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SPECIAL ISSUE: CONCEPTS AND CONTROVERSIES IN TIDAL MARSH ECOLOGY REVISITED

Climate Change Implications for Tidal Marshes and Food Web Linkages to Estuarine and Coastal Nekton

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Abstract

Climate change is altering naturally fluctuating environmental conditions in coastal and estuarine ecosystems across the globe. Departures from long-term averages and ranges of environmental variables are increasingly being observed as directional changes [e.g., rising sea levels, sea surface temperatures (SST)] and less predictable periodic cycles (e.g., Atlantic or Pacific decadal oscillations) and extremes (e.g., coastal flooding, marine heatwaves). Quantifying the short- and long-term impacts of climate change on tidal marsh seascape structure and function for nekton is a critical step toward fisheries conservation and management. The multiple stressor framework provides a promising approach for advancing integrative, cross-disciplinary research on tidal marshes and food web dynamics. It can be used to quantify climate change effects on and interactions between coastal oceans (e.g., SST, ocean currents, waves) and watersheds (e.g., precipitation, river flows), tidal marsh geomorphology (e.g., vegetation structure, elevation capital, sedimentation), and estuarine and coastal nekton (e.g., species distributions, life history adaptations, predator-prey dynamics). However, disentangling the cumulative impacts of multiple interacting stressors on tidal marshes, whether the effects are additive, synergistic, or antagonistic, and the time scales at which they occur, poses a significant research challenge. This perspective highlights the key physical and ecological processes affecting tidal marshes, with an emphasis on the trophic linkages between marsh production and estuarine and coastal nekton, recommended for consideration in future climate change studies. Such studies are urgently needed to understand climate change effects on tidal marshes now and into the future.

Keywords Tidal wetlands · Seascapes · Multiple stressors · Ecosystem resilience · Trophic relays

Introduction

Tidal marshes are vegetated intertidal habitats that occur at the land-sea interface and thus serve as critical transition zones linking marine, freshwater, and terrestrial processes (Boström et al. 2011). Recent research demonstrates the urgent need to understand both short- and long-term impacts of climate change and sea level rise (SLR) on tidal marsh ecosystem function, food webs, and fisheries support (Able this issue; Baker et al. 2020; Gilby et al. 2020). The cumulative impacts of multiple interacting stressors, and whether the net effects are additive, synergistic, or antagonistic, are receiving increased attention in the ecological literature (Crain et al. 2008; Przeslawski et al. 2015; Jackson et al. 2016; Lauchlan and Nagelkerken 2020). To further advance this area of research, we revisit established concepts published in *Concepts and Controversies in Tidal Marsh Ecology* (Weinstein and Kreeger 2000) through the lens of climate change and the multiple stressor framework. We explore the question: how is climate change expected to impact the trophic linkages between marsh production and estuarine and coastal nekton (free-swimming fishes and invertebrates), now and into the future?

Tidal marshes evolved in dynamic coastal and estuarine settings, and their position at the land-sea interface exposes

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them to a variety of environmental drivers (e.g., ocean currents, watershed hydrology) and environmental gradients (e.g., salinity, temperature, dissolved oxygen; Lauchlan and Nagelkerken 2020). Mounting evidence suggests that some directional, periodic, and stochastic variation in environmental conditions is intensifying under climate change [e.g., global or regional SLR, sea surface temperature (SST), and anomalous droughts, floods, or heatwaves, respectively; Trenberth 2011; Boyd et al. 2015; Nerem et al. 2018]. While coastal and estuarine ecosystems can resist and recover from minor to moderate natural disturbances, multiple stressors interacting synergistically, whereby the combined effects are greater than the sum of the individual (additive) effects, may lead to novel ecological responses (Crain et al. 2008; Jackson et al. 2016) or exceed critical ecological thresholds that result in fundamental state changes (Boström et al. 2011). Quantifying the combined effects of climate-related stressors on costal and estuarine nekton, and their associated fisheries, is of great conservation, restoration, and socio-economic concern (zu Ermgassen et al. this issue; Waltham et al. 2021; Baker et al. 2020; Gilby et al. 2020). Yet disentangling the drivers of change and ecological outcomes remains a major challenge to researchers and managers. We highlight key climate change implications for tidal marshes and food web linkages to estuarine and coastal nekton to inform future studies.

Climate Change Impacts at the Land-Sea Interface

Coastal Oceans and Watersheds

Broad-scale climatic changes are already shifting the timing, magnitude, and duration of naturally fluctuating environmental conditions (e.g., SLR, SST, ocean currents, waves, tides, precipitation) in marine, estuarine, and freshwater environments (see Table 1; Pörtner et al. 2014; Haigh et al. 2020; Konapala et al. 2020; Laufkötter et al. 2020). While natural variability is often directional or periodic with an element of stochasticity, climate change can increase the rate of change, amplify extreme

Table 1 Broad-scale environmental drivers to consider for studies addressing the questions: *How do climate change–induced shifts in environmental drivers across the marine-freshwater gradient potentially interact? How do these individual drivers or their interactions alter tidal marsh structure, hydrodynamics, water quality, nutrients, vegetation, and ultimately nekton and food webs?*

	Coastal ocean				*Watershed/ estuary*	
Broad-scale environmental drivers altered by climate change	Ocean currents, waves, tides, upwelling	Weather, precipitation, wind, storminess	Sea surface temperature (SST), marine heatwaves	Relative sea level rise (RSLR)	Weather, precipitation, storminess	Freshwater flows, drought vs. flood
Nature of variation	Periodic, stochastic	Periodic, stochastic	Directional, periodic, stochastic	Directional	Periodic, stochastic	Periodic, stochastic
Marsh structure, hydrodynamics, water quality, nutrients, vegetation	Hydroperiod, sedimentation, accretion, erosion, subsidence, scouring, vegetation *community, structure, biomass, growth*, temperature, salinity, turbidity, dissolved oxygen, pH, acidification, nutrient loading	Hydroperiod, coastal flooding, marsh pore water exchange, sediment delivery and exchange, accretion, erosion, subsidence, scouring, temperature, salinity, turbidity, dissolved oxygen, pH, acidification, nutrient delivery and exchange, vegetation community, structure, biomass, growth	Temperature, dissolved oxygen, vegetation *community, structure, biomass, growth*	Hydroperiod, coastal flooding, sediment delivery, accretion, erosion, subsidence, scouring, vegetation *community, structure, biomass, growth*	Hydroperiod, river flooding, surface water runoff, groundwater and marsh pore water exchange, sediment delivery and exchange, accretion, erosion, scouring, temperature, salinity, turbidity, dissolved oxygen, hypoxia, deoxygenation, nutrient delivery and exchange, eutrophication, harmful algal blooms, vegetation community, structure, biomass, growth	
Marsh nekton communities and food web dynamics	Species distribution, abundance, biomass, community composition, life history, diversity, species invasions, physiology, phenology, ontogenetic shifts, migrations, foraging, growth, survival, recruitment, spawning, competition, primary production, food web pathways, outwelling, *secondary production, predator-prey interactions, trophic relays*					

events, and shift the timing of variability. As a result, climate change impacts on coastal oceans and watersheds, which influence marshes from seaward and landward directions, respectively, may not only shift in timing individually but also generate simultaneous or consecutive applications of multiple stressors (Crain et al. 2008; Jackson et al. 2016).

Ocean climate variability regulates SST trends, which naturally vary in amplitude and frequency on annual and decadal scales (e.g., Atlantic and Pacific decadal oscillations; Xie and Tanimoto 1998; Mantua and Hare 2002). When viewed over decades, increasing SST is a progressive, directional process; however, departures from long-term averages (i.e., marine heatwaves) occur on daily, monthly, or seasonal timescales (Laufkötter et al. 2020). Coastal watershed hydrology is also regulated by atmospheric climate variability, which influences the timing and magnitude of precipitation, evapotranspiration, and groundwater interactions (Williamson et al. 2009). While long-term averages may be trending in one direction (e.g., drier conditions overall in Mediterranean climates), periodic extremes may also occur (e.g., severe droughts and floods due to changes in seasonal rainfall and snowpack in California, USA; Belmecheri et al. 2016).

Overall, the combined effects of climate change on ocean and watershed processes are connected and poised to interact with each other. This is especially the case in tidal marshes, which are dynamic and structurally complex biogenic habitats that are shaped by tidal and fluvial processes (e.g., tides, surface water runoff, groundwater and marsh porewater exchange; Davis and Dalrymple 2011). Several scenarios suggest that multiple interacting stressors may result in marsh conversion to open water or mudflat (Fagherazzi 2013). For example, the co-occurrence of accelerating regional SLR with increasing frequencies and/or magnitudes of high amplitude “king” tides and storm surges may synergistically worsen flooding and eventually result in marsh drowning (Cayan et al. 2008; Marsooli et al. 2019; Dominicis et al. 2020). Similarly, accelerating regional SLR and seasonal drought interactions may increase the frequency and/or magnitude of salinity intrusion into freshwater/brackish zones in estuaries which has been shown to threaten less salt-tolerant vegetation (Parker et al. 2011; Lauchlan and Nagelkerken 2020). Globally, more frequent and intense deviations from long-term averages and ranges, whether occurring on daily, seasonal, annual, or decadal scales, are likely to lead to novel changes in ecosystem dynamics.

Tidal Marsh Hydrogeomorphology

Elevation and sediment Marsh surface elevation is the primary factor influencing whether marshes can tolerate and recover from accelerating global or regional SLR impacts due to feedback mechanisms between tidal inundation, above- and belowground plant biomass, and sediment trapping and accretion (Morris et al. 2002; Cahoon et al. 2020). Marshes situated at a higher position within the potential vegetation growth range possess greater “elevation capital” and have a higher capacity to persist under accelerated SLR (Morris et al. 2002; Reed 2002; Cahoon and Guntenspergen 2010; Cahoon et al. 2020). Elevation capital can be maintained if vertical sediment and organic matter accretion rates match or exceed the rate of relative SLR (RSLR), a region-specific measurement of SLR that incorporates vertical land motion (Cahoon 2015). Elevation deficits can occur if marshes experience subsidence, soil erosion, or low sediment supply or plant production, and can be further exacerbated when RSLR exceeds sediment accretion rates (Kirwan and Megonigal 2013). While marshes with high elevation capital can tolerate deficits for long periods (e.g., decades to centuries), marshes with low elevation capital are more vulnerable to threshold effects (or ‘tipping points’; see Table 2). That is, they may only be able to persist with deficits for a short period before they deteriorate due to channel expansion, marsh-edge erosion, runaway pond expansion, and/or drowning (Cahoon 2015; Mariotti 2016; Mariotti 2020; Schepers et al. 2020). If accretion rates cannot keep pace with RSLR, marsh migration (or “transgression”) into adjacent uplands is the remaining mechanism for the natural maintenance of marsh habitat (Brinson et al. 1995; Kirwan et al. 2016; Schuerch et al. 2018; Kirwan and Gedan 2019). However, marsh migration depends on accommodation space, upland topography, slope, and connectivity, and can be greatly reduced due to shoreline armoring and urbanization, resulting in “coastal squeeze” (see Fig. 1, as well as Pontee 2013; Waltham et al. 2021).

Nutrient dynamics Tidal marsh hydrogeomorphology regulates the exchange of water, sediment, and nutrients across the land-water interface (Davis and Dalrymple 2011), and as a result, multiple interacting stressors may alter organic matter processing, nutrient cycling, and primary productivity (O’Meara et al. 2017). For example, increased rainfall may interact with topography, sediment grain size, and sediment organic matter content to influence the rate and amount of surface water runoff, groundwater and marsh porewater exchange, and ultimately, delivery of upland sediment (Sparks et al. 2014; Sparks et al. 2015). Increased sediment delivery to marshes may then combine with resuspended marsh sediment due to erosion from wave energy to enhance vertical accretion and emergent marsh sustainability (Mudd 2011). However, increased nutrient delivery may counteract this process. For example, nutrient enrichment may alter above- and belowground biomass of saltmarsh cordgrass (*Spartina alterniflora*; Darby and Turner 2008; Deegan et al. 2012; Hanson et al. 2016) and accelerate microbial decomposition of soil organic matter (Drake et al. 2009; Bulseco et al. 2019). Collectively, these effects can interact synergistically with RSLR and storm surges to physically weaken edges of tidal

Table 2 Summary of eleven estimates of annual increases in relative sea level rise (RSLR) that, when exceeded, are predicted to lead to the conversion of marsh to open water in each system. Such threshold values are commonly referred to as marsh "tipping points"

Tipping points (mm year^{-1})	Study description and location	Reference
2 to 10	Mangrove presence/absence and paleo-botany record in the Pacific	Fujimoto et al. 1996
4 to 6	Field observations in New England, USA	Watson et al. 2017
4 to 10	Field experiments and model of high and low sediment marshes on the East Coast, USA	Mudd et al. 2010
5	Model based on 5075 samples from 33 salt marshes	Morris et al. 2016
5 to 10	Model of varying tidal ranges and suspended sediment concentrations on the East and Gulf coasts, USA	Kirwan et al. 2010
5 to 10	Determination of the rate of SLR when 36 deltas formed across the globe	Turner et al. 2018
6 to 9	Paleo-marsh record on the Gulf Coast, USA	Törnqvist et al. 2020
6.1	Paleo-record of mangrove vertical accretion records compared to modeled rates of RSLR at multiple locations globally	Saintilan et al. 2020
7.1	780 Holocene evolution reconstructions in Great Britain	Horton et al. 2018
7.99	Multiple metrics model on the Gulf Coast, USA	Wu 2019
8.49	Total area model on the Gulf Coast, USA	Wu 2019
12	Salt marshes with high sedimentation rates on the East Coast, USA	Morris et al. 2002

creeks and increase erosion (Deegan et al. 2012) or to increase the amount of open water due to an increase in the number and size of ponds on the marsh platform (Able this issue). In addition, interactions between nutrients, residence time or tidal flushing, and warming may lead to harmful algal blooms, deoxygenation, and hypoxia (Bricker et al. 2008).

Tidal Marsh Vegetation Plant community structure may respond to climate change in a variety of ways due to species-specific anatomical and physiological adaptations (Brinson et al. 1995). Plant species in a low-elevation marsh are adapted to frequent flooding, whereas those in a high-elevation marsh may only tolerate infrequent flooding. As a result, marsh response to an increased hydroperiod (i.e., frequency, duration, and amplitude of tidal flooding) because of RSLR varies depending on the position of the tidal frame. Increased tidal flooding of high marsh vegetation may exceed plant stress tolerances to saltwater inundation and exacerbate soil anoxia, both of which can lead to high marsh plant loss or replacement by low marsh species (Brinson et al. 1995; Fagherazzi 2013).

Marsh response to increased storms and wave energy may also vary. Marshes dominated by structurally rigid plant species may experience folding and breaking of stems, while marshes with more flexible species may tolerate higher wave energy levels, as has been shown with *Elymus athericus* and *Puccinellia maritima*, respectively, in a European salt marsh (Rupprecht et al. 2017). However, at very high wave energy levels, conditions may be unsuitable even for highly flexible species, resulting in total plant loss. Positive feedback loops may be exacerbated by climate change, whereby declines in plant density and changes in plant traits can decrease attenuation of wave energy, sediment trapping efficiency, shoreline stabilization, and storm buffering (Temmerman et al. 2005; Möller 2006; Mudd et al. 2010; Ozeren et al. 2014; Morris et al. 2016).

Altered climatic conditions are also predicted to drive changes in foundation species, and the biogenic habitat they provide, in multiple and often non-intuitive ways. Warming-induced increases in the growing season may increase overall community photosynthesis and marsh plant biomass (Gedan and Bertness 2010). While elevated CO_2 concentrations may cause a similar overall ecosystem stimulus (Langley et al. 2002), this stimulation may be preferentially beneficial to C3 plants (i.e., forbs), which are currently sub-dominant in many saline marshes, compared to the C4 grasses (e.g., *Spartina patens* and *S. alterniflora*) that more commonly dominate those systems (Erickson et al. 2007). "Tropicalization" occurs when decreases in the frequency and duration of extreme cold events allow the expansion of tropical and subtropical macrophytes into temperate areas. For example, woody black mangroves (*Avicennia germinans*) are replacing *S. alterniflora* in marshes of the southeastern USA (McKee and Rooth 2008; Cavanaugh et al. 2019). Changing environmental conditions may also affect phenological characteristics such as propagule establishment, peak biomass, senescence, and ultimately marsh surface elevation, as has been observed with increased temperature and shifts in flowering timing in *S. alterniflora* (Crosby et al. 2015). These types of preferential adaptations may imply substantial shifts in future wetland (i.e., marsh and mangrove) community structure, food web pathways, and fisheries support.

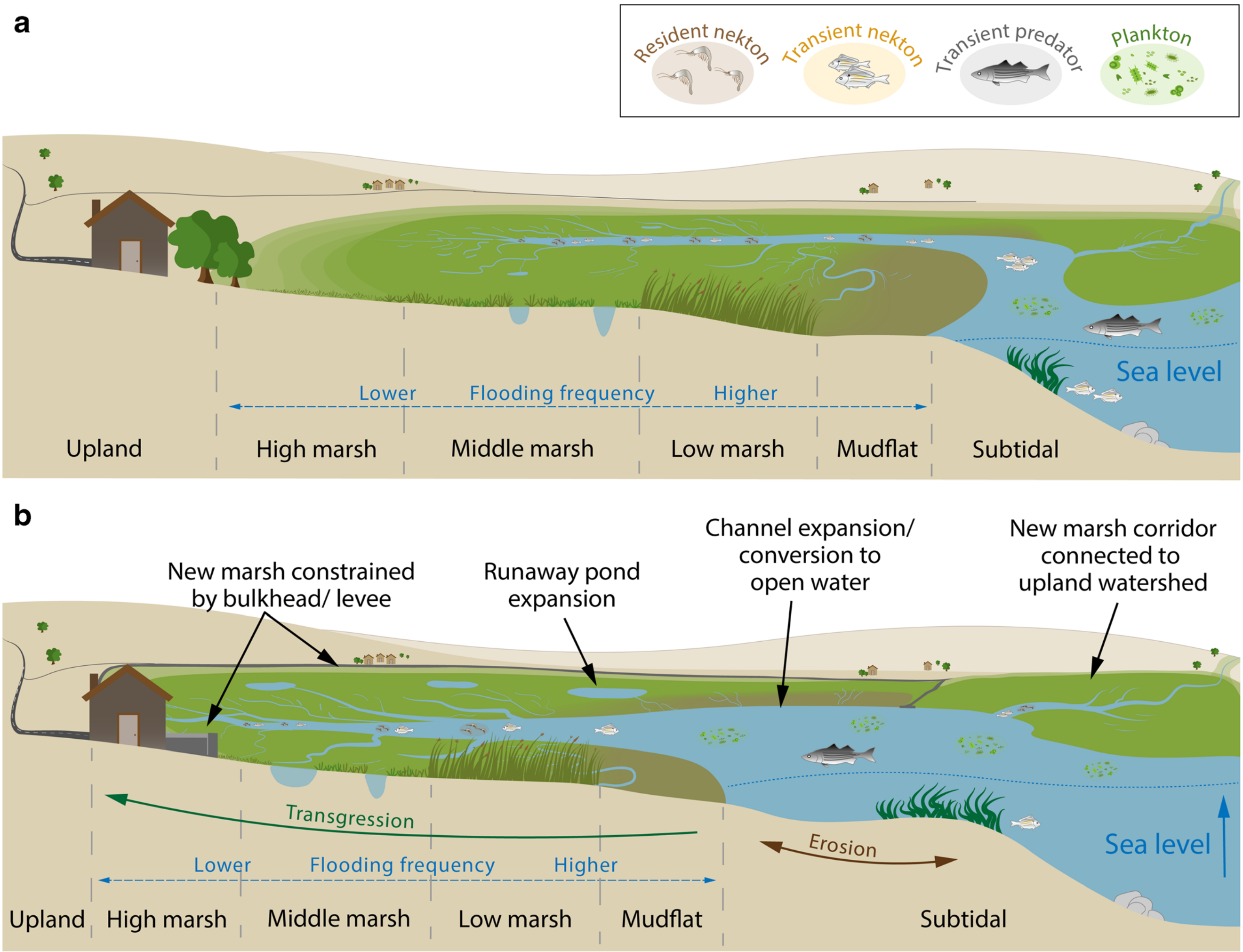

Fig. 1 Comparison of two scenarios: a tidal marsh seascape **a** under historic rates of sea level rise (SLR) and **b** under accelerated SLR. In scenario **b**, SLR leads to erosion and transgression, which shift the location and extent of each habitat type (e.g., subtidal, mudflat, low marsh, middle marsh, high marsh, ponds) laterally and vertically. In areas where human infrastructure constrains marsh transgression, coastal squeeze leads to a higher risk of flooding along levees, roads, and houses. In areas connected to upland watersheds, marsh migration is unimpeded. Implications for food web dynamics in squeezed areas are (1) reduced marsh area for resident nekton and juvenile transient nekton but increased access for larger transient marine predators and (2) shifts in the relative contributions of food web pathways, represented here as a higher biomass of plankton (i.e., phytoplankton and zooplankton) due to expanding open water habitat

Climate Change Impacts on Nekton Communities

Potentially profound consequences of climate change arise from alterations to the complex suite of interacting physical, biogeochemical, and ecological processes affecting estuarine and coastal nekton. Here, we explore multiple stressor impacts on species distributions, life history adaptations, and food web dynamics, with an emphasis on the trophic linkages between marsh production and nekton communities. For example, marine transient primary and intermediate consumers [e.g., juvenile shrimp (Penaeidae) and pinfish (*Lagodon rhomboides*), respectively] accumulate marsh production while feeding on the marsh surface or in channels before recruiting to estuarine or coastal waters where they are subsequently consumed (Fry et al. 2003). These production transfers or “trophic relays” also occur when larger marine transient predators [e.g., striped bass (*Morone saxatilis*), white perch (*Morone americana*)] make “feeding forays” into marshes to consume both resident [e.g., mummichog (*Fundulus heteroclitus*)] and transient prey (Tupper and Able 2000; Weinstein et al. 2000; Baker et al. 2016). We use this framework (Kneib 2000) to illustrate how trophic relays, the primary mechanism of energy transport from tidal marshes to estuarine and coastal ecosystems, may be fundamentally altered by climate change.

Species Distributions Changes in macroclimate may redistribute species and alter ecosystem function (Thompson et al. 2012). Species range expansions are particularly evident in marine systems (e.g., coastal salt marshes) whereby nekton are responding to warming temperatures (Sorte et al. 2010; Burrows et al. 2011; Morley et al. 2020). Historical comparisons of bivalves (Berge et al. 2005), gastropods (Mieszkowska et al. 2006), amphipods (Foster et al. 2004), crabs (Spivak and Luppi 2005; Hollebone and Hay 2007), and fishes (Fodrie et al. 2010; Morson et al. 2012) have all demonstrated poleward expansions. Species distributions within estuaries may expand or contract depending on changes in the spatial and temporal variability of environmental drivers and gradients (e.g., temperature, salinity, dissolved oxygen, pH; Lauchlan and Nagelkerken 2020). In addition, species invasions into new areas may lead to unprecedented combinations of species in estuarine and coastal nekton communities, with unforeseen consequences to species interactions and food web structure (Hobbs et al. 2009).

Life History Adaptations Climate change can affect the phenology, physiology, and behavior of tidal marsh fauna. Plant responses to shifts in the timing and magnitude of environmental fluctuations (e.g., seasonal temperature maxima) may alter the availability of structural habitat (i.e., cover), foraging substrate, and nutritional quality to consumers (Renner and Zohner 2018; Lauchlan and Nagelkerken 2020). In addition, the timing of peak nekton abundance may shift in response to changing environmental conditions. In the southeastern USA, for example, the timing of peak ingress of larval fishes [e.g., Atlantic croaker (*Micropogonias undulates*), summer flounder (*Paralichthys dentatus*), pinfish] from the coastal ocean to estuarine nurseries is shifting earlier in warm years, with projections of future shifts in response to warming SST on the order of weeks or months, but is delayed in years with strong northerly winds (Thaxton et al. 2020).

Physiological performance (e.g., growth, calcification, maximum body size), behavior (e.g., predator detection, escape response, freshwater dependence), and inter- and intraspecific competition and non-consumptive indirect effects may also be affected by climate change (Miller et al. 2000; Pörtner and Peck 2010; Nagelkerken and Munday 2016). The consequences may vary among species, depending on life history flexibility (Lord et al. 2017; Lauchlan and Nagelkerken 2020). For example, changes to physiochemical conditions have the potential to negatively affect secondary nekton production directly through changes in feeding rate, growth, and survival [juvenile weakfish (*Cynoscion regalis*); Lankford and Targett 1994] or indirectly through mediating the overlap of nekton and their predators [age-0 winter flounder (*Pseudopleuronectes americanus*); Manderson et al. 2006].

Climate change may lead to ecological mismatches between nekton and critical resources at important points in their life cycles, which often occur in pulses or bottlenecks (Lauchlan and Nagelkerken 2020). For example, shifts in the timing of primary production pulses may create a temporal mismatch in feeding and food availability for larval fishes, thus affecting growth and survival (Houde 2016). Altered predator-prey interactions may also impact early survival rates of nekton due to increased predation on newly settled recruits (Almany and Webster 2004), which has the potential to scale up to large effects on population persistence (Levin and Stunz 2005; Baker et al. 2014). Other documented ecological mismatches arise when different life history types, species, or populations exhibit differential responses to spatial or temporal changes in environmental conditions (Durant et al. 2007; Millette et al. 2020). Nekton adapted to moving between marine, estuarine, and freshwater environments at different life stages or events may be uniquely affected by altered timing of their preferred conditions due to climate change (Davis et al. 2014).

Tidal Marsh Food Webs Tidal marsh integration of complex physical, biogeochemical, and ecological processes is reflected in the diversity of primary producers, such as emergent vegetation, phytoplankton, benthic algae, or aquatic macrophytes, which support marsh resident and transient nekton (Currin et al. 1995). Due to the fact that marshes are embedded in seascape mosaics linked by an overlying water column that integrates multiple interacting processes (Childers et al. 2000), consumers that are able to exploit different resources in space and time may be more resilient to change (Young et al. 2020). However, if consumers are reliant on marsh-derived organic matter, a reduction in its availability resulting from marsh plant loss could have cascading effects on nekton growth and recruitment (Litvin and Weinstein 2004; Litvin et al. 2018), foraging success (Colombano et al. 2021), energy reserves (Litvin et al. 2014), and trophic relays (Childers et al. 2000; Deegan et al. 2000; Kneib 2000).

Impacts on biogenic habitat structure may profoundly impact food web dynamics (see Fig. 1). For example, hydroperiod and marsh-edge morphology govern nekton access to the marsh surface, marsh primary production, and prey resources; marsh residence time; and the frequency that organisms are transported off the marsh surface to aquatic habitats (Minello et al. 2012; Ziegler et al. 2020). As a result, any changes to these factors may affect direct consumption of marsh-derived organic matter, feeding forays by transient nekton, and trophic relays (Childers et al. 2000; Deegan et al. 2000; Kneib 2000). Increased tidal flooding height due to RSLR may influence nekton access and predator-prey interactions on the marsh platform, whereby increased flooding duration may affect the amount of marsh production supporting estuarine and coastal food webs (Ziegler et al. 2019). Conversely, marsh-edge erosion that leads to scarp formations may limit the ability of primary consumers to access the marsh surface during periods of tidal flooding, thus limiting the amount of energy consumers transfer from the marsh surface to the aquatic food web and make available to consumers (Nelson et al. 2019; Lesser et al. 2020).

Climate change impacts on food web dynamics may also scale up to estuarine and coastal nekton communities and population persistence. Such impacts are already being observed in the Gulf of Mexico, USA, where nekton communities are receiving less energetic benefit from foraging in mangroves, which are increasingly encroaching into marshes due to tropicalization (Harris et al. 2020). Other changes in habitat complexity (e.g., foraging substrate, cover in interstitial spaces) due to climate change and RSLR may reduce the nursery function (i.e., growth and survival of juvenile resident and transient nekton) and, ultimately, reduce recruitment from marshes to adult populations inhabiting other estuarine or marine habitats (Minello et al. 2003; Nagelkerken et al. 2015).

Threshold Effects on Tidal Marsh Food Webs The cumulative impacts of multiple interacting stressors on tidal marshes may yield immediate, delayed, or non-linear responses, or may exceed critical ecological thresholds, with important implications for energy flows to recipient consumers and ecosystems. For example, as seaward marshes submerge under accelerated RSLR, nekton production may increase in response to fragmentation and associated increases in marsh edge-to-area ratios (Minello et al. 1994; Gittman et al. 2018). Therefore, if submergence stimulates nekton production, and transgression compensates for seaward losses, the net effect of RSLR could be an increase in nekton production and consumption by marine transient predators (Chesney et al. 2000). However, these increases in food web support of nekton may only be temporary if significant marsh loss occurs over the long term, with uncertain but potentially catastrophic outcomes for trophic relays from marsh resident to transient nekton (Weinstein et al. 2000). Overall, the resulting net losses of marsh contributions of secondary production to estuarine and coastal food webs may occur over short (e.g., years; Nelson et al. 2019; Harris et al. 2020) or long timescales (e.g., decades, centuries; Able this issue). Understanding what characteristics of tidal marsh ecosystem structure and function underlie nekton support, and their resilience to climate change, is now a clear research and management priority.

Considering Climate Change Impacts in Future Tidal Marsh Research

Climate change is a rapidly evolving topic that can be incorporated into all tidal marsh research efforts and resource management decisions due to the prevalence and range of effects on present and future tidal marshes globally. Our goals are to promote awareness of climate change impacts and to stimulate discussion among coastal and estuarine scientists and managers. We offer the following recommendations with the aim of encouraging tidal marsh researchers to conduct more holistic and cross-disciplinary climate change studies, which are critically needed for present and future management and conservation of nekton and fisheries that rely on marshes.

- Climate change affects a diverse suite of physical and biological processes that directly and indirectly influence tidal marsh ecosystems. Future studies should focus on drivers of short- and long-term ecosystem change and variability, including those originating from coastal oceans and watersheds (Table 1).
- Research opportunities on climate change impacts on tidal marshes abound, especially in the context of the multiple stressor framework (Table 1) and the critical ecological threshold framework (“tipping points”; Table 2). Quantitative studies on the net effects of multiple stressors will provide important insight into the magnitude, direction, and timing of change that is likely to occur in tidal marsh ecosystems.
- Secondary production offers a composite metric reflecting ecosystem structure and function (Layman and Rypel 2020) and, thus, in the context of this perspective, partially reflects the complex physical, biogeochemical, and ecological processes mediating multiple energetic pathways through which tidal marsh production supports estuarine and coastal nekton. In addition to trophic relays, marsh-derived organic matter exported in the form of particulate or dissolved organic matter may also support nekton (i.e., the “outwelling hypothesis”; Teal 1962; Nixon 1980; Childers et al. 2000; Odum 2000), but this mechanism has received less attention over recent decades (Duarte et al. 2017; Najjar et al. 2018). Studies quantifying tidal marsh energy flows (e.g., g m^{-2} $year^{-1}$) through both mechanisms are needed to track climate change effects on food web resilience and recovery.
- Advancing integrative research on climate change impacts on tidal marsh ecosystems requires diverse, collaborative teams of theoreticians, empiricists, and statisticians. Open science practices allow for tidal marsh researchers and managers across the globe to tackle pressing climate change issues together (Kimball et al. this issue).

Furthermore, there are numerous other high-priority tidal marsh ecology topics that need to be evaluated in the context of climate change. Examples are listed below.

- Climate change interactions with anthropogenic drivers of seascape change (Gilby et al. 2020)
- Geographic variation in climate change impacts on tidal marsh structure and function (Ziegler et al. 2021)
- Strategies to mitigate the effects of climate change and urbanization through restoration techniques (Waltham et al. 2021)

- Emerging technologies to study climate change impacts on nekton communities and food web dynamics (Kimball et al. this issue)
- Climate change threats to the provision of marsh-supported fisheries to humans (zu Ermgassen et al. this issue)

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