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Impacts of Climate Change on Marine Foundation Species

Thomas Wernberg,[1,2] Mads S. Thomsen,[3,4] Julia K. Baum,[5,*] Melanie J. Bishop,[6,*] John F. Bruno,[7,*] Melinda A. Coleman,[8,*] Karen Filbee-Dexter,[1,2,*] Karine Gagnon,[2,*] Qiang He,[9,*] Daniel Murdiyarso,[10,11,*] Kerrylee Rogers,[12,*] Brian R. Silliman,[13,*] Dan A. Smale,[14,*] Samuel Starko,[1,*] and Mathew A. Vanderklift[15,*]

[1] Oceans Institute and School of Biological Sciences, University of Western Australia, Crawley, Western Australia, Australia; email: thomas.wernberg@uwa.edu.au

[2] Flødevigen Research Station, Institute of Marine Research, His, Norway

[3] Marine Ecology Research Group, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

[4] Department of Ecoscience, Aarhus University, Roskilde, Denmark

[5] Department of Biology, University of Victoria, Victoria, British Columbia, Canada

[6] School of Natural Sciences, Macquarie University, Macquarie Park, New South Wales, Australia

[7] Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA

[8] National Marine Science Centre, New South Wales Department of Primary Industries, Coffs Harbour, New South Wales, Australia

[9] Coastal Ecology Lab, MOE Key Laboratory for Biodiversity Science and Ecological Engineering, School of Life Sciences, Fudan University, Shanghai, China

[10] Center for International Forestry Research–World Agroforestry (CIFOR-ICRAF), Bogor, Indonesia

[11] Department of Geophysics and Meteorology, IPB University, Bogor, Indonesia

[12] School of Earth, Atmospheric, and Life Sciences, University of Wollongong, Wollongong, New South Wales, Australia

[13] Nicholas School of the Environment, Duke University, Durham, North Carolina, USA

[14] Marine Biological Association of the United Kingdom, Plymouth, United Kingdom

[15] Indian Ocean Marine Research Centre, Commonwealth Scientific and Industrial Research Organisation (CSIRO), Crawley, Western Australia, Australia

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*These authors are listed alphabetically

Keyword

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Abstract

Marine foundation species are the biotic basis for many of the world's coastal ecosystems, providing structural habitat, food, and protection for myriad plants and animals as well as many ecosystem services. However, climate change poses a significant threat to foundation species and the ecosystems they support. We review the impacts of climate change on common marine foundation species, including corals, kelps, seagrasses, salt marsh plants, mangroves, and bivalves. It is evident that marine foundation species have already been severely impacted by several climate change drivers, often through interactive effects with other human stressors, such as pollution, overfishing, and coastal development. Despite considerable variation in geographical, environmental, and ecological contexts, direct and indirect effects of gradual warming and subsequent heatwaves have emerged as the most pervasive drivers of observed impact and potent threat across all marine foundation species, but effects from sea level rise, ocean acidification, and increased storminess are expected to increase. Documented impacts include changes in the genetic structures, physiology, abundance, and distribution of the foundation species themselves and changes to their interactions with other species, with flow-on effects to associated communities, biodiversity, and ecosystem functioning. We discuss strategies to support marine foundation species into the Anthropocene, in order to increase their resilience and ensure the persistence of the ecosystem services they provide.

1. INTRODUCTION

Marine ecosystems provide vast benefits to human societies, including food and raw materials, nutrient cycling, climate regulation, and cultural and spiritual connections (Barbier et al. 2011, Filbee-Dexter et al. 2022b). The capacity of marine ecosystems to deliver these services depends on the species that inhabit them, their ecological functions, and the processes that control these functions. Human activities increasingly affect physical, chemical, and biological processes at local, regional, and planetary scales (Duarte 2014). These impacts alter the performance of species and the strength and direction of biological interactions, which in turn rearranges ecological communities (He & Silliman 2019, Pinsky et al. 2020, Smith et al. 2023, Vergés et al. 2014), with serious implications for the provision of benefits from Earth's ecosystems (Cooley et al. 2022a, Filbee-Dexter & Wernberg 2018, Smith et al. 2021).

Marine ecologists have long recognized that some species are disproportionately more important to determining overall community structure than others (Möbius 1877). Dayton (1972) coined the term foundation species to describe "critical species which define much of the structure of a community" (p. 85). While he included in this category any species with large effects, including both herbivores and carnivores, Bruno & Bertness (2001) later redefined foundation species as those that have a large effect on community structure by modifying environmental conditions, species interactions, and resource availability through their presence rather than their actions (e.g., kelps, grasses, mussels, and corals). Other authors have called such species structural species (Huston 1994), autogenic ecosystem engineers (Jones et al. 1997), keystone structures (Tews et al. 2004) and habitat-forming species (Thomsen et al. 2010).

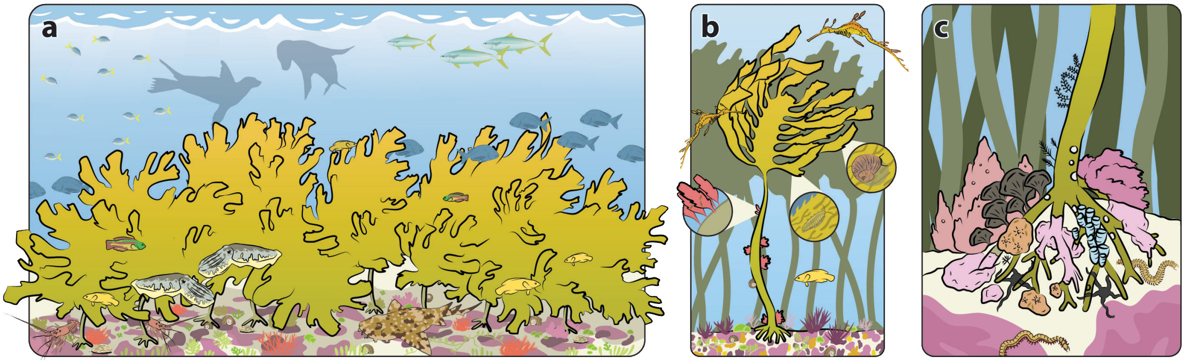

Figure 1

Foundation species support associated species and communities. Foundation species affect communities through their presence, not their actions. They define ecosystems by providing a physical framework for associated species, and these community-wide effects occur across multiple scales. For example, at the seascape scale (panel *a*), a kelp forest provides a unique environment and habitat for large, highly mobile species, including mammals, fish, cuttlefish, and other invertebrates. On a smaller scale, individual kelp (panel *b*) are home to epiphytes, small fish, and invertebrates, and even specific parts of the kelp, such as the holdfast (panel *c*), create a unique physical structure that is home to rich and sometimes specialized communities.

Foundation species facilitate the presence of associated species and underpin entire ecosystems by creating biogenic structures that, in turn, modify environmental conditions, offer refuge from predation, and ameliorate environmental stress. Unlike keystone species, which have a disproportionate impact on the structure of an ecosystem relative to their abundance (i.e., they represent a small proportion of community biomass) (Power et al. 1996), foundation species play a crucial role in shaping the structure and function of entire ecosystems by providing the physical framework that supports other species (**Figure 1**). Consequently, they are among the most important components of marine communities (Dayton 1972). Indeed, experimental removal or wholesale loss of foundation species can cause the loss of entire suites of species (Ling 2008, Silliman et al. 2011). The most common and widely known marine foundation species and their biogenic structures include coral reefs, kelp forests, seagrass meadows, salt marshes, mangrove forests, and bivalve reefs (**Table 1**).

Climate change has already substantially altered the marine environment, and these changes will continue into the foreseeable future. Anthropogenic greenhouse gas emissions drive long-term changes in environmental conditions such as altered circulation patterns, higher air and sea temperatures, reduced sea ice cover, higher sea levels, and lower pH, as well as increased frequency, intensity, or duration of extreme events such as heatwaves, storms, precipitation, and floods (IPCC 2021, 2022). These changes impact physical and chemical systems that support marine communities, causing a range of complex biological responses (**Figure 2**) and impacts across organizational levels, habitats, ecosystems, and biogeographical regions (Bellard et al. 2012, Stenseth et al. 2002, Walther et al. 2002). Whereas short-term extreme events typically have negative effects on species and communities (Smale et al. 2019), longer-term changes in mean conditions can have variable effects on foundation species, ranging from negative to neutral or even positive effects, depending on the context (Duarte et al. 2018, Smale 2020). Additionally, climate change can interact—often in complex synergistic or antagonistic ways (Crain et al. 2008, Darling & Côté 2008)—with existing stressors such as pollution and overfishing, driving changes in foundation species and losses of valuable ecosystem services (e.g., Baum et al. 2023, Filbee-Dexter & Wernberg 2018, He & Silliman 2019). Foundation species and the ecosystems they underpin are increasingly recognized as being under threat (**Figure 3**), and understanding these complex interactions is crucial for

Table 1 Overview of key marine foundation species and their approximate areal extents, major climate and nonclimate stresses, estimated rates of change, and economic valuations

Foundation species/ecosystem	Brief description	Global extent	Major climate drivers of change	Major nonclimate drivers of change	Rate of change	Estimated value
Coral reefs	Marine subtidal reef-building stony corals, ~750 species worldwide (Muir & Pichon 2019)	154,049–301,110 km^2 (Li et al. 2020) 284,000 km^2 (Davidson et al. 2019, McKenzie et al. 2020)	Warming; more prolonged, intense, and frequent marine heatwaves; secondary climate drivers include ocean acidification, sea level rise, and stronger storms (IPCC 2022)	Turbidity, sedimentation, nutrient enrichment, pollution, fishing, diseases, invasive species, plastics	50% of coral cover lost since 1870, accelerating loss in recent decades due to climate change exacerbating other drivers (Eddy et al. 2021) 50–75% decline in coral cover over the last 30–40 years (Bruno et al. 2019)	US\$36 billion y^{-1} in reef-related tourism (Spalding et al. 2017). >US\$4 billion y^{-1} in storm protection by living reefs (Beck et al. 2018). US\$1.8 billion y^{-1} in flood risk reduction in the United States by coral reefs (Reguero et al. 2021) US\$10.02 × 10^{12} y^{-1} (Davidson et al. 2019)
Kelp forests	Large subtidal brown seaweeds, >100 species worldwide (Bolton 2010)	2,033,936 km^2 (Jayathilake & Costello 2021) 1.70 and 2.57 million km^2 of Laminariales and Fucales, respectively (Fragkopoulou et al. 2022)	Warming, stronger heatwaves	Overfishing of predators causing overgrazing by sea urchins; turbidity; sedimentation; nutrient enrichment; pollution; urban development	Declines in 61% of time series over 20 years (Wernberg et al. 2019) ~2% decline per year (Krumhansl et al. 2016)	US\$500,000–1,000,000 per kilometer of coastline per year (Filbee-Dexter & Wernberg 2018) 620,000 km coastline globally × 38% with kelp forests × US\$750 million km^{-1} = US\$1.7 × 10^{11} y^{-1}
Seagrass meadows	Intertidal and subtidal vascular flowering marine plants, ~60 species worldwide (Short et al. 2007)	177,000–600,000 km^2 (McKenzie et al. 2020) 788,000 km^2 (Davidson et al. 2019) 1,646,788 km^2 (Jayathilake & Costello 2018)	Warming, stronger heatwaves, stronger storms (wave damage and rainfall-induced turbidity)	Turbidity, sedimentation, nutrient enrichment, coastal development, aquaculture	19% loss of surveyed area since 1880 (Dunic et al. 2021) 7% per year (Waycott et al. 2009)	No global valuation estimates (see table 3 in Dewsbury et al. 2016) for values from local studies/single-ecosystem services US\$2.28 × 10^{12} y^{-1} (Davidson et al. 2019)
Salt marshes	Intertidal and supratidal vascular plants and shrubs, ~600 species worldwide (Silliman 2014)	2.2–40 Mha (Pendleton et al. 2012) 5,495,089 ha (McOwen et al. 2017) 55,000 km^2 (Davidson et al. 2019, McKenzie et al. 2020)	Warming, extreme drought, sea level rise	Overgrazing, invasive species, nutrient pollution, urban development, conversion to agriculture	Global net salt marsh loss of 1,452.84 km^2 from 2000 to 2019 (Campbell et al. 2022)	US\$15–15,000 $acre^{-1}$ (Barbier et al. 2011) US\$1.07 × 10^{12} y^{-1} (Davidson et al. 2019)

(*Continued*)

Table 1 (*Continued*)

Foundation species/ecosystem	Brief description	Global extent	Major climate drivers of change	Major nonclimate drivers of change	Rate of change	Estimated value
Mangrove forests	Intertidal vascular trees and shrubs adapted to high salinity, ~70 species worldwide (Sandilyan & Kathiresan 2012)	138,000 km^2 (Davidson et al. 2019) ~147,000 km^2 (Bunting et al. 2022) 152,361 km^2 (McKenzie et al. 2020)	Stronger storms, sea level rise; warming and stronger heatwaves sometimes inhibit and sometime facilitate mangroves	Burning, cutting, urbanization, aquaculture, agriculture development; sedimentation may inhibit or facilitate mangroves	Net mangrove loss of 5,807.1 km^2 from 1996 to 2016 (Campbell et al. 2022)	US$2.68 $\times 10^{12}$ y^{-1} (Davidson et al. 2019)
Bivalve reefs	Aggregations of oysters and/or mussels, ~70 oyster species (Sigwart et al. 2021) and ~400 mussel species (Mytilidae) (WoRMS Ed. Board 2023) worldwide, very few of which are reef builders	Unknown but extensive	Warming, stronger heatwaves, salinity changes from altered precipitation, ocean acidification (evidence limited to aquaculture to date), warming-induced diseases	Overharvesting; changes in salinity, sedimentation, hypoxia, and flow due to catchment and shoreline modification, disease, and pollution (Beck et al. 2011)	~85% loss of oyster reefs globally since industrialization (Beck et al. 2011), similar loss likely for mussel beds	Conservatively, US$5,500–99,000 ha^{-1} y^{-1} (Grabowski et al. 2012)
Lesser-known marine foundation species	Rockweeds, sponges, bryozoans, cold-water corals, hydroids, gardening polychaetas, maerl beds, and floating *Sargassum*	Unknown but extensive and common from the intertidal zone to the deep sea, across all biogeographical realms, and from polar to tropical latitudes	Warming, stronger heatwaves, ocean acidification (particularly for calcareous species), sea level rise (particularly for intertidal polychaetas)	Eutrophication, algal epiphytes, trawling, resource extractions (particularly for deep-water sponges, hydroids, bryozoans, and corals)	Unknown/undescribed	Unknown/undescribed

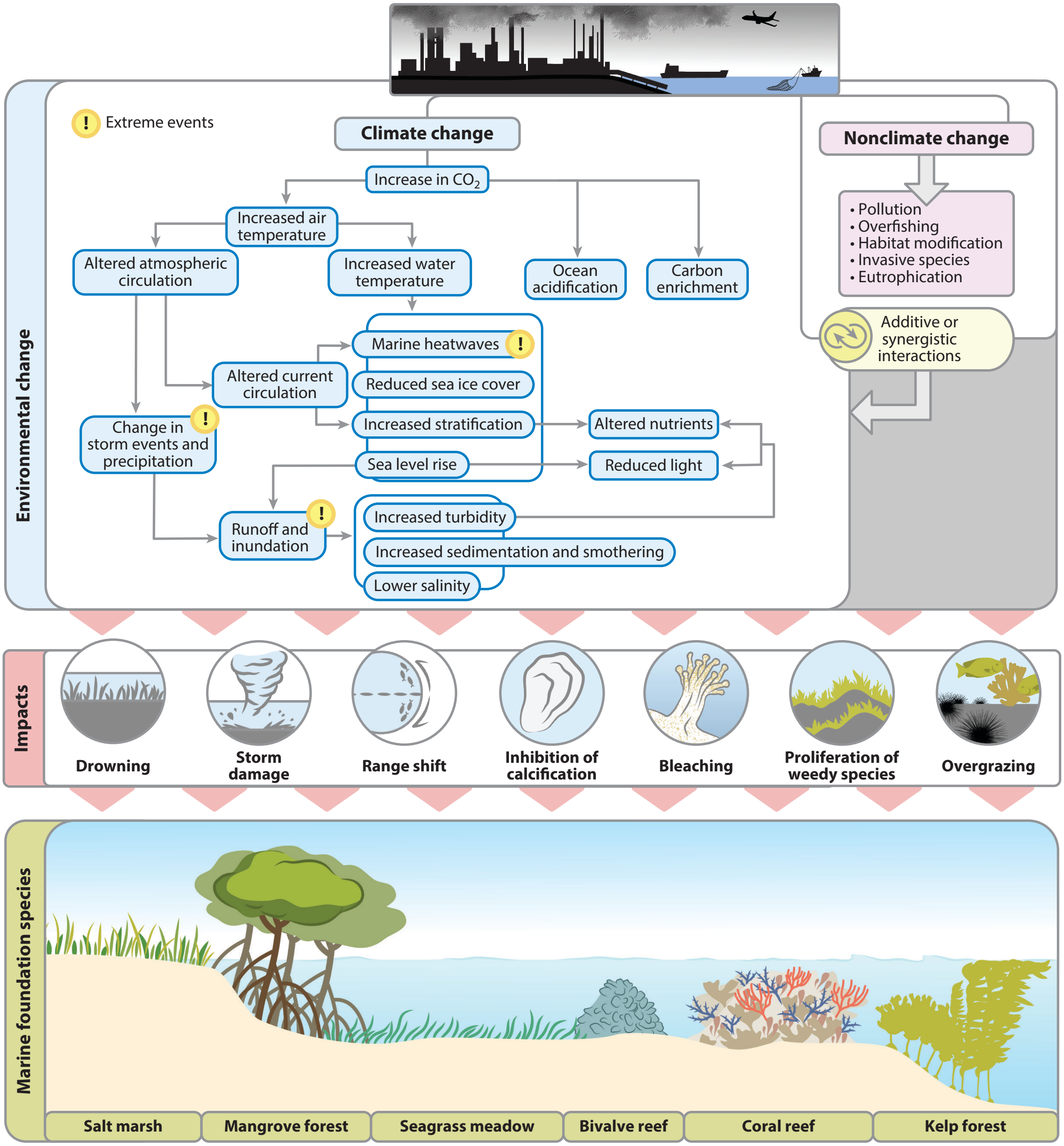

Figure 2

Humans cause environmental changes that drive impacts to foundation species. In the Anthropocene, human greenhouse gas emissions and other activities cause complex climate and nonclimate changes to the environment. These changes interact to drive a range of physical and biological impacts to foundation species. Impacts and foundation species are representative and not to scale.

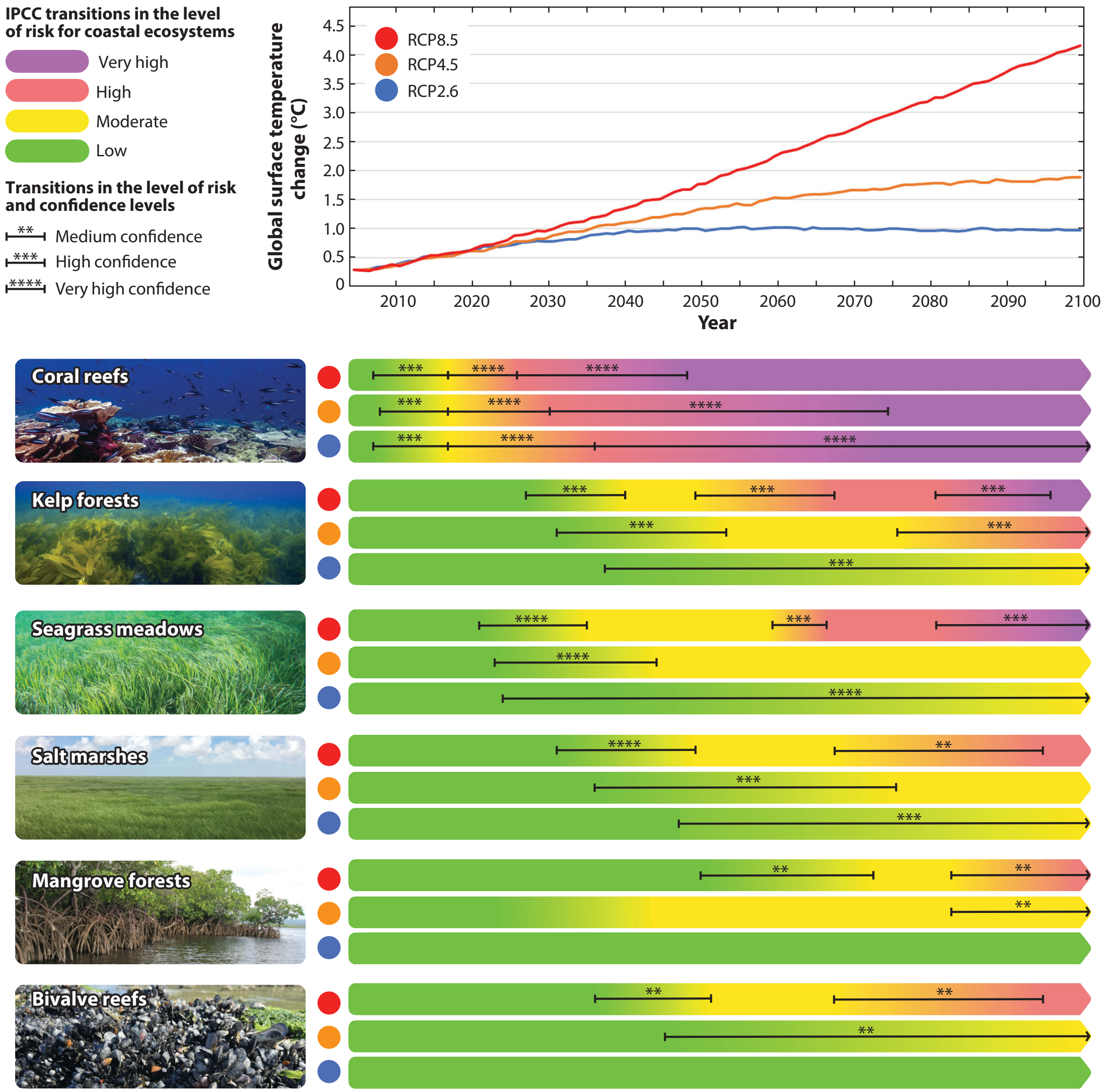

Figure 3

Marine foundation species are at risk of climate-mediated impact and collapse. The trajectory of global surface temperatures will depend on the global greenhouse gas emission scenario [Representative Concentration Pathway (RCP)]. Ranked top to bottom according to overall risk, all common marine foundation species are at moderate risk within the next ~15 years following RCP8.5. Risks to bivalve reefs are based on threats to rocky reefs. Data are from the Intergovernmental Panel on Climate Change (IPCC) (Collins et al. 2013, Cooley et al. 2022b); for photo credits, see the captions for **Figures 4*a*–9*a***, respectively.

managing their health and resilience. Here, we review knowledge of the impacts of climate-driven threats to marine foundation species. Our goal is to provide an overview of the current state and future of key marine foundation species and to identify areas for future research and management to ensure their persistence and functioning under climate change.

2. GLOBAL AND LOCAL STRESSORS OF MARINE FOUNDATION SPECIES

Marine foundation species are pervasive throughout the coastal zone, and they are under immense and increasing pressure from climate change superimposed onto other anthropogenic stressors (**Figure 3**). Over the past few decades, climate changes have caused substantial declines in all foundation species and their associated communities, resulting in the loss of ecosystem services valued in the billions regionally and trillions globally each year (**Table 1**).

Background warming and heatwaves have caused poleward range shifts in many taxa and bioregions, as warming results in slow colonization of new poleward regions but is offset by rapid loss from their equatorial ranges (Bates et al. 2014, Kitchel et al. 2022, Poloczanska et al. 2013). However, loss is inevitable when new thermal conditions exceed the maximum temperature tolerance of species and poleward colonization is restricted by barriers such as landscape features, countercurrents, low and poor propagule production and dispersal traits, human-established barriers, or a lack of other necessary resources or conditions. Such wholesale community range shifts have already been observed for seaweed (Wernberg et al. 2011, 2016), mangroves (Saintilan et al. 2014), and corals (Precht & Aronson 2004) and will most likely ultimately be reported for all foundation species. Furthermore, in addition to poleward range shifts, all community dynamics within ranges will experience myriad changes, as temperature-dependent physiological processes such as metabolism, growth, and reproduction will modify all community-scale competitive hierarchies and consumer interactions (e.g., Kordas et al. 2011). Superimposed onto gradual warming are episodic short heatwaves that accelerate range shifts and can cause sudden dramatic loss of marine foundation species. Such dramatic short-term loss of entire seascape structures over only a few months has already been observed for kelps, fucoids, and seagrasses (Kendrick et al. 2019, Thomsen et al. 2019, Wernberg et al. 2016) and is a major driver of increasing bleaching events on coral reefs (Donovan et al. 2021). Temperature-dependent impacts from continued gradual warming and future longer and stronger heatwaves will likely accelerate dramatic reshuffling of marine foundation species in the near future (Oliver et al. 2019).

Climate-driven heatwaves and sea level rise can also cause vertical range shifts, as desiccation stress, light, turbidity, sedimentation, and wave action can change dramatically over a few vertical meters in the intertidal and upper subtidal zones (Whalen et al. 2023). Sea level rise has had the strongest effects on intertidal foundation species, which have been pushed upward on the shore. Here, terrestrial habitats have typically been drowned, and marine foundation species have been outcompeted at their lower vertical distribution levels. Yet these shifts are constrained, as most of these marine species have experienced reduced vertical ranges because human structures built to protect human-dominated landscapes, agriculture, and built environments—including causeways, seawalls, and levees—now limit landward migration of marine and coastal foundation species (Doody 2004, Pontee et al. 2022).

Ocean acidification, driven by anthropogenic CO_2 emissions, differs from the relatively obvious ecological effects of warming, heatwaves, and sea level rise, as effects have rarely been directly observable in natural ecosystems. Instead, they have been inferred from comparative experiments along pH gradients near hydrothermal vents or from laboratory experiments (Doney et al. 2020, Leung et al. 2022). Typically, these studies suggest that calcifying foundation species (corals, mussels, oysters, and coralline algae) will be disproportionately inhibited because more energy will be required to build and maintain calcareous shell structures.

Strong storms have had devastating ecological impacts on marine foundation species, particularly those with large, rigid, upright forms with large drag and high stiffness, such as mangroves and upright corals (Madden et al. 2023, Taillie et al. 2020). Although attribution of storminess to climate change is highly complicated and often debated, recent studies suggest that storms in many areas are becoming stronger and more frequent (Emanuel 2020, Moon et al. 2019), and if this trend continues, uprooting and breakage of marine foundation species will accelerate in the near future.

Climate change stressors, like temperature, have well-described effects on marine foundation species, but interactive effects between climate and nonclimate stressors remain a critical knowledge gap. For example, understanding interactive effects between climate change and habitat modification, invasive species, pollution, eutrophication, and fisheries will be critical to predict the true impact of climate change on foundation species. Indeed, meta-analyses have shown that additive and synergistic (elevated) effects between co-occurring stressors are common in marine ecosystems (Crain et al. 2008, Darling & Côté 2008). For example, heatwaves and elevated turbidity and riverine inputs in concert have caused massive losses of seagrass (Kendrick et al. 2019) and decimated giant kelp forests (Tait et al. 2021), and ocean acidification may increase impacts from stronger storms (Hudson et al. 2023).

Marine foundation species impacted by climate change are often replaced by alternative foundation species or smaller, fast-growing weedy species, or they are transformed in ways that provide little to no cover of sessile species. Examples of the substitution of one primary foundation species with an alternative foundation species include conversions of large bull kelp forests to beds of smaller fucoids and invasive Japanese kelp (Thomsen et al. 2019), mussel-dominated reefs to oyster-dominated reefs (Kochmann et al. 2008), or oysters to mangroves (McClenachan et al. 2021). Elsewhere, often immediately following the loss of foundation species or in systems with additional human stressors (such as eutrophication), primary foundation species may instead be replaced by smaller weedy species, such as small turf-forming and filamentous seaweed that can replace kelp (Filbee-Dexter & Wernberg 2018), seagrass (Thomsen et al. 2012), and corals (Anton et al. 2020). Finally, in extreme cases, kelp forests, seagrass meadows, and salt marshes can collapse into structurally depauperate states such as bare rock or mudflats (Ling 2008, Silliman et al. 2005). Many of these new habitat configurations exhibit positive feedback mechanisms and hysteresis that may, in concert with the continued increase of climate change stressors, prevent recovery of foundation species (Filbee-Dexter & Wernberg 2018).

3. CORAL REEFS

Coral reefs are biogenic calcium carbonate accretions generated by scleractinian stony corals distributed throughout the tropics. Tropical coral reefs are especially vulnerable to climate change (Cooley et al. 2022a) (**Figure 3**) due to the high thermal sensitivity of corals. Temperature stress as little as 1°C above local background temperatures can disrupt the vital partnership between the coral animal and its photosynthetic endosymbionts (Symbiodiniaceae), causing bleaching as the coral skeleton becomes visible following symbiont expulsion (Glynn 1993). Prolonged temperature stress often leads to coral mortality (Hughes et al. 2017) (**Figure 4**). Many coral reefs also have a long history of local human impacts, ranging from fishing to coastal development, and these stressors, coupled with climate change, have already resulted in significant coral reef degradation globally. It is estimated that ~50% of all coral cover has already been lost, and current IPCC projections suggest that almost all corals could be lost with warming of 1.5–2°C (Cooley et al. 2022a) (**Table 1**).

Marine heatwaves amplified by anthropogenic global warming now pose the greatest threat to coral reefs. Coral mass mortality events were first documented and attributed to anthropogenic warming in the 1980s in the Caribbean and eastern Pacific (e.g., Glynn 1993). Mass bleaching became more common in the 1990s, and in 1998, the first global bleaching event caused widespread losses (Aronson et al. 2002, Baird & Marshall 1998, Bruno et al. 2001). A second global coral

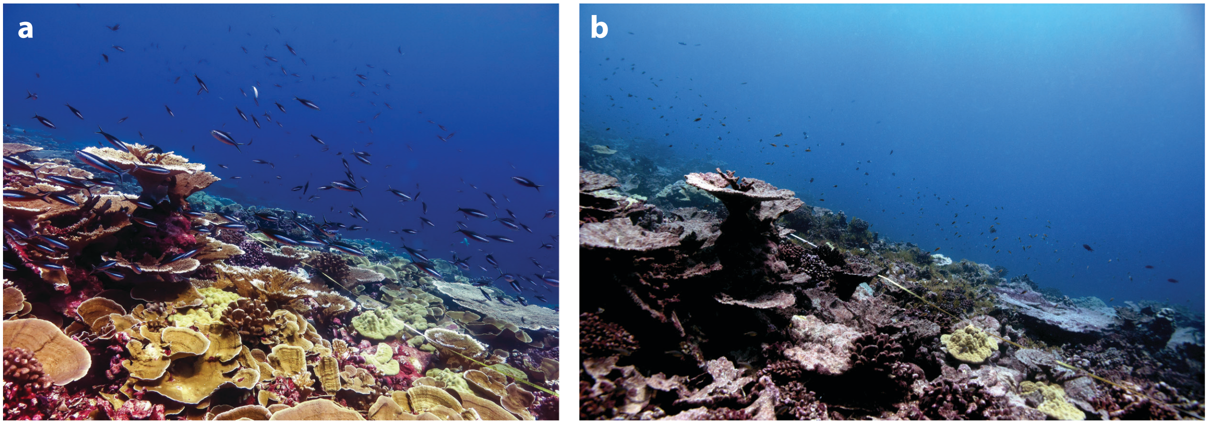

Figure 4

Pristine versus climate-impacted coral reefs. Shown is a reef with mixed scleractinian species (*a*) before and (*b*) after a marine heatwave caused coral bleaching in Kiritimati. Photos in panels *a* and *b* by K. Cox and K. Tietjen, respectively, and adapted with permission from Baum et al. (2023) (CC BY-NC 4.0).

bleaching event followed in 2010. The 2014–2017 global coral bleaching event was the most prolonged and widespread on record, with losses occurring on some of the world's best-managed (e.g., the Great Barrier Reef; Hughes et al. 2017) and most remote (e.g., the Chagos Archipelago; Sheppard et al. 2020) coral reefs. At its epicenter, the central equatorial ocean, both Jarvis Island and Kiritimati Atoll sustained more than 25 degree heating weeks, a magnitude not previously thought likely to occur until the mid-twenty-first century (Hoegh-Guldberg 2011). Both reefs suffered extensive coral mortality (~90%; Baum et al. 2023). The persistence of the world's coral reefs is jeopardized not only by the increased intensity and duration of marine heatwaves but also by their increasing frequency, which leaves insufficient time for coral recovery between successive disturbances (Hughes et al. 2018). Additionally, over longer timescales, ocean acidification, sea level rise, and other climate change–related environmental changes will further jeopardize coral populations and reef habitats (Cooley et al. 2022a).

Ocean warming is not only driving massive losses in living coral cover but also significantly altering the composition of coral communities. Species sensitive to temperature extremes are being replaced by more thermally tolerant taxa (Loya et al. 2001, Selig et al. 2010). The resulting change in coral species composition may increase resilience, but it also alters ecosystem processes, as low-cover reefs dominated by weedy taxa may be less susceptible to heatwaves but are not functionally equivalent to pristine reefs. Additionally, continued warming (and other threats) could wipe out even these survivors. Similarly, in some locations (e.g., much of the Caribbean), the functional role of corals is being fulfilled by other habitat-forming taxa that are replacing corals as the dominant space holder of tropical reefs. Seaweeds, sponges, and upright gorgonians provide microhabitat that can attract and facilitate reef fishes and invertebrates. Although these climate change winners probably benefit reef biodiversity, they do not appear to be functionally equivalent to corals in terms of habitat provision, and they will not form reef frameworks over thousands of years via deposition of calcium carbonate skeletons, as hard corals have.

Coral reefs support exceptionally high biodiversity (an estimated 25% of all marine species) despite covering less than 0.1% of the ocean's surface. As such, declines in living coral cover and habitat complexity have major impacts on the abundance, composition, and richness of associated communities. Impacts of coral loss on fishes are especially well documented (Magel et al.

2020). Following the Kiritimati bleaching in 2015–2016, overall reef fish abundance dropped by half, but most functional groups had recovered within two years, suggesting that fishes had simply temporarily relocated to cooler, deeper waters (Magel et al. 2020). However, corallivore numbers remained depressed following the mass bleaching event. Presumably there were also knock-on effects on numerous invertebrate taxa, but these remain largely unexplored. Coral mass mortality can lead to a variety of outcomes, including compositional shifts and spatial homogenization of the taxonomic and functional richness of fishes (Richardson et al. 2018), rapid recovery and relatively minor impacts despite the collapse of dense coral populations (Wismer et al. 2019), spatial mismatch (of coral and fish declines) (Wismer et al. 2019), and increased herbivorous fish biomass following mass bleaching and macroalgal blooms (Lindahl et al. 2001). Clearly, the indirect effects of coral loss on other reef inhabitants are context dependent, species specific, and complex. Beyond biodiversity loss, millions of people depend on healthy coral populations for jobs and food via fisheries and tourism (Spalding et al. 2017) and for protection from storms and waves (Harris et al. 2018).

Unfortunately, corals have limited capacity to move or adapt at the scale or pace required under current climate change. Although the movement of reef fishes and corals into warming areas previously dominated by kelp ecosystems has been documented along some continental margins (Vergés et al. 2014), overall, the potential for corals to shift their ranges is very limited (Madin et al. 2016). Moreover, modeling studies suggest that the adaptive capacity of coral symbionts is outpaced by warming under high-emission scenarios, although corals shifting to more thermally tolerant symbionts can delay or prevent widespread coral mortality under Representative Concentration Pathway 2.6 (RCP2.6) and RCP4.5 (Logan et al. 2021). While identifying climate refugia has gained traction in coral reef management (Beyer et al. 2018), recent studies caution that such efforts will likely only be effective in the short term, with most local refugia being lost even at planetary warming of 1.5°C (Dixon et al. 2022).

4. KELP FORESTS

Kelp forests are formed by large brown seaweeds (macroalgae), predominantly from the order Laminariales (**Figure 5**) (Wernberg & Filbee-Dexter 2019). These ecosystems are among the most abundant and productive coastal ecosystems in the world (Pessarrodona et al. 2022)

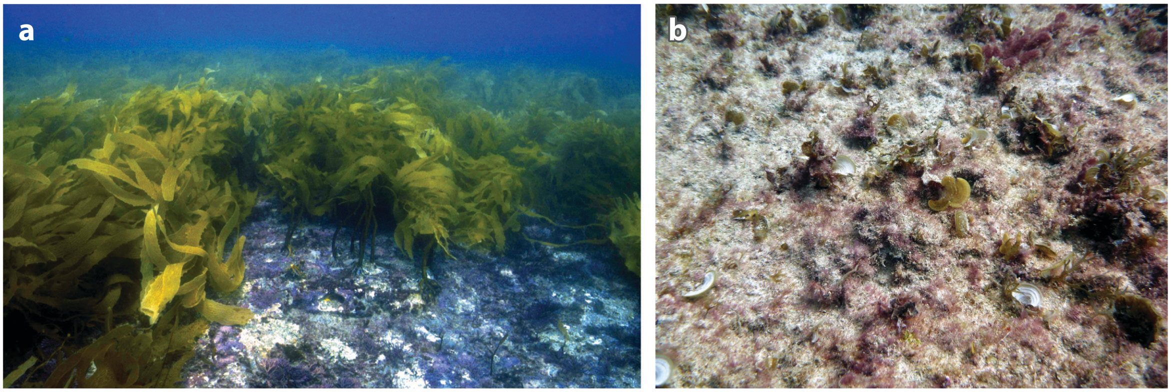

Figure 5

Pristine versus climate-impacted kelp forests. Shown is an *Ecklonia radiata* forest (*a*) before and (*b*) after a severe marine heatwave in Western Australia. Photos by T. Wernberg.

(**Table 1**) but are also considered to be the most vulnerable temperate marine ecosystems to climate change (Cooley et al. 2022a) (**Figure 3**). As most kelps live only a few years or less, kelp forests respond quickly to the environment, leading to rapid changes in their structure, function, and extent (e.g., Krumhansl et al. 2016).

Kelps are cool-water species found mainly at temperate to Arctic latitudes, and their distributions are strongly linked to temperature (Bolton 2010). Consequently, ocean warming can have a range of direct and indirect effects on kelp performance and persistence (Smale 2020, Wernberg et al. 2019). Direct effects typically occur in regions where temperatures are at or above the optimum for kelps, with warming and marine heatwaves leading to mortality (Filbee-Dexter et al. 2020, Wernberg et al. 2016) or sublethal damage such as reduced growth, reproduction, or tissue health (Simonson et al. 2015, Xiao et al. 2015). Indirect effects of warming commonly include climate-mediated shifts in grazers, such as the increases in sea urchin overgrazing in southeastern Australia following the shifting East Australian Current (Ling et al. 2009) and in the northeastern Pacific following marine heatwave-driven loss of predatory sea stars (Rogers-Bennett & Catton 2019, Starko et al. 2022). Overgrowth by epibiota (e.g., Saunders et al. 2010) and grazing pressure from range-extending fish (Vergés et al. 2014) can also increase with warming and drive or cement kelp loss. At cooler leading range edges in the Arctic, kelp forests are predicted to expand deeper and increase in cover and biomass (Filbee-Dexter et al. 2019), largely due to loss of sea ice and increased light providing more suitable habitat. Models predict an increase in kelp distribution of between ~70,000 and ~123,000 km^2 in Arctic regions by 2100 (Assis et al. 2022). However, these predicted gains may be overestimates given that increased turbidity from melting land ice and glaciers is also expected in some areas and may limit kelp expansion (Bonsell & Dunton 2018).

The total area of kelp forest impacted by climate change is uncertain due to large unmapped and unmonitored portions of their global range and the relative lack of long-term time series (Krumhansl et al. 2016). The most extensive climate-driven losses of kelp forests, exceeding tens of thousands of hectares, have been reported in Norway (accelerated by eutrophication) (Gundersen et al. 2017), Western Australia (Wernberg et al. 2016), and Japan (Tanaka et al. 2012). Less extensive losses, on the order of hundreds to thousands of hectares and including some localized extinctions, have increasingly been reported for many areas in the North Atlantic (Filbee-Dexter et al. 2020), New Zealand (Tait et al. 2021), Oman (Coleman et al. 2022), and the northeastern Pacific (Rogers-Bennett & Catton 2019, Starko et al. 2022). Kelp forests in areas with strong upwelling or eastern boundary currents flowing toward the equator, such as Chile, southern Africa, and parts of California, appear generally to be more stable or even increasing over time, possibly representing regions of high resistance to climate warming (Krumhansl et al. 2016, Mora-Soto et al. 2021). Long-term records (>20 years) of kelp forests suggest that ~60% have been declining and only ~5% have been increasing over the past few decades (Wernberg et al. 2019).

Climate change and warming can also cause sublethal effects that are less dramatic compared with complete die-offs but nevertheless can modify the structure and function of kelp forests. Climate change can directly impact species or populations by altering vital rates such as growth (Pessarrodona et al. 2018) and decomposition (Filbee-Dexter et al. 2022a). These impacts can lead to reduced carbon capture and export by kelp forests, limiting their capacity to support secondary production and their overall importance in carbon cycling (Pessarrodona et al. 2022). Warmer temperatures can also drive declines in the overall size of kelp (Pessarrodona et al. 2018), leading to a reduction in the amount of habitat available for associated species and in the standing biomass present in forests. Increased decomposition rates under a warming climate may also limit the capacity of kelp-derived carbon to be exported from kelp forests, reducing the capacity for spatial subsidies and carbon drawdown potential (e.g., in the deep sea) (Filbee-Dexter et al. 2022a). Warming can also alter the genetic makeup of kelp populations (e.g., Coleman et al. 2020a), potentially limiting their ability to adapt and respond to future change (Coleman & Wernberg 2020). In Australia, for example, a marine heatwave caused declines in the genetic diversity and shifts toward genotypes associated with warm waters (Coleman et al. 2020a, Gurgel et al. 2020).

Climate change can alter the species composition of kelp forests, with cold-adapted species replaced by ones tolerant of higher temperatures. This has already occurred in the northeastern Atlantic (*Laminaria hyperborea* replaced by *Laminaria ochroleuca*; Smale et al. 2015) and the northeastern Pacific (*Pterygophora californica* replaced by *Eisenia arborea*; Watson et al. 2021). These species substitutions can have important functional implications for the kelp forest. In Europe, where *L. hyperborea* is being replaced by *L. ochroleuca*, epifaunal communities have been impacted (reduced), because *L. ochroleuca* has substantially fewer stipe epiphytes (Teagle & Smale 2018), which has ramifications for the wider food web (Smale et al. 2022). This substitution may also limit carbon export due to differences in production and decomposition rate between kelp species (Wright et al. 2022).

Climate-driven loss of kelp often results in regime shifts to alternative ecosystem states, such as turf-dominated reefs (Filbee-Dexter & Wernberg 2018), smaller fucoid species (Thomsen & South 2019), or sea urchin barrens (Filbee-Dexter & Scheibling 2014), all of which have been observed across the distribution of kelps. Urchin barrens are primarily dominated by encrusting coralline algae, with high abundances of urchins and little foliose macroalgal cover. Turf reefs are dominated by many species of small, finely branched algae that can trap sediment and tend to have high cover and turnover (Pessarrodona et al. 2022). These states are stabilized by feedback mechanisms that can prevent kelp recovery even if environmental conditions improve, such as recruitment inhibition or high grazing pressure (Wernberg et al. 2019). Gradual warming can also result in tropicalization of kelp forests, with increases in coral abundance or tropical *Sargassum* documented in kelp forests in Japan (Tanaka et al. 2012) and Australia (Wernberg et al. 2016).

5. SEAGRASS MEADOWS

Seagrasses are flowering plants that have adapted to live in marine environments (**Figure 6**; **Table 1**). They build extensive meadows in shallow sedimentary habitats, typically through vegetative clonal spread. They have been affected by climate changes, including warming and marine heatwaves, sea level rise, altered storm patterns, and (perhaps) ocean acidification (Duarte et al. 2018, Guerrero-Meseguer et al. 2020).

Temperature effects are well documented in comparison with other climate stressors. Seagrasses generally respond to long-term increases in mean temperature through poleward shifts of range edges (Hyndes et al. 2016, Wilson & Lotze 2019). However, not all species have the same capacity for range shifts, as fast-growing species are better able to keep pace with temperature changes than slow-growing species, leading to changes in their relative abundance and distribution (Hyndes et al. 2016, Richardson et al. 2018). Rapid range extension requires sexual reproduction and long-distance dispersal on the order of kilometers per year. Where clonal growth is predominant, range extension will be limited to the rate of belowground clonal expansion, typically no more than a few meters per year. Reduced sea ice at high latitudes may increase the growing season and reduce ice scouring but could also lead to increased potential for winter storms affecting seagrass without the protective ice cover.

Warming can also influence nutrient cycling (e.g., Alexandre et al. 2020) and decomposition (Trevathan-Tackett et al. 2020) in seagrass meadows, and can create conditions that favor net CO_2

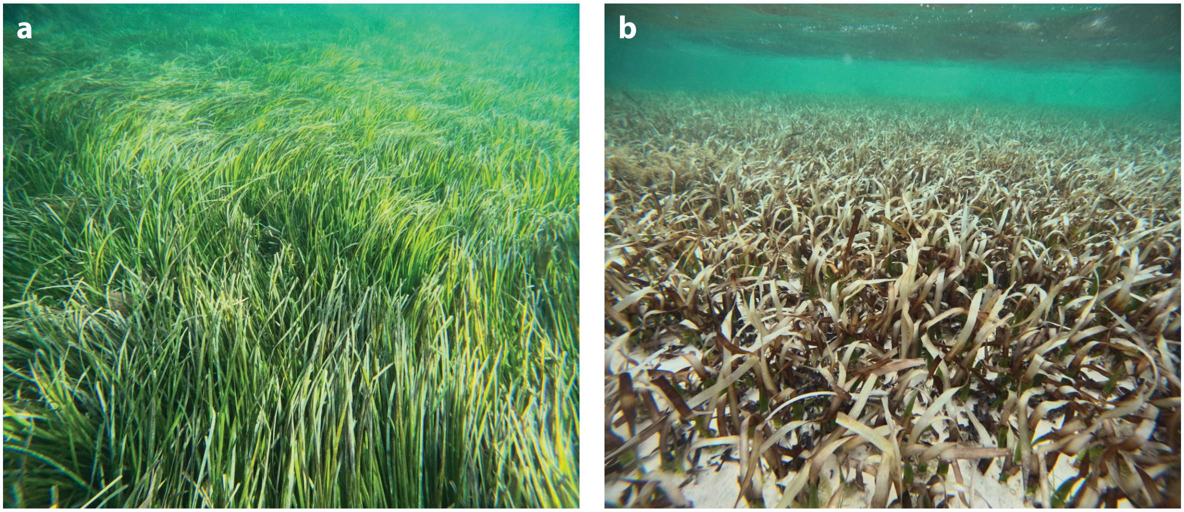

Figure 6

Pristine versus climate-impacted seagrass meadows. Shown are *Posidonia* sp. meadows (*a*) before and (*b*) after a heating and bleaching event in Western Australia. Photos by M.S. Thomsen.

and CH_4 flux from sediment to water (Burkholz et al. 2020). In addition, multiple co-occurring species will respond differently to the same temperature changes, causing species interactions to change. Warming has also facilitated colonization of nonindigenous seagrass species (*Halophila* spp. in the Mediterranean and Caribbean; Beca-Carretero et al. 2020, Wesselmann et al. 2021). These shifts in species identity can have cascading effects on associated species and community structure and function (e.g., Viana et al. 2019). Estuarine intertidal seagrass species, which naturally experience large daily and seasonal temperature fluctuations, appear to have highly variable responses to warming and heatwaves (Clemente et al. 2023, Magel et al. 2022). Still, heat-associated mortality has been reported on intertidal seagrass, particularly when high water and air temperatures coincide with midday low spring tides and high solar radiation (Rasheed & Unsworth 2011). Furthermore, high mortality and massive loss of large seagrass meadows has been reported after extreme marine heatwaves, particularly in shallow, less wave-exposed waters and near species' poleward latitudinal distribution limits, as in the Mediterranean Sea and Shark Bay in Australia (e.g., Marbà & Duarte 2010, Strydom et al. 2020). For example, in Shark Bay, 36% of all seagrass meadows were damaged following a marine heatwave in 2010–2011, causing dramatic cascading impacts on small animals and megafauna such as dugongs and turtles, as well as effects on carbon storage as sediment carbon was rereleased to the atmosphere (Arias-Ortiz et al. 2018, Nowicki et al. 2021).

Few studies have tested the impacts of ocean acidification on seagrasses; experimental studies suggest relatively little overall effect (e.g., Guerrero-Meseguer et al. 2020), although associated species, like shell-producing snails and bivalves, and ecosystem functioning might be more affected (Ravaglioli et al. 2020). However, rates of photosynthesis and growth can, for some seagrass species, be favored by increased CO_2 (Koch et al. 2013). Evidence for the impacts of sea level rise on seagrasses is also scarce, and model predictions vary; sediment accumulation rates in many seagrass meadows likely allow them to keep pace with sea level rise (e.g., Saderne et al. 2018). Sea level rise might create new space for seagrasses to colonize in some areas, but this could be hampered if coastal development creates barriers (Raw et al. 2021). In other areas, they could be pushed into shallower areas prone to high temperatures (Carr et al. 2012) or ice scouring.

Effects of climate change are likely to differ between perennial persistent and ephemeral colonizing seagrasses, which vary in their response to and recovery from disturbance (Kilminster et al. 2015). Both types can be greatly impacted by warming events, but recovery of persistent species is slow or absent, while colonizing taxa are typically adapted to recover more quickly (e.g., Strydom et al. 2020). Overall, this may result in composition shifts toward fast-growing species becoming more dominant after heatwaves (Kendrick et al. 2019). Mortality events can also reduce genetic diversity within a meadow (Chefaoui et al. 2018), which could lead to reduced capacity to adapt to future stressors and changes. Beyond impacts on seagrasses themselves, extreme events can also exert profound changes on ecosystem functioning and services, such as reducing sediment carbon stocks (Arias-Ortiz et al. 2018) and the carbon sequestration capacity of seagrass meadows (George et al. 2020).

In several places, the fauna inhabiting seagrass meadows has been altered by warming (e.g., Fodrie et al. 2010, Zarco-Perello et al. 2020). Changes in trophic interactions or feeding behavior can lead to either increased grazing on seagrasses themselves (Buñuel et al. 2021) or altered grazing pressure on epiphytic algae, although the direction of this effect varies among species (Pillay & Waspe 2019). Gradual warming and heatwaves can also interfere with mutualisms between seagrasses and other species, leading to increased mortality from other stressors, such as sulfide (e.g., de Fouw et al. 2022). Finally, climate change—and warming and heatwaves in particular—may also impact host–pathogen dynamics, for example, by increasing the prevalence of seagrass wasting diseases (Groner et al. 2021).

6. SALT MARSHES

Salt marshes are dominated by salt-tolerant, vascular, herbaceous plants and small shrubs that inhabit wave-protected sedimentary shorelines throughout the world (Adam 1990) (**Figure 7**). The extent of salt marshes is limited in the tropics by competition with mangrove forests and in polar regions by ice scour. The primary foundation species of salt marshes are grasses, sedges and

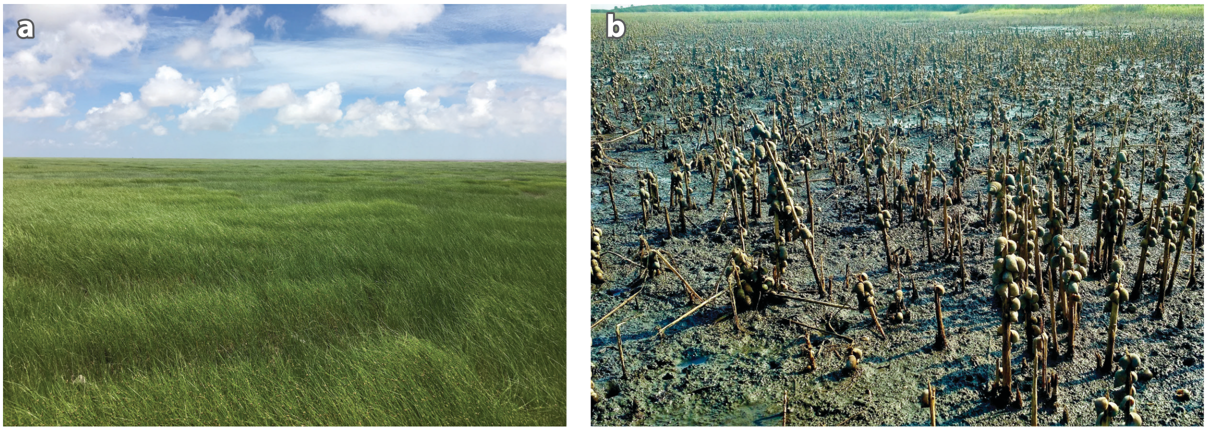

Figure 7

Pristine versus climate-impacted salt marshes. Shown are (*a*) a healthy marsh dominated by *Scirpus mariqueter*, China, and (*b*) a degraded *Spartina alterniflora* marsh after a severe drought followed by runaway grazing by *Littorina*, US east coast. Photos in panels *a* and *b* by Q. He and B.R. Silliman, respectively.

rushes, and succulents, depending on geographic location. Some animal species, such as the ribbed mussel, *Geukensia demissa* (Bertness 1984), also act as foundation species in salt marshes, though they are less prominent. An increasing number of studies have investigated the effects of climate change on these foundation species, and both positive and negative responses have been observed (**Table 1**).

Many studies have investigated the direct effects of CO_2 enrichment on the growth and function of salt marsh plants. A general pattern has emerged that both the current higher levels of CO_2 and future increases in CO_2 may increase the aboveground growth of many marsh species, with C_3 plants expected to respond more positively than C_4 plants (Arp et al. 1993). In addition to increasing aboveground growth, a 33-year study showed that, when exposed to higher levels of CO_2, the sedge *Schoenoplectus americanus* increased root and rhizome biomass and became a better forager for growth-limiting nitrogen, although this effect was diminished with increases in sea level rise (Zhu et al. 2022).

While CO_2 enrichment increases the growth of salt marsh plants, increasing temperatures can have both positive and negative impacts depending on geographic and within-marsh location. In Maine, USA, experimental warming of more heavily saturated marsh pannes increased the dominance of *Spartina patens* but decreased plant diversity (Gedan & Bertness 2009). The mechanism was experimental warming-induced drying of the pannes, allowing stress-intolerant, competitive *S. patens* to move in and outcompete a guild of nonfoundational halophytic forbs. While warming at colder latitudes tends to increase the growth of marsh plants, warming at the tropical range limits of salt marshes tends to decrease or have no impact on the growth of marsh plants and could even facilitate overgrowth by encroaching mangroves (Coldren et al. 2019). Warming has also been predicted to increase the invasion of exotic marsh species and the replacement of native marsh species (Borges et al. 2021).

The rate of sea level rise is increasing due to climate change, and where coastal land is not increasing elevation at rates equaling or exceeding sea level rise, salt marsh plants will become increasingly stressed by higher inundation frequencies, greater flooding depths, modified salinity regimes, greater wave energy, and wrack deposition (Fagherazzi et al. 2020, Li et al. 2018). Marsh plants are dependent on tidally borne sediments for their survival and also contribute organic material to substrates that improves resilience to sea level rise. Where sea level rise allows tides to extend beyond the landward boundaries of salt marshes, increasing inundation frequencies and elevated substrate salinity can affect the condition and survival of adjacent coastal forests, making way for the advancement and landward expansion of salt marsh plants (Kirwan & Gedan 2019). This expansion can be curtailed by steep topography, conflicting land use (e.g., coastal development), and engineering structures (e.g., sea defenses, levees, and revetments) that prevent tidal incursion into the margins of salt marshes. Consequently, there is increasing concern that drowning, internal breakup, and erosion of seaward margins of salt marshes and barriers to landward retreat will cause coastal squeeze effects, which have severe implications for salt marsh extent (Torio & Chmura 2013), with global projections indicating that large-scale loss could be reduced if sufficient landward space is available for the advance of salt marsh foundational species (Schuerch et al. 2018).

The effects of climate change on salt marshes are often driven by a combination of co-occurring stressors. For example, salt marshes are highly vulnerable to increasing storm intensity induced by climate change (Beck et al. 2011), particularly when oyster reefs in front of marshes are removed. Likewise, drought during the summer months in marshes can lead to elevated salinities in marsh soils. Elevated soil salinities then induce water stress in marsh plants, decreasing their growth, increasing their vulnerability to herbivores, and, when the stress is intense enough, leading to massive die-offs. Indeed, in China (He et al. 2017) and the United States (Silliman et al. 2005), severe drought has weakened marsh plants (e.g., *Spartina alterniflora* and *Suaeda salsa*), increased top-down control by common grazers, and led to runaway die-offs of marsh ecosystems due to the interaction of drought and overgrazing (Silliman & Bertness 2002, Silliman et al. 2005). While fire has been used as a salt marsh management tool to prevent woody plant invasion and manage cattle impacts (Williams-Jara et al. 2022), the increasing intensity and frequency of wildfires and bushfires are of growing concern because of the fires' physical impacts on plant condition (Glasby et al. 2023), soil structure (Smith 2001), and invertebrate communities (Ross et al. 2019).

While the independent effects of climate change drivers on salt marsh species have been increasingly studied, climate change drivers often interact with each other (e.g., the El Niño/ Southern Oscillation and drought) or with localized human influences to impact marsh species (He & Silliman 2019). These effects may be synergistic, additive, or antagonistic but remain poorly understood in salt marshes. For example, interactions between hydrodynamic forcing arising from sea level rise and other climate change drivers variably indicate the compounding effect of warming temperatures and elevated CO_2 on salt marsh responses to sea level rise. Some species respond favorably, with increasing biomass (Pérez-Romero et al. 2019), while others exhibit decreased belowground biomass allocation, higher rates of peat decomposition, and increasing exposure to the effects of sea level rise (Crosby et al. 2017). In some cases, the plant architecture changes to improve resilience to sea level rise with warming and CO_2 enrichment, increasing extension above rising sea levels and stem rigidity in the face of increasing wave energy (Paul et al. 2022). Where mangroves and salt marshes co-occur, the additive effects of warming and CO_2 may also favor the establishment of advancing mangrove seedlings (Manea et al. 2020).

7. MANGROVE FORESTS

Mangroves are salt-tolerant trees, shrubs, and palms that occur in the upper intertidal zone along low-energy sedimentary coastlines predominantly in the tropics, with few species able to tolerate the cool temperatures of temperate coastlines (**Figure 8**). Mangrove distribution is limited by the 20°C isotherm based on atmospheric (Walsh 1974) or ocean temperatures (Duke et al. 1998), extreme freezing events at the poleward limit of their latitudinal distribution (Cavanaugh et al. 2014),

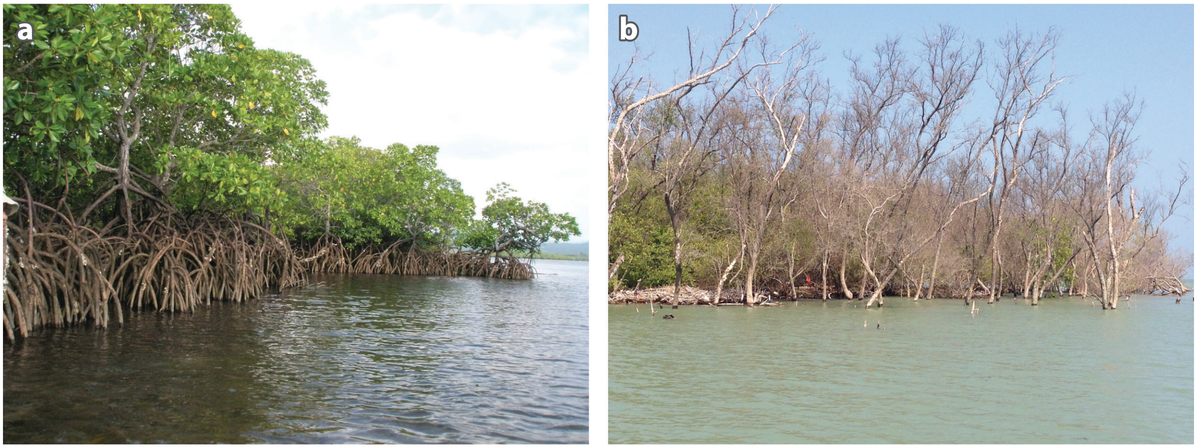

Figure 8

Pristine versus climate-impacted mangrove forests. Shown are (*a*) healthy fringing *Rhizophora apiculata* mangroves, Indonesia, and (*b*) a dying *Avicennia alba* mangrove due to prolonged inundation, Indonesia. Photos by D. Murdiyarso/CIFOR-ICRAF.

or geomorphological barriers (Raw et al. 2019, Rogers & Krauss 2019). Mangroves are affected by physical processes operating on the land, ocean, and atmosphere and are therefore exposed to a broad range of climate change drivers (**Table 1**).

Mangroves typically cope with modest warming, although this may reduce aboveground biomass (Ward et al. 2016), particularly in arid areas dominated by *Avicennia* species. Warming has been implicated in mangrove range extensions along many coastlines extending across latitudinal ranges (Fazlioglu et al. 2020, Saintilan et al. 2014). For example, in the southeastern United States, warming has reduced the frequency of freeze events (Cavanaugh et al. 2014), leading to the expansion of *Avicennia germinans*, *Rhizophora mangle*, and *Laguncularia racemosa*. Projections suggest that warming near mangrove range limits will increase their height and biomass (Gabler et al. 2017), providing a competitive advantage over adjacent salt marshes (Osland et al. 2013), and facilitate poleward expansion at 2.2–3.2 km y^{-1} (Cavanaugh et al. 2014), although propagule predation may limit expansion in some regions (Langston et al. 2017).

Whereas increasing temperatures have resulted in poleward range expansion, higher atmospheric CO_2 levels increase mangrove productivity because they enhance photosynthetic and water use efficiency (McKee et al. 2012). For example, *R. mangle*, from the Atlantic–East Pacific region, exhibited significant increases in stem length, maturation rates, and total leaf area in greenhouse experiments conducted on propagules (Farnsworth et al. 1996). However, this enhanced efficiency did not provide a productivity subsidy for *A. germinans* when exposed to suboptimal salinity regimes (Reef et al. 2015) or for *Avicennia marina* and *Rhizophora stylosa* when exposed to flooding regimes that simulated sea level rise (Jacotot et al. 2018). Indeed, CO_2 enrichment has been proposed as a contributing factor to global expansions of mangrove into salt marsh habitats, interacting with sea level rise, altered inundation regimes, and modified substrate salinity (Saintilan & Rogers 2015).

The productivity and tree heights of mangroves generally also increase with precipitation (Simard et al. 2019), which reduces substrate salinities, improves access to freshwater, facilitates flushing of toxicity from roots, and modifies competitive hierarchies and zonation patterns (Ribeiro et al. 2019). For example, growth of *Avicennia*, *Rhizophora*, and *Laguncularia* species in Venezuela was inhibited by salinity stress where rainfall is low (Medina & Francisco 1997), while expansion into salt marshes in subtropical Australia has been linked with freshening arising from sea level rise and increasing rainfall (Eslami-Andargoli et al. 2009). Precipitation also modifies the sediment supply and deposition, hydrological regimes, and sulfate toxicity in substrates in mangrove environments (Adams & Rajkaran 2021). However, projections of changing precipitation based on future climate change scenarios indicate that most mangroves will have reduced access to freshwater and an increasingly drier climate (Sippo et al. 2018). Reduced access to freshwater, associated with coupled negative phases of the Indian Ocean Dipole and the El Niño/Southern Oscillation, has already been implicated in widespread drought-induced mangrove dieback across northern Australia (Duke et al. 2021).

Traditionally, mangroves were thought to adapt to sea level rise by accumulating sediments, but greenhouse experiments on *R. mangle* indicate that initial rapid growth was followed by reduced growth (Ellison & Farnsworth 1997). Furthermore, organic matter addition from roots can allow mangroves to maintain their intertidal position, particularly when mineral sediment supply is low (McKee 2011). The importance of mangrove roots in relation to sea level rise is now well established, as is their capacity to buffer wave energy, bind sediments, add organic matter, dampen erosion, and contribute to the vertical growth of substrates as sea level increases (Krauss et al. 2014). However, if mineral and organic matter accumulation does not match sea level rise, then mangroves' intertidal position can transition to lower elevations that are less suitable for survival and will expose them to higher wave energy (Woodroffe et al. 2016). The paleo record indicates limited threshold tolerance for adaptation when sea level rise exceeds ~7 mm y^{-1} (Saintilan et al. 2020), a rate that likely will be surpassed by the end of the twenty-first century. With predicted sea level rise, landward retreat will become increasingly important, although retreat will be limited where land use and tidal barriers cause coastal squeeze (Leo et al. 2019, Phan et al. 2014).

Mangroves can be uprooted and destroyed by climate change–induced cyclones and storms (**Figure 2**), but they can also buffer storm surges and reduce erosion (Marois & Mitsch 2015) and are therefore important coastal defenses against extreme weather events. Postcyclone recovery of mangroves depends on the severity of the cyclone, exposure, degree of physical damage, and mangrove traits (Krauss & Osland 2020). For example, Rhizophoraceae are sensitive to wind effects (Asbridge et al. 2018, Aung et al. 2013), which have a significant influence on recovery trajectories. In contrast, *Avicennia* and *Laguncularia* species have a stronger recovery capacity because they are semideciduous (Paling et al. 2008) and can resprout from coppiced stems or lateral roots (Saenger 2002), their seedlings are protected from wind and storm surges, and postcyclone propagule supply is often high (Krauss & Osland 2020). However, storm-induced geomorphological or hydrological changes can reduce recovery by causing peat collapse, organic matter decomposition, loss of substrate elevation, and extreme sedimentation that buries aerial roots and reduces oxygen availability (Paling et al. 2008) as well as impounding tidal waters, which leads to reduced or persistent inundation (Cahoon et al. 2003, Lagomasino et al. 2021). Paradoxically, extreme weather events may improve mangrove forest resilience by providing nutrients that enhance productivity (Rasquinha & Mishra 2021) and sediment that increases resilience to sea level rise (Feher et al. 2020). Storm-related recovery is time dependent, and species that recover fastest will have a long-term influence on canopy structure (Baldwin et al. 2001, Paling et al. 2008). For example, where cyclone frequency is high, mangroves exhibit lower biomass and have fewer canopy emergents (Lugo & Snedaker 1974), while species diversity and structural complexity are higher where cyclone frequency is low and/or mangroves have had more time for recovery (Simard et al. 2019).

8. BIVALVE REEFS

Bivalve reefs or beds are complex raised structures created by aggregations of oysters and/or mussels. Besides providing an important food source to humans and other species (e.g., birds, fish, crabs, and whelks), their three-dimensional structures offer habitats to fish and invertebrates, enhance shoreline stabilization and wave attenuation, and provide water filtration and nutrient cycling. Consequently, they can exert large influences on ecosystem structure and function beyond their structural footprint.

Bivalve reefs are found in estuarine and coastal waters of temperate to tropical regions, spanning intertidal to subtidal habitats (Keith et al. 2022) (**Figure 9**). For many species, the availability of hard substrate (including rock and the shells of live or dead conspecifics) limits the establishment of reefs, though some species, such as pen shells, occur on soft bottoms. The fundamental niches of these species are shaped by biophysical factors such as temperature, salinity, dissolved oxygen, pH, and turbidity (Theuerkauf & Lipcius 2016). However, present-day distributions also strongly reflect historical and contemporary anthropogenic activities (Beck et al. 2011), like overharvest that has removed 85% of oyster reefs globally (Beck et al. 2011), recently scaled-up restoration of oyster and mussel populations, and deliberate (i.e., for aquaculture) and unintentional (e.g., as hull fouling) species translocations beyond their native ranges (Ruesink et al. 2005). Furthermore, predation and disease, which are also often mediated by human activities, are key drivers of bivalve distributions at local scales (Bushek et al. 2012, Paine 1966).

Figure 9

Pristine versus climate-impacted bivalve reefs. Shown are (*a*) a healthy *Mytilus trossulus* reef and (*b*) a dying *Mytilus trossulus* reef with gaping valves after the western North American heat dome, British Columbia. Photos by C. Harley and adapted with permission.

Among physicochemical factors, ocean temperature is the most important driver of bivalve distributions and hence the most significant climate stressor of bivalve reefs (Zippay & Helmuth 2012). Poleward range shifts in some reef-building bivalve species have already been detected coincident with warming (Sorte et al. 2010), leading to cascading ecological impacts (e.g., Andriana et al. 2020). For example, in the Wadden Sea (Germany and Denmark), warming summers have accelerated Pacific oyster (*Magallana gigas*) invasion (Diederich et al. 2005), while warming winters have driven recruitment failure and population declines in native bed-forming mussels (*Mytilus edulis*, *Macoma balthica*, and *Cerastoderma edule*) by synchronizing the timing of their settlement with seasonal biomass peaks in their main predators (Beukema & Dekker 2014). Increases in Pacific oyster numbers have, in part, ecologically compensated for the loss of blue mussels, as there is some functional redundancy in their provision of habitat to other invertebrates (Markert et al. 2010, 2013) and of food and habitat to shorebirds (Markert et al. 2013).

There are, however, also functional differences among these species (Kochmann et al. 2008). For example, whereas oysters promote green algae of low biomass and habitat complexity, blue mussels promote high-biomass, high-complexity meadows of the habitat-forming brown seaweed (*Fucus*) (Andriana et al. 2020). Unable to move to thermal refugia, reef-forming bivalves are also highly vulnerable to heatwaves (Harley 2008). Intertidal populations are particularly vulnerable, especially when low tides occur during midday in periods of calm, warm weather (Helmuth et al. 2002). Direct heatwave mortality of oysters and mussels is often heterogeneous, with animals living on equatorward-facing surfaces (Harley 2008), in solitary configurations (McAfee et al. 2018), or in the top layer of mussel beds being more vulnerable (Mislan & Wethey 2015). Aggregating behavior decreases thermal stress to individuals, and associated species, because of shading and moisture retention (McAfee et al. 2018). Parasitic endoliths may also reduce shellfish vulnerability to heat stress by providing a white discoloration that reflects solar radiation (Zardi et al. 2016).

In addition to directly affecting bivalve distributions, warming and heatwaves can alter biological interactions (Zippay & Helmuth 2012). For example, the predator–prey interaction between *Pisaster* sea stars and *Mytilus* mussels, which controls intertidal rocky shore community structure in the northeastern Pacific (Paine 1966), is sensitive to temperature (Sanford 1999). Furthermore, warming winters in Florida have been correlated with an ecosystem shift from intertidal oyster reefs (as also noted above for salt marshes) to mangroves (McClenachan et al. 2021). Warming and heatwaves have also been implicated in outbreaks of diseases, such as the ostreid herpesvirus (e.g., de Kantzow et al. 2016), which has spread from cultivated populations of Pacific oysters onto reefs and to co-occurring *C. edule*, an important infaunal bioengineer (reefs and bioturbation) and food source for protected bird species (Bookelaar et al. 2020). Indirect effects of warming and heatwaves may also occur where they cause shifts in the availability and/or species composition of phytoplankton (food) resources that negatively influence the development, survival, and competitive ability of bivalve species (Correia-Martins et al. 2022).

Temperature, salinity, and dissolved oxygen are also important drivers of bivalve distributions, influencing their development, growth, and survival (Clark & Gobler 2016) as well as disease dynamics of established populations (Bushek et al. 2012). Dissolved oxygen is declining in marine systems due in part to rising temperatures as well as increased nutrient loading into coastal systems (Breitburg et al. 2018), while intense precipitation events, associated with flooding and low salinity, are increasing. Besides causing mass mortality associated with prolonged severe hypoxia (~5 days) (Lenihan & Peterson 1998), diel cyclic hypoxia caused by changes in photosynthesis and exacerbated by warming can impact bivalves and their ecosystem services (Donelan et al. 2023). Altered rainfall and runoff patterns have been implicated in disease cycles, such as dermo occurrence in *Crassostrea virginica* oyster populations on the US Gulf and East Coasts (Bushek et al. 2012). Additionally, though shellfish can persist through short-term anomalies in salinity by closing their valves and shifting to anaerobic metabolism, flood events can result in mass mortality (Gledhill et al. 2020).

Although ocean acidification poses a potential threat to bivalves, most studies documenting impacts have come from experimental studies focused on early life history stages of cultivated populations (Parker et al. 2009). The persistence of bivalve reefs in highly acidified estuaries affected by acid-sulfate runoff and along coasts with strong diel and seasonal metabolic shifts in CO_2 suggests that there may be some capacity of bivalves to resist this stressor (e.g., Amaral et al. 2011). Nevertheless, in a mesocosm study examining effects of warming and ocean acidification on mussel reef communities, elevated $p\mathrm{CO_2}$ reduced the growth of *Trichomya hirsuta* but not that of *Mytilus galloprovincialis*, and warming and $p\mathrm{CO_2}$ influenced the infauna that colonized both species of mussels (Cole et al. 2021).

9. LESSER-KNOWN MARINE FOUNDATION SPECIES

Several lesser-known marine organisms not discussed above can dominate biomass and control biodiversity and community interactions; examples include sponges, bryozoans, tunicates, sessile crustaceans such as barnacles, calcareous reef-forming polychaetes, noncoral cnidarians such as hydroids or gorgonians, maerl beds composed of calcareous red algae, intertidal fucoid beds, and floating *Sargassum* forests. These foundation species are found across most marine ecosystems.

Most of these species have also been impacted by climate change. For example, intertidal fucoid beds are generally susceptible to the same stressors as kelp forests, with warming being a main driver of impacts (Thomsen et al. 2019). In contrast, floating *Sargassum* forests may benefit from warming, with expansion documented in some areas (Bach et al. 2021). Warming has also caused decreases in abundances of gorgonians (Chimienti et al. 2021), and heatwaves have caused mass mortality of barnacles (Hesketh & Harley 2023), gorgonians, sponges, bryozoans, cockles, and clams (Cerrano & Bavestrello 2008, Garrabou et al. 2009, Raymond et al. 2022). Moreover, lower pH increases energetic costs in calcareous foundation species such as clams, cockles, maerl, and many polychaetes, and these species can therefore be negatively affected by ocean acidification (Martin & Hall-Spencer 2017, Ong et al. 2017, Smith et al. 2013).

As for most other foundation species, there is evidence that co-occurring stressors modify impacts. For example, heatwaves were most severe on intertidal barnacles in wave-sheltered harbors and on low, sunlit sloping rocks, and cockles were more affected when heatwaves coincided with spring low tides in the middle of the day (Hesketh & Harley 2023). Furthermore, high temperatures can increase diseases by facilitating infections by pathogens and parasites (Cerrano & Bavestrello 2008), sometimes resulting in increased susceptibility to predation (Magalhães et al. 2018). Strong marine heatwaves in the Mediterranean Sea have also caused deeper and stronger vertical stratification, thereby reducing food for suspension-feeding gorgonians, bryozoans, and hydroids (Cerrano & Bavestrello 2008, Garrabou et al. 2009).

10. SUPPORTING FOUNDATION SPECIES IN THE ANTHROPOCENE

There is a clear trend for continued decline in the extent, cover, and condition of foundation species in a future of increasing climatic stress. Prompt and proactive management, protection, and restoration actions can help slow or reverse these trends. While reducing greenhouse gas emissions must remain a priority, we must also invest in ameliorating other interacting coastal stressors. It is also important to recognize that some pristine areas still exist, and protection of these bright spots, which may represent future refugia, will also be important. For example, given the dire prognosis for the world's coral reefs (Cooley et al. 2022a), much research is now focused on developing methods that will enhance the thermal tolerance of corals. Approaches such as assisted evolution—including selective breeding of corals, stress exposure of corals to induce acclimatization, laboratory evolution of Symbiodiniaceae through mutagenesis and/or selection, and active modification of the community composition of the coral microbiome (eukaryotic and prokaryotic)—are being proposed to help corals adapt to climate change (van Oppen et al. 2015), and similar approaches are increasingly proposed for other foundation species as well (e.g., Coleman et al. 2020b). Even previously controversial interventions to develop super-corals have become more broadly accepted since the devastation of the 2014–2017 global bleaching event (Voolstra et al. 2021), but such approaches have had limited success in producing persistent changes in thermal tolerance. Even if successful, the capacity to implement reef restoration at the scales required to make a meaningful difference remains questionable. At best, such approaches could buy foundation species some time at very small scales while greenhouse gas emissions are being reduced. Directly mitigating climate change is inarguably the only way to ensure the persistence of foundation species and their ecosystems into the future.

While reducing stressors is essential for the continued persistence of foundation species, reversing the damage is possible in many places through restoration of lost or degraded ecosystems. The history and success of restoration vary among taxa, but such restorations can be difficult, costly, and prone to failure, particularly for subtidal foundation species. Substantial advances have been made in our ability to restore some ecosystems, like mangroves, salt marshes, oyster reefs, and even seagrasses. Cost-effective and scalable methods involve harnessing passive restoration methods and using propagules instead of transplanting mature individuals (Fredriksen et al. 2020, Vanderklift et al. 2020). Concurrent with restoration, incorporation of nature-based design principles into coastal planning can help maintain populations of foundation species within urban environments, integrating space for foundation species within coastal infrastructure like seawalls, and designing future infrastructure to be compatible with the likely need for landward migration (Firth et al. 2016).

In this era of rapid environmental change, there is also a need for proactive actions to boost the resilience of foundation species to climate change (Coleman et al. 2020b, van Oppen et al. 2015). Such actions could be combined with restoration (see above) or could be done proactively in healthy populations that are vulnerable to future change. Strategies include assisted adaptation or evolution, assisted gene flow, genetic rescue, and assisted migration (e.g., Coleman et al. 2020b, van Oppen et al. 2015). While the terminology varies, these strategies generally revolve around moving, introducing, or increasing the frequency of putatively resilient genotypes in populations, which could be thermally resilient genotypes or those that have a higher tolerance for other stressors that are predicted to increase in the future. Another, albeit more controversial, strategy to boost the resilience of foundation species is hybridization between species or genetic engineering. Tools such as CRISPR-Cas9 can be used to insert genes that might change the performance of individuals under stress, and this has been done in terrestrial settings. For marine foundation species, this technique has been trialed in the laboratory for corals (Cleves et al. 2020) but has not yet been extended to other species. The underpinning genomic knowledge for almost all foundation species is currently lacking to facilitate these approaches, and this lack remains a large gap to overcome before progress can be made.

There is also the option of accepting and adapting to climate-induced change in foundation species, including the rearrangement of foundational ecosystems. There are many instances where it will be futile to try to maintain the current status of foundation species (e.g., the position of warm range edges) or where the resources required to boost resilience will outweigh the benefits. Central to the decision of whether to act will be understanding how ecosystems will rearrange and what ecosystem services might flow from future foundation species. Rather than attempting to maintain individual species in certain areas, we could seek to maintain critical ecological functions and ecosystem services and accept that there are also new opportunities and services provided in future states.

Marine foundation species play a critical role in maintaining the integrity of marine ecosystems and extensive benefits to coastal peoples. However, rising ocean temperatures, marine heatwaves, extreme weather, sea level rise, and ocean acidification are pushing these important species to their limits, jeopardizing entire ecosystems. While treating the symptoms of climate change through conservation efforts and habitat restoration is important, we must recognize the urgency of addressing the root cause—greenhouse gas emissions—and prioritize reducing our carbon footprint. Only by taking bold action to mitigate emissions can we safeguard the future of marine foundation species and the invaluable services they provide.

SUMMARY POINTS

1. Foundation species are dominant species that provide a physical framework for associated communities. The most well-known marine foundation species include corals, kelps, seagrasses, salt marsh plants, mangroves, and bivalves.
2. The distribution, abundance, and ecological performance of foundation species have already been modified by climate change, particularly gradual atmospheric and ocean warming, stronger and more frequent heatwaves, and (to a lesser extent) ocean acidification, sea level rise, and perhaps stronger storms.
3. Impacts on foundation species have caused dramatic cascading changes to ecological communities, ecosystem functioning, and provision of ecosystem services.
4. Direct effects of climate change on foundation species are exacerbated by co-occurring anthropogenic stressors, including coastal development and seawalls, which increase habitat homogenization and coastal squeeze during sea level rise; overfishing of

predators, which can increase herbivory from sea urchins or fishes; and pollution and eutrophication, which reduce water quality, compromising the health of foundation species and facilitating weedy species.

5. Already documented impacts to foundation species are predicted to accelerate over the next 50–80 years if climate changes follow current model projections.
6. Because mitigating or reversing direct climate change drivers is nearly impossible at local scales, immediate local actions should focus on management of the foundation species themselves (e.g., protection of organisms that are still healthy, restoration using strains that can tolerate higher temperatures, or assisted colonization of species that can tolerate higher temperatures), combined with management of co-occurring stressors (e.g., reducing nutrient pollution, removing barriers to upland migration, coplanting alkaline shells, or reducing fishing of apex predators).

FUTURE ISSUES

1. We need better maps of the distribution, abundance, and condition of marine foundation species, particularly for foundation species that are difficult to see on satellite images (subtidal species as well as intertidal species with narrow vertical ranges).
2. We need to build conceptual and predictive quantitative models for interaction effects within and between different climate change stressors and other human stressors on different foundation species.
3. We need to study and better understand limitations to climate change–related range shifts, like poleward and upward range changes.
4. We need to study and better understand complex, counterintuitive, and cascading impacts from climate changes such as acidification, which may decrease predation pressure and indirectly increase grazing rates from shell-forming herbivores.
5. We need to study and better understand when and where primary foundation species are replaced with alternative foundation species, the likelihood and factors influencing recovery, and associated changes to ecosystem services.
6. We need to apply the full management toolbox to maintain marine foundation species and the ecosystem functioning and services they provide, including consideration of increasing heat tolerance (e.g., via genetic strain selections) and various forms of active restoration.
7. We need to focus on solution-oriented research to improve restoration success and reduce restoration costs, as well as to integrate foundation species into coastal infrastructure to create opportunities for species maintenance and migration while protecting coastal assets.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

AUTHOR CONTRIBUTIONS

T.W. and M.S.T. led the manuscript preparation process based on overall conceptualization by T.W., M.S.T., K.F.-D., D.A.S., and M.A.C. The first drafts of Sections 1, 2, and 10 were written by M.S.T., T.W., M.A.C., and D.A.S. The first drafts of the other sections were written by J.K.B. and J.F.B. (Section 3); K.F.-D. and S.S. (Section 4); K.G. and M.A.V. (Section 5); B.S., Q.H., and K.R. (Section 6); K.R., D.M., and M.A.V. (Section 7); M.J.B. and M.S.T. (Section 8); and M.S.T. (Section 9). All authors provided critical edits to the full manuscript.

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Contents

Errata

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