore, studies quantifying the magnitude, frequency, and

duration of disturbance events and their direct and indirect impacts on habitat structure and nekton are of increasing importance for comparing and contrasting current states and future trajectories of geographically distinct salt marshes.

Climate-driven ecological thresholds and regime shifts are common in coastal wetlands (Feher et al. 2017). Warmer winters can trigger the encroachment of mangroves into salt marshes (Saintilan et al. 2014), and drier precipitation regimes (days of precipitation or days of drought annually) can result in the conversion of tidal wetlands to salt flats (Gabler et al. 2017) regardless of geographic region. The potential implications of these shifts on salt marsh support of fisheries are beginning to be explored (Nelson et al. 2019b), and add further complexity to geographic variations and climate change in salt marsh function.

Sediment supply and riverine input. Both sediment deposition and accrual of organic matter are important processes for salt marsh structure and function (Table 1). The degree to which salt marshes rely on sediment deposition versus biogenic accumulation of plant biomass for elevation maintenance or gain (horizontal and vertical change in the marsh; Table 1) is variable across space and with latitude (Crosby et al. 2017). When large and persistent reductions in sediment supply occur, sediment deposition and accrual onto the salt marsh surface (net rate of sediment deposition) are also reduced and, as a result, the marsh begins to erode or sink relative to sea-level (see Able this issue). Persistent erosion leads to decreased structural integrity of the salt marsh soil and, eventually, to salt marsh fragmentation and loss (Rogers et al. 2015).

Geographical gradients in sediment delivery into coastal systems are primarily controlled by the presence of large rivers (distance from nearest major river) with high sediment inputs, or sediment resuspension from eroded material (in situ discharge, peak riverine discharge). For instance, the Mississippi River accounts for approximately 85% of the total sediment delivery

into the Gulf of Mexico (Allison et al. 2012) and marshes can be extensive, diverse, and productive throughout the deltaic landforms (Osland et al. 2014, example marsh in Louisiana: Figure 1). By contrast, many salt marshes far from large rivers or constrained by levees are sustained by the erosion, resuspension, and tidal deposition of internal sediment (Virgin et al. 2020). The interaction among the distribution of rivers, land use within their catchments (human activities, Table 1), river modifications that impact sediment delivery (e.g., land use change, channelization, levees and dams), and rainfall combine to create a spatial mosaic of sediment delivery to coastal salt marshes that impacts the structure and function of these systems.

Salinity. Relationships between salinity and the distribution of organisms within estuaries has received considerable attention (e.g., Rakocinski et al. 1992, Elliott et al. 2007). While marsh habitats can be found across estuaries, ranging from fully fresh (salinity = 0) to hypersaline systems (salinity > 35; in situ salinity), the salinity regime (in conjunction with hydroperiod and geomorphology) of a given marsh affects the species composition of both the plant and nekton assemblages (Table 1). Across salinity gradients, spatial patterns in species richness are apparent with the greatest species richness in fully saline areas adjacent to the ocean and decreases with declining salinity (Gilby et al. 2018). Salinity regime (categorical salinity regime, mean annual salinity range) can be more important than habitat type in determining fish community composition (Bradley et al. 2019). The habitat value of estuarine salt marshes can change with season or year as the salinity regimes of these habitats respond to changes in freshwater input (i.e., snowmelt [San Francisco Bay Estuary, Figure 1], floods, droughts; annual days of low salinity). For example, during drought years, upper estuary (low salinity) marshes may become more valuable habitat for penaeid shrimps as increasing salinity becomes more favorable and the extent of suitable habitat expands estuary-wide (Mace and Rozas 2017). Shifts

in salinity occur across seasonal and interannual scales and may increase in frequency and intensity with changes in climate (Cloern et al. 2017). Understanding how salinity regime of a given marsh site influences the overall species assemblage and functional diversity may be key in understanding broad-scale patterns in marsh function across regional and continental scales.

Vegetation composition. Salt marshes are structured by vegetation characteristics that in turn influence habitat use by nekton (Table 1). Plant zonation along marsh elevation gradients occurs in bands of (or near complete) monocultures in response to submergence frequency. Shoot density, diameter, and height are key traits that determine the structure of these plant zones within salt marshes (Turner 1976). Collectively, these factors govern salt marsh patch size, complexity, species richness, and productivity, and influence physical access by nekton (Lewis and Eby 2002). However, nekton may use salt marshes with similar vegetation structure differently due to temporal (e.g. timing of plant growth and senescence) or spatial (e.g. latitude-stem density relationships) differences (Pennings et al. 2001).

Direct effects of vegetation structure on resident and transient nekton include provision of habitat (e.g. foraging substrate, cover for avoiding predators), whereas indirect effects include support of marsh prey resources for consumers (Kneib 1997). Evidence from *Spartina alterniflora*-dominated marshes that are invaded by *Phragmites australis* shows an increase in stem density and overall productivity, but a decrease in fish biomass (Warren et al. 2001; Hagan et al. 2007). These examples demonstrate that salt marshes, which often function as refuge and transfer energy to nekton communities, are defined by differences in plant species diversity and overall vegetation productivity, ranging from patch and local to regional and global scales.

Recommendations

Understanding geographic variation is key to finding commonalities across salt marsh ecosystems and predicting how global change may influence salt marsh-associated species. However, a big-picture understanding of variation (and thus commonalities and differences) among salt marshes of the world is lacking. Much of the research on the importance of marsh habitats for fisheries production has been conducted in the Gulf of Mexico and along the Atlantic Coast of the USA, and particularly from a few well studied locations within this region. Largely from this work, salt marshes in general have been deemed critical nursery habitats for many fishes and crustaceans. However, this generalization is based on the assumption that all salt marshes function equally across space and time, an oversimplification that has hampered our ability to effectively understand and manage these systems. To advance understanding of the broad commonalities and drivers of regional differences in marsh function, we propose investigations that are necessarily limited in scope (spatially and temporally) should use a consistent list of drivers (and suggested metrics for their sources of variation, e.g., Table 1) to characterize structure and function. Syntheses (e.g., meta-analyses) of studies aiming to search for commonalities and differences in salt marsh and their support of nekton (geographically) should consider the drivers and measurements examined in our paper. Further, the establishment of an organized network of scientists using an open science framework to run standardized experiments in local marshes would provide a wealth of information on both site or local scale marsh structure and function, and clarify global-scale patterns in marsh functionality for nekton (e.g., nursery function, secondary production).

Recommendation 1: Consistent collection and reporting of data across sites.

Developing a mechanistic understanding of environmental factors that drive the structure and function of salt marshes will allow scientists to make meaningful comparisons among salt

marshes spanning large geographic regions. This approach has been considered for many other coastal habitat types (e.g., coral reefs, seagrass) and suggested previously for salt marsh habitats (Rozas 1995, Connolly 1999). While our list of environmental variables is extensive (Table 1), many environmental drivers or habitat metrics can be easily collected during field sampling or remotely sensed with novel technologies to bolster current studies of salt marsh function for fauna (Kimball et al. this issue). We acknowledge that not all variables will be possible to obtain for all sites, as some can be field intensive or beyond the scope of individual studies (e.g., sediment supply). We encourage scientists to report some or all variables whenever possible in supplemental material or appendices of published manuscripts. Collecting and reporting of environmental measurements across future salt marsh studies will allow for a more unified understanding of salt marsh structure and function and allow for increased comparison and synthesis of marsh function globally using meta-analytic techniques. We also recognize that this approach holds true for the sampling of nekton within and across salt marsh systems. Due to the variation in salt marsh structure, consistent sampling procedures for nekton may be difficult (e.g., seining where water levels are too deep or trawling near shellfish reefs). However, we emphasize that data must be reported in consistent ways (frequency of occurrence, CPUE, individuals m⁻²) with clear descriptions of sampling methodology such as gear type (e.g., fyke net), size (e.g., mesh size, wing width), soak time, distance or area sampled, and tidal stage. Consistent reporting of data and use of the environmental drivers (addressed above) in future studies is also critical for managing locations that are traditionally data poor. Managers and conservationists in these areas, using limited information from their sites, will be better able to assess the relevance of data or understanding derived from other regions to make inferences and determine how to best protect, conserve, or restore local marshes for enhanced functionality.

Recommendation 2: Establishment of a network of scientists to perform simple, standardized experiments across the globe. We propose that organized efforts be taken by scientists at multiple sites to perform simultaneous surveys and experiments to determine patterns and processes that influence marsh function for crustaceans and fishes. This type of network would emphasize the collection of data that are consistent across both space and time (focused on the environmental drivers discussed, Table 1). Networks of this kind have been previously established (e.g., Long-Term Ecological Research [LTER] network, National Ecological Observatory Network [NEON]) and have been important in paving the way for future collaborative programs. However, in many cases due the vast scope of these projects, data are not always collected comparably across all sites (terrestrial and aquatic). Other large-scale networks (e.g., Zostera Experimental Network [ZEN], StreamPULSE, Reef Life Survey, Smithsonian MarineGEO) focusing on one or two habitat types have been able to run manipulative experiments with consistent data collection across space and time to identify both site-specific and larger-scale patterns (Duffy et al, 2015b; Bernhardt et al 2017; Edgar et al. 2017; Whalen et al, 2020). Networks of this kind focused in marsh habitats would provide information on local or regional processes that can be used by conservation and restoration practitioners as well as fisheries managers. In addition, these simple experiments would allow scientists to scale up to clarify macroecological or global-scale patterns in how salt marshes function for fisheries species. Determining these patterns may provide insight into how marshes and associated fisheries may be altered by future climate change scenarios. Ideally, this network should operate based on ‘open science’ principles, allowing the development of large datasets across physical and biological disciplines that can be universally accessed to stimulate interdisciplinary salt marsh research (Kimball et al. this issue).

Conclusion

Developing a unified framework (consistent collection and reporting of data) to determine commonality across distinct salt marsh systems would provide insight into not only the attributes that account for fundamental commonalities and differences but also how marsh function will change under future climate scenarios. Continued habitat loss and fragmentation in conjunction with sea-level rise (Able this issue, Colombano et al. this issue, Gilby et al. this issue) will influence the structure and function of salt marshes for nekton communities in unique ways in different locations. Therefore, a more comprehensive understanding of geographic variation in marsh structure and functionality is essential to increase predictive power, assess the success of restoration and conservation efforts (Waltham et al. this issue), and preserve overall coastal ecosystem functioning into the future.

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Table 1. Drivers of variation in salt marsh function for nekton, key variables for data collection, and relevant spatial scales to consider for each variable (P: patch (10s of meters), L: local (100s of meters), R: regional (kms), and G: global).

Drivers of Variation in Salt Marshes	Sources of variation to be reported	Relevant spatial scales
<i>Hydroperiod</i>		
	Flooding duration	P, L, R
	Flooding frequency	P, L, R
	Flooding depth	P, L, R
	Tidal regime	R
	Average tidal range	L, R
<i>Seascape</i>		
	Area	P, L
	Edge	P, L
	Isolation/distance to nearest structured habitat	P, L
	Animal pool	P, L, R
<i>Geomorphology</i>		
	Latitude and longitude	R, G
	Local geomorphology or positioning	L
	Marsh surface elevation	P, L
	Edge morphology and slope	P, L
	Degree of channelization	P, L
	Ratio of vegetated to non-vegetated habitat	P, L
	Number of open water pools/ponds	P, L
<i>Climatic Region</i>		
	In situ water temperature	P, L
	Average water temperature range	P, L, R
	Mean annual or seasonal precipitation	P, L, R
	Days of precipitation (annual)	L, R
	Days of drought (annual)	L, R
	Disturbance regime	L, R, G
<i>Sediment Supply/Riverine Input</i>		
	Distance to nearest major river	L, R
	Net rate of sediment deposition	P, L, R
	Horizontal change in marsh over time	L
	Vertical change in marsh elevation over time	L
	In situ riverine discharge	L, R
	Peak riverine discharge	L, R
<i>Salinity</i>		
	In situ salinity	P, L
	Mean annual or seasonal salinity range	P, L, R
	Categorical salinity regime	P, L
	Days of low salinity (annual)	L, R
<i>Vegetation</i>		
	Plant diversity	P, L, R
	Shoot density	P, L
	Aboveground biomass	P, L
	Shoot height	P, L
<i>Human Activities</i>		
	Human population density in catchment	P, L, R
	Distance to urban structures	P, L
	Proportion of land use categories in area surrounding marsh	P, L, R
	Proportion of human-induced channelization, ditching, dredging	P, L
	Presence of invasive species	P, L, R
	Distance to nearest port	P, L

657 **Figure 1.** Map of global distribution of salt marshes (data source: Global Biodiversity
658 Information Facility [GBIF] and occurrence data for dominant taxa). Stars indicate location of
659 corresponding marshes from distinct locations across the globe. Each marsh is described by key
660 ecological drivers that influence functionality for nekton (Photo credit: San Francisco Bay
661 Estuary: D. Colombano; Gulf of Mexico: S. Ziegler, and N. Queensland: N. Waltham).
662

Figure 1

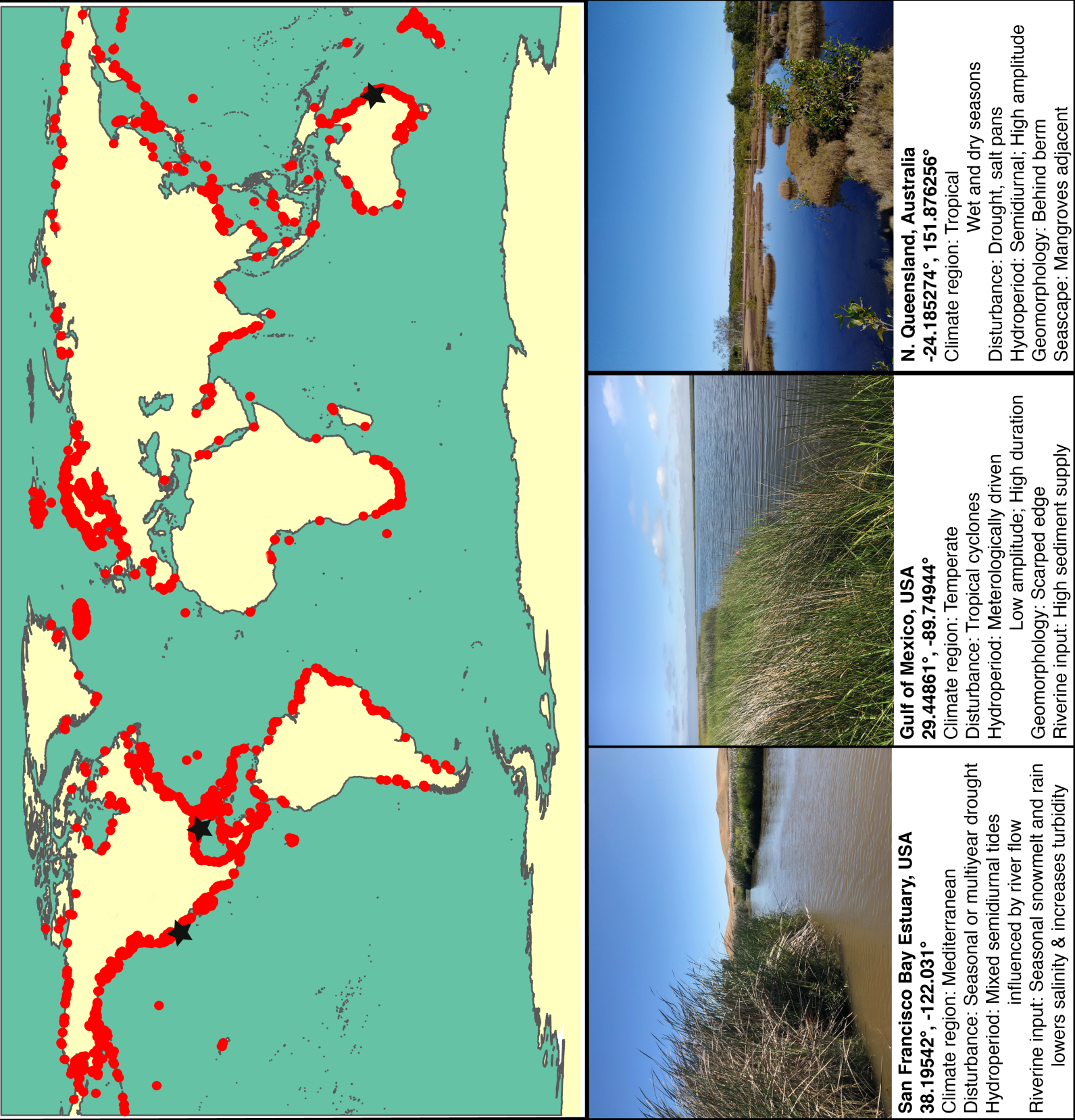


Table 1

Drivers of Variation in Salt Marshes	Sources of variation to be reported	Relevant spatial scales
<i>Hydroperiod</i>		
	Flooding duration	P, L, R
	Flooding frequency	P, L, R
	Flooding depth	P, L, R
	Tidal regime	R
	Average tidal range	L, R
<i>Seascape</i>		
	Area	P, L
	Edge	P, L
	Isolation/Distance to nearest structured habitat	P, L
	Animal pool	P, L, R
<i>Geomorphology</i>		
	Latitude and Longitude	R, G
	Local geomorphology or positioning	L
	Marsh surface elevation	P, L
	Edge morphology and slope	P, L
	Degree of channelization	P, L
	Ratio of vegetated to non-vegetated habitat	P, L
	Number of open water pools/ponds	P, L
<i>Climatic Region</i>		
	In situ water temperature	P, L
	Average water temperature range	P, L, R
	Mean annual or seasonal precipitation	P, L, R
	Days of precipitation	L, R
	Days of drought (annual)	L, R
	Disturbance regime	L, R, G
<i>Sediment Supply/Riverine Input</i>		
	Distance to nearest major river	L, R
	Net rate of sediment deposition	P, L, R
	Horizontal change in marsh over time	L
	Vertical change in marsh elevation over time	L
	In situ riverine discharge	L, R
	Peak riverine discharge	L, R
<i>Salinity</i>		
	In situ salinity	P, L
	Mean annual or seasonal salinity range	P, L, R
	Categorical salinity regime	P, L
	Days of low salinity (annual)	L, R
<i>Vegetation</i>		
	Plant diversity	P, L, R
	Shoot density	P, L
	Aboveground Biomass	P, L
	Shoot height	P, L
<i>Human Activities</i>		
	Human population density in catchment	P, L, R
	Distance to urban structures	P, L
	Proportion of land use categories in area surrounding marsh	P, L, R
	Proportion of human-induced channelization, ditching, dredging	P, L
	Presence of invasive species	P, L, R
	Distance to nearest port	P, L