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# Oceans and Coastal Ecosystems and Their Services

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## Executive Summary

Ocean and coastal ecosystems support life on Earth and many aspects of human well-being. Covering two-thirds of the planet, the ocean hosts vast biodiversity and modulates the global climate system by regulating cycles of heat, water and elements, including carbon. Marine systems are central to many cultures, and they also provide food, minerals, energy and employment to people. Since previous assessments<sup>1</sup>, new laboratory studies, field observations and process studies, a wider range of model simulations, Indigenous knowledge, and local knowledge have provided increasing evidence on the impacts of climate change on ocean and coastal systems, how human communities are experiencing these impacts, and the potential solutions for ecological and human adaptation.

### *Observations: vulnerabilities and impacts*

**Anthropogenic climate change has exposed ocean and coastal ecosystems to conditions that are unprecedented over millennia (*high confidence*<sup>2</sup>), and this has greatly impacted life in the ocean and along its coasts (*very high confidence*).** Fundamental changes in the physical and chemical characteristics of the ocean acting individually and together are changing the timing of seasonal activities (*very high confidence*), distribution (*very high confidence*) and abundance (*very high confidence*) of oceanic and coastal organisms, from microbes to mammals and from individuals to ecosystems, in every region. Evidence of these changes is apparent from multi-decadal observations, laboratory studies and mesocosms, as well as meta-analyses of published data. Geographic range shifts of marine species generally follow the pace and direction of climate warming (*high confidence*): surface warming since the 1950s has shifted marine taxa and communities poleward at an average (mean  $\pm$  *very likely*<sup>3</sup> range) of  $59.2 \pm 15.5$  km per decade (*high confidence*), with substantial variation in responses among taxa and regions. Seasonal events occur  $4.3 \pm 1.8$  d to  $7.5 \pm 1.5$  d earlier per decade among planktonic organisms (*very high confidence*) and on average  $3 \pm 2.1$  d earlier per decade for fish (*very high confidence*). Warming, acidification and deoxygenation are altering ecological communities by increasing the spread of physiologically suboptimal conditions for many marine fish and invertebrates (*medium confidence*). These and other responses have subsequently driven habitat loss (*very high confidence*), population declines (*high confidence*), increased risks of species extirpations and extinctions (*medium confidence*) and rearrangement of marine food webs (*medium to high confidence*, depending on ecosystem). {3.2, 3.3, 3.3.2, 3.3.3, 3.3.3.2, 3.4.2.1, 3.4.2.3–3.4.2.8, 3.4.2.10, 3.4.3.1, 3.4.3.2, 3.4.3.3, Box 3.2}

**Marine heatwaves lasting weeks to several months are exposing species and ecosystems to environmental conditions beyond their tolerance and acclimation limits (*very high confidence*).** WGI AR6 concluded that marine heatwaves are more frequent (*high confidence*), more intense and longer (*medium confidence*) since the 1980s, and since at least 2006 *very likely* attributable to anthropogenic climate change. Open-ocean, coastal and shelf-sea ecosystems, including coral reefs, rocky shores, kelp forests, seagrasses, mangroves, the Arctic Ocean and semi-enclosed seas, have recently undergone mass mortalities from marine heatwaves (*very high confidence*). Marine heatwaves, including well-documented events along the west coast of North America (2013–2016) and east coast of Australia (2015–2016, 2016–2017 and 2020), drive abrupt shifts in community composition that may persist for years (*very high confidence*), with associated biodiversity loss (*very high confidence*), collapse of regional fisheries and aquaculture (*high confidence*) and reduced capacity of habitat-forming species to protect shorelines (*high confidence*). {WGI AR6 Chapter 9, 3.2.2.1, 3.4.2.1–3.4.2.5, 3.4.2.7, 3.4.2.10, 3.4.2.3, 3.4.3.3.3, 3.5.3}

**At local to regional scales, climate change worsens the impacts on marine life of non-climate anthropogenic drivers, such as habitat degradation, marine pollution, overfishing and overharvesting, nutrient enrichment and introduction of non-indigenous species (*very high confidence*).** Although impacts of multiple climate and non-climate drivers can be beneficial or neutral to marine life, most are detrimental (*high confidence*). Warming exacerbates coastal eutrophication and associated hypoxia, causing ‘dead zones’ (*very high confidence*), which drive severe impacts on coastal and shelf-sea ecosystems (*very high confidence*), including mass mortalities, habitat reduction and fisheries disruptions (*medium confidence*). Overfishing exacerbates effects of multiple climate-induced drivers on predators at the top of the marine food chain (*medium confidence*). Urbanisation and associated changes in freshwater and sediment dynamics increase the vulnerability of coastal ecosystems like sandy beaches, salt marshes and mangrove forests to sea level rise and changes in wave energy (*very high confidence*). Although these non-climate drivers confound attribution of impacts to climate change, adaptive, inclusive and evidence-based management reduces the cumulative pressure on ocean and coastal ecosystems, which will decrease their vulnerability to climate change (*high confidence*). {3.3, 3.3.3, 3.4.2.4–3.4.2.8, 3.4.3.4, 3.5.3, 3.6.2, Cross-Chapter Box SLR in Chapter 3}

**Climate-driven impacts on ocean and coastal environments have caused measurable changes in specific industries, economic losses, emotional harm and altered cultural and recreational activities around the world (*high confidence*).** Climate-driven movement of fish stocks is causing commercial, small-scale, artisanal

1 Previous IPCC assessments include the IPCC Fifth Assessment Report (AR5) (IPCC, 2013; IPCC, 2014b; IPCC, 2014c; IPCC, 2014d), the Special Report on Global Warming of 1.5°C (SR1.5) (IPCC, 2018), the Special Report on Ocean and Cryosphere in a Changing Climate (SROCC) (IPCC, 2019b) and the IPCC Sixth Assessment Report Working Group I (WGI AR6).

2 In this Report, the following summary terms are used to describe the available evidence: limited, medium or robust; and for the degree of agreement: low, medium or high. A level of confidence is expressed using five qualifiers: very low, low, medium, high and very high, and is typeset in italics (e.g., *medium confidence*). For a given evidence and agreement statement, different confidence levels can be assigned, but increasing levels of evidence and degrees of agreement are correlated with increasing confidence.

3 In this Report, the following terms are used to indicate the assessed likelihood of an outcome or a result: virtually certain 99–100% probability, very likely 90–100%, likely 66–100%, about as likely as not 33–66%, unlikely 0–33%, very unlikely 0–10% and exceptionally unlikely 0–1%. Additional terms (extremely likely 95–100%, more likely than not >50–100% and extremely unlikely 0–5%) may also be used when appropriate. Assessed likelihood is typeset in italics (e.g., *very likely*). This Report also uses the term ‘likely range’ to indicate that the assessed likelihood of an outcome lies within the 17–83% probability range.

and recreational fishing activities to shift poleward and diversify harvests (*high confidence*). Climate change is increasing the geographic spread and risk of marine-borne pathogens like *Vibrio* sp. (*very high confidence*), which endanger human health and decrease provisioning and cultural ecosystem services (*high confidence*). Interacting climate-induced drivers and non-climate drivers are enhancing movement and bioaccumulation of toxins and contaminants into marine food webs (*medium evidence, high agreement*), and increasing salinity of coastal waters, aquifers and soils (*very high confidence*), which endangers human health (*very high confidence*). Combined climate-induced drivers and non-climate drivers also expose densely populated coastal zones to flooding (*high confidence*) and decrease physical protection of people, property and culturally important sites (*very high confidence*). {3.4.2.10, 3.5.3, 3.5.5, 3.5.5.3, 3.5.6, Cross-Chapter Box SLR in Chapter 3}

#### *Projections: vulnerabilities, risks and impacts*

**3**  
**Ocean conditions are projected to continue diverging from a pre-industrial state (*virtually certain*), with the magnitude of warming, acidification, deoxygenation, sea level rise and other climate-induced drivers depending on the emission scenario (*very high confidence*), and to increase risk of regional extirpations and global extinctions of marine species (*medium confidence*).** Marine species richness near the equator and in the Arctic is projected to continue declining, even with less than 2°C warming by the end of the century (*medium confidence*). In the deep ocean, all global warming levels will cause faster movements of temperature niches by 2100 than those that have driven extensive reorganisation of marine biodiversity at the ocean surface over the past 50 years (*medium confidence*). At warming levels beyond 2°C by 2100, risks of extirpation, extinction and ecosystem collapse escalate rapidly (*high confidence*). Paleorecords indicate that at extreme global warming levels (>5.2°C), mass extinction of marine species may occur (*medium confidence*). {Box 3.2, 3.2.2.1, 3.4.2.5, 3.4.2.10, 3.4.3.3, Cross-Chapter Box PALEO in Chapter 1}

**Climate impacts on ocean and coastal ecosystems will be exacerbated by increases in intensity, reoccurrence and duration of marine heatwaves (*high confidence*), in some cases, leading to species extirpation, habitat collapse or surpassing ecological tipping points (*very high confidence*).** Some habitat-forming coastal ecosystems including many coral reefs, kelp forests and seagrass meadows, will undergo irreversible phase shifts due to marine heatwaves with global warming levels >1.5°C and are at high risk this century even in <1.5°C scenarios that include periods of temperature overshoot beyond 1.5°C (*high confidence*). Under SSP1-2.6, coral reefs are at risk of widespread decline, loss of structural integrity and transitioning to net erosion by mid-century due to increasing intensity and frequency of marine heatwaves (*very high confidence*). Due to these impacts, the rate of sea level rise is *very likely* to exceed that of reef growth by 2050, absent adaptation. Other coastal ecosystems, including kelp forests, mangroves and seagrasses, are vulnerable to phase shifts towards alternate states as marine heatwaves intensify (*high confidence*). Loss of kelp forests are expected to be greatest at the low-latitude warm edge of species' ranges (*high confidence*). {3.4.2.1, 3.4.2.3, 3.4.2.5, 3.4.4}

**Escalating impacts of climate change on marine life will further alter biomass of marine animals (*medium confidence*), the timing of seasonal ecological events (*medium confidence*) and the geographic ranges of coastal and ocean taxa (*medium confidence*), disrupting life cycles (*medium confidence*), food webs (*medium confidence*) and ecological connectivity throughout the water column (*medium confidence*).** Multiple lines of evidence suggest that climate-change responses are *very likely* to amplify up marine food webs over large regions of the ocean. Modest projected declines in global phytoplankton biomass translate into larger declines of total animal biomass (by 2080–2099 relative to 1995–2014) ranging from (mean ± *very likely* range)  $-5.7 \pm 4.1\%$  to  $-15.5 \pm 8.5\%$  under SSP1-2.6 and SSP5-8.5, respectively (*medium confidence*). Projected declines in upper-ocean nutrient concentrations, *likely* associated with increases in stratification, will reduce carbon export flux to the mesopelagic and deep-sea ecosystems (*medium confidence*). This will lead to a decline in the biomass of abyssal meio- and macrofauna (by 2081–2100 relative to 1995–2014) by  $-9.8\%$  and  $-13.0\%$  under SSP1-2.6 and SSP5-8.5, respectively (*limited evidence*). By 2100,  $18.8 \pm 19.0\%$  to  $38.9 \pm 9.4\%$  of the ocean will *very likely* undergo a change of more than 20 d (advances and delays) in the start of the phytoplankton growth period under SSP1-2.6 and SSP5-8.5, respectively (*low confidence*). This altered timing increases the risk of temporal mismatches between plankton blooms and fish spawning seasons (*medium to high confidence*) and increases the risk of fish-recruitment failure for species with restricted spawning locations, especially in mid-to-high latitudes of the Northern Hemisphere (*low confidence*). Projected range shifts among marine species (*medium confidence*) suggest extirpations and strongly decreasing tropical biodiversity. At higher latitudes, range expansions will drive increased homogenisation of biodiversity. The projected loss of biodiversity ultimately threatens marine ecosystem resilience (*medium to high confidence*), with subsequent effects on service provisioning (*medium to high confidence*). {3.2.2.3, 3.4.2.10, 3.4.3.1–3.4.3.5, 3.5, WGI AR6 Section 2.3.4.2.3}

**Risks from sea level rise for coastal ecosystems and people are *very likely* to increase tenfold well before 2100 without adaptation and mitigation action as agreed by Parties to the Paris Agreement (*very high confidence*).** Sea level rise under emission scenarios that do not limit warming to 1.5°C will increase the risk of coastal erosion and submergence of coastal land (*high confidence*), loss of coastal habitat and ecosystems (*high confidence*) and worsen salinisation of groundwater (*high confidence*), compromising coastal ecosystems and livelihoods (*high confidence*). Under SSP1-2.6, most coral reefs (*very high confidence*), mangroves (*likely, medium confidence*) and salt marshes (*likely, medium confidence*) will be unable to keep up with sea level rise by 2050, with ecological impacts escalating rapidly beyond 2050, especially for scenarios coupling high emissions with aggressive coastal development (*very high confidence*). Resultant decreases in natural shoreline protection will place increasing numbers of people at risk (*very high confidence*). The ability to adapt to current coastal impacts, cope with future coastal risks and prevent further acceleration of sea level rise beyond 2050 depends on immediate implementation of mitigation and adaptation actions (*very high confidence*). {3.4.2.1, 3.4.2.4, 3.4.2.5, 3.4.2.6, 3.5.5.3, Cross-Chapter Box SLR in Chapter 3}

Climate change will alter many ecosystem services provided by marine systems (*high confidence*), but impacts to human communities will depend on people's overall vulnerability, which is strongly influenced by local context and development pathways (*very high confidence*). Catch composition and diversity of regional fisheries will change (*high confidence*), and fishers who are able to move, diversify and leverage technology to sustain harvests decrease their own vulnerability (*medium confidence*). Management that eliminates overfishing facilitates successful future adaptation of fisheries to climate change (*very high confidence*). Marine-dependent communities, including Indigenous Peoples and local peoples, will be at increased risk of losing cultural heritage and traditional seafood-sourced nutrition (*medium confidence*). Without adaptation, seafood-dependent people face increased risk of exposure to toxins, pathogens and contaminants (*high confidence*), and coastal communities face increasing risk from salinisation of groundwater and soil (*high confidence*). Early-warning systems and public education about environmental change, developed and implemented within the local and cultural context, can decrease those risks (*high confidence*). Coastal development and management informed by sea level rise projections will reduce the number of people and amount of property at risk (*high confidence*), but historical coastal development and policies impede change (*high confidence*). Current financial flows are globally uneven and overall insufficient to meet the projected costs of climate impacts on coastal and marine social–ecological systems (*very high confidence*). Inclusive governance that (a) accommodates geographically shifting marine life, (b) financially supports needed human transformations, (c) provides effective public education and (d) incorporates scientific evidence, Indigenous knowledge and local knowledge to manage resources sustainably shows greatest promise for decreasing human vulnerability to all of these projected changes in ocean and coastal ecosystem services (*very high confidence*). {3.5.3, 3.5.5, 3.5.6, 3.6.3, Box 3.4, Cross-Chapter Box ILLNESS in Chapter 2, Cross-Chapter Box SLR in Chapter 3}

#### *Solutions, trade-offs, residual risk, decisions and governance*

**Humans are already adapting to climate-driven changes in marine systems, and while further adaptations are required even under low-emission scenarios (*high confidence*), transformative adaptation will be essential under high-emission scenarios (*high confidence*).** Low-emission scenarios permit a wider array of feasible, effective and low-risk nature-based adaptation options (e.g., restoration, revegetation, conservation, early-warning systems for extreme events and public education) (*high confidence*). Under high-emission scenarios, adaptation options (e.g., hard infrastructure for coastal protection, assisted migration or evolution, livelihood diversification, migration and relocation of people) are more uncertain and require transformative governance changes (*high confidence*). Transformative climate adaptation will reinvent institutions to overcome obstacles arising from historical precedents, reducing current barriers to climate adaptation in cultural, financial and governance sectors (*high confidence*). Without transformation, global inequities will likely increase between regions (*high confidence*) and conflicts between jurisdictions may emerge and escalate. {3.5, 3.5.2, 3.5.5.3, 3.6, 3.6.2.1, 3.6.3.1, 3.6.3.2, 3.6.3.3, 3.6.4.1, 3.6.4.2, 3.6.5, Cross-Chapter Box SLR in Chapter 3, Cross-Chapter Box ILLNESS in Chapter 2}

Available adaptation options are unable to offset climate-change impacts on marine ecosystems and the services they provide (*high confidence*). Adaptation solutions implemented at appropriate scales, when combined with ambitious and urgent mitigation measures, can meaningfully reduce impacts (*high confidence*). Increasing evidence from implemented adaptations indicates that multi-level governance, early-warning systems for climate-associated marine hazards, seasonal and dynamic forecasts, habitat restoration, ecosystem-based management, climate-adaptive management and sustainable harvesting tend to be both feasible and effective (*high confidence*). Marine protected areas (MPAs), as currently implemented, do not confer resilience against warming and heatwaves (*medium confidence*) and are not expected to provide substantial protection against climate impacts past 2050 (*high confidence*). However, MPAs can contribute substantially to adaptation and mitigation if they are designed to address climate change, strategically implemented and well governed (*high confidence*). Habitat restoration limits climate-change-related loss of ecosystem services, including biodiversity, coastal protection, recreational use and tourism (*medium confidence*), provides mitigation benefits on local to regional scales (e.g., via carbon-storing 'blue carbon' ecosystems) (*high confidence*) and may safeguard fish-stock production in a warmer climate (*limited evidence*). Ambitious and swift global mitigation offers more adaptation options and pathways to sustain ecosystems and their services (*high confidence*). {3.4.2, 3.4.3.3, 3.5, 3.5.2, 3.5.3, 3.5.5.4, 3.5.5.5, 3.6.2.1, 3.6.2.2, 3.6.2.3, 3.6.3.1, 3.6.3.2, 3.6.3.3, 3.6.5, Figure 3.24, Figure 3.25}

**Nature-based solutions for adaptation of ocean and coastal ecosystems can achieve multiple benefits when well designed and implemented (*high confidence*), but their effectiveness declines without ambitious and urgent mitigation (*high confidence*).** Nature-based solutions, such as ecosystem-based management, climate-smart conservation approaches (i.e., climate-adaptive fisheries and conservation) and coastal habitat restoration, can be cost-effective and generate social, economic and cultural co-benefits while contributing to the conservation of marine biodiversity and reducing cumulative anthropogenic drivers (*high confidence*). The effectiveness of nature-based solutions declines with warming; conservation and restoration alone will be insufficient to protect coral reefs beyond 2030 (*high confidence*) and to protect mangroves beyond the 2040s (*high confidence*). The multidimensionality of climate-change impacts and their interactions with other anthropogenic stressors calls for integrated approaches that identify trade-offs and synergies across sectors and scales in space and time to build resilience of ocean and coastal ecosystems and the services they deliver (*high confidence*). {3.4.2, 3.5.2, 3.5.3, 3.5.5.3, 3.5.5.4, 3.5.5.5, 3.6.2.2, 3.6.3.2, 3.6.5, Figure 3.25, Table 3.SM.6}

**Ocean-focused adaptations, especially those that employ nature-based solutions, address existing inequalities, and incorporate just and inclusive decision-making and implementation processes, support the UN Sustainable Development Goals (SDGs) (*high confidence*).** There are predominantly positive synergies between adaptation options for Life Below Water (SDG14), Climate Action (SDG13) and social, economic and governance SDGs (SDG1–12, 16–17) (*high confidence*), but the ability of ocean adaptation to contribute to the

SDGs is constrained by the degree of mitigation action (*high confidence*). Furthermore, existing inequalities and entrenched practices limit effective and just responses to climate change in coastal communities (*high confidence*). Momentum is growing towards transformative international and regional governance that will support comprehensive, equitable ocean and coastal adaptation while also achieving SDG14 (*robust evidence*), without compromising achievement of other SDGs. {3.6.4.0, 3.6.4.2, 3.6.4.3, Figure 3.26}.

### 3.1 Point of Departure

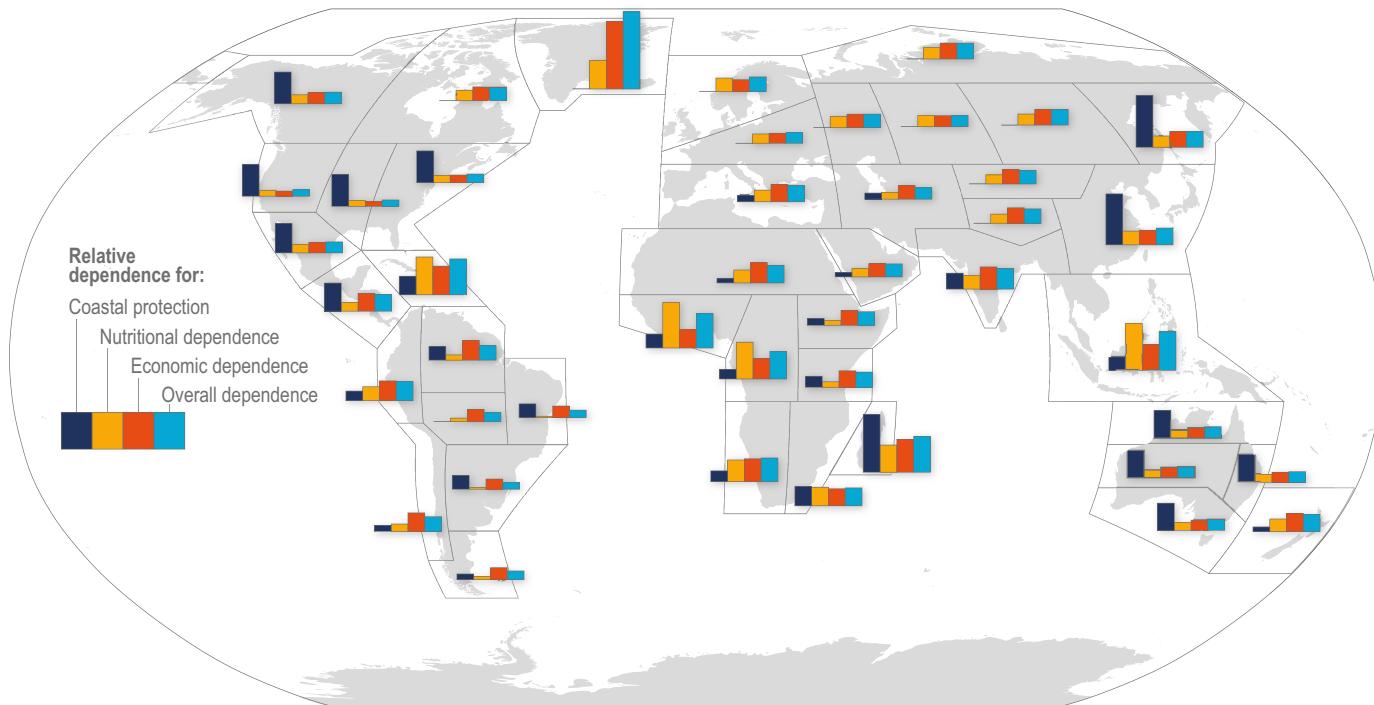
The ocean contains approximately 97% of Earth's water within a system of interconnected basins that cover 71% of its surface. Coastal systems mostly extend seaward from the high-water mark, or just beyond, to the edge of the continental shelf and include shores of soft sediments, rocky shores and reefs, embayments, estuaries, deltas and shelf systems. Oceanic systems comprise waters beyond the shelf edge, from ~200 m to nearly 11,000 m deep (Stewart and Jamieson, 2019), with an average depth of approximately 3700 m. The epipelagic zone, or upper 200 m of the ocean, is illuminated by sufficient sunlight to sustain photosynthesis that supports the rich marine food web. Below the epipelagic zone lies the barely lit mesopelagic zone (200–1000 m), the perpetually dark bathypelagic zone (depth >1000 m) and the deep seafloor (benthic ecosystems at depths >200 m), which spans rocky and sedimentary habitats on seamounts, mid-ocean ridges and canyons, abyssal plains and sedimented margins. Semi-enclosed seas (SES) include both coastal and oceanic systems.

The ocean sustains life on Earth by providing essential resources and modulating planetary flows of energy and materials. Together, harvests from the ocean and inland waters provide more than 20% of dietary animal protein for more than 3.3 billion people worldwide and livelihoods for about 60 million people (FAO, 2020b). The global ocean is centrally involved in sequestering anthropogenic atmospheric CO<sub>2</sub> and recycling many elements, and it regulates the global climate system

by redistributing heat and water (WGI AR6 Chapter 9; Fox-Kemper et al., 2021). The ocean also provides a wealth of aesthetic and cultural resources (Barbier et al., 2011), contains vast biodiversity (Appeltans et al., 2012), supports more animal biomass than on land (Bar-On et al., 2018) and produces at least half the world's photosynthetic oxygen (Field et al., 1998). Ecosystem services (Annex II: Glossary) delivered by ocean and coastal ecosystems support humanity by protecting coastlines, providing nutrition and economic opportunities (Figure 3.1; Selig et al., 2019) and providing many intangible benefits. Even though ecosystem services and biodiversity underpin human well-being and support climate mitigation and adaptation (Pörtner et al., 2021b), there are also ethical arguments for preserving biodiversity and ecosystem functions regardless of the beneficiary (e.g., Taylor et al., 2020). This chapter assesses the impact of climate change on the full spectrum of ocean and coastal ecosystems, on their services and on related human activities, and it assesses marine-related opportunities within both ecological and social systems to adapt to climate change.

Previous IPCC Assessment Reports (IPCC, 2014b; IPCC, 2014c; IPCC, 2018; IPCC, 2019b) have expressed growing confidence in the detection of climate-change impacts in the ocean and their attribution to anthropogenic greenhouse gas emissions. Heat and CO<sub>2</sub> taken up by the ocean (*high to very high confidence*) (IPCC, 2021b) directly affect marine systems, and the resultant "climatic impact-drivers (CIDs) (e.g., ocean temperature and heatwaves, sea level, dissolved oxygen levels, acidification; Annex II: Glossary, WGI Figure SPM.9; IPCC, 2021b)

#### Estimated relative human dependence on marine ecosystems



**Figure 3.1 | Estimated relative human dependence on marine ecosystems for coastal protection, nutrition, fisheries economic benefits and overall.** Each bar represents an index value that semi-quantitatively integrates the magnitude, vulnerability to loss and substitutability of the benefit. Indices synthesize information on people's consumption of marine protein and nutritional status, gross domestic product, fishing revenues, unemployment, education, governance and coastal characteristics. Overall dependence is the mean of the three index values after standardisation from 0–1. (Details regarding component indices are found in Table 1 and Supplementary Material of Selig et al., 2019.) The overall index does not include the economic benefits from tourism or other ocean industries, and data limitations prevented including artisanal or recreational fisheries or the protective impact of salt marshes (Selig et al., 2019). Values for reference regions established in the WGI AR6 Atlas (Gutiérrez et al., 2021) were computed as area-weighted means from original country-level data (Table S6 in Selig et al., 2019).

also influence ocean and coastal systems (Section 3.2; Cross-Chapter Box SLR in Chapter 3; Cross-Chapter Box EXTREMES in Chapter 2; Figure 3.SM.1), from individual biophysical processes to dependent human activities. Several marine outcomes of CIDs are themselves drivers of ecological change (e.g., climate velocities, stratification, sea ice changes). This chapter updates and extends the assessment of SROCC (IPCC, 2019b) and WGI AR6 by assessing the ecosystem effects of the CIDs in WGI AR6 Figure SPM.9 (IPCC, 2021b) and their biologically relevant marine outcomes (detailed in Section 3.2), which are referred to collectively hereafter as ‘climate-induced drivers’<sup>4</sup>.

Detrimental human impacts on ocean and coastal ecosystems are not only caused by climate. Other anthropogenic activities are increasingly affecting the physical, chemical and biological conditions of the ocean (Doney, 2010; Halpern et al., 2019), and these ‘non-climate drivers’<sup>5</sup> also alter marine ecosystems and their services. Fishing and other extractive activities are major non-climate drivers in many ocean and coastal systems (Steneck and Pauly, 2019). Many activities, such as coastal development, shoreline hardening and habitat destruction, physically alter marine spaces (Suchley and Alvarez-Filip, 2018; Ducrotoy et al., 2019; Leo et al., 2019; Newton et al., 2020; Raw et al., 2020). Other human activities decrease water quality by overloading coastal water with terrestrial nutrients (eutrophication) and by releasing runoff containing chemical, biological and physical pollutants, toxins, and pathogens (Jambeck et al., 2015; Luek et al., 2017; Breitburg et al., 2018; Froelich and Daines, 2020). Some human activities disturb marine organisms by generating excess noise and light (Davies et al., 2014; Duarte et al., 2021), while others decrease natural light penetration into the ocean (Wollschläger et al., 2021). Several anthropogenic activities alter processes that span the land–sea interface by changing coastal hydrology or causing coastal subsidence (Michael et al., 2017; Phlips et al., 2020; Bagheri-Gavkosh et al., 2021). Atmospheric pollutants can harm marine systems or unbalance natural marine processes (Doney et al., 2007; Hagens et al., 2014; Lamborg et al., 2014; Ito et al., 2016). Organisms frequently experience non-climate drivers simultaneously with climate-induced drivers (Section 3.4), and feedbacks may exist between climate-induced drivers and non-climate drivers that enhance the effects of climate change (Rocha et al., 2015; Ortiz et al., 2018; Wolff et al., 2018; Cabral et al., 2019; Bowler et al., 2020; Gissi et al., 2021). SROCC assessed with *high confidence* that reduction of pollution and other stressors, along with protection, restoration and precautionary management, supports ocean and coastal ecosystems and their services (IPCC, 2019b). This chapter examines the combined influence of climate-induced drivers and primary non-climate drivers on many ecosystems assessed.

Detecting changes and attributing them to specific drivers has been especially difficult in ocean and coastal ecosystems because drivers, responses and scales (temporal, spatial, organisational) often overlap and interact (IPCC, 2014b; IPCC, 2014c; Abram et al., 2019; Gissi et al., 2021). In addition, some marine systems have short, heterogeneous or geographically biased observational records, which exacerbate the interpretation challenge (Beaulieu et al., 2013; Christian, 2014; Huggel et al., 2016; Benway et al., 2019). It is even more challenging to detect

and attribute climate impacts on marine-dependent human systems, where culture, governance and society also strongly influence observed outcomes. To assess climate-driven change in natural and social systems robustly, IPCC reports rely on multiple lines of evidence, and the available types of evidence differ depending on the system under study (Section 1.3.2.1, Cross-Working Group Box ATTRIB). Lines of evidence used for ocean and coastal ecosystems for this and previous assessments include observed phenomena, laboratory and field experiments, long-term monitoring, empirical and dynamical model analyses, Indigenous knowledge (IK) and local knowledge (LK), and paleorecords (IPCC, 2014b; IPCC, 2014c; IPCC, 2019b). The growing body of climate research for ocean and coastal ecosystems and their services increasingly provides multiple independent lines of evidence whose conclusions support each other, raising the overall confidence in detection and attribution of impacts over time (Section 1.3.2.1, Cross-Working Group Box ATTRIB in Chapter 3).

Natural adaptation to climate change in ocean and coastal systems includes an array of responses taking place at scales from cells to ecosystems. Previous IPCC assessments have established that many marine species ‘have shifted their geographic ranges, seasonal activities, migration patterns, abundances and species interactions in response to climate change’ (*high confidence*) (IPCC, 2014b; IPCC, 2014c), which has had global impacts on species composition, abundance and biomass, and on ecosystem structure and function (*medium confidence*) (IPCC, 2019b). Warming and acidification have affected coastal ecosystems in concert with non-climate drivers (*high confidence*), which have affected habitat area, biodiversity, ecosystem function and services (*high confidence*) (IPCC, 2019b). Confidence has grown in these assessments over time as observational datasets have lengthened and other lines of evidence have corroborated observations. AR5 and SROCC assessed how physiological sensitivity to climate-induced drivers is the underlying cause of most marine organisms’ vulnerability to climate (*high confidence*) (Pörtner et al., 2014; Bindoff et al., 2019a). Since those assessments, more evidence supports the empirical physiological models of tolerance and plasticity (Sections 3.3.2, 3.3.4) and of interactions among multiple (climate and non-climate) drivers at individual to ecosystem scales (Sections 3.3.3, 3.4.5). New experimental evidence about evolutionary adaptation (Section 3.3.4) bolsters previous assessments that adaptation options to climate change are limited for eukaryotic organisms. Tools such as ecosystem models can now constrain probable ecosystem states (Sections 3.3.4, 3.3.5, 3.4). Observations have increased understanding of how extreme events affect individuals, populations and ecosystems, helping refine understanding of both ecological tolerance to climate impacts and ecological transformations (Section 3.4).

Human adaptation to climate impacts on ocean and coastal systems spans a variety of actions that change human activity to maintain marine ecosystem services. After AR5 concluded that coastal adaptation could reduce the effects of climate impacts on coastal human communities (*high agreement, limited evidence*) (Wong et al., 2014), SROCC confirmed that mostly risk-reducing ocean and coastal adaptation responses were underway (Bindoff et al., 2019a). However,

<sup>4</sup> We henceforth use the term ‘climate-induced drivers’ in reference to all drivers of ecological change that are related directly to climate change (IPCC, 2021a) as well as those that emerge in response to CIDs.

<sup>5</sup> We henceforth use the term ‘non-climate drivers’ in reference to drivers of ecological change that are not caused by climate change.

## Frequently Asked Questions

**FAQ 3.1 | How do we know which changes to marine ecosystems are specifically caused by climate change?**

*To attribute changes in marine ecosystems to human-induced climate change, scientists use paleorecords (reconstructing the links between climate, evolutionary and ecological changes in the geological past), contemporary observations (assessing current climate and ecological responses in the field and through experiments) and models. We refer to these as multiple lines of evidence, meaning that the evidence comes from diverse approaches, as described below.*

Emissions of greenhouse gases like carbon dioxide from human activity cause ocean warming, acidification, oxygen loss, and other physical and chemical changes that are affecting marine ecosystems around the world. At the same time, natural climate variability and direct human impacts, such as overfishing and pollution, also affect marine ecosystems locally, regionally and globally. These climate and non-climate impact drivers counteract each other, add up or multiply to produce smaller or larger changes than expected from individual drivers. Attribution of changes in marine ecosystems requires evaluating the often-interacting roles of natural climate variability, non-climate drivers, and human-induced climate change. To do this work, scientists use

- paleorecords: reconstructing the links between climate and evolutionary and ecological changes of the past;
- contemporary observations: assessing current climate and ecological responses;
- manipulation experiments: measuring responses of organisms and ecosystems to different climate conditions; and
- models: testing whether we understand how organisms and ecosystems are impacted by different stressors, and quantifying the relative importance of different stressors.

Paleorecords can be used to trace the correlation between past changes in climate and marine life. Paleoclimate is reconstructed from the chemical composition of shells and teeth or from sediments and ice cores. Changes to sea life signalled by changing biodiversity, extinction or distributional shifts are reconstructed from fossils. Using large datasets, we can infer the effects of climate change on sea life over relatively long time scales—usually hundreds to millions of years. The advantage of paleorecords is that they provide insights into how climate change affects life from organisms to ecosystems, without the complicating influence of direct human impacts. A key drawback is that the paleo and modern worlds do not have fully comparable paleoclimate regimes, dominant marine species and rates of climate change. Nevertheless, the paleorecord can be used to derive fundamental rules by which organisms, ecosystems, environments and regions are typically most affected by climate change. For example, the paleorecord shows that coral reefs repeatedly underwent declines during past warming events, supporting the inference that corals may not be able to adapt to current climate warming.

Contemporary observations over recent decades allow scientists to relate the status of marine species and ecosystems to changes in climate or other factors. For example, scientists compile large datasets to determine whether species usually associated with warm water are appearing in traditionally cool-water areas that are rapidly warming. A similar pattern observed in multiple regions and over several decades (i.e., longer than time scales of natural variability) provides confidence that climate change is altering community structure. This evidence is weighed against findings from other approaches, such as manipulation experiments, to provide a robust picture of climate-change impacts in the modern ocean.

In manipulation experiments, scientists expose organisms or communities of organisms to multiple stressors, for example, elevated CO<sub>2</sub>, high temperature, or both, based on values drawn from future climate projections. Such experiments will involve multiple treatments (e.g., in different aquarium tanks) in which organisms are exposed to different combinations of the stressors. This approach enables scientists to understand the effects of individual stressors as well as their interactions to explore physiological thresholds of marine organisms and communities. The scale of manipulation experiments can range from small tabletop tanks to large installations or natural ocean experiments involving tens of thousands of litres of water.

Ecological effects of climate change are also explored within models developed from fundamental scientific principles and observations. Using these numerical representations of marine ecosystems, scientists can explore how different levels of climate change and non-climate stressors influence species and ecosystems at scales not possible with experiments. Models are commonly used to simulate the ecological response to climate change over recent decades and centuries. Convergence between the model results and the observations suggests that our understanding of the key processes is sufficient to attribute the observed ecological changes to climate change, and to use the models to project future ecological changes. Differences between model results and observations indicate gaps in knowledge to be filled in order to better detect and attribute the impacts of climate change on marine life.

## Box FAQ 3.1 (continued)

Using peer-reviewed research spanning the full range of scientific approaches (paleorecords, observations, experiments and models), we can assess the level of confidence in the impact of climate change on observed modifications in marine ecosystems. We refer to this as multiple lines of evidence, meaning that the evidence comes from the diverse approaches described above. This allows policymakers and managers to address the specific actions needed to reduce climate change and other impacts.

### Examples of well-known impacts of anthropogenic climate change

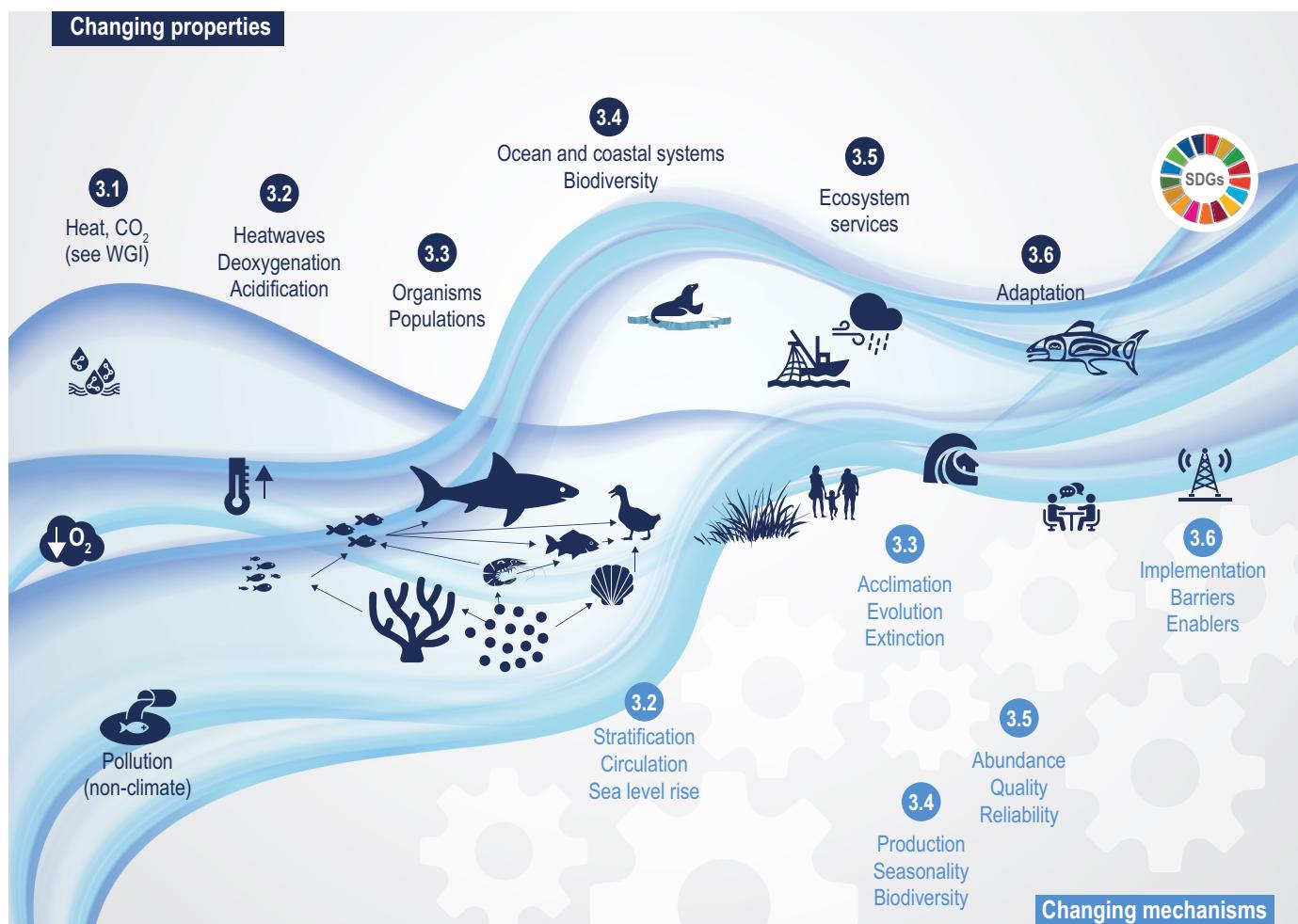
Impacts	Evidence of impacts	Examples of nature-based adaptation solutions
<b>Coral reefs</b> 	 Paleorecord   Observations   Experiments   Model	Restoration and conservation
<b>Mangroves</b> 	 Paleorecord   Observations   Experiments   Model	Restoration and conservation
<b>Beaches</b> 	 Observations   Experiments   Paleorecord   Model	Recovery of sand dunes
<b>Fisheries</b> 	 Observations   Experiments   Paleorecord   Model	Ecosystem-based management
<b>Evidence availability</b>	 Robust  Medium  Limited	

**Figure FAQ3.1.1 | Examples of well-known impacts of anthropogenic climate change and associated nature-based adaptation.** To attribute changes in marine ecosystems to anthropogenic climate change, scientists use multiple lines of evidence including paleorecords, contemporary observations, manipulation experiments and models.

overlapping climate-induced drivers and non-climate drivers confound implementation and assessment of the success of marine adaptation, revealing the complexity of attempting to maintain marine ecosystems and services through adaptation. SROCC assessed with *high confidence* that while the benefits of many locally implemented adaptations exceed their disadvantages, others are marginally effective and have large disadvantages, and overall, adaptation has a limited ability to reduce the probable risks from climate change, being at best a temporary solution (Bindoff et al., 2019a). SROCC also concluded that a portfolio of many different types of adaptation actions, effective and inclusive governance, and mitigation must be combined for successful adaptation (Bindoff et al., 2019a). The portfolio of adaptation measures has now been defined (Section 3.6.2), and individual and combined adaptation solutions have been implemented in several marine sectors (Section 3.6.3). Delays in marine adaptation have been partly attributed to the complexity of ocean governance (Section 3.6.4; Cross-Chapter Box 3 and Figure CB3.1 in Abram et al., 2019) and to the low priority accorded the ocean in international development goals (Nash et al., 2020), but in recent years the ocean is being increasingly incorporated in international climate policy and multilateral environmental agreements (Section 3.6.4).

This chapter assesses the current understanding of climate-induced drivers, ecological vulnerability and adaptability, risks to coastal and ocean ecosystems, and human vulnerability and adaptation to resulting changes in ocean benefits, now and in the future (Figure 3.2). It starts by assessing the biologically relevant outcomes of anthropogenic climate-induced drivers (Section 3.2). Next, it sets out the mechanisms that determine the responses of ocean and coastal organisms to individual and combined drivers from the genetic to the ecosystem level (Section 3.3). This supports a detailed assessment of the observed and projected responses of coastal and ocean ecosystems to these hazards, placing them in context using the paleorecord (Section 3.4). These observed and projected impacts are used to quantify consequent risks to delivery of ecosystem services and the socioeconomic sectors that depend on them, with attention to the vulnerability, resilience and adaptive capacity of social–ecological systems (Section 3.5). The chapter concludes by assessing the state of adaptation and governance actions available to address these emerging threats while also advancing human development (Section 3.6). Abbreviations used repeatedly in the chapter are defined in Table 3.1.

## WGII AR6 Chapter 3 concept map



**Figure 3.2 | WGII AR6 Chapter 3 concept map.** Climate changes both the properties (top of wave; Sections 3.1–3.6) and the mechanisms (below wave; Sections 3.2–3.6) that influence the ocean and coastal social–ecological system. The Sustainable Development Goals (top right) represent ideal outcomes and achievement of equitable, healthy and sustainable ocean and coastal social–ecological systems.

**Table 3.1** | Abbreviations frequently used in this chapter, with brief definitions

Abbreviation	Definition
ABNJ	Areas beyond national jurisdiction: the water column beyond the exclusive economic zone called the high seas and the seabed beyond the limits of the continental shelf; established in conformity with United Nations Convention on the Law of the Sea
AMOC	Atlantic meridional overturning circulation (WGI AR6 Glossary, IPCC, 2021a)
AR5	The IPCC Fifth Assessment Report (IPCC, 2013; IPCC, 2014b; IPCC, 2014c; IPCC, 2014d)
CBD	Convention on Biological Diversity: an international legal instrument that has been ratified by 196 nations to conserve biological diversity, sustainably use its components and share its benefits fairly and equitably
CE	Common era
CID	Climatic impact-driver (WGI AR6 Glossary, IPCC, 2021a)
CMIP5, CMIP6	The Coupled Model Intercomparison Project, Phase 5 or 6 (WGI AR6 Glossary, IPCC, 2021a)
EbA	Ecosystem-based adaptation: the use of ecosystem management activities to increase the resilience and reduce the vulnerability of people and ecosystems to climate change
EBUS	Eastern boundary upwelling system (WGI AR6 Glossary, IPCC, 2021a)
EEZ	Exclusive economic zone: the area from the coast to 200 nautical miles (370 km) off the coast, where a nation exercises its sovereign rights and exclusive management authority
ESM	Earth system model: a coupled atmosphere–ocean general circulation model (AOGCM, WGI AR6 Glossary, IPCC, 2021a) in which a representation of the carbon cycle is included, allowing for interactive calculation of atmospheric CO <sub>2</sub> or compatible emissions
Fish-MIP	The Fisheries and Marine Ecosystem Model Intercomparison Project: a component of the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) that explores the long-term impacts of climate change on fisheries and marine ecosystems using scenarios from CMIP models
GMSL/GMSLR	Global mean sea level/global mean sea level rise (sea level change, WGI AR6 Glossary, IPCC, 2021a)
HAB	Harmful algal bloom: an algal bloom composed of phytoplankton known to naturally produce biotoxins that are harmful to the resident population as well as humans
ICZM	Integrated coastal zone management: a dynamic, multidisciplinary and iterative process to promote sustainable management of coastal zones (European Environmental Agency)
IKLK	Indigenous knowledge and local knowledge (SROCC Glossary, IPCC, 2019a)
MHW	Marine heatwaves (WGI AR6 Glossary, IPCC, 2021a)
MPA	Marine protected area: an area-based management approach, commonly intended to conserve, preserve or restore biodiversity and habitat, protect species or manage resources (especially fisheries)
NbS	Nature-based Solution: actions to protect, sustainably manage and restore natural or modified ecosystems that address societal challenges effectively and adaptively, simultaneously providing human well-being and biodiversity benefits (IUCN, 2016)
NDC	Nationally determined contribution by parties to the Paris Agreement
NPP	Net primary production: the difference between how much CO <sub>2</sub> vegetation takes in during photosynthesis (gross primary production) and how much CO <sub>2</sub> the plants release during respiration
OECM	Other effective area-based conservation measures: a conservation designation for areas that are achieving the effective <i>in situ</i> conservation of biodiversity outside of protected areas
OMZ	Oxygen minimum zone (WGI AR6 Glossary, IPCC, 2021a)
pCO <sub>2</sub>	Partial pressure of carbon dioxide. For seawater, pCO <sub>2</sub> is used to measure the amount of carbon dioxide dissolved in seawater.
pH	Potential of hydrogen (WGI AR6 Glossary, IPCC, 2021a)
POC	Particulate organic carbon: a fraction of total organic carbon operationally defined as that which does not pass through a filter pore size $\geq 0.2 \mu\text{m}$
SDG	Sustainable Development Goals: the 17 global goals for development for all countries established by the United Nations through a participatory process and elaborated in the 2030 Agenda for Sustainable Development
SES	Semi-enclosed sea: a gulf, basin or sea surrounded by land and connected to another sea by a narrow outlet
SIDS	Small Island Developing States (WGI AR6 Glossary, IPCC, 2021a)
SLR/RSLR/RLS	Sea level rise/relative sea level rise/relative sea level (sea level change, WGI AR6 Glossary, IPCC, 2021a)
SR15	The IPCC Special Report on 1.5°C (IPCC, 2018)
SROCC	The IPCC Special Report on the Ocean and Cryosphere in a Changing Climate (IPCC, 2019b)
SSP/RCP	Shared Socioeconomic Pathway/Representative Concentration Pathway (Pathways; IPCC, 2021a)
SST	Sea surface temperature (WGI AR6 Glossary, IPCC, 2021a)
$\Omega_{\text{aragonite}}$	Saturation state of seawater with respect to the calcium carbonate mineral aragonite, used as a proxy measurement for ocean acidification

**Table 3.2 |** Overview of the main global ocean climatic impact-drivers and their observed and projected trends from WGI AR6, with corresponding confidence levels and links to WGI chapters where these trends are assessed in detail

Climatic impact-drivers (hazards)	Observed trends over the historical period	WGI section	Projected trends over the 21st century	WGI section
<i>Ocean temperature</i>				
Ocean warming	'At the ocean surface, temperature has on average increased by 0.88 [0.68–1.01] °C from 1850–1900 to 2011–2020.'	2.3.3.1, 9.2.1 (Fox-Kemper et al., 2021; Gulev et al., 2021)	Ocean warming will continue over the 21st century ( <i>virtually certain</i> ), with the rate of global ocean warming starting to be scenario-dependent from about the mid-21st century ( <i>medium confidence</i> ).	9.2.1 (Fox-Kemper et al., 2021)
Marine heatwaves (MHWs)	MHWs became more frequent ( <i>high confidence</i> ), more intense and longer ( <i>medium confidence</i> ) over the 20th and early 21st centuries.	Box 9.2 (Fox-Kemper et al., 2021)	MHWs will become '4 [2–9, <i>likely range</i> ] times more frequent in 2081–2100 compared with 1995–2014 under SSP1-2.6, and 8 [3–15, <i>likely range</i> ] times more frequent under SSP5-8.5.'	Box 9.2 (Fox-Kemper et al., 2021)
Climate velocities	Not assessed in WGI		Not assessed in WGI	
<i>Sea level</i>				
Global mean sea level (GMSL)	'Since 1901, GMSL has risen by 0.20 [0.15–0.25] m', and the rate of rise is accelerating.	2.3.3, 9.6.1 (Fox-Kemper et al., 2021; Gulev et al., 2021)	There will be continued rise in GMSL throughout the 21st century under all assessed SSPs ( <i>virtually certain</i> ).	4.3.2.2, 9.6.3 (Fox-Kemper et al., 2021; Lee et al., 2021)
Extreme sea levels	Relative sea level rise is driving a global increase in the frequency of extreme sea levels ( <i>high confidence</i> ).	9.6.4 (Fox-Kemper et al., 2021)	Rising mean relative sea level will continue to drive an increase in the frequency of extreme sea levels ( <i>high confidence</i> ).	9.6.4 (Fox-Kemper et al., 2021)
<i>Ocean circulation</i>				
Ocean stratification	'The upper ocean has become more stably stratified since at least 1970 [...] ( <i>virtually certain</i> ).'	9.2.1.3 (Fox-Kemper et al., 2021)	'Upper-ocean stratification will continue to increase throughout the 21st century ( <i>virtually certain</i> ).'	9.2.1.3 (Fox-Kemper et al., 2021)
Eastern boundary upwelling systems	'Only the California current system has experienced some large-scale upwelling-favourable wind intensification since the 1980s ( <i>medium confidence</i> ).'	9.2.5 (Fox-Kemper et al., 2021)	'Eastern boundary upwelling systems will change, with a dipole spatial pattern within each system of reduction at low latitude and enhancement at high latitude ( <i>high confidence</i> ).'	9.2.5 (Fox-Kemper et al., 2021)
Atlantic overturning circulation (AMOC)	There is <i>low confidence</i> in reconstructed and modelled AMOC changes for the 20 <sup>th</sup> century.	2.3.3.4, 9.2.3 (Fox-Kemper et al., 2021; Gulev et al., 2021)	The AMOC will decline over the 21st century ( <i>high confidence</i> , but <i>low confidence</i> for quantitative projections).	4.3.2.3, 9.2.3 (Fox-Kemper et al., 2021; Lee et al., 2021)
<i>Sea ice</i>				
Arctic sea ice changes	'Current Arctic sea ice coverage levels are the lowest since at least 1850 for both annual mean and late-summer values ( <i>high confidence</i> ).'	2.3.2.1, 9.3.1 (Fox-Kemper et al., 2021; Gulev et al., 2021)	'The Arctic will become practically ice-free in September by the end of the 21st century under SSP2-4.5, SSP3-7.0 and SSP5-8.5[...] ( <i>high confidence</i> ).'	4.3.2.1, 9.3.1 (Fox-Kemper et al., 2021; Lee et al., 2021)
Antarctic sea ice changes	There is no global significant trend in Antarctic sea ice area from 1979 to 2020 ( <i>high confidence</i> ).	2.3.2.1, 9.3.2 (Fox-Kemper et al., 2021; Gulev et al., 2021)	There is <i>low confidence</i> in model simulations of future Antarctic sea ice.	9.3.2 (Fox-Kemper et al., 2021)
<i>Ocean chemistry</i>				
Changes in salinity	The 'large-scale, near-surface salinity contrasts have intensified since at least 1950 [...] ( <i>virtually certain</i> ).'	2.3.3.2, 9.2.2.2 (Fox-Kemper et al., 2021; Gulev et al., 2021)	'Fresh ocean regions will continue to get fresher and salty ocean regions will continue to get saltier in the 21st century ( <i>medium confidence</i> ).'	9.2.2.2 (Fox-Kemper et al., 2021)
Ocean acidification	Ocean surface pH has declined globally over the past four decades ( <i>virtually certain</i> ).	2.3.3.5, 5.3.2.2 (Canadell et al., 2021; Gulev et al., 2021)	Ocean surface pH will continue to decrease 'through the 21st century, except for the lower-emission scenarios SSP1-1.9 and SSP1-2.6 [...] ( <i>high confidence</i> ).'	4.3.2.5, 4.5.2.2, 5.3.4.1 (Lee et al., 2021; Canadell et al., 2021)
Ocean deoxygenation	Deoxygenation has occurred in most open ocean regions since the mid-20th century ( <i>high confidence</i> ).	2.3.3.6, 5.3.3.2 (Canadell et al., 2021; Gulev et al., 2021)	Subsurface oxygen content 'is projected to transition to historically unprecedented condition with decline over the 21st century ( <i>medium confidence</i> ).'	5.3.3.2 (Canadell et al., 2021)
Changes in nutrient concentrations	Not assessed in WGI		Not assessed in WGI	

## 3.2 Observed Trends and Projections of Climatic Impact-Drivers in the Global Ocean

### 3.2.1 Introduction

Climate change exposes ocean and coastal ecosystems to changing environmental conditions, including ocean warming, SLR, acidification, deoxygenation and other climatic impact-drivers (CIDs), which have distinct regional and temporal characteristics (Gruber, 2011; IPCC, 2018). This section aims to build on the WGI AR6 assessment (Table 3.2) to provide an ecosystem-oriented framing of CIDs. Updating SROCC, projected trends assessed here are based on a new range of scenarios (Shared Socioeconomic Pathways, SSPs), as used in the Coupled Model Intercomparison Project Phase 6 (CMIP6; Section 1.2.2).

### 3.2.2 Physical Changes

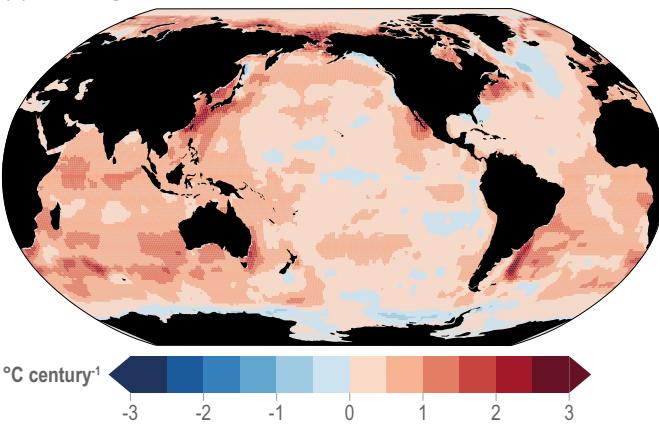
#### 3.2.2.1 Ocean Warming, Climate Velocities and Marine Heatwaves

Global mean SST has increased since the beginning of the 20th century by  $0.88^{\circ}\text{C}$  (*very likely* range:  $0.68\text{--}1.01^{\circ}\text{C}$ ), and it is *virtually certain* that the global ocean has warmed since at least 1971 (WGI AR6 Section 9.2; Fox-Kemper et al., 2021). A key characteristic of ocean temperature change relevant for ecosystems is climate velocity, a measure of the speed and direction at which isotherms move under climate change (Burrows et al., 2011), which gives the rate at which species must migrate to maintain constant climate conditions. It has been shown to be a useful and simple predictor of species distribution shifts in marine ecosystems (Chen et al., 2011; Pinsky et al., 2013; Lenoir et al., 2020). Median climate velocity in the surface ocean has been 21.7 km per decade since 1960, with higher values in the Arctic/sub-Arctic and within  $15^{\circ}$  of the Equator (Figure 3.3; Burrows et al., 2011). While climate velocity has been slower in the mesopelagic layer (200–1000 m) than in the epipelagic layer (0–200 m) over the past 50 years, it has been shown to be faster in the bathypelagic (1000–4000 m) and abyssopelagic (>4000 m) layers (Figure 3.4; Brito-Morales et al., 2020), suggesting that deep-ocean species could be as exposed to effects of warming as species in the surface ocean (Brito-Morales et al., 2020).

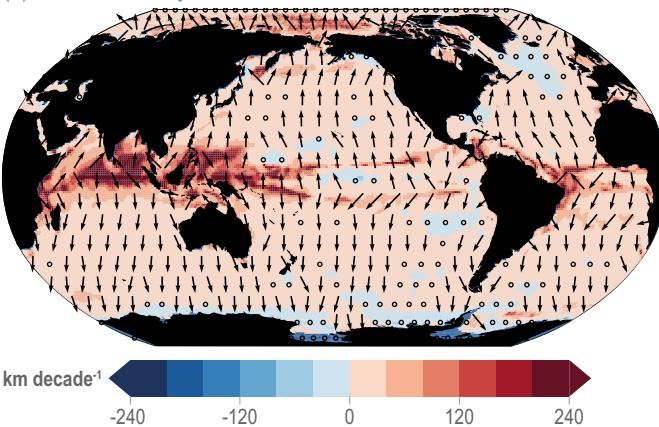
Marine heatwaves (MHWs) are periods of extreme seawater temperature relative to the long-term mean seasonal cycle, that persist for days to months, and that may carry severe consequences for marine ecosystems and their services (WGI AR6 Box 9.2; Hobday et al., 2016a; Smale et al., 2019; Fox-Kemper et al., 2021). MHWs became more frequent over the 20th century (*high confidence*) and into the beginning of the 21st century, approximately doubling in frequency (*high confidence*) and becoming more intense and longer since the 1980s (*medium confidence*) (WGI AR6 Box 9.2; Fox-Kemper et al., 2021). These trends in MHWs are explained by an increase in ocean mean temperatures (Oliver et al., 2018), and human influence has *very likely* contributed to 84–90% of them since at least 2006 (WGI AR6 Box 9.2; Fox-Kemper et al., 2021). The probability of occurrence (as well as duration and intensity) of the largest and most impactful MHWs that have occurred in the past 30 years has increased more than 20-fold due to anthropogenic climate change (Laufkötter et al., 2020).

### Observed surface ocean warming, surface climate velocity and reconstructed changes in marine heatwaves over the last 100 years

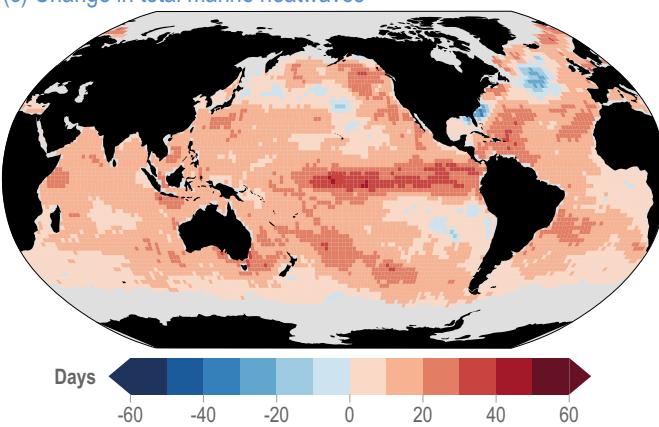
#### (a) Warming rate



#### (b) Climate velocity



#### (c) Change in total marine heatwaves



**Figure 3.3 | Observed surface ocean warming, surface climate velocity and reconstructed changes in marine heatwaves (MHWs) over the past 100 years.**  
 (a) Sea surface temperature trend (degrees Celsius per century) over 1925–2016 from Hadley Centre Sea Ice and Sea Surface Temperature 1.1 (HadISST1.1); (b) surface climate velocity (kilometres per decade) over 1925–2016 computed from HadISST1.1 and (c) change in total MHW days for the surface ocean over 1925–1954 to 1987–2016 based on monthly proxies. (Data from Oliver et al., 2018).

Ocean warming will continue over the 21st century (*virtually certain*), with the rate of global ocean warming starting to be scenario-dependent from about the mid-21st century (*medium confidence*). At the ocean surface, it is *virtually certain* that SST will continue to increase throughout the 21st century, with increasing hazards to many marine ecosystems (WGI AR6 Box 9.2; Fox-Kemper et al., 2021). The future global mean SST increase projected by CMIP6 models for the period 1995–2014 to 2081–2100 is  $0.86^{\circ}\text{C}$  (*very likely* range:  $0.43\text{--}1.47^{\circ}\text{C}$ ) under SSP1-2.6,  $1.51^{\circ}\text{C}$  ( $1.02\text{--}2.19^{\circ}\text{C}$ ) under SSP2-4.5,  $2.19^{\circ}\text{C}$  ( $1.56\text{--}3.30^{\circ}\text{C}$ ) under SSP3-7.0 and  $2.89^{\circ}\text{C}$  ( $2.01\text{--}4.07^{\circ}\text{C}$ ) under SSP5-8.5 (WGI AR6 Section 9.2.1; Fox-Kemper et al., 2021). Stronger surface warming occurs in parts of the tropics, in the North Pacific, and in the Arctic Ocean, where SST increases by  $>4^{\circ}\text{C}$  in 2080–2099 under SSP5-8.5 (Kwiatkowski et al., 2020). The CMIP6 climate models also project ocean warming at the seafloor, with the magnitude of projected changes being less than that of surface waters but having larger uncertainties (Kwiatkowski et al., 2020). The projected end-of-the-century warming in CMIP6 as reported here is greater than assessed with Coupled Model Intercomparison Project 5 (CMIP5) models in AR5 and in SROCC for similar radiative forcing scenarios (Figure 3.5; Kwiatkowski et al., 2020), because of greater climate sensitivity in the CMIP6 model ensemble than in CMIP5 (WGI AR6 Chapter 4; Forster et al., 2020; Lee et al., 2021).

Marine heatwaves will continue to increase in frequency, with a *likely* global increase of 2–9 times in 2081–2100 compared with 1995–2014

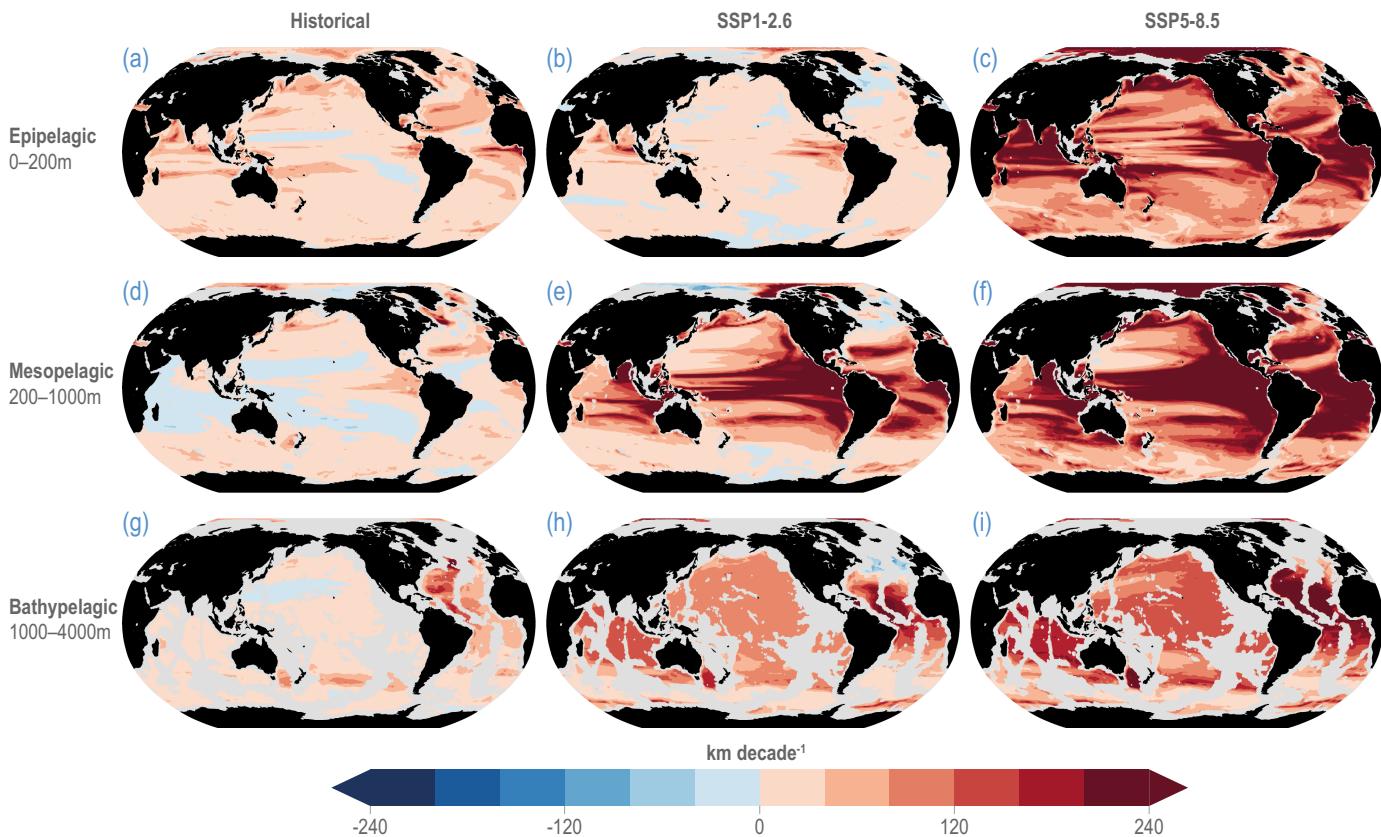
under SSP1-2.6, and 3–15 times under SSP5-8.5, with the largest increases in tropical and Arctic oceans (WGI AR6 Box 9.2; Frölicher et al., 2018; Fox-Kemper et al., 2021).

### 3.2.2.2 Sea Level Rise and Extreme Sea Levels

Global mean sea level (GMSL) (Cross-Chapter Box SLR in Chapter 3) has risen by about 0.20 m since 1901 and continues to accelerate (WGI AR6 Section 2.3.3.3; Church and White, 2011; Jevrejeva et al., 2014; Hay et al., 2015; Kopp et al., 2016; Dangendorf et al., 2017; WCRP Global Sea Level Budget Group, 2018; Kemp et al., 2018; Ablain et al., 2019; Gulev et al., 2021).

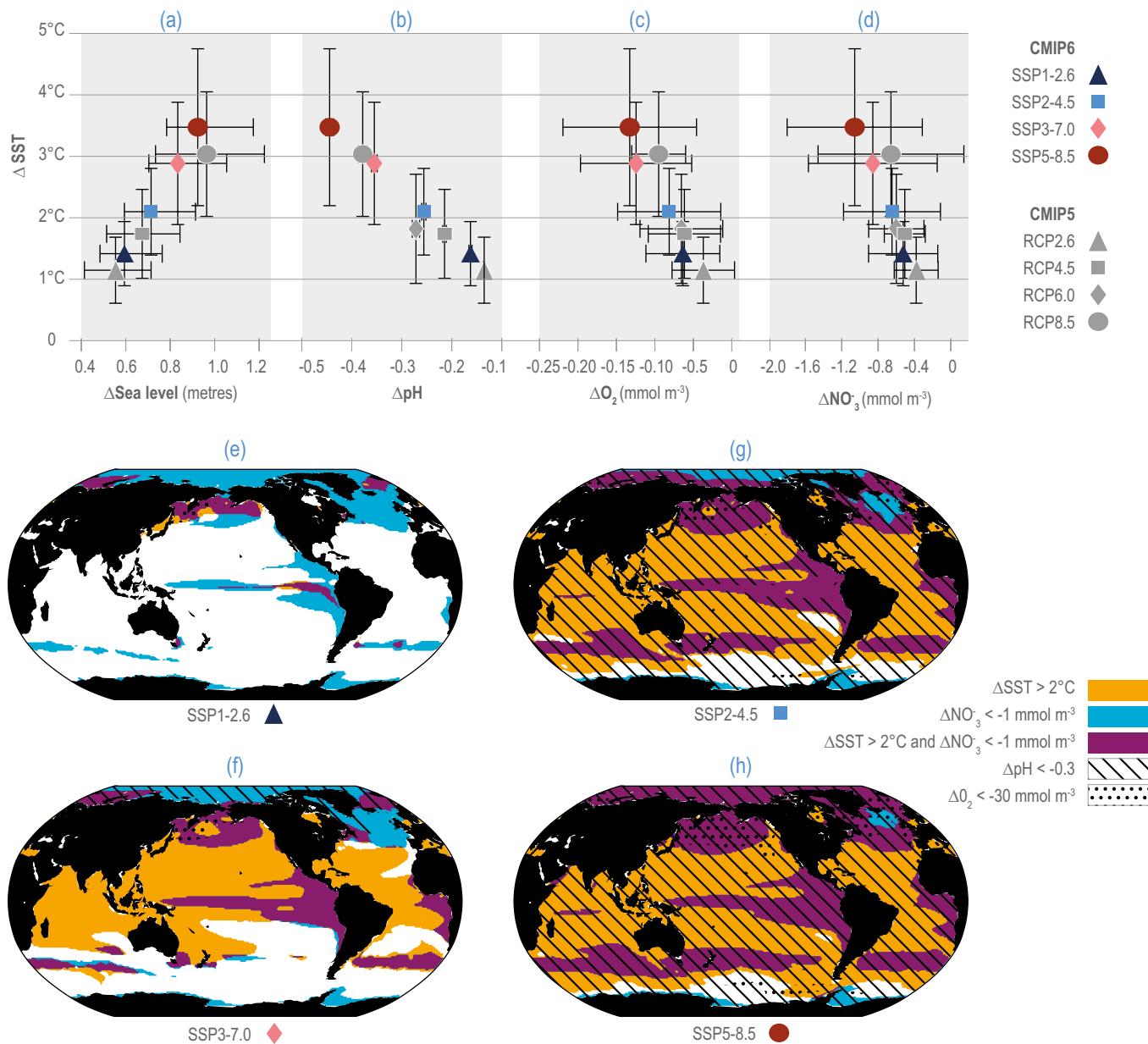
Most coastal ecosystems (mangroves, seagrasses, salt marshes, shallow coral reefs, rocky shores and sandy beaches) are affected by changes in relative sea level (RSL, the change in the mean sea level relative to the land; Section 3.4.2). Regional rates of RSL rise differ from the global mean due to a range of factors, including local subsidence driven by anthropogenic activities such as groundwater and hydrocarbon extraction (WGI AR6 Box 9.1; Fox-Kemper et al., 2021). In many deltaic regions, anthropogenic subsidence is currently the dominant driver of RSL rise (WGI AR6 Section 9.6.3.2; Tessler et al., 2018; Fox-Kemper et al., 2021). RSL rise is driving a global increase in the frequency of extreme sea levels (*high confidence*) (WGI AR6 Section 9.6.4.1; Fox-Kemper et al., 2021).

## Historical and projected climate velocity



**Figure 3.4 | Historical and projected climate velocity.** Climate velocities (in kilometres per decade) are shown for the (a,d,g) historical period (1965–2014), and the last 50 years of the 21st century (2051–2100), under (b,e,h) SSP1-2.6 and (c,f,i) SSP5-8.5. Also shown are the epipelagic (0–200 m), mesopelagic (200–1000 m) and bathypelagic (1000–4000 m) domains. Updated figure from Brito-Morales et al. (2020), with Coupled Model Intercomparison Project 6 models used in Kwiatkowski et al. (2020).

## Projected trends in climatic impact-drivers for ocean ecosystems



**Figure 3.5 | Projected trends in climatic impact-drivers for ocean ecosystems.** Panels (a,b,c,d) represent Coupled Model Intercomparison Project 5 (CMIP5) Representative Concentration Pathway (RCP) and CMIP6 Shared Socioeconomic Pathway (SSP) end-of-century changes in (a) global sea level; (b) average surface pH; (c) subsurface (100–600 m) dissolved oxygen concentration and (d) euphotic-zone (0–100 m) nitrate (NO<sub>3</sub>) concentration against anomalies in sea surface temperature. All anomalies are model-ensemble averages over 2080–2099 relative to the 1870–1899 baseline period (from Kwiatkowski et al., 2020), except for sea level, which shows model-ensemble median in 2100 relative to 1901 (from AR6 WGI Chapter 9). Error bars represent very likely ranges, except for SLR where they represent likely ranges. Very likely ranges for pH changes are too narrow to appear in the figure (see text). Panels (e,f,g,h) show regions where end-of-century projected CMIP6 surface warming exceeds 2°C, where surface ocean pH decline exceeds 0.3, where subsurface dissolved oxygen decline exceeds 30 mmol m<sup>-3</sup> and where euphotic-zone (0–100 m) nitrate decline exceeds 1 mmol m<sup>-3</sup> in (e) SSP1-2.6, (f) SSP2-4.5, (g) SSP3-7.0 and (h) SSP5-8.5. All anomalies are 2080–2099 relative to the 1870–1899 baseline period. (Modified from Kwiatkowski et al., 2020).

GMSL rise through the middle of the 21st century exhibits limited dependence on emissions scenario; between 1995–2014 and 2050, GMSL is likely to rise by 0.15–0.23 m under SSP1-1.9 and 0.20–0.30 m under SSP5-8.5 (WGI AR6 Section 9.6.3; Fox-Kemper et al., 2021). Beyond 2050, GMSL and RSL projections are increasingly sensitive to the differences among emission scenarios. Considering only processes in which there is at least medium confidence (e.g., thermal expansion, land-water storage, land-ice surface mass balance and some ice-sheet

dynamic processes), GMSL between 1995–2014 and 2100 is likely to rise by 0.28–0.55 m under SSP1-1.9, 0.33–0.61 m under SSP1-2.6, 0.44–0.76 m under SSP2-4.5, 0.55–0.90 m under SSP3-7.0 and 0.63–1.02 m under SSP5-8.5 (Figure 3.5). Under high-emission scenarios, ice-sheet processes in which there is low confidence and deep uncertainty might contribute more than one additional metre to GMSL rise by 2100 (WGI AR6 Chapter 9; Fox-Kemper et al., 2021).

Rising mean RSL will continue to drive an increase in the frequency of extreme sea levels (*high confidence*). The expected frequency of the current 1-in-100-year extreme sea level is projected to increase by a median of 20–30 times across tide-gauge sites by 2050, regardless of emission scenario (*medium confidence*). In addition, extreme-sea-level frequency may be affected by changes in tropical cyclone climatology (*low confidence*), wave climatology (*low confidence*) and tides (*high confidence*) associated with climate change and sea level change (WGI AR6 Section 9.6.4.2; Fox-Kemper et al., 2021).

### 3.2.2.3 Changes in Ocean Circulation, Stratification and Coastal Upwelling

Ocean circulation and its variations are key to the evolution of the physical, chemical and biological properties of the ocean. Vertical mixing and upwelling are critical factors affecting the supply of nutrients to the sunlit ocean and hence the magnitude of primary productivity. Ocean currents not only transport heat, salt, carbon and nutrients, but they also control the dispersion of many organisms and the connectivity between distant populations.

Ocean stratification is an important factor controlling biogeochemical cycles and affecting marine ecosystems. WGI AR6 Section 9.2.1.3 (Fox-Kemper et al., 2021) assessed that it is *virtually certain* that stratification in the upper 200 m of the ocean has been increasing since 1970. Recent evidence has strengthened estimates of the rate of change (Yamaguchi and Suga, 2019; Li et al., 2020a; Sallée et al., 2021), with an estimated increase of  $1.0 \pm 0.3\%$  (*very likely* range) per decade over the period 1970–2018 (*high confidence*) (WGI AR6 Section 9.2.1.3; Fox-Kemper et al., 2021), higher than assessed in SROCC. It is *very likely* that stratification in the upper few hundred metres of the ocean will increase substantially in the 21st century in all ocean basins, driven by intensified surface warming and near-surface freshening at high latitudes (WGI AR6 Section 9.2.1.3; Capotondi et al., 2012; Fu et al., 2016; Bindoff et al., 2019a; Kwiatkowski et al., 2020; Fox-Kemper et al., 2021).

Contrasting changes among the major eastern boundary coastal upwelling systems (EBUS) were identified in AR5 (Hoegh-Guldberg et al., 2014). While SROCC assessed with *high confidence* that three (Benguela, Peru-Humboldt, California) out of the four major EBUS have experienced upwelling-favourable wind intensification in the past 60 years (Sydeman et al., 2014; Bindoff et al., 2019a), WGI AR6 revisited this assessment based on evidence showing *low agreement* between studies that have investigated trends over past decades (Varela et al., 2015). WGI AR6 assessed that only the California Current system has undergone large-scale upwelling-favourable wind intensification since the 1980s (*medium confidence*) (WGI AR6 Section 9.2.1.5; García-Reyes and Largier, 2010; Seo et al., 2012; Fox-Kemper et al., 2021).

While no consistent pattern of contemporary changes in upwelling-favourable winds emerges from observation-based studies, numerical and theoretical work projects that summertime winds near poleward boundaries of upwelling zones will intensify, while winds near equatorward boundaries will weaken (*high confidence*) (WGI AR6 Section 9.2.3.5; García-Reyes et al., 2015; Rykaczewski et al., 2015; Wang et al., 2015; Aguirre et al., 2019; Fox-Kemper et al., 2021).

Nevertheless, projected future annual cumulative upwelling wind changes at most locations and seasons remain within  $\pm 10\text{--}20\%$  of present-day values (*medium confidence*) (WGI AR6 Section 9.2.3.5; Fox-Kemper et al., 2021).

Continuous observation of the Atlantic meridional overturning circulation (AMOC) has improved the understanding of its variability (Frajka-Williams et al., 2019), but there is *low confidence* in the quantification of AMOC changes in the 20th century because of *low agreement* in quantitative reconstructed and simulated trends (WGI AR6 Sections 2.3.3, 9.2.3.1; Fox-Kemper et al., 2021; Gulev et al., 2021). Direct observational records since the mid-2000s remain too short to determine the relative contributions of internal variability, natural forcing and anthropogenic forcing to AMOC change (*high confidence*) (WGI AR6 Sections 2.3.3, 9.2.3.1; Fox-Kemper et al., 2021; Gulev et al., 2021). Over the 21st century, AMOC will *very likely* decline for all SSP scenarios but will not involve an abrupt collapse before 2100 (WGI AR6 Sections 4.3.2, 9.2.3.1; Fox-Kemper et al., 2021; Lee et al., 2021).

### 3.2.2.4 Sea Ice Changes

Sea ice is a key driver of polar marine life, hosting unique ecosystems and affecting diverse marine organisms and food webs through its impact on light penetration and supplies of nutrients and organic matter (Arrigo, 2014). Since the late 1970s, Arctic sea ice area has decreased for all months, with an estimated decrease of 2 million km<sup>2</sup> (or 25%) for summer sea ice (averaged for August, September and October) in 2010–2019 as compared with 1979–1988 (WGI AR6 Section 9.3.1.1; Fox-Kemper et al., 2021). For Antarctic sea ice there is no significant global trend in satellite-observed sea ice area from 1979 to 2020 in either winter or summer, due to regionally opposing trends and large internal variability (WGI AR6 Section 9.3.2.1; Maksym, 2019; Fox-Kemper et al., 2021).

CMIP6 simulations project that the Arctic Ocean will *likely* become practically sea ice free (area below 1 million km<sup>2</sup>) for the first time before 2050 and in the seasonal sea ice minimum in each of the four emission scenarios SSP1-1.9, SSP1-2.6, SSP2-4.5 and SSP5-8.5 (Figure 3.7; WGI AR6 Section 9.3.2.2; Notz and SIMIP Community, 2020; Fox-Kemper et al., 2021). Antarctic sea ice area is also projected to decrease during the 21st century, but due to mismatches between model simulations and observations, combined with a lack of understanding of reasons for substantial inter-model spread, there is *low confidence* in model projections of future Antarctic sea ice changes, particularly at the regional level (WGI AR6 Section 9.3.2.2; Roach et al., 2020; Fox-Kemper et al., 2021).

### 3.2.3 Chemical Changes

#### 3.2.3.1 Ocean Acidification

The ocean's uptake of anthropogenic carbon affects its chemistry in a process referred to as ocean acidification, which increases the concentrations of aqueous CO<sub>2</sub>, bicarbonate and hydrogen ions, and decreases pH, carbonate ion concentrations and calcium carbonate mineral saturation states (Doney et al., 2009). Ocean acidification

affects a variety of biological processes with, for example, lower calcium carbonate saturation states reducing net calcification rates for some shell-forming organisms and higher CO<sub>2</sub> concentrations increasing photosynthesis for some phytoplankton and macroalgal species (Section 3.3.2).

Direct measurements of ocean acidity from ocean time series, as well as pH changes determined from other shipboard studies, show consistent decreases in ocean surface pH over the past few decades (*virtually certain*) (WGI AR6 Section 5.3.2.2; Takahashi et al., 2014; Bindoff et al., 2019a; Sutton et al., 2019; Canadell et al., 2021).

Since the 1980s, surface ocean pH has declined by a *very likely* rate of 0.016–0.020 per decade in the subtropics and 0.002–0.026 per decade in the subpolar and polar zones (WGI AR6 Section 5.3.2.2; Canadell et al., 2021). Typically, the pH of global surface waters has decreased from 8.2 to 8.1 since the pre-industrial era (1750 CE), a trend attributable to rising atmospheric CO<sub>2</sub> (*virtually certain*) (Orr et al., 2005; Jiang et al., 2019).

Ocean acidification is also developing in the ocean interior (*very high confidence*) due to the transport of anthropogenic CO<sub>2</sub> to depth by ocean currents and mixing (WGI AR6 Section 5.3.3.1; Canadell et al., 2021). There, it leads to the shoaling of saturation horizons of aragonite and calcite (*high confidence*) (WGI AR6 Section 5.3.3.1; Canadell et al., 2021), below which dissolution of these calcium carbonate minerals is thermodynamically favoured. The calcite or aragonite saturation horizons have migrated upwards in the North Pacific (1–2 m yr<sup>-1</sup> over 1991–2006) (Feely et al., 2012) and in the Irminger Sea (10–15 m yr<sup>-1</sup> for the aragonite saturation horizon over 1991–2016) (Perez et al., 2018). In some locations of the western Atlantic Ocean, calcite saturation depth has risen by ~300 m since the pre-industrial era due to increasing concentrations of deep-ocean dissolved inorganic carbon (Sulpis et al., 2018). In the Arctic, where some coastal surface waters are already undersaturated with respect to aragonite due to the degradation of terrestrial organic matter (Mathis et al., 2015; Semiletov et al., 2016), the deep aragonite saturation horizon shoaled on average 270 ± 60 m during 1765–2005 (Terhaar et al., 2020).

Detection and attribution of ocean acidification in coastal environments are more difficult than in the open ocean due to larger spatio-temporal variability of carbonate chemistry (Duarte et al., 2013; Laruelle et al., 2017; Torres et al., 2021) and to the influence of other natural acidification drivers such as freshwater and high-nutrient riverine inputs (Cai et al., 2011; Laurent et al., 2017; Fennel et al., 2019; Cai et al., 2020) or anthropogenic acidification drivers (Section 3.1) like atmospherically deposited nitrogen and sulphur (Doney et al., 2007; Hagens et al., 2014). Since AR5, the observing network in coastal oceans has expanded substantially, improving understanding of both the drivers and amplitude of observed variability (Sutton et al., 2016). Recent studies indicate that two more decades of observations may be required before anthropogenic ocean acidification emerges over natural variability in some coastal sites and regions (WGI AR6 Section 5.3.5.2; Sutton et al., 2019; Turk et al., 2019; Canadell et al., 2021).

Mean open-ocean surface pH is projected to decline by 0.08 ± 0.003 (*very likely range*), 0.17 ± 0.003, 0.27 ± 0.005 and 0.37 ± 0.007 pH

units in 2081–2100 relative to 1995–2014, for SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5, respectively (Figure 3.5; WGI AR6 Section 4.3.2; Kwiatkowski et al., 2020; Lee et al., 2021). Projected changes in surface pH are relatively uniform in contrast with those of other surface-ocean variables, but they are largest in the Arctic Ocean (Figure 3.6; WGI AR6 Section 5.3.4.1; Canadell et al., 2021). Similar declines in the concentration of carbonate ions are projected by Earth system models (ESMs; Bopp et al., 2013; Gattuso et al., 2015; Kwiatkowski et al., 2020). The North Pacific, the Southern Ocean and Arctic Ocean regions will become undersaturated for calcium carbonate minerals first (Orr et al., 2005; Pörtner et al., 2014). Concurrent impacts on the seasonal amplitude of carbonate chemistry variables are anticipated (i.e., increased amplitude for pCO<sub>2</sub> and hydrogen ions, decreased amplitude for carbonate ions; McNeil and Sasse, 2016; Kwiatkowski and Orr, 2018; Kwiatkowski et al., 2020).

Future declines in subsurface pH (Figure 3.6) will be modulated by changes in ocean overturning and water-mass subduction (Resplandy et al., 2013), and in organic matter remineralisation (Chen et al., 2017). In particular, decreases in pH will be less consistent at the seafloor than at the surface and will be linked to the transport of surface anomalies to depth. For example, >20% of the North Atlantic seafloor deeper than 500 m, including canyons and seamounts designated as marine protected areas (MPAs), will experience pH reductions >0.2 by 2100 under RCP8.5 (Gehlen et al., 2014). Changes in pH in the abyssal ocean (>3000 m deep) are greatest in the Atlantic and Arctic Oceans, with lesser impacts in the Southern and Pacific Oceans by 2100, mainly due to ventilation time scales (Sweetman et al., 2017).

### 3.2.3.2 Ocean Deoxygenation

Ocean deoxygenation, the loss of oxygen in the ocean, results from ocean warming, through a reduction in oxygen saturation, increased oxygen consumption, increased ocean stratification and ventilation changes (Keeling et al., 2010; IPCC, 2019a). In recent decades, anthropogenic inputs of nutrients and organic matter (Section 3.1) have increased the extent, duration and intensity of coastal hypoxia events worldwide (Diaz and Rosenberg, 2008; Rabalais et al., 2010; Breitburg et al., 2018), while pollution-induced atmospheric deposition of soluble iron over the ocean has accelerated open-ocean deoxygenation (Ito et al., 2016). Deoxygenation and acidification often coincide because biological consumption of oxygen produces CO<sub>2</sub>. Deoxygenation can have a range of detrimental effects on marine organisms and reduce the extent of marine habitats (Sections 3.3.2, 3.4.3.1; Vaquer-Sunyer and Duarte, 2008; Chu and Tunnicliffe, 2015).

Changes in ocean oxygen concentrations have been analysed from compilations of *in situ* data dating back to the 1960s (Helm et al., 2011; Ito et al., 2017; Schmidtko et al., 2017). SROCC concluded that a loss of oxygen had occurred in the upper 1000 m of the ocean (*medium confidence*), with a global mean decrease of 0.5–3.3% (*very likely range*) over 1970–2010 (Bindoff et al., 2019a). Based on new regional assessments (Queste et al., 2018; Bronselaer et al., 2020; Cummins and Ross, 2020; Stramma et al., 2020), WGI AR6 assesses that ocean deoxygenation has occurred in most regions of the open ocean since the mid-20th century (*high confidence*), but it is modified by climate variability on interannual and inter-decadal time scales

(medium confidence) (WGI AR6 Sections 2.3.3.6, 5.3.3.2; Canadell et al., 2021; Gulev et al., 2021). New findings since SROCC also confirm that the volume of oxygen minimum zones (OMZs) are expanding at many locations (high confidence) (WGI AR6 Section 5.3.3.2; Canadell et al., 2021).

The most recent estimates of future oxygen loss in the subsurface ocean (100–600 m), using CMIP6 models, amount to  $-4.1 \pm 4.2$  (very likely range),  $-6.6 \pm 5.7$ ,  $-10.1 \pm 6.7$  and  $-11.2 \pm 7.7\%$  in 2081–2100 relative to 1995–2014 for SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5, respectively (Figure 3.5; Kwiatkowski et al., 2020). Based on these CMIP6 projections, WGI AR6 concludes that the oxygen content of the subsurface ocean is projected to decline to historically unprecedented conditions over the 21st century (medium confidence) (WGI AR6 Section 5.3.3.2; Canadell et al., 2021). These declines are greater (by 31–72%) than simulated by the CMIP5 models in their Representative Concentration Pathway (RCP) analogues, a likely consequence of enhanced surface warming and stratification in CMIP6 models (Figure 3.5; Kwiatkowski et al., 2020). At the regional scale and for subsurface waters, projected changes are not spatially uniform, and there is lower agreement among models than they show for the global mean trend (Bopp et al., 2013; Kwiatkowski et al., 2020). In particular, large uncertainties remain for these future projections of ocean deoxygenation in the subsurface tropical oceans, where the major OMZs are located (Cabré et al., 2015; Bopp et al., 2017).

### 3.2.3.3 Changes in Nutrient Availability

The availability of nutrients in the surface ocean often limits primary productivity, with implications for marine food webs and the biological carbon pump. Nitrogen availability tends to limit phytoplankton productivity throughout most of the low-latitude ocean, whereas dissolved iron availability limits productivity in high-nutrient, low-chlorophyll regions, such as in the main upwelling region of the Southern Ocean and the Eastern Equatorial Pacific (high confidence) (Moore et al., 2013; IPCC, 2019b). Phosphorus, silicon, other micronutrients such as zinc, and vitamins can also co-limit marine phytoplankton productivity in some ocean regions (Moore et al., 2013). Whereas some studies have shown coupling between climate variability and nutrient trends in specific regions, such as in the North Atlantic (Hátún et al., 2016), North Pacific (Di Lorenzo et al., 2009; Yasunaka et al., 2014) and tropical (Stramma and Schmidtko, 2021) Oceans, very few studies have been able to detect long-term changes in ocean nutrient concentrations (but see Yasunaka et al., 2016).

Future changes in nutrient concentrations have been estimated using ESMs, with future increases in stratification generally leading to decreased nutrient levels in surface waters (IPCC, 2019b). CMIP6 models project a decline in the nitrate concentration of the upper 100 m in 2080–2099 relative to 1995–2014 of  $-0.46 \pm 0.45$  (very likely range),  $-0.60 \pm 0.58$ ,  $-0.80 \pm 0.77$  and  $-1.00 \pm 0.78 \text{ mmol m}^{-3}$  under SSP1-2.6, SSP2-4.5 and SSP5-8.5, respectively (Figure 3.5; Kwiatkowski et al., 2020). These declines in nitrate concentration are greater than simulated by the CMIP5 models in their RCP analogues, a likely consequence of enhanced surface warming and stratification in CMIP6 models (Figure 3.5; Kwiatkowski et al., 2020). It is concluded

that the surface ocean will encounter reduced nitrate concentrations in the 21st century (medium confidence).

## 3.2.4 Global Synthesis on Multiple Climate-induced Drivers

In the 21st century, ocean and coastal ecosystems are projected to face conditions unprecedented over past centuries to millennia (high confidence) (Section 3.2; WGI AR6 Chapters 4, 9; Fox-Kemper et al., 2021; Lee et al., 2021), with increased temperatures (virtually certain) and frequency and severity of MHWs (very high confidence), stronger upper-ocean stratification (high confidence), continued rise in GMSL throughout the 21st century (high confidence) and increased frequency of extreme sea levels (high confidence), further acidification (virtually certain), oxygen decline (high confidence) and decreased surface nitrate inventories (medium confidence).

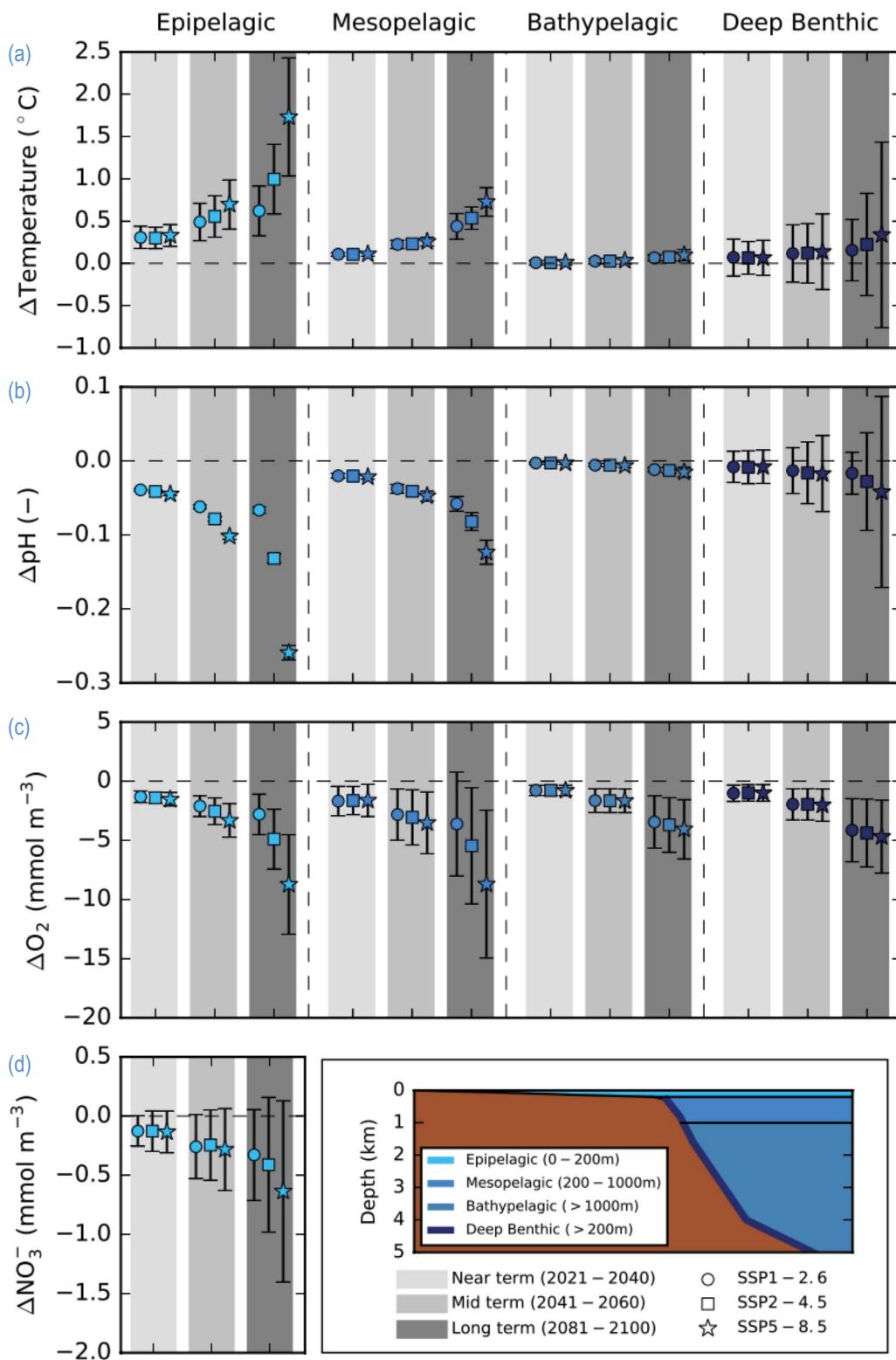
The rates and magnitudes of these changes largely depend on the extent of future emissions (very high confidence), with surface ocean warming and acidification (very likely range) at  $+3.47^\circ\text{C} \pm 1.28^\circ\text{C}$  and  $-0.44 \text{ pH units} \pm 0.008 \text{ pH units}$  in 2080–2099 (relative to 1870–1899) for SSP5-8.5 compared with  $+1.42^\circ\text{C} \pm 0.53^\circ\text{C}$  and  $-0.16 \text{ pH units} \pm 0.003 \text{ pH units}$  for SSP1-2.6 (Figure 3.5; Kwiatkowski et al., 2020).

### 3.2.4.1 Compound Changes in the 21st century

Earth system models project distinct regional evolutions of the different CIDs over the 21st century (very high confidence) (Figures 3.5, 3.6, 3.7; Kwiatkowski et al., 2020). Tropical and subtropical oceans are characterised by projected warming and acidification, accompanied by declining nitrate concentrations in equatorial upwelling regions. The North Atlantic is characterised by a high exposure to acidification and declining nitrate concentrations. The North Pacific is characterised by high sensitivity to compound changes, with high rates of warming, acidification, deoxygenation and nutrient depletion. In contrast, the development of compound hazards is limited in the Southern Ocean, where rates of warming and nutrient depletion are lower. The Arctic Ocean is characterised by the highest rates of acidification and warming, strong nutrient depletion, and it will likely become practically sea ice free in the September mean for the first time before the year 2050 in all SSP scenarios (high confidence) (Figures 3.5, 3.6, 3.7; Sections 3.2.2, 3.2.3).

In general, the projected changes in climate-induced drivers are less in absolute terms in the deep-sea (mesopelagic and bathypelagic domains and deep-sea habitats) than in the surface ocean and in shallow-water habitats (e.g., kelp ecosystems, warm-water corals) (very high confidence) (Figures 3.6, 3.7; Mora et al., 2013; Sweetman et al., 2017). The mesopelagic domain will be nevertheless exposed to high rates of deoxygenation (Figure 3.6) and high climate velocities (Figure 3.4; Section 3.2.2.1), as well as impacted by the shoaling of aragonite or calcite saturation horizon (Section 3.2.3.2). Significant differences in projected trends between the SSPs show that mitigation strategies will limit exposure of deep-sea ecosystems to potential warming, acidification and deoxygenation during the 21st century (very high confidence) (Figure 3.6; Kwiatkowski et al., 2020).

### Projected trends across open-ocean systems



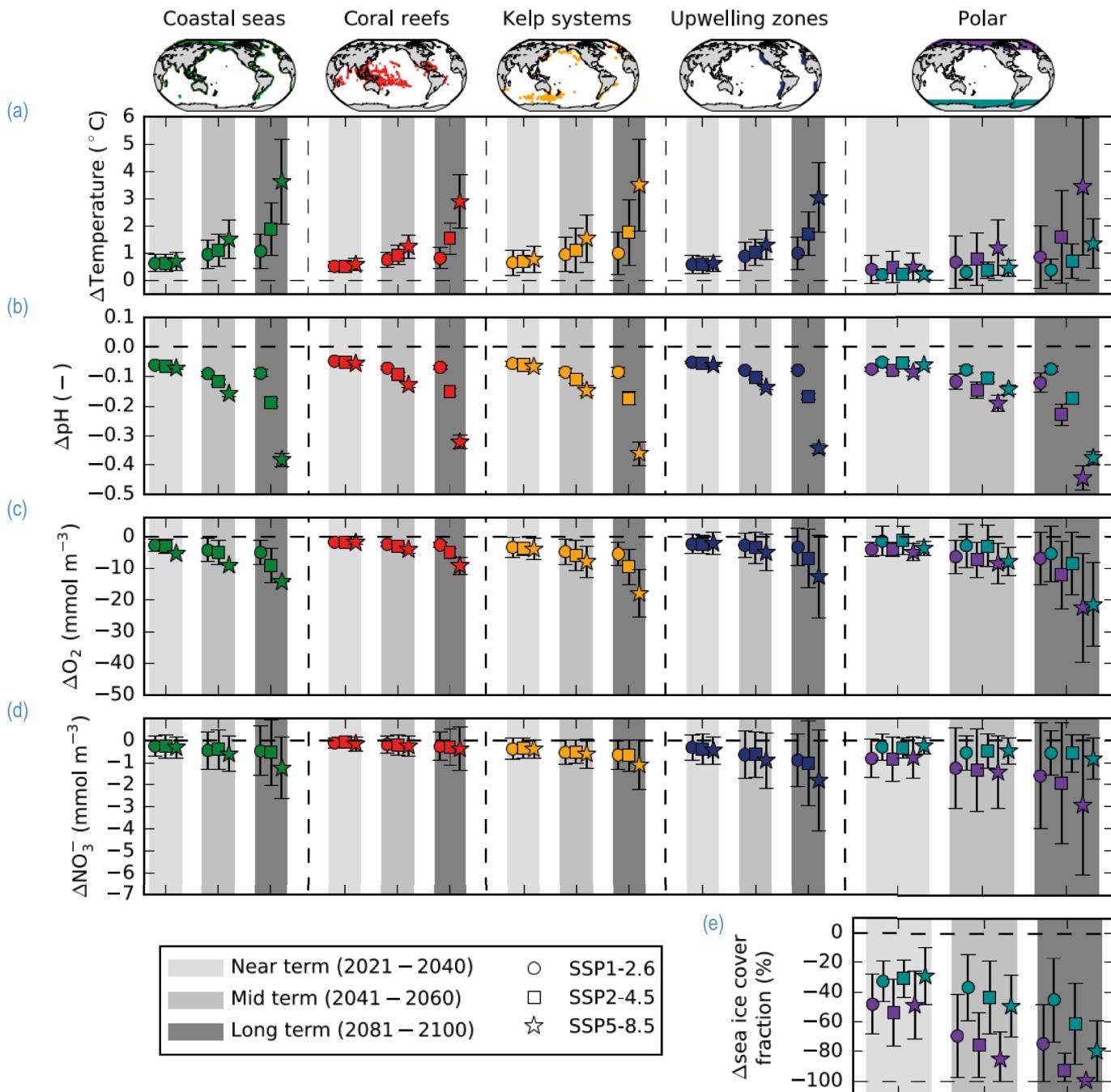
**Figure 3.6 | Projected trends across open-ocean systems.** Projected annual and global (a) average warming, (b) acidification, (c) changes in dissolved oxygen concentrations and (d) changes in nitrate ( $\text{NO}_3^-$ ) concentrations for four open-ocean systems, including the epipelagic (0–200 m depth), mesopelagic (200–1000 m), bathypelagic (>1000 m) domains and deep benthic waters (>200 m). All projections are based on Coupled Model Intercomparison Project 6 models and for three Shared Socioeconomic Pathways (SSPs): SSP1-2.6, SSP2-4.5 and SSP5-8.5 (Kwiatkowski et al., 2020). Anomalies in the near-term (2020–2041), mid-term (2041–2060) and long-term (2081–2100) are all relative to 1985–2014. Error bars represent *very likely* ranges.

### 3.2.4.2 Time of Emergence

Anthropogenic changes in climate-induced drivers assessed here exhibit vastly distinct times of emergence, which is the time scale over which an anthropogenic signal related to climate change is statistically detected to emerge from the background noise of natural

climate for a specific region (Christensen et al., 2007; Hawkins and Sutton, 2012). SROCC concluded that for ocean properties, the time of emergence ranges from under a decade (e.g., surface ocean pH) to over a century (e.g., net primary production; see Section 3.4.3.3.4 for time of emergence of biological properties; Bindoff et al., 2019a).

## Projected trends across coastal-ocean ecosystems



**Figure 3.7 | Projected trends across coastal-ocean ecosystems.** Projected (a) warming, (b) acidification, (c) changes in dissolved oxygen concentrations, (d) changes in nitrate ( $\text{NO}_3^-$ ) concentrations and (e) changes in summer sea ice cover fraction (September and north of  $66^{\circ}\text{N}$  for the Northern Polar Oceans, and March and south of  $66^{\circ}\text{S}$  for the Southern Polar Ocean) for five coastal-ocean ecosystems. All projected trends are for the surface ocean, except oxygen concentration changes that are computed for the subsurface ocean (100–600 m depth) for the upwelling ecosystems and the polar seas. All projections are based on Coupled Model Intercomparison Project 6 (CMIP6) models and for three Shared Socioeconomic Pathways (SSPs): SSP1-2.6, SSP2-4.5 and SSP5-8.5 (Kwiatkowski et al., 2020). Anomalies in the near term (2020–2041), mid term (2041–2060) and long term (2081–2100) are all relative to 1985–2014. Error bars represent *very likely* ranges. Coastal seas are defined on a  $1^{\circ} \times 1^{\circ}$  grid when bathymetry is less than 200 m deep. Distribution of warm-water corals is from UNEP-WCMC et al. (2018). Distribution of kelp ecosystems is from OBIS (2020). Upwelling areas are defined according to Rykaczewski et al. (2015).

The literature assessed in SROCC mainly focused on surface ocean properties and gradual mean changes. Since then, the time of emergence has also been investigated for subsurface properties, ocean extreme events and particularly vulnerable regions, such as the Arctic Ocean (Hameau et al., 2019; Oliver et al., 2019; Burger et al., 2020; Landrum and Holland, 2020; Schlunegger et al., 2020), but subsequent assessments are *low confidence* due to *limited evidence*. Below the surface, changes in temperature typically emerge from internal variability prior to changes in oxygen; however, in about a third of the global thermocline, deoxygenation emerges prior to warming (Hameau et al., 2019). Permanent MHW states, defined as when SST exceeds the MHW threshold continuously over a full calendar year, will emerge during the 21st century in many parts of the surface ocean (Oliver et al., 2019). Ocean acidification extremes have already emerged from background natural internal variability during the 20th century in most of the surface ocean (Burger et al., 2020). In the Arctic, anthropogenic sea ice changes have already emerged from the background internal variability, and anthropogenic alteration of air temperatures will emerge in the early- to mid-21st century (Landrum and Holland, 2020).

#### 3.2.4.4 Perspectives from Paleoclimatology Data

3

Paleoclimatology observations are useful to assess multiple hazards of environmental change while excluding direct anthropogenic impacts (Section 3.4.3.3). Ancient intervals of rapid climate warming that occurred between 300 and 50 million years ago (Ma) were triggered by the release of greenhouse gases (*high confidence*). The sources of greenhouse gases varied but include volcanic degassing from continental flood basalts and methane hydrates stored in marine sediments and soils (Foster et al., 2018). Six extreme ancient hyperthermal events are known from the last 300 Ma, when tropical SSTs reached 1.5°C–10°C warmer than pre-industrial conditions, and with substantial impacts on ancient life (Cross-Chapter Box PALEO in Chapter 1). Warming and deoxygenation in the oceans were closely associated in hyperthermal events (*high confidence*), with anoxia reaching the photic zone and abyssal depths (Kaiho et al., 2014; Müller et al., 2017; Penn et al., 2018; Weissert, 2019), whereas ocean acidification has not been demonstrated consistently (*medium confidence*) (Hönisch et al., 2012; Penman et al., 2014; Clarkson et al., 2015; Harper et al., 2020a; Jurikova et al., 2020; Müller et al., 2020).

Greenhouse gases also contributed substantially to shaping the longer-term climate trends over the past 50 million years, although changes in continental configuration and ocean circulation as well as planetary orbital cycles were equally important (WGI AR6 Cross-Chapter Box 2.1 in Chapter 2; Westerhold et al., 2020; Gulev et al., 2021). There is little evidence for ocean acidification in the past 2.6 Ma (*low confidence*) (Hönisch et al., 2012), but ocean ventilation was highly sensitive to even modest warming such as observed in the past 10,000 years (*medium confidence*) (Jaccard and Galbraith, 2012; Lembke-Jene et al., 2018).

### 3.3 Linking Biological Responses to Climate-induced Drivers

#### 3.3.1 Introduction

This section assesses new evidence since AR5 (Pörtner et al., 2014) and SROCC (Bindoff et al., 2019a) regarding biotic responses to multiple environmental drivers. It assesses differential sensitivities among life stages within individual organisms, changing responses across scales of biological organisation and the potential for evolutionary adaptation to climate change (e.g., Przeslawski et al., 2015; Boyd et al., 2018; Reddin et al., 2020), providing examples and identifying key gaps and uncertainties that limit our ability to project the ecological impact of multiple climate-induced drivers (Figure 3.8a). The assessment includes physiological responses to single environmental drivers and their underlying mechanisms (Section 3.3.2), the characteristics of multiple drivers and organisms' responses to them (Section 3.3.3), short-term acclimation and longer-term evolutionary adaptation of populations (Section 3.3.4), and it concludes with an assessment of progress in upscaling laboratory findings to ecosystems within *in situ* settings (Figure 3.8b; Section 3.3.5).

#### 3.3.2 Responses to Single Drivers

Anthropogenic CO<sub>2</sub> emissions trigger a suite of changes that alter ocean temperature, pH and CO<sub>2</sub> concentration, oxygen concentration and nutrient supply at global scales (Section 3.2). The response pathways of these climate-induced drivers have been investigated primarily as single variables.

Temperature affects the movement and transport of molecules and, thereby, the rates of all biochemical reactions; thus, ongoing and projected warming (Section 3.2.2.1) that remains below an organism's physiological optimum will generally raise metabolic rates (*very high confidence*) (Pörtner et al., 2014). Beyond this optimum (T<sub>opt</sub>; Figure 3.9), metabolism typically decreases sharply, finally reaching a critical threshold (T<sub>crit</sub>) beyond which enzymes become thermally inactivated and cells undergo oxidative stress. Local and regional adaptation affect the heat tolerance thresholds of organisms. For example, organisms adapted to thermally stable environments (e.g., tropical, polar, deep sea) are often more sensitive to warming than those from thermally variable environments (e.g., estuaries) (*very high confidence*) (Section 3.4; Sunday et al., 2019; Collins et al., 2020). Heat tolerance also decreases with increasing organisational complexity (Storch et al., 2014; Pörtner and Gutt, 2016) and is lower in eggs, embryos and spawning fish than for their larval stages or adults outside the spawning season (*high confidence*) (Dahlke et al., 2020b). By altering physiological responses, projected changes in ocean warming (Section 3.2.2.1) will modify growth, migration, distribution, competition, survival and reproduction (*very high confidence*) (Messmer et al., 2017; Dahlke et al., 2018; Andrews et al., 2019; Pinsky et al., 2019; Anton et al., 2020).

Altered seawater carbonate chemistry (Section 3.2.3.1) affects specific processes to varying degrees. For example, higher CO<sub>2</sub> concentrations can increase photosynthesis and growth in some phytoplankton,

macroalgal and seagrass species (*high confidence*) (Pörtner et al., 2014; Seifert et al., 2020; Zimmerman, 2021), while lower pH levels decrease calcification (*high confidence*) (Pörtner et al., 2014; Falkenberg et al., 2018; Doney et al., 2020; Fox et al., 2020; Reddin et al., 2020) or silicification (*low confidence*) (Petrou et al., 2019). Organisms' capacity to compensate for or resist acidification of internal fluids depends on their capacity for acid–base regulation, which differs due to organisms' wide-ranging biological complexity and adaptive abilities (*low to medium confidence*) (Vargas et al., 2017; Melzner et al., 2020). Detrimental impacts of acidification include decreased growth and survival, and altered development, especially in early life stages (*high confidence*) (Dahlke et al., 2018; Onitsuka et al., 2018; Hancock et al., 2020), along with lowered recruitment and altered behaviour in animals (Kroeker et al., 2013a; Wittmann and Pörtner, 2013; Clements and Hunt, 2015; Cattano et al., 2018; Esbaugh, 2018; Bednaršek et al., 2019; Reddin et al., 2020). For finfish, laboratory studies of behavioural and sensory consequences of ocean acidification showed mixed results (Rossi et al., 2018; Nagelkerken et al., 2019; Stiasny et al., 2019; Velez et al., 2019; Clark et al., 2020; Munday et al., 2020). Calcifiers are generally more sensitive to acidification (e.g., for growth and survival) than non-calcifying groups (*high confidence*) (Kroeker et al., 2013a; Wittmann and Pörtner, 2013; Clements and Hunt, 2015; Cattano et al., 2018; Bednaršek et al., 2019; Reddin et al., 2020; Seifert et al., 2020). For calcifying primary producers, including phytoplankton and coralline algae, ocean acidification has different, often opposing effects, for example, decreasing calcification while photosynthetic rates increase (*high confidence*) (Riebesell et al., 2000; Van de Waal et al., 2013; Bach et al., 2015; Cornwall et al., 2017b; Gafar et al., 2019).

Oxygen concentrations affect aerobic and anaerobic processes, including energy metabolism and denitrification. Projected decreases in dissolved oxygen concentration (Section 3.2.3.2) will thus impact organisms and their biogeography in ways dependent upon their oxygen requirements (Deutsch et al., 2020), which are highest for large, multicellular organisms (Pörtner et al., 2014). The upper ocean generally contains high dissolved-oxygen concentrations due to air–sea exchange and photosynthesis, but in subsurface waters, deoxygenation may impair aerobic organisms in multiple ways (Oschlies et al., 2018; Galic et al., 2019; Thomas et al., 2019; Sampaio et al., 2021). Many processes contribute to lowered oxygen levels: altered ventilation and stratification; microbial respiration enhanced by nearshore eutrophication; and less oxygen solubility in warmer waters. For example, deoxygenation in highly eutrophic estuarine and coastal marine ecosystems (Section 3.4.2) can result from accelerated microbial activity, leading to acute organismal responses. Under hypoxia (oxygen concentrations  $\leq 2 \text{ mg l}^{-1}$ ; Limburg et al., 2020), physiological and ecological processes are impaired and communities undergo species migration, replacement and loss, transforming community composition (*very high confidence*) (Chu and Tunnicliffe, 2015; Gobler and Baumann, 2016; Sampaio et al., 2021). Hypoxia can lead to expanding OMZs, which will favour specialised microbes and hypoxia-tolerant organisms (*medium confidence*) (Breitburg et al., 2018; Ramírez-Flandes et al., 2019). As respiration consumes oxygen and produces CO<sub>2</sub>, lowered oxygen levels are often interlinked with acidification in coastal and tropical habitats (Rosa et al., 2013; Gobler and Baumann, 2016; Feely et al., 2018) and is an example of a compound hazard (Sections 3.2.4.1, 3.4.2.4).

Increased density stratification and mixed-layer shallowing, caused by warming, freshening and sea ice decline, can alter light climate and nutrient availability within the surface mixed layer (*high confidence*) (Section 3.2.2.3). As light and nutrient levels drive photosynthesis, changes in these drivers directly affect primary producers, often in different directions (Matsumoto et al., 2014; Deppele and Davidson, 2017). Decreased upward nutrient supply is expected to decrease primary production in the low-latitude ocean (*medium confidence*) (Section 3.4.4.2.1; Moore et al., 2018a; Kwiatkowski et al., 2019). Alternatively, higher mean underwater light levels resulting from changes in sea ice and/or mixed layer shallowing can increase primary production in high-latitude offshore regions, provided nutrient levels remain sufficiently high (*medium confidence*) (Section 3.4.4.2.1; Cross-Chapter Paper 6; Vancoppenolle et al., 2013; Deppele and Davidson, 2017; Tedesco et al., 2019; Ardyna and Arrigo, 2020; Lannuzel et al., 2020). In some parts of the open Southern Ocean, where iron limitation largely controls primary productivity (Tagliabue et al., 2017), changes in wind fields will deepen the summer mixed-layer depth (Panassa et al., 2018), entrain more nutrients, and raise primary productivity in the future (*medium confidence*) (Cross-Chapter Paper 6; Hauck et al., 2015; Leung et al., 2015; Moore et al., 2018a; Kwiatkowski et al., 2020).

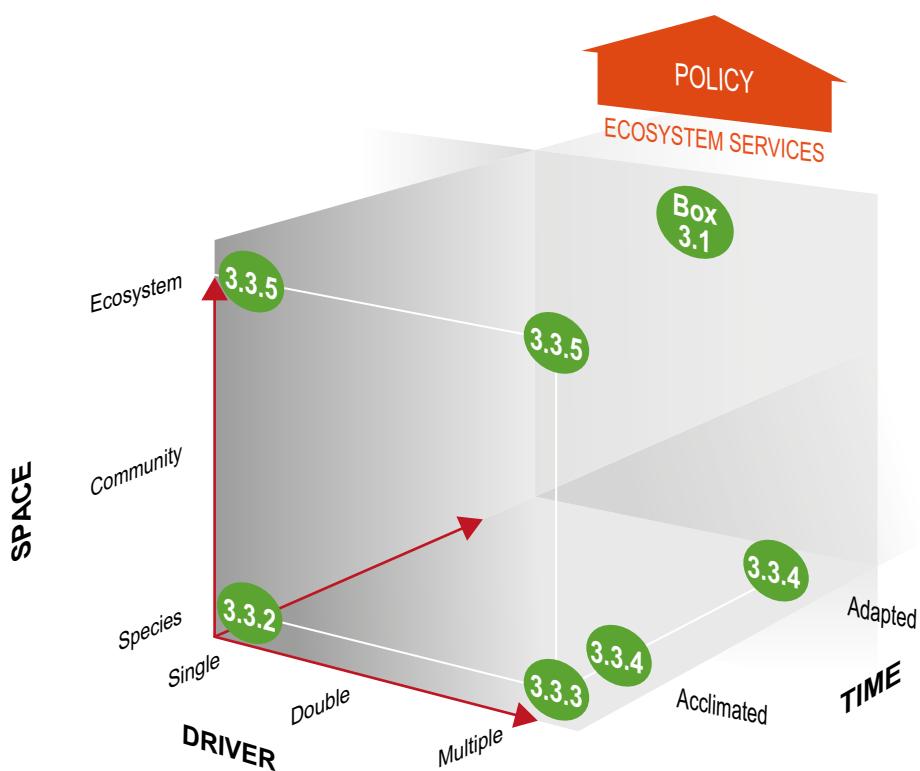
Climate-induced drivers fluctuate on time scales ranging from diurnal to annual, with potential consequences for organismal responses (Figure 3.10), but these fluctuations are commonly not incorporated experimentally. Experiments that simulate natural fluctuations in drivers, especially beyond tidal or diel cycles, can result in more detrimental impacts than those based on quasi-constant conditions (Eriander et al., 2015; Sunday et al., 2019), but can also ameliorate effects (Comeau et al., 2014; Laubenstein et al., 2020; Cabrerizo et al., 2021), confirming that the influence of environmental variability requires evaluation (Dowd et al., 2015). Marine heatwaves exacerbate the impacts of rising mean temperatures, with major ecological consequences (*very high confidence*) (Frölicher et al., 2018; IPCC, 2018; Arafeh-Dalmau et al., 2020; Laufkötter et al., 2020). Higher temperature variability decreased phytoplankton growth and calcification in *Emiliania huxleyi* relative to a stable warming regime (Wang et al., 2019b). Diel fluctuations (i.e., over 24 h) in carbonate chemistry superimposed on current and future pCO<sub>2</sub> levels influenced diatom species differently, depending on their habitat (Li et al., 2016). CO<sub>2</sub> fluctuations overlaid on changing mean values also altered phenotypic evolutionary outcomes of picoeukaryotic algae (Schaum et al., 2016). In the bivalve *Mytilus edulis*, fluctuating pH regimes exerted higher metabolic costs (Mangan et al., 2017), while salinity fluctuations might be more influential than pH fluctuations in other bivalves (Velez et al., 2016). The amplitude of diel and seasonal pH and CO<sub>2</sub> changes are projected to increase in the future due to lowered CO<sub>2</sub> seawater buffering capacity (*very high confidence*) (Section 3.2.3.1; Burger et al., 2020), which can impose additional stress on organisms.

### 3.3.3 Responses to Multiple Drivers

Each organism encounters a unique combination of local and climate-induced drivers, which vary in space and time. The contribution of these drivers to an organism's overall biological response, and thereby also potential risks for the organism, depends on the intensity and

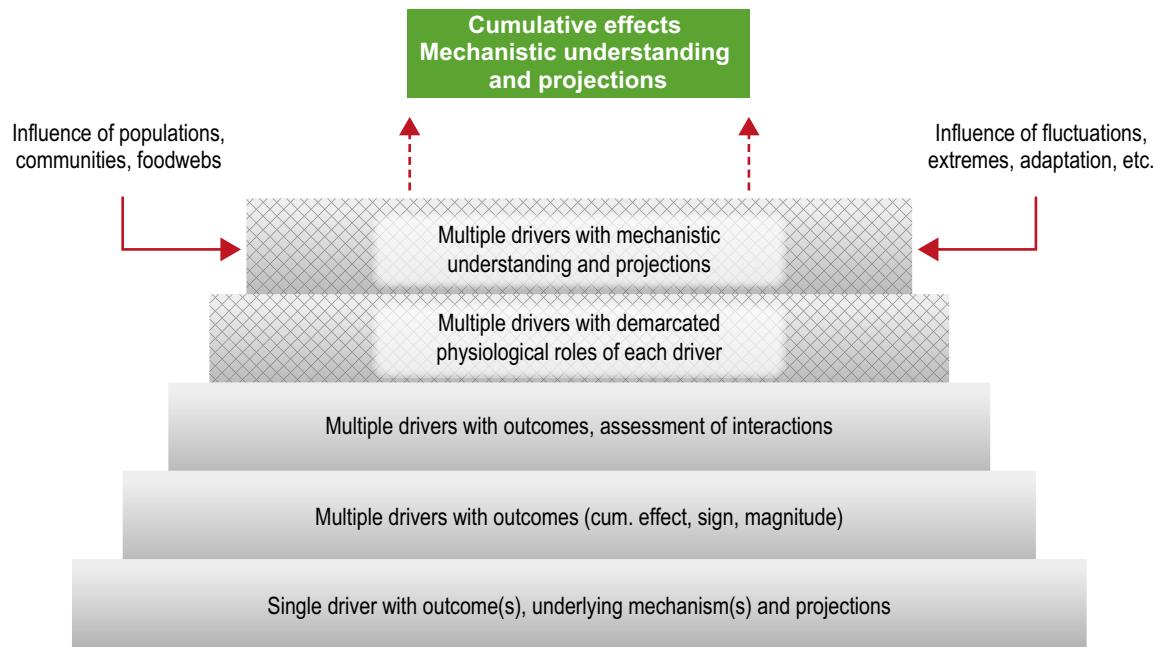
## The state of knowledge regarding ecological responses to environmental drivers in experimental settings

(a)



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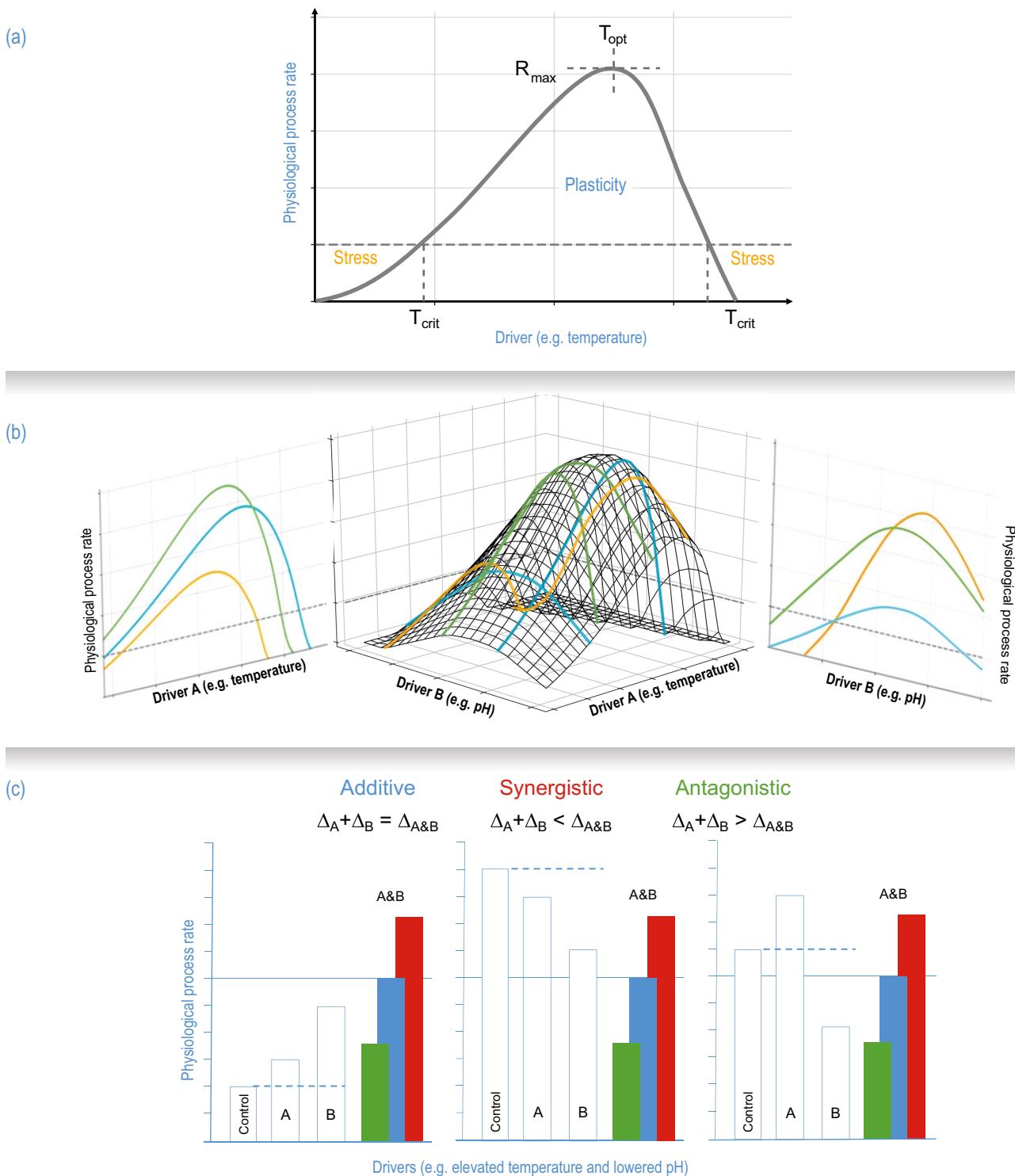
(b)



**Figure 3.8 | The state of knowledge regarding ecological responses to environmental drivers in experimental settings.**

- (a) Schematic indicates where themes are discussed within Section 3.3, and how they jointly inform policy. (Adapted from Riebesell and Gattuso, 2014).
- (b) The hierarchy of accumulating physiological knowledge (grey layers), from single (e.g., Pörtner et al., 2012) to multiple drivers, and from simple outcomes (e.g., Sciandra et al., 2003), interactions among drivers (e.g., Crain et al., 2008) and identification of physiological roles of drivers (e.g., Bach et al., 2015) to mechanistic understanding of drivers (e.g., Thomas et al., 2017). At present, the upper grey layer has been achieved, in full, for two drivers (e.g., temperature and nutrient concentrations), with validation of dual controls on phytoplankton growth rate (Thomas et al., 2017). Hatched layers denote major advances since WGII AR5 Chapter 6 (Pörtner et al., 2014). The green layer indicates the level of understanding potentially needed to project the response of marine life subjected to multiple drivers. Red horizontal arrows indicate the influence of confounding factors on our current understanding, including population genetics, fluctuating oceanic conditions or extreme events.

## Organismal responses to single and multiple drivers



**Figure 3.9 | Organismal responses to single and multiple drivers.**

**(a)** The generic temperature–response curve shows physiological process rates as a nonlinear function of a particular driver (e.g., temperature) with maximum rates ( $R_{max}$ ) and temperature optima ( $T_{opt}$ ). The driver range that keeps physiological rates above a certain threshold represents the organism’s range of phenotypic plasticity, while below that threshold, the critical temperature ( $T_{crit}$ ), physiological performance is so low as to constitute stressful conditions.

**(b)** The response curve for one driver can depend on other drivers, here exemplified for temperature and pH in the central panel. This interaction causes rates as well as optima to change with pH (left) and temperature (right), indicated by the coloured lines. **(c)** Impacts of multiple drivers on processes can be additive (blue), synergistic (red) or antagonistic (green), that is, the cumulative effects of two (or more) drivers are equal to, larger than or smaller than the sum of their individual effects, respectively. Potential experimental outcomes affected by additive, synergistic and antagonistic interactions are shown for scenarios where drivers increase rates (left), decrease rates (centre) or cause opposite responses (right), showing how experimental outcomes can mask these mechanistic interactions. (For a quantitative analysis of effects of driver pairs on animals, see Figure 3.SM.2.) (Adapted from Crain et al., 2008 and Piggott et al., 2015).

duration of its exposure to these drivers and associated sensitivities. Both geographic location (e.g., polar, tropical) and marine habitat (e.g., benthic, pelagic) strongly affect the combination of climate and non-climate drivers to which organisms are exposed. Non-climate drivers (Section 3.1) can dominate outcomes or amplify vulnerability to climate-induced drivers, with mostly detrimental effects such as extirpation (*very high confidence*) (Section 3.4; Boyd et al., 2018; Gissi et al., 2021), and unique feedbacks may exist between climate change and drivers like habitat loss or invasive species that further confound climate-change effects (Ortiz et al., 2018; Wolff et al., 2018; Gissi et al., 2021). Individual responses are further influenced by an organism's behaviour, trophic level and life-history strategy (Figure 3.10; Przeslawski et al., 2015; Boyd et al., 2018). Evidence is increasing that some life-history stages are more sensitive to specific drivers than others (Dahlke et al., 2020b). To identify the most influential drivers for an organism requires targeting key traits (e.g., calcification, reproduction). The trophic level of the organism must also be considered, because autotrophs directly depend on light and nutrients while invertebrates are often more sensitive to changes in oxygen or altered prey, but temperature plays a key role for both groups (Figure 3.10b).

Co-occurring environmental drivers often cause complex organismal responses (*high confidence*) (Pörtner et al., 2014). Individual drivers can have detrimental, neutral or beneficial effects, depending on the relationship between driver and physiological process (Section 3.3.2; Figure 3.9a). Multiple drivers can have interactive effects, where the response to one driver alters the sensitivity to another, and outcomes cannot be deduced from individual drivers' effects (Figure 3.9b). Impacts of multiple drivers can be additive, synergistic or antagonistic (Figure 3.9c; Crain et al., 2008; Piggott et al., 2015; Boyd et al., 2018; Bindoff et al., 2019a). Well-controlled laboratory studies on multiple-driver effects have revealed insights into the mode of action of individual drivers and their interdependence (Kroeker et al., 2017; Gao et al., 2019; Reddin et al., 2020; Seifert et al., 2020; Green et al., 2021b; Sampaio et al., 2021). Understanding the outcomes of interactive drivers is important for robustly assessing risks to organisms under different climate-change scenarios.

### 3.3.3.1 Effects of Multiple Drivers on Primary Producers

Warming and rising CO<sub>2</sub> concentrations enhance growth and/or photosynthetic rates in many species of cyanobacteria, picoeukaryotes, coccolithophores, dinoflagellates and diatoms (*high confidence*) (Fu et al., 2007; Sett et al., 2014; Hoppe et al., 2018a; Wolf et al., 2018; Brandenburg et al., 2019), and the optimum pCO<sub>2</sub> for growth and/or primary production shifts upward under warming (*medium confidence*) (Sett et al., 2014; Hoppe et al., 2018a). Warming and ocean acidification appear to jointly favour the proliferation and toxicity of harmful algal bloom (HAB) species (*limited evidence, high agreement*) (Section 3.5.5.3; Bindoff et al., 2019a; Brandenburg et al., 2019; Griffith et al., 2019a; Wells et al., 2020), but a 2021 analysis found no uniform global trend in HABs or their distribution over 1985–2018 once field data were adjusted for regional variations in monitoring effort (Hallegraeff et al., 2021). The predominantly detrimental impacts of ocean acidification on coccolithophores can partly be offset by warming (Seifert et al., 2020) but also be exacerbated, depending on the magnitudes of drivers (D'Amario et al., 2020). For non-calcifying

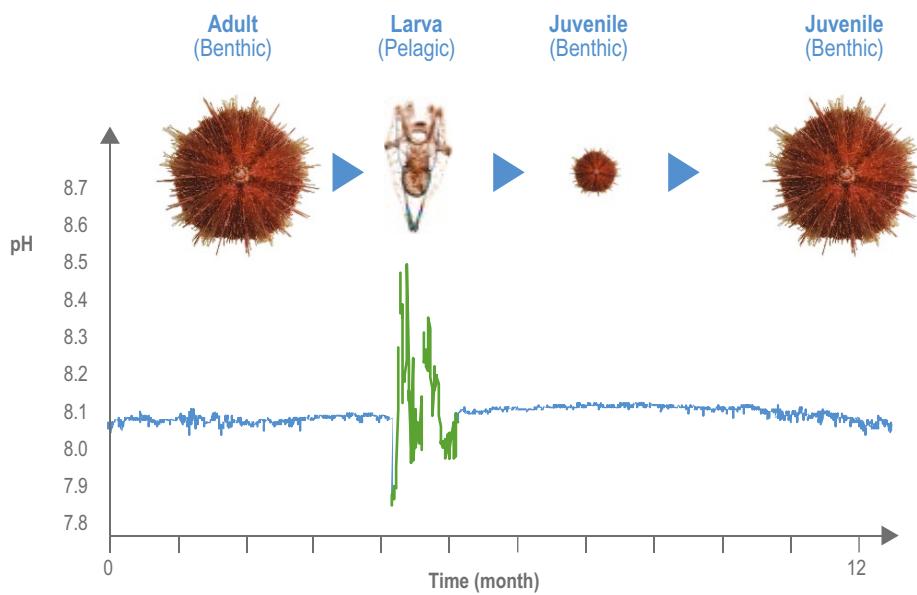
macroalgae, responses are highly species specific and often indicate synergistic interactions between warming and acidification (Kram et al., 2016; Falkenberg et al., 2018). Ocean acidification poses a large risk for coralline algae that is further amplified by warming (*medium confidence*) (Section 3.4.2.2; Cornwall et al., 2019). However, temperatures up to 5°C above ambient do not decrease calcification (Cornwall et al., 2019), and there is *limited evidence* that some species have the physiological capacity to resist acidification via pH upregulation at the calcification site (Cornwall et al., 2017a). For seagrass, warming beyond a species' thermal tolerance will limit growth and impact germination, but ocean acidification appears to increase thermal tolerance of some eelgrass species by increasing the photosynthesis-to-respiration ratio (*medium confidence*) (Egea et al., 2018; Scalpone et al., 2020; Zimmerman, 2021).

Thermal sensitivity of pelagic primary producers changes with nutrient supply (*high confidence*) (Thomas et al., 2017; Marañón et al., 2018; Fernández et al., 2020). Phosphorus limitation lowers the temperature optimum for growth of phytoplankton, making these organisms more prone to heat stress (Thomas et al., 2017; Bestion et al., 2018). This trend may hold for open-ocean phytoplankton, which are often iron-limited (*medium confidence*) (Boyd, 2019). Such temperature-nutrient interactions might be especially relevant during summer MHWs (Section 3.2.2.1; Cross-Chapter Box EXTREMES in Chapter 2; IPCC, 2018; Holbrook et al., 2019; DeCarlo et al., 2020; Hayashida et al., 2020), when primary producers are often nutrient-limited and near their thermal limits. Increasingly frequent and intense MHWs along with projected decreases in nutrient availability (Section 3.2.3.3) may push some primary producers beyond tolerance thresholds. Temperature-nutrient interactions can also alter the photosynthesis-to-respiration ratio in phytoplankton (Marañón et al., 2018). Overall, rising metabolic rates due to warming will be restricted to primary producers in high-nutrient regions (*medium confidence*) (Thomas et al., 2017; Marañón et al., 2018). For zoxanthellae-containing corals, nutrient supply from upwelling or from runoff can increase coral susceptibility to bleaching during warm-season MHWs (DeCarlo et al., 2020; Wooldridge, 2020).

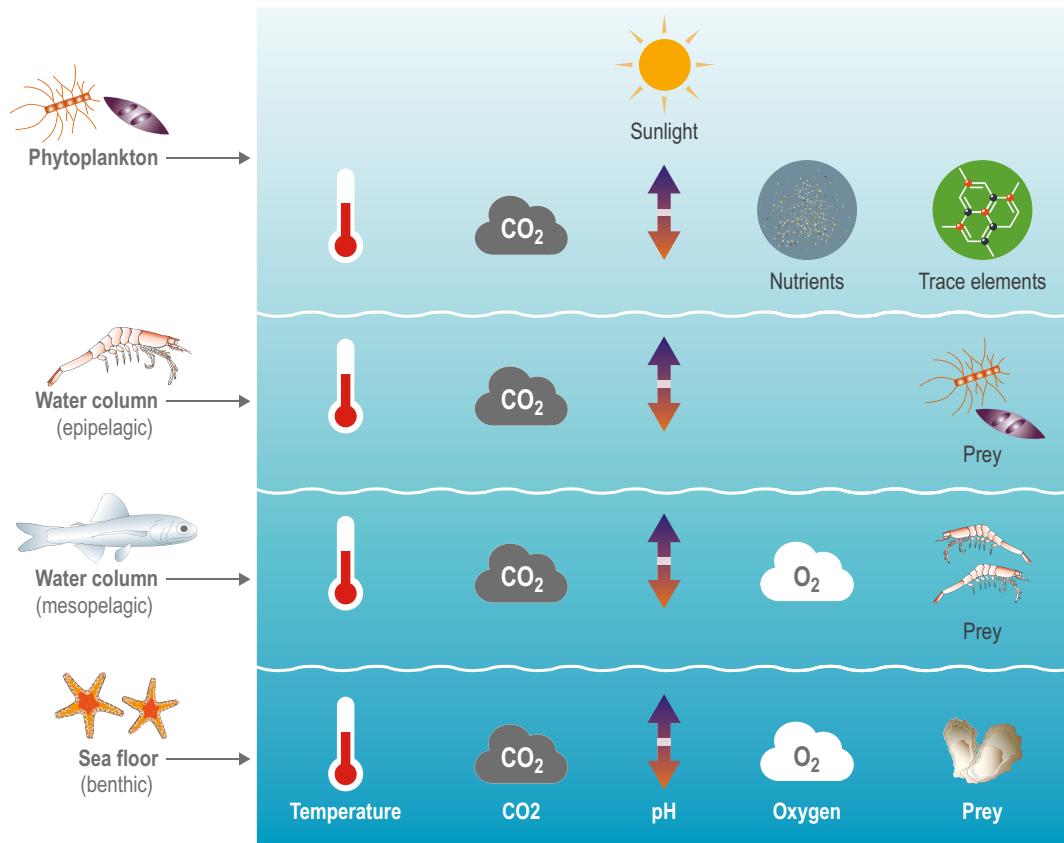
The effects of ocean acidification on growth, metabolic rates or elemental composition of primary producers changes with nutrient availability and light conditions (*high confidence*) (Gao et al., 2019; Seifert et al., 2020). While interactions with nutrients are often additive in phytoplankton, diatoms revealed predominantly synergistic interactions (Seifert et al., 2020). Growth or photosynthesis of some diatom and HAB species, for instance, are stimulated by ocean acidification only if nutrients are replete (Hoppe et al., 2013; Boyd et al., 2015b; Eberlein et al., 2016; Griffith et al., 2019a). Interactions with light are more complex because relative effects of ocean acidification are larger under limiting irradiances, while saturating light levels decrease beneficial or detrimental effects on these processes (Kranz et al., 2010; Garcia et al., 2011; Rokitta and Rost, 2012; Heiden et al., 2016). For the coccolithophore *Emiliana huxleyi*, for example, the impacts of ocean acidification are less detrimental under high light availability, which could partly explain why this species is moving poleward (Winter et al., 2014; Kondrik et al., 2017; Neukermans et al., 2018), although acidification is more pronounced in polar waters (Section 3.2.3.1; Cross-Chapter Paper 6). Under excess light, however, the detrimental impacts of ocean acidification are amplified for many

## Effect of environmental drivers varies depending on several factors

(a)



(b)



3

**Figure 3.10 | The effect of environmental drivers differs depending upon organisms' life history, and trophic strategy or habitat.**

(a) pH variability differs for benthic invertebrates, such as sea urchins (in blue), and their pelagic larvae (in green); pH fluctuations over the annual cycle can be much larger in the water column (due to primary production) relative to the seafloor. Variability associated with behaviour and life stage strongly defines organisms' niches and sensitivities to present and future conditions.

(b) Examples of organisms that are influenced by different suites of drivers that are set jointly by their habitat (e.g., benthic versus epipelagic settings) and trophic strategy (e.g., nutrients for phytoplankton, prey characteristics for grazers).

species (*high confidence*) (Gao et al., 2012; Li and Campbell, 2013; Zhang et al., 2015; Kottmeier et al., 2016; Gafar et al., 2019). Lowered photo-physiological capacity to cope with high-light stress and avoid photodamage (Gao et al., 2012; Li and Campbell, 2013; Hoppe et al., 2015; Kvernvik et al., 2020) is also consistent with observations that dynamic light regimes can become more stressful under ocean acidification (Jin et al., 2013; Hoppe et al., 2015). Given the expected mixed-layer shallowing in some regions (Section 3.2.2.3), the exposure to overall higher mean irradiances could shift the effects of acidification from beneficial to detrimental for some primary producers, depending on species and organismal traits (*medium confidence*) (Gao et al., 2019; Seifert et al., 2020).

Studies investigating two drivers provide most of the information on the wide range of interactive effects of drivers on phytoplankton (Gao et al., 2019; Seifert et al., 2020), although climate change alters several oceanic drivers concurrently (Section 3.2). The few experimental studies that have addressed three or more drivers (Xu et al., 2014; Boyd et al., 2015b; Brennan and Collins, 2015; Brennan et al., 2017; Hoppe et al., 2018b; Moreno-Marín et al., 2018) indicate that one or two drivers generally dominate the cumulative outcome, with others playing a subordinate role (*medium confidence*). In these studies, temperature had a disproportionately large influence, while other drivers differed in importance, depending on the type of primary producer, ecosystem characteristics and selected driver values.

### 3.3.3.2 Effects of Multiple Drivers on Animals

When changing CO<sub>2</sub> concentrations affect marine ectotherms, they typically combine additively or synergistically with warming (*medium confidence*) (e.g., Lefevre, 2016; Reddin et al., 2020; Sampaio et al., 2021), and their cumulative effects can lead to detrimental, neutral or beneficial effects (*high confidence*) (Figure 3.9a; Bennett et al., 2017; Büscher et al., 2017; Dahlke et al., 2017; Foo and Byrne, 2017; Johnson et al., 2017b; Cominassi et al., 2019). Higher ocean CO<sub>2</sub> influences the thermal tolerance of species adapted to extreme but stable habitats in tropical and polar regions, more than that of thermally tolerant generalists (*high confidence*) (Byrne et al., 2013; Schiffer et al., 2014; Flynn et al., 2015; Kunz et al., 2016; Pörtner et al., 2017; Kunz et al., 2018; Bindoff et al., 2019a; but see Ern et al., 2017), especially in early life stages (Dahlke et al., 2020a). In thermal generalists from temperate and subtropical species, warming and ocean acidification generally have detrimental effects on growth and survival (e.g., Gao et al., 2020), but warming can also alleviate the detrimental effects of ocean acidification by increasing metabolic rate and/or growth (Garzke et al., 2020), provided that other conditions (e.g., thermal niche, food availability) are beneficial. For example, larval growth and survival of Australasian snapper (*Pagrus auratus*) appear to benefit from combined acidification and warming (but see Watson et al., 2018; McMahon et al., 2020), introducing major uncertainties to population modelling (Section 3.3.4; Parsons et al., 2020).

As with ocean acidification, reduced oxygen availability further alters the influence of warming on metabolic rates (*high confidence*). Acidification and hypoxia can contribute to a decrease or shift in thermal tolerance, while the magnitude of this effect depends on the duration of exposure (Tripp-Valdez et al., 2017; Cattano et al., 2018; Calderón-

Liévanos et al., 2019; Schwieterman et al., 2019). Warming and hypoxia are mostly positively correlated and tolerances to both phenomena are often linked after long-term acclimation (e.g., Bouyoucos et al., 2020). Acute short-term heat shocks can impair hypoxia tolerance, for instance, in intertidal fish (McArley et al., 2020). This is relevant for shallow waters, specifically for MHWs (Section 3.2.2.1; Hobday et al., 2016a; IPCC, 2018; Collins et al., 2019a). Ocean acidification can increase hypoxia tolerance in some cases, possibly by downregulating activity (Faleiro et al., 2015) and/or changing blood oxygenation (Montgomery et al., 2019). Other studies, however, reported additive negative effects of acidification and warming on hypoxia tolerance (Schwieterman et al., 2019; Götze et al., 2020), in line with the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis presented in AR5 (Pörtner et al., 2014): Warming causes increased metabolic rates and oxygen demand in ectotherms, which at some point exceed supply capacities (which also depend on environmental oxygen availability) and reduce aerobic scope. In consequence, expansion of OMZs and other regions where warming, hypoxia and acidification combine will further reduce habitat for many fish and invertebrates (*high confidence*) (Sections 3.4.3.2, 3.4.3.3).

Food availability modulates, and may be more influential than, other driver responses by affecting the energetic and nutritional status of animals (Cole et al., 2016; Stiasny et al., 2019; Cominassi et al., 2020). Laboratory studies conducted under an excess of food risk underestimating the ecological effects of climate-induced drivers, because increased feeding rates may help mitigate adverse effects (Nowicki et al., 2012; Towle et al., 2015; Cominassi et al., 2020). Lowered food availability from reduced open-ocean primary production (Sections 3.2.3.3, 3.4.4.2.1) will act as an additional driver, amplifying the detrimental effects of other drivers. However, warming and higher CO<sub>2</sub> availability may increase primary productivity in some coastal areas (Section 3.4.4.1), ameliorating the adverse direct effects on animals (e.g., Sswat et al., 2018). Due to the few studies addressing food availability under multiple-driver scenarios (Thomsen et al., 2013; Pistevos et al., 2015; Towle et al., 2015; Ramajo et al., 2016; Brown et al., 2018a; Cominassi et al., 2020), there is *medium confidence* in its modulating effect on climate-induced driver responses.

Animal behaviour can be affected by ocean acidification, warming and hypoxia. While warming and hypoxia mostly induce avoidance behaviour, potentially leading to migration and habitat compression (Section 3.4; McCormick and Levin, 2017; Limburg et al., 2020), the effects of acidification appear more complex. Some studies reported that acidification dominates behavioural effects (Schmidt et al., 2017), although outcomes vary with experimental design and duration of exposure (*low confidence, low agreement*) (Maximino and de Brito, 2010; Munday et al., 2016; Laubenstein et al., 2018; Munday et al., 2019; Sundin et al., 2019; Clark et al., 2020; Munday et al., 2020; Williamson et al., 2021). Behaviour represents an integrated phenomenon that can be influenced both directly and indirectly by multiple drivers. For instance, increased pCO<sub>2</sub> can directly act on neuronal signalling pathways (e.g., Gamma-aminobutyric acid hypothesis; Nilsson et al., 2012; Thomas et al., 2020) and influence learning (Chivers et al., 2014), vision (Chung et al., 2014), and choice and escape behaviour (Watson et al., 2014; Wang et al., 2017b). There is further evidence that observed alterations in fish olfactory behaviour

under ocean acidification may result from physiological and molecular changes of the olfactory epithelium, influencing olfactory receptors (Roggatz et al., 2016; Porteus et al., 2018; Velez et al., 2019; Mazurais et al., 2020). Temperature mainly drives metabolic processes and thus energetic requirements, which can indirectly influence behaviour, including increased risk-taking during feeding (Marangon et al., 2020). Ocean warming also accelerates the biochemical reactions and metabolic processes that are primarily influenced by acidification. It is therefore difficult to generalise to what extent co-occurring ocean warming ameliorates or exacerbates effects of acidification on behaviour (Lauenstein et al., 2019); outcomes depend upon species and life stage (Faleiro et al., 2015; Chan et al., 2016; Tills et al., 2016; Wang et al., 2018b; Jarrold et al., 2020), interactions between species (e.g., Paula et al., 2019) along with confounding factors including food availability and salinity (*medium confidence*) (Ferrari et al., 2015; Pistevos et al., 2015; Pimentel et al., 2016; Pistevos et al., 2017; Horwitz et al., 2020).

While hypoxia can dominate multiple-driver responses locally (Sampaio et al., 2021), warming is the fundamental physiological driver for most marine ectotherms, globally, as it directly affects their entire biochemistry and energy metabolism. Other influential drivers include ocean acidification, salinity (*high confidence*) (Lefevre, 2016; Whiteley et al., 2018; Reddin et al., 2020) or food availability/quality (*medium confidence*) (Nagelkerken and Munday, 2016; Gao et al., 2020). Fluctuating and decreasing salinity may aggravate the detrimental effects of warming and elevated CO<sub>2</sub>, because dilution with freshwater lowers acid–base buffering capacity, resulting in lower pH and calcium carbonate saturation state (Dickinson et al., 2012; Shrivastava et al., 2019; Melzner et al., 2020).

### 3.3.4 Acclimation and Evolutionary Adaptation

Climate change is and will continue to be a major driver of natural selection, causing important changes in fitness-related (e.g., growth, reproduction, survival) and functional (e.g., body/cell size, morphology, physiology) traits, and in the genetic diversity of natural populations (*medium confidence*) (Pauls et al., 2013; Merilä and Hendry, 2014). Climate-change impacts will continue to be exacerbated by interactions with non-climate drivers such as habitat fragmentation or loss, pollution or resource overexploitation, which limit the adaptive potential of populations to future conditions (Trathan et al., 2015; Gaitán-Espitia and Hobday, 2021). However the ultimate responses to complex change are conditioned by the rate and magnitude of environmental change, organisms' capacity for acclimation, the degree of local adaptation of natural populations and populations' potential for adaptive evolution (Figure 3.11; Pespeni et al., 2013; Calosi et al., 2017; Vargas et al., 2017). These controlling factors are mainly determined by local environmental conditions encountered by populations across their geographic distribution (Boyd et al., 2016). In highly fluctuating environments (e.g., upwelling regions, coastal zones), multiple drivers can change and interact across temporal and spatial scales, generating geographic mosaics of tolerances and sensitivities to environmental and climate change in marine organisms (*medium confidence*) (Pespeni et al., 2013; Boyd et al., 2016; Vargas et al., 2017; Li et al., 2018a). A further challenge for marine life lies in its ability to cope with extreme

events such as MHWs (Cross-Chapter Box EXTREMES in Chapter 2). The interplay between the abruptness, intensity, duration, magnitude and reoccurrence of extreme events may alter or prevent evolutionary responses (e.g., adaptation) to climate change and the potential for acclimation to extreme conditions such as MHWs (Cheung and Frölicher, 2020; Coleman et al., 2020a; Gurgel et al., 2020; Gruber et al., 2021).

Some studies have documented higher phenotypic plasticity and tolerance to ocean warming and acidification in marine invertebrates (Dam, 2013; Kelly et al., 2013; Pespeni et al., 2013; Gaitán-Espitia et al., 2017a; Vargas et al., 2017; Li et al., 2018a), seaweeds (Noisette et al., 2013; Padilla-Gamiño et al., 2016; Machado Monteiro et al., 2019) and fish (*medium confidence*) (Sandoval-Castillo et al., 2020; Enbody et al., 2021) living in coastal zones characterised by strong temporal fluctuations in temperature, pH, pCO<sub>2</sub>, light and nutrients. For these populations, strong directional selection with intense and highly fluctuating conditions may have favoured local adaptation and increased tolerance to environmental stress (*low confidence, low evidence*) (Hong and Shurin, 2015; Gaitán-Espitia et al., 2017b; Li et al., 2018a).

Other mechanisms acting within and across generations can influence selection and inter-population tolerances to environmental and climate-induced drivers. For instance, transgenerational effects and/or developmental acclimation, both 'carry-over effects' (where the early-life environment affects the expression of traits in later life stages or generations), can influence within- and cross-generational changes in the tolerances of marine organisms (*medium confidence*) to ocean warming (Balogh and Byrne, 2020) and acidification (Parker et al., 2012). Over longer time scales, increasing tolerance to these drivers may be mediated by mechanisms such as transgenerational plasticity (Murray et al., 2014), leading to locally adapted genotypes as seen in bivalves (Thomsen et al., 2017), annelids (Rodríguez-Romero et al., 2016; Thibault et al., 2020), corals (Putnam et al., 2020) and coralline algae (Cornwall et al., 2020). However, transgenerational plasticity is species specific (Byrne et al., 2020; Thibault et al., 2020) and, depending on the rate and magnitude of environmental change, it may either be insufficient for evolutionary rescue (Morgan et al., 2020) or could induce maladaptive responses (i.e., reduced fitness) in marine organisms exposed to multiple drivers (*medium confidence, low evidence*) (Figure 3.11; Griffith and Gobler, 2017; Parker et al., 2017; Byrne et al., 2020).

Acclimation to environmental pressures and climate change via phenotypic plasticity (Section 3.3.3; Collins et al., 2020) enables species to undergo niche shifts such that their present-day climatic niche is altered to incorporate new or shifted conditions (Fox et al., 2019). Although plasticity provides an adaptive mechanism, it is *unlikely* to provide a long-term solution for species undergoing sustained directional environmental change (e.g., global warming) (*medium confidence*) (Fox et al., 2019; Gaitán-Espitia and Hobday, 2021). Beyond the limits for plastic responses (Figure 3.9; DeWitt et al., 1998; Valladares et al., 2007), genetic adjustments are required to persist in a changing world (Figure 3.11; Fox et al., 2019). The ability of species and populations to undergo these adjustments (i.e., adaptive evolution) depends on extrinsic factors including the rate and magnitude of environmental change (important determinants of the strength and form of selection; Hoffmann and Sgrò, 2011;

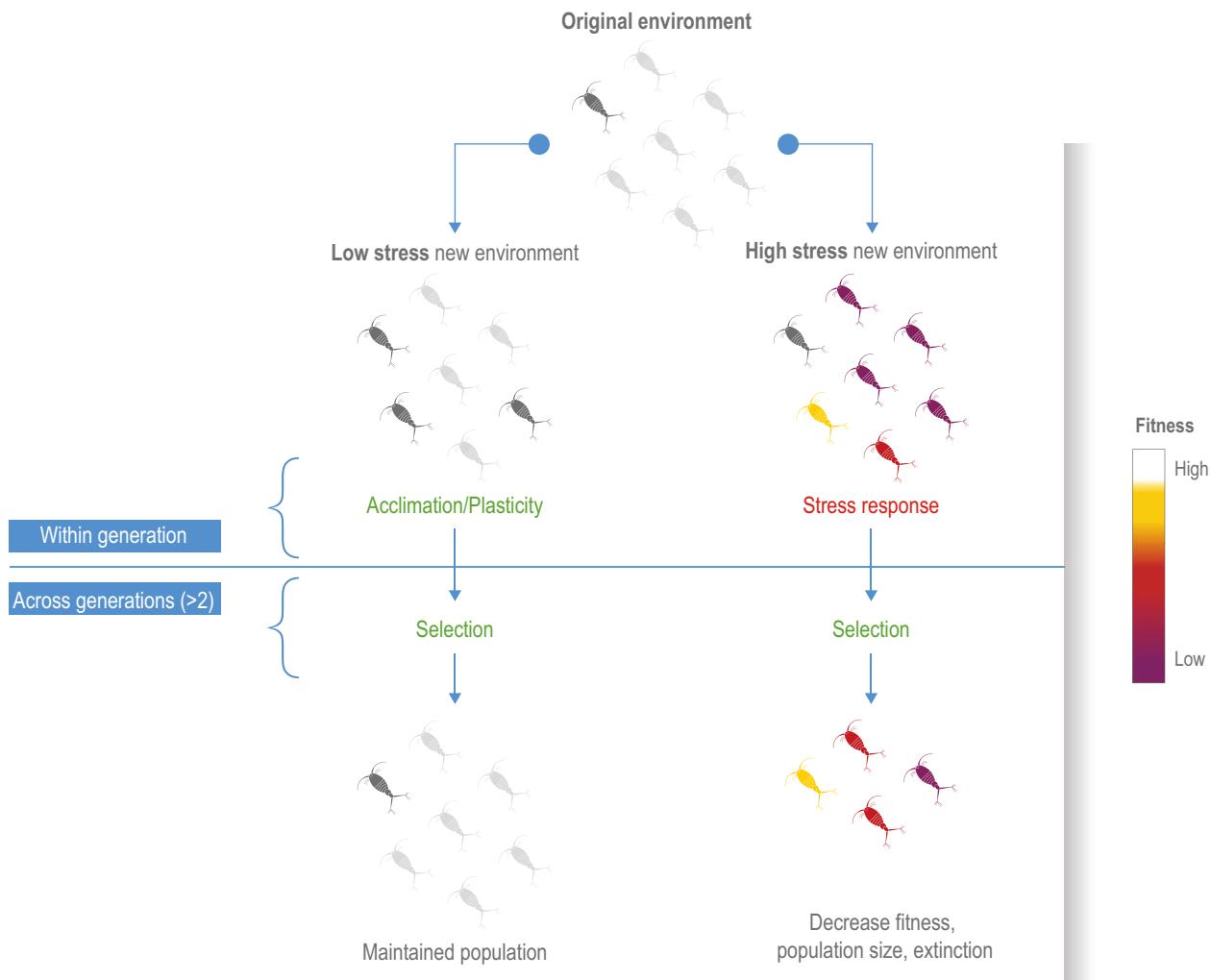
Munday et al., 2013), along with intrinsic factors such as generation times and standing genetic variation (Mitchell-Olds et al., 2007; Lohbeck et al., 2012). Accurately assessing the degree of acclimation and/or adaptation across space and time is difficult and constrains studying adaptive evolution in natural populations. There is a major gap in climate-change biology related to the study of evolutionary responses in complex and long-lived multicellular organisms. Insights on organismal acclimation, adaptation and evolution rely on studies of small, short-lived marine organisms, such as phytoplankton, which divide rapidly and contain high genetic variation in large populations. (Schaum et al., 2016; Cavicchioli et al., 2019; Collins et al., 2020).

Experimental evolution suggests that microbial populations can rapidly adapt (i.e., over 1–2 years) to environmental changes mimicking projected effects of climate change (*medium confidence*). Phytoplankton adaptive mechanisms include intraspecific strain sorting and genetic changes (Bach et al., 2018; Hoppe et al., 2018b; Wolf et al.,

2019). The evolutionary responses of microbes are conditioned by the number and characteristics of interacting drivers (*low confidence*) (Brennan et al., 2017). For example, in a high-salinity adapted strain of the phytoplankton *Chlamydomonas reinhardtii*, the selection intensity and the adaptation rate increased with the number of environmental drivers, accelerating the adaptive evolutionary response (Brennan et al., 2017). For this and other phytoplankton species, a few dominant drivers explain most of the phenotypic and evolutionary changes observed (Boyd et al., 2015a; Brennan and Collins, 2015; Brennan et al., 2017).

Adaptation can be impeded, delayed or constrained in eukaryotic microbial populations as a result of reduced genetic diversity and/or the presence of functional and evolutionary trade-offs (Aranguren-Gassis et al., 2019; Lindberg and Collins, 2020; Walworth et al., 2020). In the marine diatom *Chaetoceros simplex*, a functional trade-off between high-temperature tolerance and increased nitrogen requirements

## Micro-evolutionary dynamics in response to environmental change



**Figure 3.11 | Micro-evolutionary dynamics in response to environmental change.** Simplified conceptual framework shows two main eco-evolutionary trajectories for natural populations over time (vertical axis from top to bottom). If environmental stress is low, rapid responses (within a generation) through plastic phenotypic adjustments and selection (across generations) sustain fitness, enhancing maintenance of viable populations across generations. In contrast, if environmental stress is high, ongoing phenotypic plasticity and acclimation may be insufficient to buffer the negative effects, exacerbating the loss of fitness (change of colour to orange/yellow/red). Ultimately, very high stress conditions accelerate population decline, enhancing the risk of species extinction.