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REVIEW

Human-induced salinity changes impact marine organisms and ecosystems

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Abstract

Climate change is fundamentally altering marine and coastal ecosystems on a global scale. While the effects of ocean warming and acidification on ecology and ecosystem functions and services are being comprehensively researched, less attention is directed toward understanding the impacts of human-driven ocean salinity changes. The global water cycle operates through water fluxes expressed as precipitation, evaporation, and freshwater runoff from land. Changes to these in turn modulate ocean salinity and shape the marine and coastal environment by affecting ocean currents, stratification, oxygen saturation, and sea level rise. Besides the direct impact on ocean physical processes, salinity changes impact ocean biological functions with the ecophysiological consequences are being poorly understood. This is surprising as salinity changes may impact diversity, ecosystem and habitat structure loss, and community shifts including trophic cascades. Climate model future projections (of end of the century salinity changes) indicate magnitudes that lead to modification of open ocean plankton community structure and habitat suitability of coral reef communities. Such salinity changes are also capable of affecting the diversity and metabolic capacity of coastal microorganisms and impairing the photosynthetic capacity of (coastal and open ocean) phytoplankton, macroalgae, and seagrass, with downstream ramifications on global biogeochemical cycling. The scarcity of comprehensive salinity data

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in dynamic coastal regions warrants additional attention. Such datasets are crucial to quantify salinity-based ecosystem function relationships and project such changes that ultimately link into carbon sequestration and freshwater as well as food availability to human populations around the globe. It is critical to integrate vigorous high-quality salinity data with interacting key environmental parameters (e.g., temperature, nutrients, oxygen) for a comprehensive understanding of anthropogenically induced marine changes and its impact on human health and the global economy.

KEYWORDS
algae, coastal, coral reef, deep-sea, ecosystem services, mangrove, plankton, polar, seagrass, tidal marsh

1 | INTRODUCTION

Climate change is transforming the world as we know it, driving fundamental changes to the physical climate and subsequently impacting biodiversity, ecosystem functioning, and our socioeconomic livelihood (IPCC, 2023). In the marine and coastal biosphere, the current body of research on the ecological impact of climate change primarily addresses the effects of ocean warming and ocean acidification (Doney et al., 2012; Henson et al., 2017). By comparison, salinity shifts due to the changing water cycle (Durack et al., 2012) and its hydrological extremes (Westra et al., 2014), melting ice (Haumann et al., 2016), and altered terrestrial runoff (Lenderink & Van Meijgaard, 2008) have received less attention, similar to ocean deoxygenation (Hughes et al., 2020), despite its considerable impact on marine biota, ecosystems, and human livelihood (Newell, 1976). Here, we highlight the central role that salinity plays in the context of human-induced environmental change both for current and future climate change scenarios and show that for certain ecosystems, salinity changes are the leading physical driver of biological response. We explore interactions between key environmental parameters that often accompany salinity changes, such as temperature, oxygen solubility, nutrient concentration, and sedimentation. We discuss both long- and short-term salinity changes and how they will shape the evolution of oceans, its ecosystems, and inhabitants.

2 | SALINITY—A KEY VARIABLE IN A CHANGING ENVIRONMENT

Open ocean and coastal salinity are driven by water cycle variability and change that modulate the physical ocean system. The ocean is responding to the dual forcings of surface-driven warming and an enhanced atmospheric water cycling at its interface and boundaries (cryosphere and terrestrial runoff) (Durack, 2015). The complex interactions in response to these dual forcings are modulating surface ocean properties, which are subducted into the ocean interior (Durack & Wijffels, 2010). For example, coastal and estuarine ecosystems are strongly impacted by freshwater availability from rainfall and the associated runoff, with sensitivities to extreme flood and drought events (Gibson et al., 2002). For the global ocean, salinity is a marker for water cycle change, with the ocean integrating changing freshwater fluxes from the atmosphere, cryosphere, and land surface. A clear and robust pattern of salinity change, demarking changes to the oceanic water cycle, has been observed since the 1950s and since then reproduced by key studies (Stocker et al., 2013). To date, we have already observed changes in ocean salinity at an order of 0.05 to 0.01 per decade on the Practical Salinity Scale (PSS-78) at an accelerating rate (~0.2 to ~0.35 per 50 years (Durack et al., 2012); Figure 1a). These changes indicate that the open ocean is following the global idealized ‘wet gets wetter, dry gets drier’ pattern of water cycle change caused by increasing atmospheric temperatures (Chou & Neelin, 2004; Held & Soden, 2006). Fresh regions accordingly appear to becoming fresher and salty regions saltier, evident in the ocean near-surface upper layers and extending through intermediate depths (Durack et al., 2012; Durack & Wijffels, 2010). For the near surface, salinity increases in the subtropics (10–40°N/S) and freshens in the tropics (0–10°N/S) and subpolar and polar regions (40–90°N/S). Changes at depth generally follow the same patterns, with salinity changes following the subduction and circulation pathways into the ocean interior (Durack & Wijffels, 2010).

Future projections using the previous CMIP5 model suite (Taylor et al., 2012) are indicating these currently observed changes are likely to intensify (Stocker et al., 2013). By the end of the century, near-surface changes are projected to increase markedly, by an order of ~0.5 to 1.0 PSS-78 (Stocker et al., 2013), and in the deep by about 0.05 PSS-78 (Heuzé et al., 2015) (Figure 1b–d). Their magnitude is proportionally linked to the rate of global mean surface air temperature increase, with larger atmospheric CO_2 concentrations driving stronger warming and salinity responses (Stocker et al., 2013; Tebaldi et al., 2021). Water mixing through ocean currents and in particular the thermohaline circulation (THC) is largely salinity (and temperature) driven, with regional changes resulting from even small perturbations driving changes to Earth's climate directly (Carmack et al., 2016). For example, ocean freshening from melting glaciers, ice sheets, and other terrestrial water, particularly in coastal regions, is contributing to enhanced ocean stratification (Li et al., 2020). Continued high latitude terrestrial freshwater input seems to contribute to slowing of the THC (Boers, 2021).

BOX 1: Key terms and definitions

An **ecotone** is a transition area where two (or more) communities meet and integrate.

Harmful algal blooms (**HAB**) occur when algal populations reproduce exponentially and produce toxic or harmful effects on humans and/or marine organisms.

A **holobiont** encompasses a host organism and all of its associated microorganisms that directly or indirectly affect the resultant metaorganism's health and functioning.

Hydrological cycling represents the flow of freshwater through Earth's Systems, including the ocean, cryosphere, atmosphere, and land in all phases (i.e., solid (ice), liquid, and vapor).

Microbiome is the sum of microorganisms, including viral, prokaryotic, and microeukaryotic members and their genetic material. Microbiomes can be free-living or associated with non-living substrates (soil, sediment) and living hosts.

Based on osmotic stress, **osmoacclimation** refers to (reversible) biochemical, biophysical, and physiological modifications in cellular structure and/or function, while **osmoadaptation** refers to genotypic changes.

Practical-Salinity-Scale 1978 (PSS-78) is a defined, dimensionless salinity scale based on electrical conductivity, which is influenced by the ambient water temperature and pressure.

Salinization is the increase in salt concentration or salt accumulation. Salinization can occur in soils or water/porewater.

Sea level rise (**SLR**) is an increase in the level of the world's oceans due to the effects of climate change. This includes thermal water expansion related to increasing ocean temperatures (**thermosteric effect**), mass/water addition from melting ice reservoirs and transfer of terrestrial (surface and subsurface) water to the ocean (**eustatic effect**), and changes in salinity (and thus water density, with an expansion for freshening and contraction for salinization; **halosteric effect**).

Sea surface salinity (SSS) is the amount of dissolved salts in the **near-surface** layer of the ocean–atmosphere interface. Concentrations are measured in situ as well as by satellites since 2010. Changes are driven by evaporation and precipitation patterns and ocean circulation in the open ocean, plus terrestrial runoff in the near-coastal zones.

A **thermocline/halocline** is a distinct aquatic layer in which temperature/salinity changes occur much stronger with depth than in the layers above or below. The strong gradient separates the well-mixed ocean (above), which is in equilibrium with the atmosphere directly above the ocean surface, and the ocean interior (below). Changes to both state variables may strongly contribute to ocean stratification.

The **thermohaline circulation (THC)**, a global current, is driven by temperature (thermo) and salinity (haline) related differences in water density.

While broad-scale, open ocean salinity changes are coherent and physically consistent at basin scales across observations and models, the coastal regions where ocean and land processes intersect, are more dynamic in their response to climate change. Coastal regions and estuaries are among the most productive ecosystems on Earth (Nixon et al., 1986). However, due to their close proximity to human settlements, they are arguably more directly affected by local anthropogenic impacts (e.g., land use, urbanization, drainage, river regulation and discharge, changes in vegetation, desalination discharge, and terrestrial runoff) compared to the open ocean. Concomitantly, climate change-driven water cycle amplification leads to enhanced rainfall, which enhances flooding and runoff in some parts of the globe, while in other regions its decrease is causing droughts and increased evaporation (Masson-Delmotte et al., 2021). As a result, terrestrial discharge is changing dramatically in some parts of the world (Masson-Delmotte et al., 2021), a trend projected to continue in the future (Figure 1e,f). Particularly, local anthropogenic impacts and increasing precipitation extremes, along with enhanced drying and evaporation can result in concerted pulses of terrestrial runoff, which can strongly affect coastal ecosystems (Lenderink & Van Meijgaard, 2008; Papalexiou & Montanari, 2019). However, temporal and spatial data characterizing such changes as a baseline for large-scale coastal impact assessment are currently lacking.

Coastal ecosystems are also exposed to additional stressors associated with or caused by salinity changes, for instance salinity levels together with temperature drive water density. In cold-water polar oceans, a small change in salinity results in density changes that would require a far larger temperature change, while conversely, temperature is the leading property for most of the tropics and subtropics (Griffies et al., 2014). Water density drives oxygen saturation levels (Figure 2), and freshwater stratification and nutrient driven microbial respiration can additionally trigger coastal hypoxic areas (Breitburg et al., 2018). Stratification and nutrient input are fueled by terrestrial runoff that freshens (and stratifies) coastal surface waters (Li et al., 2020), delivering increased nutrients and sediments. Deoxygenation (and particularly anoxic dead zones) (Hughes et al., 2020), nutrient enrichment (Rabalais et al., 2009), and increased sediment loads (Thrush et al., 2004)

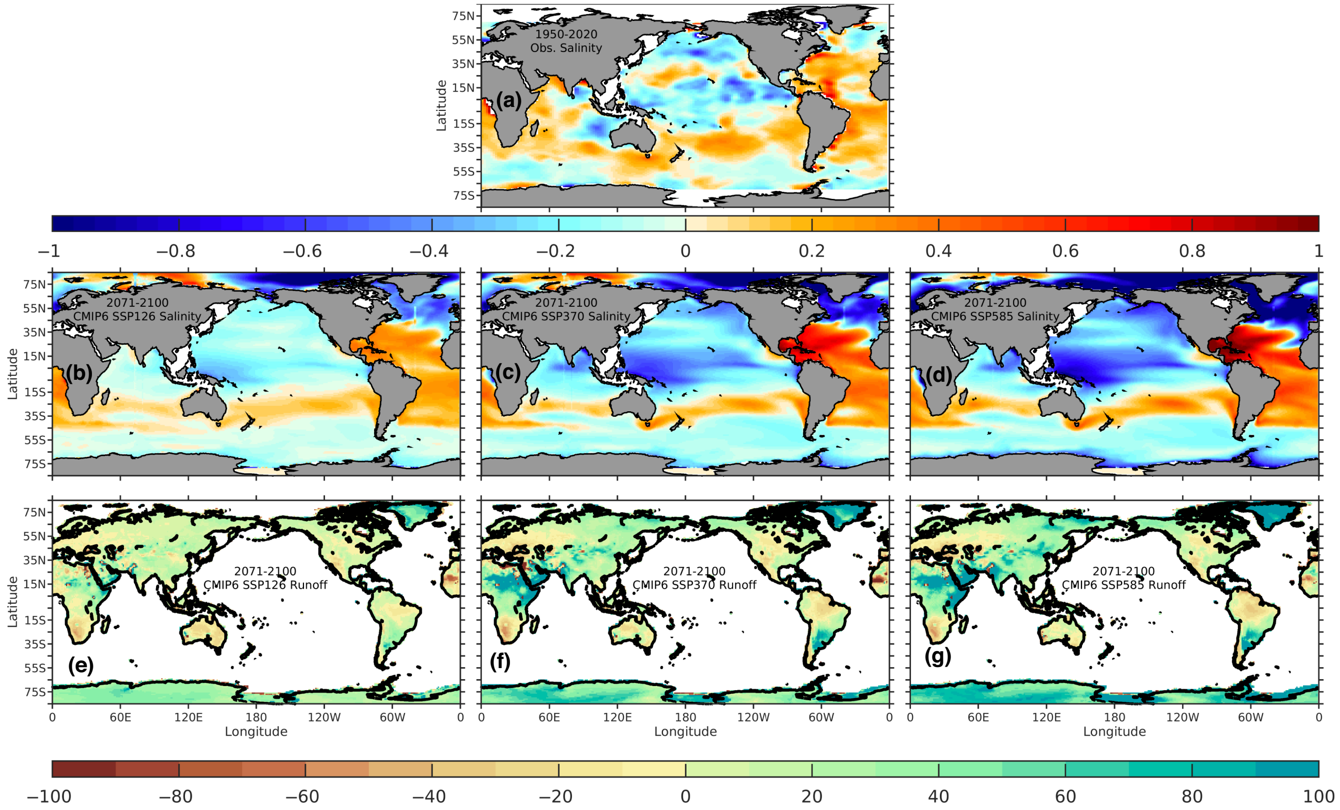


FIGURE 1 Changes in global salinity patterns and terrestrial runoff. Due to an intensified water cycle, global surface salinity patterns (a) have changed from 1950 to 2020 (PSS-78 70 years). Future projections from the phase 6 of the Coupled Model Intercomparison Project (CMIP6) multi-model mean under (b) low (Shared Socioeconomic Pathway, SSP1-2.6), (c) mid (SSP3-7.0), and (d) high (SSP5-8.5) CO_2 emission future scenarios (differences from the 1985–2014 historical counterpart) show strong salinity changes (PSS-78) that resemble the pattern of observed changes will continue, particularly under mid and high CO_2 emission scenarios. This is in concert with changes in precipitation and more direct anthropogenic impact, changes over land annual total runoff (%), that project increasing variations from (e) low (SSP1-2.6), (f) mid (SSP3-7.0), and (g) high (SSP5-8.5) CO_2 future emission scenarios. The CMIP6 Earth Systems Models (ESMs) that provide salinity and runoff change fields are detailed in the Supplementary Material & Methods (Tables S2–S4).

fundamentally transform coastal ecosystems. These stressors are all predicted to increase as a result of climate change and anthropogenic activity (Knight & Harrison, 2009; Sinha et al., 2017). Ecosystems at the coastal–terrestrial interface are also increasingly affected by local sea level rise (SLR) (Nicholls, 2010). SLR is driven by thermal expansion (thermosteric effect), freshwater addition (eustatic effect), and salinity distribution changes (halosteric effect) (Durack et al., 2014; Munk, 2003) (Figure 2). As a result, coastal and low-lying inland wetlands, islands, and estuaries are experiencing saltwater intrusion at the terrestrial–ocean interface. This salt ion increase and salinization affect ecosystem structure and function, including comprehensive changes in biogeochemical cycles for example (Herbert et al., 2015). Figure 2 illustrates the complex interplay of salinity with the physical, biological, and chemical compartments of the coasts and ocean.

3 | EFFECTS OF SALINITY ON THE GLOBAL OCEAN ECOSYSTEM

Salinity is a key variable shaping the distribution of biota across all trophic levels in marine ecosystems (Kirst, 1990; Newell, 1976) (Figure 2). In the following, we review the impacts of salinity for three key marine biomes—open ocean, polar, and coastal—due to their vulnerability to salinity changes and the breadth of impact to ecological keystone species, ocean productivity, and humans. We also outline details of the ecophysiological effects of selected keystone species in Table 1. Given the profound impact of salinity on microbiomes and their impact on downstream ecosystem structuring (Lozupone & Knight, 2007), we first consider changes across the world's ocean at large, before diving into the three key biomes. We then assess open ocean salinity effects on epipelagic and deep pelagic systems that profoundly differ in their physicochemical and biological constitution. Largely well-connected with the open ocean, we next explore polar regions that are driven by annual freezing and brine rejection cycles that fundamentally govern the ecophysiology of its inhabitants, in particular with regard to salinity (Ardyna & Arrigo, 2020). We then focus on coastal ecosystems and highlight how changes in salinity patterns affect benthic subtidal coral reefs, benthic intertidal estuaries, and the coastal photoautotrophs in the littoral zone. With their pivotal roles in ecosystem services related to carbon sequestration and storage, nutrient cycling, biodiversity, fisheries, and coastal protection,

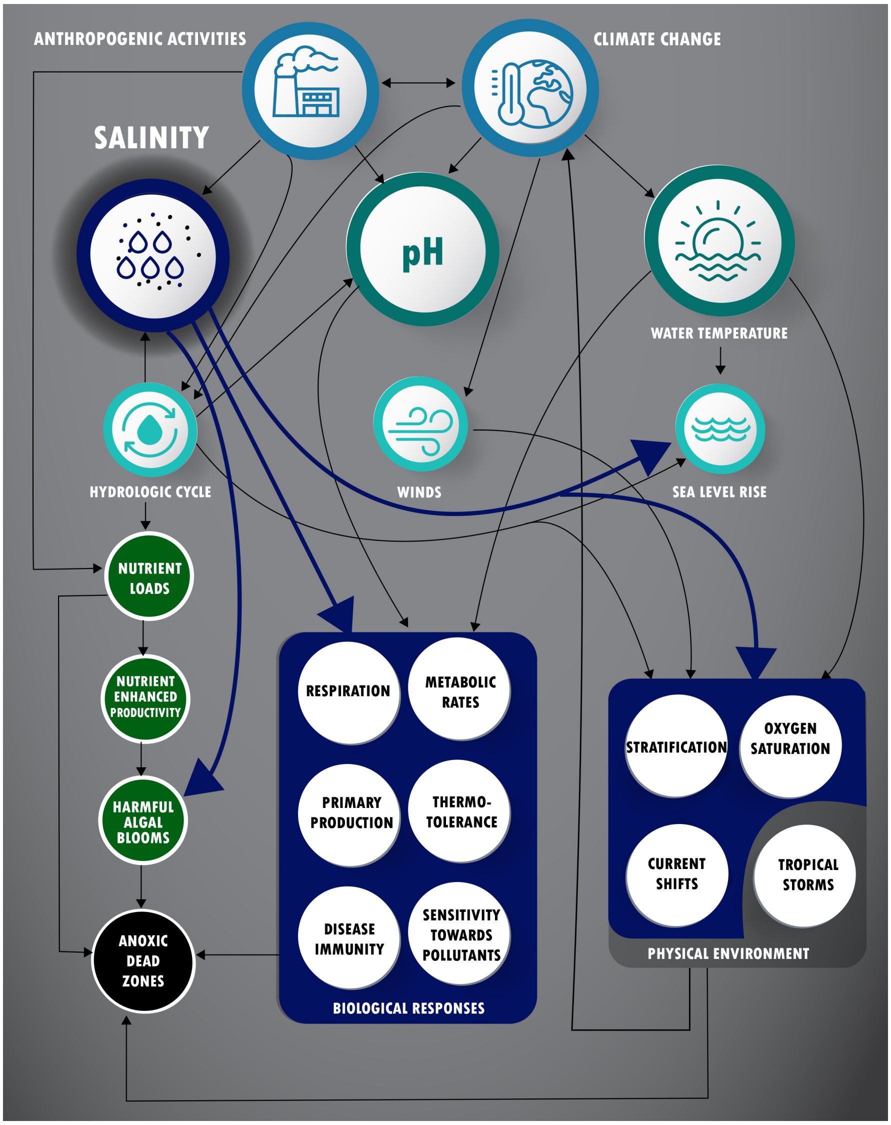


FIGURE 2 Conceptual diagram highlighting salinity's central role in structuring the physical and biological environment under human-induced environmental change. Effects of salinity are depicted in dark blue. Adapted from Doney et al. (2012).

these ecosystems are particularly important for human health and the economy. Lastly, we highlight the implications of global salinity change for human health and the global economy, and identify the most pressing research gaps, thereby providing the foundation for the inclusion of salinity changes as a key missing element in climate change research.

Salinity is a major physicochemical factor determining bacterial community composition, and salinity differences pose a particularly strong barrier for microorganismic metabolism to overcome (Jurdzinski et al., 2023). Salinity drives soil and water microbiome global composition for both, prokaryotic and eukaryotic taxa (Herlemann et al., 2011; Lozupone & Knight, 2007; Shearer et al., 2007; Telesh et al., 2013). Given the significant effect of salinity on the microbiome at such large scales (Lozupone & Knight, 2007), future shifts in salinity due to ice cap melting, precipitation variability, and SLR has the potential to alter global biogeochemical cycling, the effects of which are likely compounded by further climate change (Cavicchioli et al., 2019). Teasing apart the functional and metabolic shifts of the microbiome (or key members within) will be key to our ability in predicting biogeochemical and biological consequences of salinity change. Accordingly, biodiversity shifts are projected as a result of salinity changes due to diversification within new niches (Herbert et al., 2015; Shearer et al., 2007; Telesh et al., 2013) (Figure 3). Although many cosmopolitan microbial taxa will persist throughout regional salinity changes, their function may change (Herbert et al., 2015; Telesh et al., 2013). Additionally, salinity changes will affect key carbon- and nitrogen-cycling functional groups across all ecosystems (Table 1). For both carbon and nitrogen cycles, the quality and availability of organic carbon through sedimentation, litter production and quality, and exudates will affect what the microorganisms can degrade (enzymatic repertoire (Balmonte et al., 2020; Celussi et al., 2019)), and the efficiency at which they can do this (biogeochemical pathways (Luo et al., 2019; Neubauer et al., 2013; Santoro, 2010)). The effect of increasing salinity changes on the carbon cycle will largely depend on the organic matter–microbiome relationship, with predictions of both enhanced and suppressed carbon sequestration (Luo et al., 2018; Neubauer et al., 2013). It is further predicted that seawater intrusion and regional salinity increase will

TABLE 1 Overview on selected key ecophysiological effects of salinity changes for organisms within selected marine and coastal ecosystems (for references and additional considerations see Table S1).

Organism (ecosystem)	Physiological effect	Ecological consequence(s)	Potential socioeconomic impact
Microorganisms [soil, sediment, and water column; holobionts (host-associated microorganisms)]	Changes in enzymatic capacity and metabolic rates. Shifts in community composition. Changes in holobiont functioning either directly through association with different microbes, or indirectly, through physiological changes of the holobiont (e.g., the osmolyte metabolism). The microbiome contributes to salinity tolerance of the host.	Shift(s) in the type and rate of organic matter degradation, which will affect soil stability and accumulation. Reduced diversity, favoring euryhaline holobionts/species.	Shift(s) in the type and rate of organic matter degradation and nutrient availability will affect greenhouse gas emissions for both, the rate and the type of greenhouse gas production (CH_4, CO_2, and N_2O).
Coral (coral reef)	Changes in respiration/photosynthetic rates, reduced/heightened coral bleaching/mortality susceptibility for substantial salinity changes, lowered resilience due to low level chronic osmotic stress, changes in associated microbial community composition (pro- and eukaryotic), interactive effects with temperature changes, increased larval and in particular gamete mortality for considerable salinity drops.	Loss of coral diversity, loss of ecosystem, loss of associated diversity (coral reefs harbor estimated 30% of marine species).	Loss of ecosystem functions and value (e.g., food source, coastal protection, and tourism).
Mangroves and marshes (coastal)	Reduction in growth and seedling survival and development, and increased mortality due to elevated salinity. Ionic or sulfide stress leading to re-allocation of resources, for example, reduction in photosynthesis, may be exacerbated by other stressors, such as elevated temperature and drought. Short-term hyposalinity pulses may benefit coastal plants, including seedling success and range expansion seaward if sedimentation allows; however, long-term freshwater conditions can lead to reduction in growth or die-backs.	Reduced diversity, favoring fast-growing and adaptable taxa. Ecotone shifts, favoring halotolerant plants, or r-strategists (e.g., algae-dominant or herbaceous over woody taxa), with broad consequences to ecosystem function, trophic cascades, and lignocellulose deposits from detritus. Reduction of autochthonous carbon inputs from litter and exudates.	Estuary relocation; loss of ecosystem functions and value (e.g., ecosystem services to coral, seagrass, plankton, fish; loss of freshwater source).
Phytoplankton (coastal, open ocean, and polar regions)	Changes in respiration/photosynthetic rates and disruption of cellular processes. Toxin(s) release by harmful algal species.	Water column stratification promotes cyanobacterial success and challenges diatoms. Halotolerant and euryhaline HABs may be favored and impact ecosystem structure and function. Shifts in phytoplankton communities may trigger trophic cascades altering species composition on higher trophic levels, particularly in polar regions.	Salinity changes can trigger/ facilitate phyto- and/or bacterioplankton HABs that particularly impact shellfish, fish, marine mammal, and bird population, which in turn directly impact human health, food supply, and economy. Reduced fish stocks affected by trophic cascades.
Macroalgae (coastal)	Changes in respiration/photosynthetic rates and disruption of cellular processes.	Negative effects on sexual reproduction (e.g., lowered gamete viability, fertilization, and polyspermy) and altered disease susceptibility can lead to decreased genetic diversity that may change ecosystem structure and function.	Loss of ecosystem functions and value (e.g., ecosystem services of coral, seagrass, plankton, fish, and tidal marshes).

TABLE 1 (Continued)

Organism (ecosystem)	Physiological effect	Ecological consequence(s)	Potential socioeconomic impact
Seagrass (coastal)	Direct impacts on plant physiology: Changes in respiration/photosynthetic rates, disruption of cellular processes, and altered disease susceptibility.	Indirect effects by modifying the rate of top-down interactions with grazers and metabolic disadvantages may alter ecosystem structure and function.	Loss of ecosystem functions and value (e.g., ecosystem services of coral, seagrass, plankton, fish, and tidal marshes).
Fish, invertebrates (e.g., mussels, echinoderms, crustaceans) (coastal and polar regions)	Disruption of cellular processes and metabolic rates (e.g., caused by enhanced energetic requirements for osmo-adjustments) are common in marine fish and invertebrates and may disturb fertilization, development, and sensory perception, increase susceptibility to toxins/pollutants, and lead to changes in respiration, feeding rates and size/growth.	Reduced diversity favoring euryhaline species can result in trophic collapse (e.g., echinoderms, jellyfish, copepods, and fish) due to bottom up and/or direct impact leading to loss of ecosystem structure and function.	Loss of ecosystem functions and value, for example water quality degradation or loss of food security from fishing and/or aquaculture.

cause a shift from methanogenesis-dominated to sulfate reduction-dominated metabolism, which will likely lower CH_4 production in the short term (Neubauer et al., 2013). For the nitrogen cycle, projected increases in nitrogen mineralization and reduced coupled nitrification–denitrification could result in increased NH_4^+ export from groundwater systems (reviewed in Santoro, 2010).

Besides affecting free-living microorganisms, salinity changes can alter host-associated microbiome structure and therefore holobiont functioning. This can occur either directly through association with different taxa (e.g., Röthig et al., 2016; Yuan et al., 2016) or indirectly through physiological changes of the holobiont, such as osmolyte metabolism (Gegner et al., 2017; Ngugi et al., 2020; Ochsenkühn et al., 2017). Marine organisms in general tend to have a broad salinity tolerance, potentially due to their exposure to varying salinity levels over seasons or as a result of oceanic cycles (Velasco et al., 2019). At the same time, such altered salinity levels impact organism physiology and can affect their stress tolerance, in particular with regard to temperature stress (Gegner et al., 2017). At large, salinity has been shown to drive community structure, highlighting the ecological importance of changing salinity levels (Coles & Jokiel, 1992; Lozupone & Knight, 2007; Wilson & Dunton, 2018).

3.1 | Open ocean

In the open ocean, salinity in combination with light, temperature, nutrients, circulation, carbon dioxide, and oxygen determine the physiology of life in this biome, ultimately impacting ecosystem composition, structure, and functioning. Salinity therefore defines plankton ecological niches, affecting growth, photosynthesis, and biogeochemical activities and thus diversity (Bijma et al., 1990; Dueñas-Bohórquez et al., 2009; Mezger et al., 2016; Qasim et al., 1972) (Figure 3). Salinity changes also feedback on the physical oceanography, affecting currents and the advection of nutrients and species, shaping open ocean marine microbial community structure (Villarino et al., 2018) and thereby the ocean's biodiversity.

3.1.1 | Epipelagic ecosystems

Considering the size of the open ocean, functional implications of environmental change, for example, with regard to primary production and biogeochemical cycling, have the potential to affect all life on Earth. It is therefore important to comprehensively consider environmental key parameters, including salinity. The effect of salinity in modulating open ocean epipelagic (<200 m depth) plankton community structures, species, and functional diversity is often less highlighted when compared to the role of temperature. However, significant associations between salinity concentrations and global ocean community composition have been reported (Estrada et al., 2016; Gianoulis et al., 2009; Raes et al., 2011; Rusch et al., 2007; Sunagawa et al., 2015) (Fig. 1 in Louca et al., 2016; Fig. S12 in Salazar et al., 2019). Salinity can also affect interactions and trophic webs within marine plankton communities (Francis et al., 2012) (Figure 3). Plankton community structures (modeled via community networks) have been shown to be tightly associated with salinity in open oceans at global scales (Extended-Data-Fig. 2 in Guidi et al., 2016). More recently, salinity has even been linked to plankton predicted ecological interactions topologies (Chaffron et al., 2021). For example, a Trades-like plankton community (Figure S1) has been predicted to be vulnerable to salinity changes at tropical latitudes (Chaffron et al., 2021), where changing salinities (+~0.5–1.0 PSS-78 by the end of the century (Figure 1a,b)) are well able to profoundly impact community structure (Figure 4a).

Going forward, new satellite-based observations (http://cci.esa.int/salinity) enable further evaluation of spatiotemporal variability of sea surface salinity (SSS). This will permit the linking of SSS measurements to marine microbial omics datasets sampled across space and time (Biller et al., 2018). However, SMOS/SMAP satellites notionally detect salinity to a precision of 0.2 PSS-78 and would only allow for a coarse characterization of salinity's role in shaping open ocean (plankton) ecosystems, noting that far smaller changes having a marked impact on community structure.

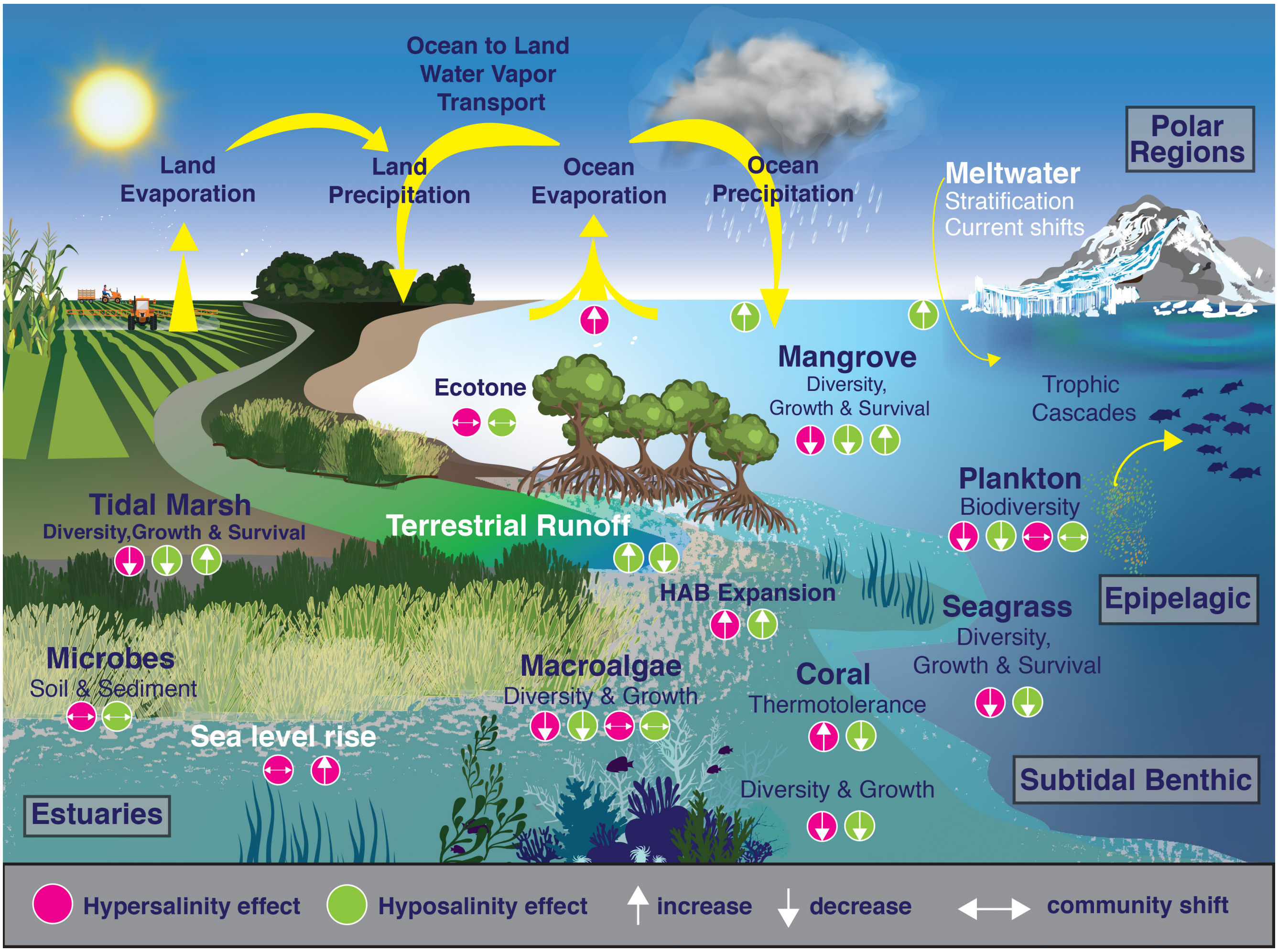
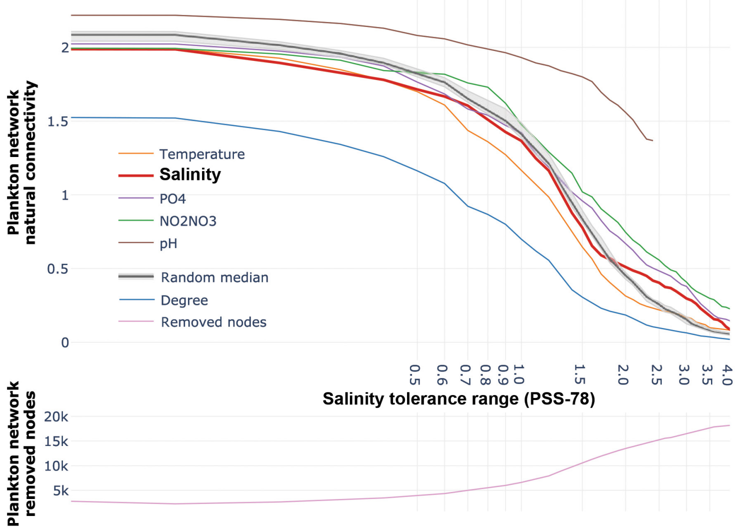


FIGURE 3 Overview of salinity changes and their influence on ecosystem function. Increasing temperatures enhance hydrological cycling, resulting in increased meltwater and shifts in evaporation and precipitation patterns that affect global ocean salinity patterns. Local anthropogenic impacts, including land use practice further modulate terrestrial runoff patterns affecting coastal ecosystems. Enhanced variation or shifts in salinity impact diversity, growth, and survival of key species. Sea level rise connected with salinization as well as ecotone shifts and trophic cascades may contribute to substantially altered ecosystem structure and functionality.

3.1.2 | Deep pelagic ecosystems

The mesopelagic zone (200–1000 m depth) differs from the epipelagic zone by the amount of incident light reaching these depths (≤1% to no light). This twilight zone and its complex food web interactions are much less understood than the euphotic environment, although they sustain key ecosystem services, such as carbon cycling (Robinson et al., 2010). While large variations in temperature are occurring in the mesopelagic (20 to 4°C), the climatological mean salinity, a temperature-independent estimation, is relatively stable (34.5–35 PSS-78). Recent efforts have identified and delineated ecoregions or biotopes defined by specific biogeochemical characteristics constrained by environmental factors mostly varying in these deeper waters (Reygondeau et al., 2018; Sutton et al., 2017). Global-scale sampling expeditions have also recently uncovered a high diversity of microbial communities in both the mesopelagic (Sunagawa et al., 2015) and the bathypelagic oceans (Salazar et al., 2016). The environmental forcing, which is driving the plankton community composition in this biome is also poorly characterized, yet salinity is known to be an important driver. For example, deep-sea pelagic particle-attached bacterial communities appear to be positively associated with salinity at the global scale (Salazar et al., 2016). Furthermore, salinity (total variation ~2 PSS-78) and depth have been found to explain zooplankton distribution at a deep Bermuda sampling site (Stefanoudis et al., 2019). Marine copepods, which account for a significant fraction of the planktonic biomass, appear to be influenced by salinity (total variation <2 PSS-78), temperature, and dissolved oxygen content of the upper mesopelagic layer in the Pacific (Hirai et al., 2020). In the North Pacific, mesopelagic fish larvae are usually distributed in high salinity waters, and even subtle drops in salinity (~1 PSS-78) may impact egg and larval survival (Sassa & Hirota, 2013). Such species could be affected by the projected end of the century salinity changes (~0.5–1.0 PSS-78; Figure 1b–d). However, our overall knowledge of the deep pelagic ecosystems is quite limited in scope and thus hinders any attempt to accurately project the impacts of salinity change. Most available


(a) Trades-like plankton community

(b) Coral distribution model based on salinity projections (2100)

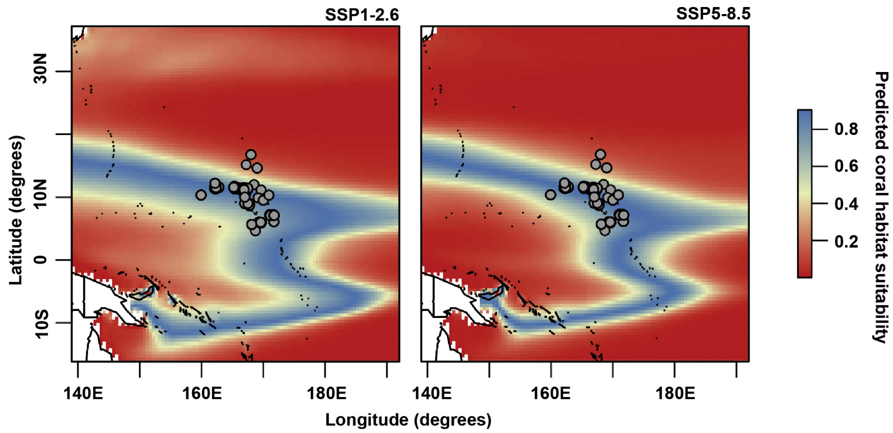


FIGURE 4 Predicted vulnerability of marine key biota by open ocean salinity changes. (a) Environmental change simulations through tolerance range perturbations on a global ocean epipelagic plankton community network (by progressively removing nodes of the network ranked by their environmental niche width) predict ecological vulnerabilities to salinity change on a Trades-like community ($p = 3.8 \times 10^{-10}$) (20,000 nodes represent 100% of the captured nodes in the community; Supplementary Material & Methods). Significant vulnerabilities to environmental changes were determined by comparing distributions of the network natural connectivity (a graph robustness measure) evolution for each abiotic factor, as compared to a random perturbation. (b) Predicted distribution of Scleractinia (hard coral) genera (occurrences as grey dots) in the Marshall Islands region for changes in near-surface salinity for the "2°C SSP1-2.6 and the high CO_2 emission SSP5-8.5 scenario" for the year 2100. These future projections stem from CMIP6; of note, the multi-model mean salinity is different from the 1985–2014 historical salinity data (see Figure 1b–d). The modeling region was defined by coral occurrence in the Marshall Islands region with a 20-degree buffer around the observations (139°E, 192°E, 16°S, 37°N). The training AUC score was 0.914 for the SSP1-2.6 scenario and 0.948 for SSP5-8.5. The legend for the model predictions ranges from blue (highest probability of occurrence >0.8) to red (lowest probability of occurrence <0.2). For details on modeling, see Supplementary Material & Methods.

data in this area stem from inferences that are acquired from better-studied systems such as the polar regions.

3.2 | Polar regions

In contrast to the open ocean, polar regions have a wealth of data on how salinity shapes the physical system, controlling circulation, stratification, and mixing. Polar regions are characterized by salinity variations mainly driven by seasonal meltwater runoff to the ocean (rivers and land ice), net precipitation, sea ice, and advection of mid-latitude waters (Figure 2). These regions are likely to undergo the most dramatic changes in salinity reduction and enhanced stratification, at least in the immediate future (Carmack et al., 2016; Skliris et al., 2014; Swart et al., 2018) (Figure 3). Climate change enhances freshwater input caused by increasing ice reservoir melting (Swart et al., 2018), sea ice transport (Haumann et al., 2016), and precipitation (Bintanja et al., 2020; Bintanja & Selten, 2014). The resulting stratification reduces vertical mixing and consequently the incoming heat flux, ocean acidification, biogeochemical cycling, nutrient supply, and primary production (Carmack et al., 2016). For example, polar ecosystems have experienced comprehensive community structure changes (Greene & Pershing, 2007) in phytoplankton biomass and production (Blais et al., 2017). Rising temperatures and the reduction in sea ice extent have prolonged the phytoplankton growing season, thus increasing net primary production, and seem to favor photosynthetic picoeukaryotes over diatoms (Ardyna & Arrigo, 2020; Blais et al., 2017). While terrestrial runoff supplies nutrients that facilitate plankton growth, salinity-enhanced stratification may at least regionally suppress plankton biomass and productivity (Ardyna & Arrigo, 2020). As primary consumer (e.g., copepods) life cycles are finely tuned toward seasonal algal blooms, particularly diatoms, changes thereof can result in trophic cascades and regime shifts and contribute to the collapse of higher-level consumer populations (Ardyna & Arrigo, 2020; Greene et al., 2008; Greene & Pershing, 2007) (Figure 3). Global warming will continue to strongly affect both polar regions (Post et al., 2019), resulting in sea ice loss and regional freshening (Figure 1b–d). This will have important consequences for future polar plankton biodiversity (Ibarbalz et al., 2019) and ecosystem functionality (Murphy et al., 2016).

3.3 | Coastal ecosystems

Salinity changes can have a profound influence on the distribution and physiological responses of diverse multicellular organisms (Figure 2, Table 1). This particularly holds true in coastal ecosystems where salinity is highly variable and influenced by terrestrial runoff. For an organism, relocation or adjustment to osmotic and ionic stress may be energetically costly, in addition to coping with other climate change impacts (Gunderson et al., 2016; Velasco et al., 2019). Therefore, projected salinity changes on the order of ~0.5 to 1.0 PSS-78 until the end of the century (Figure 1b–d) in conjunction with increased short-term variations due to precipitation and runoff pattern changes (Figure 1e,f) are anticipated to lead to ecotone (i.e., transition areas between communities) or ecosystem shifts, substituting concurrent community members with more tolerant, plastic, or adaptable species (or functional groups) (Figure 3). It is of particular interest to understand which species are predicted to be the salinity change 'losers', as these may lead to altered or, in the most extreme case, loss of entire ecosystem functions.

3.3.1 | The benthic subtidal—Coral reefs

Research on the effects of salinity changes and its implications for corals and reef ecosystems is relatively scarce, despite its established importance with respect to osmoadaptation (sensu Reed, 1984) and holobiont physiology (Coles & Jokiel, 1992). This may be due to the circumstance that 'historically' coral reefs occur in regions where salinity has been relatively stable. In addition, ongoing research largely focuses on the more imminent threat associated with ocean warming (i.e., coral bleaching) (Dietzel et al., 2020). However, salinity is considered a key environmental variable for coral distribution, and salinity changes can also lead to coral bleaching and mortality (Coles & Jokiel, 1992). For this reason, it is important to consider how salinity, either in isolation, or in combination with ocean warming and the dynamical effect of the ocean physics, along with ocean acidification will affect corals and the reef ecosystems they build. We therefore applied distribution modeling to explore the effects of open ocean near-surface salinity changes on coral habitat suitability. Our models indicate pronounced responses to projected salinity changes. Future coral reef ranges are reduced under the SSP1-2.6 scenario that details a gradual shift toward a sustainable resource and energy intensity and resultant CO_2 emission scenario. Coral reef ranges are further diminished under the SSP5-8.5 scenario that projects a fossil-fueled resource and energy intensive development, high CO_2 emission scenario (Figure 4b, Figure S2). Both scenarios predict lower near-surface salinity (Figure 1b,d) resulting in reduced areas with high habitat suitability across the Marshall Islands and surrounding South Pacific Island countries. Particularly strong reductions in habitat suitability are predicted for the Federated States of Micronesia western of the Marshall Islands for both scenarios (0.2–0.4 for SSP1-2.6 and 0–0.2 for SSP5-8.5) (Figure 4b).

The question remains, however, how well can corals osmoadapt? And how will salinity changes affect their ability to respond to other stressors? Corals already survive across a large range of salinities (from about 25 to 45 PSS-78, although most coral reefs occur in more moderate saline environments) (Röthig et al., 2016; van der Merwe et al., 2014), leading to either non-measurable or drastic effects depending on the marked change of salinity and the duration of exposure (Coles & Jokiel, 1992). Physiological responses (e.g., osmoacclimation sensu Reed, 1984) of corals to both increasing and decreasing salinity can vastly differ and some species seem more osmotolerant than others (Coles & Jokiel, 1992). In general, corals seem to cope well under high salinity conditions (e.g., ~40 PSS-78 in the Red Sea and the Persian/Arabian Gulf) and even appear to exhibit decreased bleaching susceptibility (D'Angelo et al., 2015; Ochsenkühn et al., 2017). The presumed increased thermal tolerance is supposedly mediated by osmolytes that harbor antioxidative functions and can thus counter reactive oxygen species (ROS) from heat stress (Gegner et al., 2019; Hume et al., 2016; Osman et al., 2017). By comparison, decreased salinity seems to have rather detrimental effects, as evidenced by the many studies describing reduced respiration, photosynthetic rates, and mortality (critical threshold ~20 PSS-78 for 24 h) consequential to lowered salinity levels due to heavy rainfall associated with major storms or monsoons (Coles & Jokiel, 1992; Ferrier-Pagès et al., 1999; Moberg et al., 1997) (Table 1). This may explain why the effects of decreased salinity are better represented in the scientific literature than the effects of salinity increase. While quantitative data are lacking, such short-term salinity variations may well pose a larger pressure on coral than the more consistent, long-term ocean scale salinity changes (Figure 1a,b). Taken together, even though salinity is considered a key variable for coral distribution and health, interaction effects with other stressors (e.g., ocean warming, ocean acidification, ocean deoxygenation), cellular response mechanisms (Mayfield & Gates, 2007), or the role of associated microorganisms (Röthig et al., 2016), which at least partially affect future distribution ranges, are currently unclear. This is surprising given the ecological and economic importance of tropical coral reefs matching or even surpassing estuaries. However, the latter seem to affect industrialized nations more directly, which may partially explain why salinity effects in estuaries are better understood.

3.3.2 | The benthic intertidal—Estuary continuum

The effect of salinity on mangrove and coastal/freshwater tidal marsh ecosystems in terms of physiological, reproductive, and ecological stress and adaptations has been well-summarized in several reviews over the past 10 years (e.g., Herbert et al., 2015; Parida & Jha, 2010; Pratolongo et al., 2018; Wang et al., 2011). Therefore, here we will focus on the overarching effects of salinity changes along the mangrove-marsh continuum and in the context of precipitation and salinization (Figures 1 and 3, Table 1). In contrast to coral reefs, low salinities induced by regular or relative increases in precipitation will largely benefit coastal wetlands (Figure 3). This is primarily due to the increased access to groundwater, thereby enhancing growth and biodiversity (Feher et al., 2017; Gilman et al., 2008; Janousek & Mayo, 2013); however, chronic freshwater conditions will lead to the eventual reduction or die-off of tidal marsh and mangrove plants (Wang et al., 2011) (Table 1). In instances where runoff is concomitant with increased precipitation, mangrove expansion both seaward, landward, and up-estuary will be facilitated in the long term by increased sedimentation, sediment volume, and inundation (Gilman et al., 2008; Yang et al., 2013). Additionally, some coastal tidal marsh species can grow under meso- and oligo-haline conditions, suggesting certain taxa, particularly those adapted to high marsh conditions, could migrate to fresher ecotones under SLR (Janousek & Mayo, 2013; Kirwan & Gedan, 2019; Sutter et al., 2015) (Figure 3).

Conversely, salinization caused by SLR, drought, and low tidal flushing will ultimately have a negative impact on this ecosystem and/or disrupt the health and function of emergent coastal autotrophs (Table 1). Along the estuarine continuum, freshwater tidal and upland ecosystems may be the biggest 'losers' connected to changes in salinity. Encroachment of halophyte species into fresher areas as saltwater reaches upstream may initially cause diversification of species at the ecotone and be an advantage to brackish taxa. However, these changes will ultimately be at the expense of freshwater tidal ecosystems (Kirwan & Gedan, 2019). Salinity shifts not only lead to poor competition of freshwater tidal species, but salinity and inundation stress may also create a positive feedback loop for tidal wetlands at large, whereby stress and low reproduction leads to increased plant death and decay and decreased net carbon inputs, which then cause soil compaction and subsidence (Herbert et al., 2015). The indirect salinity-induced subsidence and predicted increase in inundation would result in more stress to the ecosystem due to a loss of viable habitats, leading to less autochthonous carbon inputs into the system (Herbert et al., 2015). Salinization can also negatively impact mangrove and coastal marshes in the short-to-medium term via ion and sulfide stress (e.g., drought, low tidal flushing, high evapotranspiration (Gilman et al., 2008; Luo et al., 2019)), which can eventuate to large-scale die-backs (e.g., Alber et al., 2008; Lovelock et al., 2017). However, salinization in the context of relative SLR does show promise for coastal wetlands in scenarios where sedimentation and elevation provide new habitat and carbon sink opportunities for mangroves and tidal marsh ecosystems (Rogers et al., 2019). These contrasting impacts highlight the complexities of predicting interactive effects of salinity changes across multiple spatiotemporal scales and under future climatic conditions.

3.3.3 | The littoral zone

Ocean productivity largely refers to the production of organic matter by phytoplankton or photoautotrophs. Often distinct from the open ocean, productivity in coastal ecosystems is driven by proximity to land and its nutrient sources, the interception of organic matter by the shallow seafloor, and the propensity for coastal upwelling, all resulting in highly productive ecosystems. The response of phytoplankton to salinity changes is therefore of key importance and comparably well researched (Bijma et al., 1990; Dueñas-Bohórquez et al., 2009; Mezger et al., 2016; Qasim et al., 1972) (Table 1). However, a key challenge in predicting how coastal phytoplankton will respond to changes in salinity is drawing meaningful conclusions from the high degree of inter- and intraspecific response variability that has been reported in both laboratory and field studies (including species associated with harmful algal blooms (HAB)). These responses may be influenced by any combination of physiological osmoacclimation and phenotypic plasticity (i.e., variation within strains), genetic variation among strains, and evolutionary osmoadaptation (Burford et al., 2020). Despite this challenge, it is anticipated that the most pronounced changes in phytoplankton diversity and community structure will occur along ecotones or ecoclines of the freshwater–marine continuum (Mazzei & Gaiser, 2018; Muylaert et al., 2009; Quinlan & Phlips, 2007) (Figure 3). Particularly, genera of freshwater toxigenic phytoplankton are capable of adapting to new conditions and have already been reported in estuaries throughout North America, Australia, Europe, and Japan (Preece et al., 2017). In certain cases, HABs may be induced by salinity changes and some species can even develop enhanced toxicity under altered salinities (Fu et al., 2012). Unfortunately, there continues to be a considerable gap in our understanding of the adaptive mechanisms employed by toxic phytoplankton in response to salinity-induced stress. While some species/strains can adapt and modulate toxin production, others succumb to osmotic thresholds resulting in cell lysis and toxin release into the environment (des Aulnois et al., 2019; Ross et al., 2019; Tanabe et al., 2018).

Similar to phytoplankton, macroalgal species composition and richness can change dramatically along salinity gradients that are typically encountered in transitional coastal regions. Of particular concern are macroalgal populations that exist at the salinity range margins of a species' distribution. For example, climate change-related declining salinities in the Baltic Sea (currently ranging from 2 to 13 PSS-78 (Kniebusch et al., 2019)) are predicted to continue and push the distribution of marine species on a southerly trajectory, transitioning the community toward a more limnic state (Takolander et al., 2017). Such increases in hyposalinity have the potential to negatively affect macroalgal sexual reproduction by reducing gamete viability and fertilization and promoting polyspermy (Serrão et al., 1996; Steen, 2004). The ensuing shift to asexual reproduction promotes lower genetic diversity and may consequently impair the potential for adaptation to new selective marine regimes (Rothäusler et al., 2018) (Figure 3). Furthermore, increasingly hyposaline conditions of the Baltic Sea may also cause a shift toward the prevalence of green algae (Chlorophytes) with a concomitant decline in red (Rhodophyta) and brown algal (Phaeophyceae) species (Nielsen et al., 1995; Ojaveer et al., 2010; Snoeijs, 1999). This has the potential to affect higher trophic levels, as many green algae in this region are considered to be fast-growing, opportunistic annual species unable to provide appropriate habitat complexity for fauna compared to larger perennial taxa (Takolander et al., 2017).

Seagrasses are another photoautotroph that will be impacted by regional shifts in salinity. In subtropical seagrass beds, changes in salinity can cause a phase shift to occur from dominance of benthic rhizophytic algae to drift algae at sites experiencing lower salinity (Biber & Irlandi, 2006) (Figure 3). While rhizophytic algae can help facilitate sediment stabilization and promote seagrass succession (Thayer et al., 1994; Williams, 1990), large clumps of detached drift algae often reduce seagrass productivity and biomass via the process of over-shading (Cambridge et al., 1986; Hauxwell et al., 2001). Interestingly, despite the broad geographic range covered by seagrasses (found on all continental margins except the Antarctic), a large number of these coastal and estuarine plants have optimal growth rates between salinities of 30–40 PSS-78 (Touchette, 2007). Most species can tolerate short-term salinity fluctuations. However, prolonged exposure to hypo- or hypersaline conditions can have a significant impact on plant fitness with subsequent ecosystem ramifications (Collier et al., 2014; Robblee et al., 1991; Wilson & Dunton, 2018) (Table 1, Table S1, Figure 3). Altered salinity can not only have a direct effect on seagrass communities by affecting plant physiology (i.e., disruption of cellular processes), but can also have an indirect effect by modifying the rate of top-down interactions with grazers (Bell et al., 2019). Climate change models project decreased precipitation and increases in the occurrence of drought conditions in such regions as the Mediterranean Sea, the Gulf of Mexico, and southwest Australia (Stocker et al., 2013) (Figure 1e–g). Given that these areas support extensive seagrass meadows, plant sustainability will depend on the ability to adapt to the predicted increased saline conditions (Green et al., 2003). Hypersalinity has already been implicated as a major factor in large-scale die-offs of seagrass in the United States and southern Australia (Robblee et al., 1991; Seddon et al., 2000). As wetland hydrology and seasonal rainfall patterns continue to change, die-offs in these areas may very well increase in frequency and coverage (Duffy et al., 2019). This is of particular concern for vulnerable and near-threatened seagrass species and their associated fauna (Short et al., 2011). Other seagrass populations will have to contend with contrasting hyposaline conditions, occurring in response to enhanced rainfall, runoff, or other hydrological modifications (Figure 1b–g). For example, salinity in the Baltic Sea is expected to decrease by 8%–50% by the end of the 21st century (Meier, 2006). Populations of *Zostera marina* in Baltic subregions are genetically isolated from each other and have different salinity tolerances. Selected edge populations have lower critical salinity limits of 2–4 PSS-78 (Salo et al., 2014). However, as freshwater expands in range, it is not clear how other higher salinity-adapted populations will respond in the long term.

4 | HUMAN HEALTH, ECONOMY, AND FUTURE DIRECTIONS

In addition to the global ecological impact, the changing marine environment is causing economic losses and poses new challenges for human health (Pörtner et al., 2019). Despite clear evidence of changing ocean salinity, we have no broad, integrative understanding of how salinity alterations interact with other climate change pressures and affect global ecosystems (Figure 2). Rather, such interactions remain largely untested and therefore difficult to quantify (ecologically and economically). However, we do have evidence that changing salinity patterns can result in complete regime shifts and the loss of ecosystem function, providing a warning flag (Table 1, Table S1, Figures 3 and 4). For some ecosystems, salinity is even considered a key variable to quantify degradation (Bland et al., 2017), but knowledge on the direct effects of salinity changes on marine ecosystem function remains fragmentary.

For example, the loss of ecosystem services (such as nutrition, coastal protection, and tourism) associated with coral reefs would equate to an annual loss of US$375 billion (Costanza et al., 1997). Losing seagrass meadows, marsh grass and mangroves ecosystems, and their economically valuable species would result in an annual loss of US$22–31 million in carbon value in Australia alone (Serrano et al., 2019). Although it is likely that isolated shifts in salinity would not be the major driver of demise in these ecosystems, healthy ecosystem function is impaired by salinity changes, especially when concurrent with other stressors (e.g., ocean warming, ocean acidification). Indeed, increasing SLR has been estimated to directly threaten an estimated 0.2%–4.6% of the human population that reside in coastal regions with expected annual losses of 0.3%–9.3% of the global gross domestic product by 2100 (Hinkel et al., 2014). For instance, salinity intrusion in soils and freshwater reservoirs, partly connected to annual flooding, already impacts agricultural productivity globally and is a major driver for human migrations (Chen & Mueller, 2018). SLR and changes in terrestrial runoff patterns further affect salinity regimes in estuaries, including upstream salinization and water quality degeneration, thus limiting freshwater supply for the often highly populated coastal regions (Figure 3). Furthermore, other salinity-driven shifts in ocean productivity, such as HABs and/or anoxic dead zones, can decimate local and regional fish stocks with direct and severe consequences for fisheries, aquaculture, and human health (estimated US$8 billion global annual loss from HABs alone (Brown et al., 2019)). Aquaculture may further be directly impacted, exemplified by the economically important mussel genus *Mytilus* with a global distribution (>750,000 tons production in 2019 (FAO, 2021)). Here, decreasing salinity can cause reduced growth rates (Riisgård et al., 2013), while increasing salinity variability can affect the physiology and immunology of mussels with further anticipated economic downstream effects (Bussell et al., 2008; Duarte et al., 2018). Lastly, salinity-triggered changes to global ocean currents (including the THC) and enhanced stratification may provide direct feedback on the rate of climate change, but the direct and indirect consequences on human socioeconomics remain difficult to quantify.

This review highlights that detailed data on the effects of salinity changes on the vast majority of ecologically and economically important ecosystems are lacking, which makes the projection of consequences highly inaccurate. Existing research typically does not address spatial, diel, monthly, and seasonal variability of salinity. Enhanced short-term variability through extreme events (e.g., droughts, floodings) may well impose a stronger selective pressure on ecosystems than long-term changes and this should urgently be explored, particularly in coastal regions (Ziegler et al., 2021). Salinity is also often measured alongside other environmental parameters but rarely addressed as a central ecosystem driver, particularly in the context of environmental change. This exclusion may be linked to the inherent local complexities and variabilities that influence salinity on short-term spatiotemporal scales. Here, data are lacking at large, for instance on combined effects of salinity and SLR on benthic coastal ecosystems. This is surprising, as physiological effects of salinity changes are commonly assessed on an organismal scale for certain groups, particularly combined with other variables, such as temperature or toxins (Gunderson et al., 2016). However, for many important groups these data are also lacking, exemplified by bacterial (Baker-Austin et al., 2013) and viral (Brown et al., 2009) pathogens, the spread and infectivity of which can be affected by salinity. Existing large-scale sampling and monitoring efforts (e.g., plankton (Biller et al., 2018) and seagrass (Short et al., 2011)) should consider salinity as a central physio-ecological driver. Future research should also characterize large-scale spatiotemporal coastal salinity patterns and changes therein as a framework to integrate meaningful data such as key species' tipping points (see our modeling approaches for plankton communities and coral distribution based on open ocean salinity projections for two examples of how this can be undertaken (Figure 4)). If conducted, such data can deliver meaningful projections to inform conservation and management strategies.

5 | CONCLUSION

The physiological effects of salinity changes in the marine ecosphere have long been studied. However, in the context of climate change, salinity appears to be the 'elephant in the room'. This is particularly remarkable as there is ample evidence that ocean warming and ocean acidification directly affect and are affected by salinity changes. More work is therefore needed to integrate how all three climate change-related stressors interact and affect marine ecosystems and biota, which should be comprehensively summarized as a first step. While physiological (and mostly laboratory-based) data on salinity variations are available for a range of organisms, we are missing baseline data on the natural variability of many ecosystems, which makes any prediction of the consequences of climate change driven salinity changes challenging. In particular, salinity patterns in coastal ecosystems are lacking spatial and temporal resolution. We also need to acquire a clearer understanding of interactions of salinity with accompanying factors such as temperature, acidification, oxygen solubility, sedimentation, and nutrient input—all of which play a crucial global role for human health and economy.

AUTHOR CONTRIBUTIONS

Till Röthig, Stacey M. Trevathan-Tackett, Christian R. Voolstra, and Paul J. Durack led and Michael Sweet contributed to the design of the study. Till Röthig led, and Stacey M. Trevathan-Tackett, Christian R. Voolstra and Cliff Ross contributed to the coordination of the paper. Till Röthig, Stacey M. Trevathan-Tackett, Christian R. Voolstra, Cliff Ross, Paul J. Durack, Samuel Chaffron, and Laura M. Warmuth led the drafting of subsections and development of figures and tables. All authors contributed to writing and/or editing the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available as detailed in the following. The data source for the observation fields in Figure 1a is included in the AR6 citation: Durack, P. J. (2023): Chapter 2 of the Working Group I Contribution to the IPCC Sixth Assessment Report—Input data for Figure 2.27 (v20211112) https://catalogue.ceda.ac.uk/uuid/78ad6999f2d743d2a7db16757c27b549. NERC EDS Centre for Environmental Data Analysis, accessed 11.05.2023. Tables S2–S4 detail the respective DOIs for each of the CMIP6 model fields that were used across the three future climate projection scenarios in Figure 1b–g. Raw data associated with Figure 4a are available at the EBI under the project identifiers PRJEB402 and PRJEB7988 and at PANGAEA https://doi.pangaea.de/10.1594/PANGAEA.875582. All processed data (raw abundance matrices and interactome graphML files) needed to evaluate the conclusions of the paper in regard to plankton communities are available at https://zenodo.org/record/7684593. Data used for coral habitat predictions (Figure 4b) can be accessed at Zenodo under https://doi.org/10.5281/zenodo.8079650 and are detailed in the Supplementary Material & Methods.

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REFERENCES

Alber, M., Swenson, E. M., Adamowicz, S. C., & Mendelssohn, I. A. (2008). Salt Marsh dieback: An overview of recent events in the US. *Estuarine, Coastal and Shelf Science*, *80*(1), 1–11. https://doi.org/10.1016/j.ecss.2008.08.009

Ardyna, M., & Arrigo, K. R. (2020). Phytoplankton dynamics in a changing Arctic Ocean. *Nature Climate Change*, *10*(10), 892–903. https://doi.org/10.1038/s41558-020-0905-y

Baker-Austin, C., Trinanes, J. A., Taylor, N. G. H., Hartnell, R., Siitonen, A., & Martinez-Urtaza, J. (2013). Emerging vibrio risk at high latitudes in response to ocean warming. *Nature Climate Change*, *3*(1), 73–77. https://doi.org/10.1038/nclimate1628

Balmonte, J. P., Hasler-Sheetal, H., Glud, R. N., Andersen, T. J., Sejr, M. K., Middelboe, M., Teske, A., & Arnosti, C. (2020). Sharp contrasts between freshwater and marine microbial enzymatic capabilities, community composition, and DOM pools in a NE Greenland fjord. *Limnology and Oceanography*, *65*(1), 77–95. https://doi.org/10.1002/lno.11253

Bell, S. Y., Fraser, M. W., Statton, J., & Kendrick, G. A. (2019). Salinity stress drives herbivory rates and selective grazing in subtidal seagrass communities. *PLoS ONE*, *14*(3), e0214308. https://doi.org/10.1371/journal.pone.0214308

Biber, P. D., & Irlandi, E. A. (2006). Temporal and spatial dynamics of macroalgal communities along an anthropogenic salinity gradient in Biscayne Bay (Florida, USA). *Aquatic Botany*, *85*(1), 65–77. https://doi.org/10.1016/j.aquabot.2006.02.002

Bijma, J., Faber, W. W., & Hemleben, C. (1990). Temperature and salinity limits for growth and survival of some planktonic foraminifers in laboratory cultures. *Journal of Foraminiferal Research*, *20*(2), 95–116. https://doi.org/10.2113/gsjfr.20.2.95

Biller, S. J., Berube, P. M., Dooley, K., Williams, M., Satinsky, B. M., Hackl, T., Hogle, S. L., Coe, A., Bergauer, K., Bouman, H. A., Browning, T. J., De Corte, D., Hassler, C., Hulston, D., Jacquot, J. E., Maas, E. W., Reinthaler, T., Sintes, E., Yokokawa, T., & Chisholm, S. W. (2018). Data descriptor: Marine microbial metagenomes sampled across space and time. *Scientific Data*, *5*(1), 1–7. https://doi.org/10.1038/sdata.2018.176

Bintanja, R., & Selten, F. M. (2014). Future increases in Arctic precipitation linked to local evaporation and sea-ice retreat. *Nature*, *509*(7501), 479–482. https://doi.org/10.1038/nature13259

Bintanja, R., van der Wiel, K., van der Linden, E. C., Reusen, J., Bogerd, L., Krikken, F., & Selten, F. M. (2020). Strong future increases in Arctic precipitation variability linked to poleward moisture transport. *Science Advances*, *6*(7), 6869–6881. https://doi.org/10.1126/sciadv.aax6869

Blais, M., Ardyna, M., Gosselin, M., Dumont, D., Bélanger, S., Tremblay, J. É., Gratton, Y., Marchese, C., & Poulin, M. (2017). Contrasting interannual changes in phytoplankton productivity and community structure in the coastal Canadian Arctic Ocean. *Limnology and Oceanography*, *62*(6), 2480–2497. https://doi.org/10.1002/lno.10581

Bland, L. M., Keith, D. A., Miller, R. M., Murray, N. J., & Rodríguez, J. P. (2017). *Guidelines for the application of IUCN Red List of Ecosystems Categories and Criteria, version 1.1*. International Union for the Conservation of Nature. https://doi.org/10.2305/IUCN.CH.2016.RLE.3.en

Boers, N. (2021). Observation-based early-warning signals for a collapse of the Atlantic Meridional Overturning Circulation. *Nature Climate Change*, *11*(8), 680–688. https://doi.org/10.1038/s41558-021-01097-4

Breitburg, D., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G. S., Limburg, K. E., Montes, I., Naqvi, S. W. A., Pitcher, G. C., Rabalais, N. N., Roman, M. R., Rose, K. A., Seibel, B. A., … Zhang, J. (2018). Declining oxygen in the global ocean and coastal waters. *Science*, *359*(6371), eaam7240. https://doi.org/10.1126/science.aam7240

Brown, A. R., Lilley, M., Shutler, J., Lowe, C., Artioli, Y., Torres, R., Berdalet, E., & Tyler, C. R. (2019). Assessing risks and mitigating impacts of harmful algal blooms on mariculture and marine fisheries. *Reviews in Aquaculture*, *12*(3), raq.12403. https://doi.org/10.1111/raq.12403

Brown, J. D., Goekjian, G., Poulson, R., Valeika, S., & Stallknecht, D. E. (2009). Avian influenza virus in water: Infectivity is dependent on pH, salinity and temperature. *Veterinary Microbiology*, *136*(1–2), 20–26. https://doi.org/10.1016/j.vetmic.2008.10.027

Burford, M. A., Carey, C. C., Hamilton, D. P., Huisman, J., Paerl, H. W., Wood, S. A., & Wulff, A. (2020). Perspective: Advancing the research agenda for improving understanding of cyanobacteria in a future of global change. *Harmful Algae*, *91*, 101601. https://doi.org/10.1016/j.hal.2019.04.004

Bussell, J. A., Gidman, E. A., Causton, D. R., Gwynn-Jones, D., Malham, S. K., Jones, M. L. M., Reynolds, B., & Seed, R. (2008). Changes in the immune response and metabolic fingerprint of the mussel, *Mytilus edulis* (Linnaeus) in response to lowered salinity and physical stress. *Journal of Experimental Marine Biology and Ecology*, *358*(1), 78–85. https://doi.org/10.1016/j.jembe.2008.01.018

Cambridge, M. L., Chiffings, A. W., Brittan, C., Moore, L., & McComb, A. J. (1986). The loss of seagrass in Cockburn sound, Western Australia. II. Possible causes of seagrass decline. *Aquatic Botany*, *24*(3), 269–285. https://doi.org/10.1016/0304-3770(86)90062-8

Carmack, E. C., Yamamoto-Kawai, M., Haine, T. W. N., Bacon, S., Bluhm, B. A., Lique, C., Melling, H., Polyakov, I. V., Straneo, F., Timmermans, M. L., & Williams, W. J. (2016). Freshwater and its role in the Arctic

Marine System: Sources, disposition, storage, export, and physical and biogeochemical consequences in the Arctic and global oceans. *Journal of Geophysical Research, G: Biogeosciences*, *121*(3), 675–717. https://doi.org/10.1002/2015JG003140

Cavicchioli, R., Ripple, W. J., Timmis, K. N., Azam, F., Bakken, L. R., Baylis, M., Behrenfeld, M. J., Boetius, A., Boyd, P. W., Classen, A. T., Crowther, T. W., Danovaro, R., Foreman, C. M., Huisman, J., Hutchins, D. A., Jansson, J. K., Karl, D. M., Koskella, B., Mark Welch, D. B., … Webster, N. S. (2019). Scientists' warning to humanity: Microorganisms and climate change. *Nature Reviews Microbiology*, *1*, 569–586. https://doi.org/10.1038/s41579-019-0222-5

Celussi, M., Zoccarato, L., Bernardi Aubry, F., Bastianini, M., Casotti, R., Balestra, C., Giani, M., & Del Negro, P. (2019). Links between microbial processing of organic matter and the thermohaline and productivity features of a temperate river-influenced Mediterranean coastal area. *Estuarine, Coastal and Shelf Science*, *228*, 106378. https://doi.org/10.1016/j.ecss.2019.106378

Chaffron, S., Delage, E., Budinich, M., Vintache, D., Henry, N., Nef, C., Ardyna, M., Zayed, A. A., Junger, P. C., Galand, P. E., Lovejoy, C., Murray, A. E., Sarmento, H., Acinas, S. G., Babin, M., Iudicone, D., Jaillon, O., Karsenti, E., Wincker, P., … Eveillard, D. (2021). Environmental vulnerability of the global ocean epipelagic plankton community interactome. *Science Advances*, *7*(35). https://doi.org/10.1126/sciadv.abg1921

Chen, J., & Mueller, V. (2018). Coastal climate change, soil salinity and human migration in Bangladesh. *Nature Climate Change*, *8*(11), 981–987. https://doi.org/10.1038/s41558-018-0313-8

Chou, C., & Neelin, J. D. (2004). Mechanisms of global warming impacts on regional tropical precipitation. *Journal of Climate*, *17*(13), 2688–2701. https://doi.org/10.1175/1520-0442(2004)017%3C2688:MOGWIO%3E2.0.CO;2

Coles, S. L., & Jokiel, P. L. (1992). Effects of salinity on coral reefs. In D. W. Connell, & D. W. Hawker (Eds.), *Pollution in tropical aquatic systems* (pp. 147–166). CRC Press, Taylor & Francis Group.

Collier, C. J., Villacorta-Rath, C., van Dijk, K., Takahashi, M., & Waycott, M. (2014). Seagrass proliferation precedes mortality during hypo-salinity events: A stress-induced morphometric response. *PLoS ONE*, *9*(4), e94014. https://doi.org/10.1371/journal.pone.0094014

Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., & van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature*, *387*, 253–260. https://doi.org/10.1016/s0921-8009(98)00020-2

D'Angelo, C., Hume, B. C. C., Burt, J., Smith, E. G., Achterberg, E. P., & Wiedenmann, J. (2015). Local adaptation constrains the distribution potential of heat-tolerant Symbiodinium from the Persian/Arabian gulf. *The ISME Journal*, *9*(12), 2551–2560. https://doi.org/10.1038/ismej.2015.80

des Aulnois, M. G., Roux, P., Caruana, A., Réveillon, D., Briand, E., Hervé, F., Savar, V., Bormans, M., & Amzil, Z. (2019). Physiological and metabolic responses of freshwater and brackish-water strains of Microcystis aeruginosa acclimated to a salinity gradient: Insight into salt tolerance. *Applied and Environmental Microbiology*, *85*(21). https://doi.org/10.1128/AEM.01614-19

Dietzel, A., Bode, M., Connolly, S. R., & Hughes, T. P. (2020). Long-term shifts in the colony size structure of coral populations along the Great Barrier Reef. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1936), 20201432. https://doi.org/10.1098/rspb.2020.1432

Doney, S. C., Ruckelshaus, M., Duffy, J. E., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N. N., Sydeman, W. J., & Talley, L. D. (2012). Climate change impacts on marine ecosystems. *Annual Review of Marine Science*, *4*, 11–37. https://doi.org/10.1146/annurev-marine-041911-111611

Duarte, C., Navarro, J. M., Quijón, P. A., Loncon, D., Torres, R., Manríquez, P. H., Lardies, M. A., Vargas, C. A., & Lagos, N. A. (2018). The energetic physiology of juvenile mussels, *Mytilus chilensis* (Hupe): The prevalent role of salinity under current and predicted pCO_2 scenarios. *Environmental Pollution*, *242*, 156–163. https://doi.org/10.1016/j.envpol.2018.06.053

Dueñas-Bohórquez, A., da Rocha, R. E., Kuroyanagi, A., Bijma, J., & Reichart, G. J. (2009). Effect of salinity and seawater calcite saturation state on Mg and Sr incorporation in cultured planktonic foraminifera. *Marine Micropaleontology*, *73*(3–4), 178–189. https://doi.org/10.1016/j.marmicro.2009.09.002

Duffy, J. E., Benedetti-Cecchi, L., Trinanes, J., Muller-Karger, F. E., Ambo-Rappe, R., Boström, C., Buschmann, A. H., Byrnes, J., Coles, R. G., Creed, J., Cullen-Unsworth, L. C., Diaz-Pulido, G., Duarte, C. M., Edgar, G. J., Fortes, M., Goni, G., Hu, C., Huang, X., Hurd, C. L., … Yaakub, S. M. (2019). Toward a coordinated global observing system for seagrasses and marine macroalgae. *Frontiers in Marine Science*, *6*(July), 317. https://doi.org/10.3389/fmars.2019.00317

Durack, P. J. (2015). Ocean salinity and the global water cycle. *Oceanography*, *28*(1), 20–31. https://doi.org/10.5670/oceanog.2015.03

Durack, P. J., & Wijffels, S. E. (2010). Fifty-year trends in global ocean salinities and their relationship to broad-scale warming. *Journal of Climate*, *23*(16), 4342–4362. https://doi.org/10.1175/2010JCLI3377.1

Durack, P. J., Wijffels, S. E., & Gleckler, P. J. (2014). Long-term sea-level change revisited: The role of salinity. *Environmental Research Letters*, *9*(11), 114017. https://doi.org/10.1088/1748-9326/9/11/114017

Durack, P. J., Wijffels, S. E., & Matear, R. J. (2012). Ocean salinities reveal strong global water cycle intensification during 1950 to 2000. *Science*, *336*(6080), 455–458. https://doi.org/10.1126/science.1212222

Estrada, M., Delgado, M., Blasco, D., Latasa, M., Cabello, A. M., Benítez-Barrios, V., Fraile-Nuez, E., Mozetič, P., & Vidal, M. (2016). Phytoplankton across tropical and subtropical regions of the Atlantic, Indian and Pacific Oceans. *PLoS ONE*, *11*(3), e0151699. https://doi.org/10.1371/journal.pone.0151699

FAO Fisheries and Aquaculture Division. (2021). *Global capture production* (online query). https://www.fao.org/fishery/statistics/global-capture-production/query/en

Feher, L. C., Osland, M. J., Griffith, K. T., Grace, J. B., Howard, R. J., Stagg, C. L., Enwright, N. M., Krauss, K. W., Gabler, C. A., & Day, R. H. (2017). Linear and nonlinear effects of temperature and precipitation on ecosystem properties in tidal saline wetlands. *Ecosphere*, *8*(10), e01956. https://doi.org/10.1002/ecs2.1956

Ferrier-Pagès, C., Gattuso, J. P., & Jaubert, J. (1999). Effect of small variations in salinity on the rates of photosynthesis and respiration of the zooxanthellate coral *Stylophora pistillata*. *Marine Ecology Progress Series*, *181*, 309–314. https://doi.org/10.3354/meps181309

Francis, T. B., Scheuerell, M. D., Brodeur, R. D., Levin, P. S., Ruzicka, J. J., Tolimieri, N., & Peterson, W. T. (2012). Climate shifts the interaction web of a marine plankton community. *Global Change Biology*, *18*(8), 2498–2508. https://doi.org/10.1111/j.1365-2486.2012.02702.x

Fu, F., Tatters, A., & Hutchins, D. (2012). Global change and the future of harmful algal blooms in the ocean. *Marine Ecology Progress Series*, *470*, 207–233. https://doi.org/10.3354/meps10047

Gegner, H. M., Rädecker, N., Ochsenkühn, M., Barreto, M. M., Ziegler, M., Reichert, J., Schubert, P., Wilke, T., & Voolstra, C. R. (2019). High levels of floridoside at high salinity link osmoadaptation with bleaching susceptibility in the cnidarian-algal endosymbiosis. *Biology Open*, *8*(12). https://doi.org/10.1242/bio.045591

Gegner, H. M., Ziegler, M., Rädecker, N., Buitrago-López, C., Aranda, M., & Voolstra, C. R. (2017). High salinity conveys thermotolerance in the coral model Aiptasia. *Biology Open*, *6*(12), 1943–1948. https://doi.org/10.1242/bio.028878

Gianoulis, T. A., Raes, J., Patel, P. V., Bjornson, R., Korbel, J. O., Letunic, I., Yamada, T., Paccanaro, A., Jensen, L. J., Snyder, M., Bork, P., & Gerstein, M. B. (2009). Quantifying environmental adaptation of metabolic pathways in metagenomics. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(5), 1374–1379. https://doi.org/10.1073/pnas.0808022106

Gibson, R. N., Barnes, M., & Atkinson, R. J. A. (2002). Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. *Oceanography and Marine Biology: An Annual Review*, *40*, 233.

Gilman, E. L., Ellison, J., Duke, N. C., & Field, C. (2008). Threats to mangroves from climate change and adaptation options: A review. *Aquatic Botany*, *89*(2), 237–250. https://doi.org/10.1016/j.aquabot.2007.12.009

Green, E. P., Short, F. T., & Frederick, T. (2003). *World atlas of seagrasses*. University of California Press.

Greene, C. H., & Pershing, A. J. (2007). Climate drives sea change. *Science*, *315*(5815), 1084–1085. https://doi.org/10.1126/science.1136495

Greene, C. H., Pershing, A. J., Cronin, T. M., & Ceci, N. (2008). Arctic climate change and its impacts on the ecology of the North Atlantic. *Ecology*, *89*(11), 24–38. https://doi.org/10.1890/07-0550.1

Griffies, S. M., Yin, J., Durack, P. J., Goddard, P., Bates, S. C., Behrens, E., Bentsen, M., Bi, D., Biastoch, A., Böning, C. W., Bozec, A., Chassignet, E., Danabasoglu, G., Danilov, S., Domingues, C. M., Drange, H., Farneti, R., Fernandez, E., Greatbatch, R. J., … Zhang, X. (2014). An assessment of global and regional sea level for years 1993-2007 in a suite of interannual core-II simulations. *Ocean Modelling*, *78*, 35–89. https://doi.org/10.1016/j.ocemod.2014.03.004

Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., Darzi, Y., Audic, S., Berline, L., Brum, J. R., Coelho, L. P., Espinoza, J. C. I., Malviya, S., Sunagawa, S., Dimier, C., Kandels-Lewis, S., Picheral, M., Poulain, J., Searson, S., … Gorsky, G. (2016). Plankton networks driving carbon export in the oligotrophic ocean. *Nature*, *532*(7600), 465–470. https://doi.org/10.1038/nature16942

Gunderson, A. R., Armstrong, E. J., & Stillman, J. H. (2016). Multiple stressors in a changing world: The need for an improved perspective on physiological responses to the dynamic marine environment. *Annual Review of Marine Science*, *8*(1), 357–378. https://doi.org/10.1146/annurev-marine-122414-033953

Haumann, A. F., Gruber, N., Münnich, M., Frenger, I., & Kern, S. (2016). Sea-ice transport driving Southern Ocean salinity and its recent trends. *Nature*, *537*(7618), 89–92. https://doi.org/10.1038/nature19101

Hauxwell, J., Cebrián, J., Furlong, C., & Valiela, I. (2001). Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology*, *82*(4), 1007–1022. https://doi.org/10.1890/0012-9658(2001)082[1007:mcctez]2.0.co;2

Held, I. M., & Soden, B. J. (2006). Robust responses of the hydrological cycle to global warming. *Journal of Climate*, *19*(21), 5686–5699. https://doi.org/10.1175/JCLI3990.1

Henson, S. A., Beaulieu, C., Ilyina, T., John, J. G., Long, M., Séférian, R., Tjiputra, J., & Sarmiento, J. L. (2017). Rapid emergence of climate change in environmental drivers of marine ecosystems. *Nature Communications*, *8*(1), 1–9. https://doi.org/10.1038/ncomms14682

Herbert, E. R., Boon, P., Burgin, A. J., Neubauer, S. C., Franklin, R. B., Ardon, M., Hopfensperger, K. N., Lamers, L. P. M., Gell, P., & Langley, J. A. (2015). A global perspective on wetland salinization: Ecological consequences of a growing threat to freshwater wetlands. *Ecosphere*, *6*(10), 1–43. https://doi.org/10.1890/ES14-00534.1

Herlemann, D. P., Labrenz, M., Jürgens, K., Bertilsson, S., Waniek, J. J., & Andersson, A. F. (2011). Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *The ISME Journal*, *5*(10), 1571–1579. https://doi.org/10.1038/ismej.2011.41

Heuzé, C., Heywood, K. J., Stevens, D. P., & Ridley, J. K. (2015). Changes in global ocean bottom properties and volume transports in CMIP5 models under climate change scenarios. *Journal of Climate*, *28*(8), 2917–2944. https://doi.org/10.1175/JCLI-D-14-00381.1

Hinkel, J., Lincke, D., Vafeidis, A. T., Perrette, M., Nicholls, R. J., Tol, R. S. J., Marzeion, B., Fettweis, X., Ionescu, C., & Levermann, A. (2014). Coastal flood damage and adaptation costs under 21st century sea-level rise. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(9), 3292–3297. https://doi.org/10.1073/pnas.1222469111

Hirai, J., Tachibana, A., & Tsuda, A. (2020). Large-scale metabarcoding analysis of epipelagic and mesopelagic copepods in the Pacific. *PLoS ONE*, *15*(5), e0233189. https://doi.org/10.1371/journal.pone.0233189

Hughes, D. J., Alderdice, R., Cooney, C., Kühl, M., Pernice, M., Voolstra, C. R., & Suggett, D. J. (2020). Coral reef survival under accelerating ocean deoxygenation. *Nature Climate Change*, *10*(4), 296–307. https://doi.org/10.1038/s41558-020-0737-9

Hume, B. C. C., Voolstra, C. R., Arif, C., D'Angelo, C., Burt, J. A., Eyal, G., Loya, Y., & Wiedenmann, J. (2016). Ancestral genetic diversity associated with the rapid spread of stress-tolerant coral symbionts in response to Holocene climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(16), 4416–4421. https://doi.org/10.1073/pnas.1601910113

Ibarbalz, F. M., Henry, N., Brandão, M. C., Martini, S., Busseni, G., Byrne, H., Coelho, L. P., Endo, H., Gasol, J. M., Gregory, A. C., Mahé, F., Rigonato, J., Royo-Llonch, M., Salazar, G., Sanz-Sáez, I., Scalco, E., Soviadan, D., Zayed, A. A., Zingone, A., … Zinger, L. (2019). Global trends in marine plankton diversity across kingdoms of life. *Cell*, *179*(5), 1084–1097.e21. https://doi.org/10.1016/j.cell.2019.10.008

IPCC. (2023). Summary for policymakers. In Core Writing Team, H. Lee, & J. Romero (Eds.), *Climate change 2023: Synthesis report. A report of the Intergovernmental Panel on Climate Change. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, in press.

Janousek, C. N., & Mayo, C. (2013). Plant responses to increased inundation and salt exposure: Interactive effects on tidal marsh productivity. *Plant Ecology*, *214*(7), 917–928. https://doi.org/10.1007/s11258-013-0218-6

Jurdzinski, K. T., Mehrshad, M., Delgado, L. F., Deng, Z., Bertilsson, S., & Andersson, A. F. (2023). Large-scale phylogenomics of aquatic bacteria reveal molecular mechanisms for adaptation to salinity. *Science Advances*, *9*(21). https://doi.org/10.1126/SCIADV.ADG2059

Kirst, G. O. (1990). Salinity tolerance of eukaryotic marine algae. *Annual Review of Plant Physiology and Plant Molecular Biology*, *41*(1), 21–53. https://doi.org/10.1146/annurev.pp.41.060190.000321

Kirwan, M. L., & Gedan, K. B. (2019). Sea-level driven land conversion and the formation of ghost forests. *Nature Climate Change*, *9*(6), 450–457. https://doi.org/10.1038/s41558-019-0488-7

Kniebusch, M., Meier, H. E. M., Neumann, T., & Börgel, F. (2019). Temperature variability of the Baltic Sea since 1850 and attribution to atmospheric forcing variables. *Journal of Geophysical Research: Oceans*, *124*(6), 4168–4187. https://doi.org/10.1029/2018JC013948

Knight, J., & Harrison, S. (2009). Sediments and future climate. *Nature Geoscience*, *2*(4), 230. https://doi.org/10.1038/ngeo491

Lenderink, G., & Van Meijgaard, E. (2008). Increase in hourly precipitation extremes beyond expectations from temperature changes. *Nature Geoscience*, *1*(8), 511–514. https://doi.org/10.1038/ngeo262

Li, G., Cheng, L., Zhu, J., Trenberth, K. E., Mann, M. E., & Abraham, J. P. (2020). Increasing ocean stratification over the past half-century. *Nature Climate Change*, *10*(12), 1116–1123. https://doi.org/10.1038/s41558-020-00918-2

Louca, S., Parfrey, L. W., & Doebeli, M. (2016). Decoupling function and taxonomy in the global ocean microbiome. *Science*, *353*(6305), 1272–1277. https://doi.org/10.1126/science.aaf4507

Lovelock, C. E., Feller, I. C., Reef, R., Hickey, S., & Ball, M. C. (2017). Mangrove dieback during fluctuating sea levels. *Scientific Reports*, *7*(1), 1–8. https://doi.org/10.1038/s41598-017-01927-6

Lozupone, C. A., & Knight, R. (2007). Global patterns in bacterial diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(27), 11436–11440. https://doi.org/10.1073/pnas.0611525104

Luo, M., Huang, J.-F., Zhu, W.-F., & Tong, C. (2019). Impacts of increasing salinity and inundation on rates and pathways of organic carbon mineralization in tidal wetlands: A review. *Hydrobiologia*, *827*(1), 31–49. https://doi.org/10.1007/s10750-017-3416-8

Luo, S., Valencia, C. A., Zhang, J., Lee, N.-C., Slone, J., Gui, B., Wang, X., Li, Z., Dell, S., Brown, J., Chen, S. M., Chien, Y.-H., Hwu, W.-L., Fan, P.-C., Wong, L.-J., Atwal, P. S., & Huang, T. (2018). Biparental inheritance of mitochondrial DNA in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(51), 13039–13044. https://doi.org/10.1073/PNAS.1810946115

Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R., Maycock, T. K., Waterfield, T., Yelekçi, O., Yu, R., & Zhou, B. (2021). Climate change 2021: The physical science basis. In *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (Vol. *2*). IPCC.

Mayfield, A. B., & Gates, R. D. (2007). Osmoregulation in anthozoan–dinoflagellate symbiosis. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *147*(1), 1–10. https://doi.org/10.1016/j.cbpa.2006.12.042

Mazzei, V., & Gaiser, E. (2018). Diatoms as tools for inferring ecotone boundaries in a coastal freshwater wetland threatened by saltwater intrusion. *Ecological Indicators*, *88*, 190–204. https://doi.org/10.1016/j.ecolind.2018.01.003

Meier, H. E. M. (2006). Baltic Sea climate in the late twenty-first century: A dynamical downscaling approach using two global models and two emission scenarios. *Climate Dynamics*, *27*(1), 39–68. https://doi.org/10.1007/s00382-006-0124-x

Mezger, E. M., de Nooijer, L. J., Boer, W., Brummer, G. J. A., & Reichart, G. J. (2016). Salinity controls on Na incorporation in Red Sea planktonic foraminifera. *Paleoceanography*, *31*(12), 1562–1582. https://doi.org/10.1002/2016PA003052

Moberg, F., Nyström, M., Kautsky, N., Tedengren, M., & Jarayabhand, P. (1997). Effects of reduced salinity on the rates of photosynthesis and respiration in the hermatypic corals *Porites lutea* and *Pocillopora damicornis*. *Marine Ecology Progress Series*, *157*, 53–59. https://doi.org/10.3354/meps157053

Munk, W. (2003). Ocean freshening, sea level rising. *Science*, *300*(5628), 2041–2043. https://doi.org/10.1126/science.1085534

Murphy, E. J., Cavanagh, R. D., Drinkwater, K. F., Grant, S. M., Heymans, J. J., Hofmann, E. E., Hunt, G. L., & Johnston, N. M. (2016). Understanding the structure and functioning of polar pelagic ecosystems to predict the impacts of change. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1844), 20161646. https://doi.org/10.1098/rspb.2016.1646

Muylaert, K., Sabbe, K., & Vyverman, W. (2009). Changes in phytoplankton diversity and community composition along the salinity gradient of the Schelde estuary (Belgium/The Netherlands). *Estuarine, Coastal and Shelf Science*, *82*(2), 335–340. https://doi.org/10.1016/j.ecss.2009.01.024

Neubauer, S. C., Franklin, R. B., & Berrier, D. J. (2013). Saltwater intrusion into tidal freshwater marshes alters the biogeochemical processing of organic carbon. *Biogeosciences*, *10*(12), 8171–8183. https://doi.org/10.5194/bg-10-8171-2013

Newell, R. C. (1976). *Adaptation to environment: Essays on the physiology of marine animals*. Elsevier. https://doi.org/10.1016/C2013-0-04229-6

Ngugi, D. K., Ziegler, M., Duarte, C. M., & Voolstra, C. R. (2020). Genomic blueprint of glycine betaine metabolism in coral Metaorganisms and their contribution to reef nitrogen budgets. *IScience*, *23*(5), 101120. https://doi.org/10.1016/j.isci.2020.101120

Nicholls, R. J. (2010). Impacts of and responses to sea-level rise. In *Understanding sea-level rise and variability* (pp. 17–51). Wiley-Blackwell. https://doi.org/10.1002/9781444323276.ch2

Nielsen, R., Kristiansen, A., Mathiesen, L., & Mathiesen, H. (1995). Distributional index of the benthic marine macroalgae of the Baltic Sea area. *Acta Botanica Fennica*, *155*, 1–70.

Nixon, S. W., Oviatt, C. A., Frithsen, J., & Sullivan, B. (1986). Nutrients and the productivity of estuarine and coastal marine ecosystems. *Journal of the Limnological Society of Southern Africa*, *12*(1–2), 43–71. https://doi.org/10.1080/03779688.1986.9639398

Ochsenkühn, M. A., Röthig, T., D'Angelo, C., Wiedenmann, J., & Voolstra, C. R. (2017). The role of floridoside in osmoadaptation of coral-associated algal endosymbionts to high-salinity conditions. *Science Advances*, *3*(8), e1602047. https://doi.org/10.1126/sciadv.1602047

Ojaveer, H., Jaanus, A., MacKenzie, B. R., Martin, G., Olenin, S., Radziejewska, T., Telesh, I., Zettler, M. L., & Zaiko, A. (2010). Status of biodiversity in the Baltic Sea. *PLoS ONE*, *5*(9), e12467. https://doi.org/10.1371/journal.pone.0012467

Osman, E. O., Smith, D. J., Ziegler, M., Kürten, B., Conrad, C., El-Haddad, K. M., Voolstra, C. R., & Suggett, D. J. (2017). Thermal refugia against coral bleaching throughout the northern Red Sea. *Global Change Biology*, *24*(2), e474–e484. https://doi.org/10.1111/gcb.13895

Papalexiou, S. M., & Montanari, A. (2019). Global and regional increase of precipitation extremes under global warming. *Water Resources Research*, *55*(6), 2018WR024067. https://doi.org/10.1029/2018WR024067

Parida, A. K., & Jha, B. (2010). Salt tolerance mechanisms in mangroves: A review. *Trees*, *24*(2), 199–217. https://doi.org/10.1007/s00468-010-0417-x

Pörtner, H. O., Roberts, D. C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegría, A., Nicolai, M., Okem, A., Petzold, J., Rama, B., & Weyer, N. M. (2019). The ocean and cryosphere in a changing climate. In *IPCC special report on the ocean and cryosphere in a changing climate* (p. 1155). Cambridge University Press. https://doi.org/10.1017/9781009157964

Post, E., Alley, R. B., Christensen, T. R., Macias-Fauria, M., Forbes, B. C., Gooseff, M. N., Iler, A., Kerby, J. T., Laidre, K. L., Mann, M. E., Olofsson, J., Stroeve, J. C., Ulmer, F., Virginia, R. A., & Wang, M. (2019). The polar regions in a 2°C warmer world. *Science Advances*, *5*(12), eaaw9883. https://doi.org/10.1126/sciadv.aaw9883

Pratolongo, P., Leonardi, N., Kirby, J. R., & Plater, A. (2018). Temperate coastal wetlands. In *Coastal wetlands: An integrated ecosystem approach* (pp. 105–152). Elsevier. https://doi.org/10.1016/B978-0-444-63893-9.00003-4

Preece, E. P., Hardy, F. J., Moore, B. C., & Bryan, M. (2017). A review of microcystin detections in estuarine and marine waters: Environmental implications and human health risk. *Harmful Algae*, *61*, 31–45. https://doi.org/10.1016/j.hal.2016.11.006

Qasim, S. Z., Bhattathiri, P. M. A., & Devassy, V. P. (1972). The influence of salinity on the rate of photosynthesis and abundance of some tropical phytoplankton. *Marine Biology*, *12*(3), 200–206. https://doi.org/10.1007/BF00346767

Quinlan, E. L., & Phlips, E. J. (2007). Phytoplankton assemblages across the marine to low-salinity transition zone in a Blackwater dominated estuary. *Journal of Plankton Research*, *29*(5), 401–416. https://doi.org/10.1093/plankt/fbm024

Rabalais, N. N., Turner, R. E., Díaz, R. J., & Justić, D. (2009). Global change and eutrophication of coastal waters. *ICES Journal of Marine Science*, *66*(7), 1528–1537. https://doi.org/10.1093/icesjms/fsp047

Raes, J., Letunic, I., Yamada, T., Jensen, L. J., & Bork, P. (2011). Toward molecular trait-based ecology through integration of biogeochemical, geographical and metagenomic data. *Molecular Systems Biology*, *7*(1), 473. https://doi.org/10.1038/msb.2011.6

Reed, R. H. (1984). Use and abuse of osmo-terminology. *Plant, Cell & Environment*, *7*, 165–170. https://doi.org/10.1111/1365-3040.ep11614591

Reygondeau, G., Guidi, L., Beaugrand, G., Henson, S. A., Koubbi, P., MacKenzie, B. R., Sutton, T. T., Fioroni, M., & Maury, O. (2018). Global biogeochemical provinces of the mesopelagic zone. *Journal of Biogeography*, *45*(2), 500–514. https://doi.org/10.1111/jbi.13149

Riisgård, H. U., Lüskow, F., Pleissner, D., Lundgreen, K., & López, M. Á. P. (2013). Effect of salinity on filtration rates of mussels *Mytilus* *edulis* with special emphasis on dwarfed mussels from the low-saline Central Baltic Sea. *Helgoland Marine Research*, *67*(3), 591–598. https://doi.org/10.1007/s10152-013-0347-2

Robblee, M. B., Barber, T. R., Carlson, P. R., Durako, M. J., Fourqurean, J. W., Muehlstein, L. K., Porter, D., Yarbro, L. A., Zieman, R. T., & Zieman, J. C. (1991). Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress Series*, *71*(3), 297–299. http://www.jstor.org/stable/24817304

Robinson, C., Steinberg, D. K., Anderson, T. R., Arístegui, J., Carlson, C. A., Frost, J. R., Ghiglione, J. F., Hernández-León, S., Jackson, G. A., Koppelmann, R., Quéguiner, B., Ragueneau, O., Rassoulzadegan, F., Robison, B. H., Tamburini, C., Tanaka, T., Wishner, K. F., & Zhang, J. (2010). Mesopelagic zone ecology and biogeochemistry—A synthesis. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *57*(16), 1504–1518. https://doi.org/10.1016/j.dsr2.2010.02.018

Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., Lu, M., Schile-Beers, L., Zawadzki, A., Mazumder, D., & Woodroffe, C. D. (2019). Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature*, *567*(7746), 91–95. https://doi.org/10.1038/s41586-019-0951-7

Ross, C., Warhurst, B. C., Brown, A., Huff, C., & Ochrietor, J. D. (2019). Mesohaline conditions represent the threshold for oxidative stress, cell death and toxin release in the cyanobacterium *Microcystis aeruginosa*. *Aquatic Toxicology*, *206*, 203–211. https://doi.org/10.1016/j.aquatox.2018.11.019

Rothäusler, E., Rugiu, L., & Jormalainen, V. (2018). Forecast climate change conditions sustain growth and physiology but hamper reproduction in range-margin populations of a foundation rockweed species. *Marine Environmental Research*, *141*, 205–213. https://doi.org/10.1016/j.marenvres.2018.09.014

Röthig, T., Ochsenkühn, M. A., Roik, A., van der Merwe, R., & Voolstra, C. R. (2016). Long-term salinity tolerance is accompanied by major restructuring of the coral bacterial microbiome. *Molecular Ecology*, *25*(6), 1308–1323. https://doi.org/10.1111/mec.13567

Rusch, D. B., Halpern, A. L., Sutton, G., Heidelberg, K. B., Williamson, S., Yooseph, S., Wu, D., Eisen, J. A., Hoffman, J. M., Remington, K., Beeson, K., Tran, B., Smith, H., Baden-Tillson, H., Stewart, C., Thorpe, J., Freeman, J., Andrews-Pfannkoch, C., Venter, J. E., … Venter, J. C. (2007). The sorcerer II Global Ocean sampling expedition: Northwest Atlantic through eastern tropical Pacific. *PLoS Biology*, *5*(3), e77. https://doi.org/10.1371/journal.pbio.0050077

Salazar, G., Cornejo-Castillo, F. M., Benítez-Barrios, V., Fraile-Nuez, E., Álvarez-Salgado, X. A., Duarte, C. M., Gasol, J. M., & Acinas, S. G. (2016). Global diversity and biogeography of deep-sea pelagic prokaryotes. *ISME Journal*, *10*(3), 596–608. https://doi.org/10.1038/ismej.2015.137

Salazar, G., Paoli, L., Alberti, A., Huerta-Cepas, J., Ruscheweyh, H. J., Cuenca, M., Field, C. M., Coelho, L. P., Cruaud, C., Engelen, S., Gregory, A. C., Labadie, K., Marec, C., Pelletier, E., Royo-Llonch, M., Roux, S., Sánchez, P., Uehara, H., Zayed, A. A., … Wincker, P. (2019). Gene expression changes and community turnover differentially shape the global ocean metatranscriptome. *Cell*, *179*(5), 1068–1083.e21. https://doi.org/10.1016/j.cell.2019.10.014

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

Santoro, A. E. (2010). Microbial nitrogen cycling at the saltwater–freshwater interface. *Hydrogeology Journal*, *18*(1), 187–202. https://doi.org/10.1007/s10040-009-0526-z

Sassa, C., & Hirota, Y. (2013). Seasonal occurrence of mesopelagic fish larvae on the onshore side of the Kuroshio off southern Japan. *Deep-Sea Research Part I: Oceanographic Research Papers*, *81*, 49–61. https://doi.org/10.1016/j.dsr.2013.07.008

Seddon, S., Connolly, R. M., & Edyvane, K. S. (2000). Large-scale seagrass dieback in northern Spencer Gulf, South Australia. *Aquatic Botany*, *66*(4), 297–310. https://doi.org/10.1016/S0304-3770(99)00080-7

Serrano, O., Lovelock, C. E., Atwood, T. B., Macreadie, P. I., Canto, R., Phinn, S., Arias-Ortiz, A., Bai, L., Baldock, J., Bedulli, C., Carnell, P., Connolly, R. M., Donaldson, P., Esteban, A., Ewers Lewis, C. J., Eyre, B. D., Hayes, M. A., Horwitz, P., Hutley, L. B., … Duarte, C. M. (2019). Australian vegetated coastal ecosystems as global hotspots for climate change mitigation. *Nature Communications*, *10*(1), 1–10. https://doi.org/10.1038/s41467-019-12176-8

Serrão, E. A., Kautsky, L., & Brawley, S. H. (1996). Distributional success of the marine seaweed *Fucus vesiculosus* L. in the brackish Baltic Sea correlates with osmotic capabilities of Baltic gametes. *Oecologia*, *107*(1), 1–12. https://doi.org/10.1007/BF00582229

Shearer, C. A., Descals, E., Kohlmeyer, B., Kohlmeyer, J., Marvanová, L., Padgett, D., Porter, D., Raja, H. A., Schmit, J. P., Thorton, H. A., & Voglymayr, H. (2007). Fungal biodiversity in aquatic habitats. *Biodiversity and Conservation*, *16*(1), 49–67. https://doi.org/10.1007/s10531-006-9120-z

Short, F. T., Polidoro, B., Livingstone, S. R., Carpenter, K. E., Bandeira, S., Bujang, J. S., Calumpong, H. P., Carruthers, T. J. B., Coles, R. G., Dennison, W. C., Erftemeijer, P. L. A., Fortes, M. D., Freeman, A. S., Jagtap, T. G., Kamal, A. H. M., Kendrick, G. A., Judson Kenworthy, W., La Nafie, Y. A., Nasution, I. M., … Zieman, J. C. (2011). Extinction risk assessment of the world's seagrass species. *Biological Conservation*, *144*(7), 1961–1971. https://doi.org/10.1016/j.biocon.2011.04.010

Sinha, E., Michalak, A. M., & Balaji, V. (2017). Eutrophication will increase during the 21st century as a result of precipitation changes. *Science*, *357*(6349), 405–408. https://doi.org/10.1126/science.aan2409

Skliris, N., Marsh, R., Josey, S. A., Good, S. A., Liu, C., & Allan, R. P. (2014). Salinity changes in the World Ocean since 1950 in relation to changing surface freshwater fluxes. *Climate Dynamics*, *43*(3–4), 709–736. https://doi.org/10.1007/s00382-014-2131-7

Snoeijs, P. (1999). Marine and brackish waters. *Acta Phytogeographica Suecica*, *84*, 187–212.

Steen, H. (2004). Effects of reduced salinity on reproduction and germling development in *Sargassum muticum* (Phaeophyceae, Fucales). *European Journal of Phycology*, *39*(3), 293–299. https://doi.org/10.1080/09670260410001712581

Stefanoudis, P. V., Rivers, M., Ford, H., Yashayaev, I. M., Rogers, A. D., & Woodall, L. C. (2019). Changes in zooplankton communities from epipelagic to lower mesopelagic waters. *Marine Environmental Research*, *146*, 1–11. https://doi.org/10.1016/j.marenvres.2019.02.014

Stocker, T. F., Qin, D., Plattner, G. K., Tignor, M. M. B., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V., & Midgley, P. M. (2013). *Climate change 2013—The Physical science basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Vol. *9781107057999*). Cambridge University Press. https://doi.org/10.1017/CBO9781107415324

Sunagawa, S., Coelho, L. P., Chaffron, S., Kultima, J. R., Labadie, K., Salazar, G., Djahanschiri, B., Zeller, G., Mende, D. R., Alberti, A., Cornejo-Castillo, F. M., Costea, P. I., Cruaud, C., d'Ovidio, F., Engelen, S., Ferrera, I., Gasol, J. M., Guidi, L., Hildebrand, F., … Velayoudon, D. (2015). Structure and function of the global ocean microbiome. *Science*, *348*(6237). https://doi.org/10.1126/science.1261359

Sutter, L. A., Chambers, R. M., & Perry, J. E. (2015). Seawater intrusion mediates species transition in low salinity, tidal marsh vegetation. *Aquatic Botany*, *122*, 32–39. https://doi.org/10.1016/j.aquabot.2015.01.002

Sutton, T. T., Clark, M. R., Dunn, D. C., Halpin, P. N., Rogers, A. D., Guinotte, J., Bograd, S. J., Angel, M. V., Perez, J. A. A., Wishner, K., Haedrich, R. L., Lindsay, D. J., Drazen, J. C., Vereshchaka, A., Piatkowski, U., Morato, T., Błachowiak-Samołyk, K., Robison, B. H., Gjerde, K. M., … Heino, M. (2017). A global biogeographic classification of the mesopelagic zone. *Deep-Sea Research Part I: Oceanographic Research Papers*, *126*, 85–102. https://doi.org/10.1016/j.dsr.2017.05.006

Swart, N. C., Gille, S. T., Fyfe, J. C., & Gillett, N. P. (2018). Recent Southern Ocean warming and freshening driven by greenhouse gas emissions and ozone depletion. *Nature Geoscience*, *11*(11), 836–841. https://doi.org/10.1038/s41561-018-0226-1

Takolander, A., Leskinen, E., & Cabeza, M. (2017). Synergistic effects of extreme temperature and low salinity on foundational macroalga *Fucus vesiculosus* in the northern Baltic Sea. *Journal of Experimental Marine Biology and Ecology*, *495*, 110–118. https://doi.org/10.1016/j.jembe.2017.07.001

Tanabe, Y., Hodoki, Y., Sano, T., Tada, K., & Watanabe, M. M. (2018). Adaptation of the freshwater bloom-forming cyanobacterium *Microcystis aeruginosa* to brackish water is driven by recent horizontal transfer of sucrose genes. *Frontiers in Microbiology*, *9*(JUN), 1150. https://doi.org/10.3389/fmicb.2018.01150

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, *93*, 485–498. https://doi.org/10.1175/BAMS-D-11-00094.1

Tebaldi, C., Debeire, K., Eyring, V., Fischer, E., Fyfe, J., Friedlingstein, P., Knutti, R., Lowe, J., O'Neill, B., Sanderson, B., Van Vuuren, D., Riahi, K., Meinshausen, M., Nicholls, Z., Tokarska, K., Hurtt, G., Kriegler, E., Meehl, G., Moss, R., … Ziehn, T. (2021). Climate model projections from the Scenario Model Intercomparison Project (ScenarioMIP) of CMIP6. *Earth System Dynamics*, *12*(1), 253–293. https://doi.org/10.5194/esd-12-253-2021

Telesh, I., Schubert, H., & Skarlato, S. (2013). Life in the salinity gradient: Discovering mechanisms behind a new biodiversity pattern. *Estuarine, Coastal and Shelf Science*, *135*, 317–327. https://doi.org/10.1016/J.ECSS.2013.10.013

Thayer, G. W., Murphey, P. L., & LaCroix, M. W. (1994). Responses of plant communities in western Florida bay to the die-off of seagrasses. *Bulletin of Marine Science*, *54*(3), 718–726.

Thrush, S. F., Hewitt, J. E., Cummings, V. J., Ellis, J. I., Hatton, C., Lohrer, A., & Norkko, A. (2004). Muddy waters: Elevating sediment input to coastal and estuarine habitats. *Frontiers in Ecology and the Environment*, *2*(6), 299–306. https://doi.org/10.1890/1540-9295(2004)002[0299:MWESIT]2.0.CO;2

Touchette, B. W. (2007). Seagrass-salinity interactions: Physiological mechanisms used by submersed marine angiosperms for a life at sea. *Journal of Experimental Marine Biology and Ecology*, *350*(1–2), 194–215. https://doi.org/10.1016/j.jembe.2007.05.037

van der Merwe, R., Röthig, T., Voolstra, C. R., Ochsenkühn, M. A., Lattemann, S., & Amy, G. L. (2014). High salinity tolerance of the Red Sea coral *Fungia granulosa* under desalination concentrate discharge conditions: An in situ photophysiology experiment. *Frontiers in Marine Science*, *1*. https://doi.org/10.3389/fmars.2014.00058

Velasco, J., Gutiérrez-Cánovas, C., Botella-Cruz, M., Sánchez-Fernández, D., Arribas, P., Carbonell, J. A., Millán, A., & Pallarés, S. (2019). Effects of salinity changes on aquatic organisms in a multiple stressor context. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *374*(1764), 20180011. https://doi.org/10.1098/rstb.2018.0011

Villarino, E., Watson, J. R., Jönsson, B., Gasol, J. M., Salazar, G., Acinas, S. G., Estrada, M., Massana, R., Logares, R., Giner, C. R., Pernice, M. C., Olivar, M. P., Citores, L., Corell, J., Rodríguez-Ezpeleta, N., Acuña, J. L., Molina-Ramírez, A., González-Gordillo, J. I., Cózar, A., … Chust, G. (2018). Large-scale ocean connectivity and planktonic body size. *Nature Communications*, *9*(1), 1–13. https://doi.org/10.1038/s41467-017-02535-8

Wang, W., Yan, Z., You, S., Zhang, Y., Chen, L., & Lin, G. (2011). Mangroves: Obligate or facultative halophytes? A review. *Trees*, *25*(6), 953–963. https://doi.org/10.1007/s00468-011-0570-x

Westra, S., Fowler, H. J., Evans, J. P., Alexander, L. V., Berg, P., Johnson, F., Kendon, E. J., Lenderink, G., & Roberts, N. M. (2014). Future changes to the intensity and frequency of short-duration extreme rainfall. *Reviews of Geophysics*, *52*(3), 522–555. https://doi.org/10.1002/2014RG000464

Williams, S. L. (1990). Experimental studies of Caribbean seagrass bed development. *Ecological Monographs*, *60*(4), 449–469. https://doi.org/10.2307/1943015

Wilson, S. S., & Dunton, K. H. (2018). Hypersalinity during regional drought drives mass mortality of the seagrass *Syringodium filiforme* in a subtropical lagoon. *Estuaries and Coasts*, *41*(3), 855–865. https://doi.org/10.1007/s12237-017-0319-x

Yang, S. C., Shih, S. S., Hwang, G. W., Adams, J. B., Lee, H. Y., & Chen, C. P. (2013). The salinity gradient influences on the inundation tolerance thresholds of mangrove forests. *Ecological Engineering*, *51*, 59–65. https://doi.org/10.1016/j.ecoleng.2012.12.049

Yuan, J., Ding, W., Liu, D., Kang, H., Xiang, J., & Lin, Y. (2016). Shifts in methanogen community structure and function across a coastal marsh transect: Effects of exotic *Spartina alterniflora* invasion. *Scientific Reports*, *6*(1), 1–12. https://doi.org/10.1038/srep18777

Ziegler, M., Anton, A., Klein, S. G., Rädecker, N., Geraldi, N. R., Schmidt-Roach, S., Saderne, V., Mumby, P. J., Cziesielski, M. J., Martin, C., Frölicher, T. L., Pandolfi, J. M., Suggett, D. J., Aranda, M., Duarte, C. M., & Voolstra, C. R. (2021). Integrating environmental variability to broaden the research on coral responses to future ocean conditions. *Global Change Biology*, *27*(21), 5532–5546. https://doi.org/10.1111/gcb.15840

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