Responses of marine ecosystems to climate change impacts and their treatment in biogeochemical ecosystem models

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Abstract

To predict the effects of climate change on marine ecosystems and the effectiveness of intervention and mitigation strategies, we need reliable marine ecosystem response models such as biogeochemical models that reproduce climate change effects. We reviewed marine ecosystem parameters and processes that are modified by climate change and examined their representations in biogeochemical ecosystem models. The interactions among important aspects of marine ecosystem modelling are not often considered due to complexity: these include the use of multiple IPCC scenarios, ensemble modelling approach, independent calibration datasets, the consideration of changes in cloud cover, ocean currents, wind speed, sea-level rise, storm frequency, storm intensity, and the incorporation of species adaptation to changing environmental conditions. Including our recommendations in future marine modelling studies could help improve the accuracy and reliability of model predictions of climate change impacts on marine ecosystems.

Keywords:
Climate change, marine ecosystem, biogeochemical model, temperature, pCO$_2$

1. Introduction

Marine ecosystems help to regulate the climate, protect coastal areas from storms (Shepard et al., 2011; Barbier, 2017), provide food for human communities, and support various livelihoods and recreational activities (Costanza et al., 2014; Barbier, 2017). Unfortunately, many marine ecosystems are in decline due to climate change or as a consequence of human activities. For example, Jones et al. (2018) estimate that 13.2% ($\approx$ 55 million km^2) of the world's oceans are marine wilderness and $< 100,000$ km^2 wilderness remains in coastal ecosystems. From 1985 to 2012, coral cover on the Great Barrier Reef (GBR) declined from 28% to 13.8% (De'ath et al., 2012). Climate change impacts on marine ecosystems include

global warming, ocean acidification, changes in ocean currents, sea-level rise and sea-ice retreat (Schweiger et al., 2008; IPCC, 2014; Hogg et al., 2015; Gattuso et al., 2015; Oliver et al., 2017). Human activities affect nearly all parts of the ocean. Eroded sediments, nutrients and chemicals from agricultural and urbanised catchments drain into coastal oceans, causing pollution (Brodie et al., 2011; Devlin et al., 2012). Discarded fishing nets and plastic waste entangle marine organisms as they swim (Wilcox et al., 2015) and some marine ecosystems such as mangrove forests have been cleared for development.

Oceans absorb more than 90% of heat generated from increased greenhouse gas (GHG) emissions from human activities such as the combustion of fossil fuels and land use (IPCC, 2014). The surface temperature of oceans is projected to increase by between 0.3°C to 1.7° C under Representative Pathway Concentration 2.6 (RCP2.6), 1.1° C to 2.6° C under RCP4.5, 1.4° C to 3.1° C under RCP6.0 and 2.6° C to 4.8° C under RCP8.5 IPCC scenarios by 2100 (IPCC, 2014). Ocean warming causes marine heat waves (Cavole et al., 2016; Oliver et al., 2017; Hughes et al., 2017), oxygen depletion (Vaquer-Sunyer and Duarte, 2011; Bruno et al., 2018) and coral bleaching (Hughes et al., 2017; Barkley et al., 2018), and may cause the loss of some marine habitats. An example is the potential loss of suitable spawning habitats for Atlantic cod (*Gadus morhua*) and Polar cod (*Boreogadus saida*) due to sea surface temperature increases (Dahlke et al., 2018).

More frequent extreme weather events associated with global warming (Mills et al., 2013; Pearce and Feng, 2013; Perry et al., 2014; Beeden et al., 2015; Hughes et al., 2017) and loss of coastal protection associated with increased storminess, sea-level rise and ecosystem changes such as reduced coral reef growth (Perry et al., 2014; Beeden et al., 2015; Cheal et al., 2017) may also negatively impact coastal communities.

Ocean warming intensifies oxygen depletion and can promote the growth of harmful algal blooms (Peperzak, 2003; Paul, 2008), leading to the death of marine organisms. Because warm water holds less dissolved oxygen than cooler water, hypoxia caused by severe oxygen depletion is projected to increase by 10% for each 1°C surface warming (Deutsch et al., 2011). Hypoxia can also occur due to increased oxygen demand as organics breakdown (Chen et al., 2007; Du et al., 2018; Rodríguez-Martínez et al., 2019).

Ocean CO_2 absorption increased from $1.0 \pm 0.5 \times 10^{12}$ kg Cyr^{-1} in 1960s to $2.4 \pm 0.5 \times 10^{12}$ kg Cyr^{-1} averaged over the period from 2008 to 2017 (Le Quéré et al., 2018). Although the absorption of CO_2 by oceans mitigates the atmospheric impacts of anthropogenic CO_2 emissions, it also causes ocean acidification (Wei et al., 2009). Ocean acidification is the reduction of ocean pH due to the dissolution of CO_2 in seawater. Global surface ocean pH naturally ranges between 8.0 and 8.5 (Bates et al., 2014), but has declined by 0.1 (Feely et al., 2004; Stocker et al., 2013; Gattuso et al., 2015) and is projected to decline by 0.3 to 0.4 by the end of 2100 under RCP8.5 (Mora et al., 2013; Gattuso et al., 2015). Ocean acidification reduces the growth, development, survival and abundance of marine calcifiers, and the abundance of their predators (Doney et al., 2009; Kroeker et al., 2013). Relative to current CO_2 conditions, marine calcifiers were shown to have a $11-19\%$ reduction in growth and development, a 27% decline in calcification and survival rate, and a 15% reduction in abundance under CO_2 conditions for the year 2100 (Kroeker et al., 2013).

Recently, several marine ecosystems around the world have experienced extreme marine

heatwaves with catastrophic ecological outcomes (Filbee-Dexter et al., 2016; Hughes et al., 2017; Barkley et al., 2018; Brainard et al., 2018; Arias-Ortiz et al., 2018; Burt et al., 2019; Kendrick et al., 2019). The unprecedented coral bleaching events in the GBR in 2016 and 2017 (Hughes et al., 2017) are examples of such events. These unprecedented bleaching events reduced living hard coral cover by 51% over large areas of the GBR that experienced extreme temperatures (Stuart-Smith et al., 2018). The 2010/2011 marine heatwave damaged about 36% of seagrass meadows in Shark Bay, the largest and most diverse seagrass assemblages in the world (Arias-Ortiz et al., 2018). Ocean warming reduced mean kelp biomass by 85–99% over the past 40–60 years at Nova Scotia, Canada (Filbee-Dexter et al., 2016). However, global warming has enhanced the poleward expansion of mangrove forests into salt marshes in subtropical and temperate coastlines (Saintilan et al., 2014).

Modelling the effects of climate change on marine ecosystems can help with the predictions of climate change impacts and the effectiveness of intervention and mitigation strategies. Among the different modelling techniques, one has proven to be popular in its predictions (Fennel et al., 2019): the biogeochemical model.

Biogeochemical models – also known as ecosystem models or receiving water quality models – are process-based models that simulate optical conditions and the cycling of nutrients such as carbon (C), nitrogen (N) and phosphorous (P) throughout the ecosystem. They also simulate the effects of changes in the physical, chemical and biological environments on primary production (PP) and export of organic and inorganic matter. Biogeochemical models are different from end-to-end models as they do not simulate high trophic level (HTL) production, e.g., fishery production (Robson et al., 2017). End-to-end models simulate the effects of the physical and hydrological environments on primary production and food-web interactions (Robson et al., 2017). Biogeochemical models are ecological models but not all ecological models are biogeochemical models. Ecological models represent important processes and factors that influence ecological systems on different scales and hierarchical levels in a specific context (Jørgensen, 2008).

Among biogeochemical models, there are two main types of models: global and coastal. Global biogeochemical models simulate export of organic and inorganic matter, and water quality, but do not simulate benthic and sediment dynamics. Coastal biogeochemical models simulate water quality, organic matter, benthic and sediment dynamics. However, some coastal biogeochemical models ignore benthic and sediment dynamics and Soetaert et al. (2000) have shown that such models have poor predictions.

Research to predict climate change responses of marine ecosystems has led to the development of many biogeochemical models with varying process representations and complexities (Robson, 2014; Janssen et al., 2015). Despite these significant developments, there has until recently been little focus on the representation of climate change impacts on marine ecosystem response models. Understanding the effects of climate change on marine ecosystem processes in the laboratory and field is fundamentally important in predicting climate change impacts on marine ecosystems. Here, we review marine ecosystem parameters and processes that are expected to change as a result of climate change and ocean acidification and then present a systematic review of published marine ecosystem climate change model applications.

2. Methods

For the systematic review of marine ecosystem modelling of climate change scenarios, peer reviewed journal publications and proceeding papers were selected for inclusion based on their use of mechanistic models to project the effects of climate change on marine ecosystems. Mechanistic models represent processes through the application of known scientific laws describing the behaviour of components of the modelled system. The literature search was done on Web of Science on May 1, 2019 (Table 1). To obtain the most relevant studies, the search field "Topic" (which searches titles, abstract, author keywords and keywords plus) was selected. The search returned 353 papers published between 2005 and 2019. A subset of 131 papers was selected for inclusion based on relevance to modelling the responses of marine ecosystems to climate change impacts.

The selected 131 modelling studies used eighty-five different models, with others being different applications of the same model. References for all 131 modelling studies can be found on the Supporting Information document. The modelled systems include twenty-two coastal (including estuarine) ecosystems and 109 open ocean marine ecosystems. Further, seventy-two of these ecosystem models considered regional domains, while the remaining fifty-nine were global models.

Table 1: Literature search keywords.

Keyword type	Search keywords
Main keyword	Biogeochemical model OR ecosystem model OR water quality model
Context keyword	Climate change OR global warming OR ocean acidification
Scope keyword	Marine OR ocean OR sea OR bay OR coastal

To complement these results and expand the range of results returned, a second search was conducted using Google Scholar. Studies were selected for inclusion due to their use of field and laboratory experiments to assess the impacts of elevated temperature and pCO_2 on plankton, coral, seagrass, mangrove, kelp and microbes. These marine organisms are considered because they are important components of marine ecosystems around the world. Results from a range of latitudes and climates were included.

3. Marine ecosystem parameters modified by climate change

3.1. Meteorological conditions and sea level

Air temperatures, cloud cover, storm intensity and storm frequency have all changed and continue to change due to anthropogenically forced climate change associated with greenhouse gas emissions. Average global surface temperature increased by 0.37°C between 1925 and 1944 and by a further 0.32°C from 1978 to 1997 (Jones et al., 1999). Relative to 1850–1900, temperatures are projected to increase throughout the 21st century with an increase of over 1.5°C by the end of the century (IPCC, 2014).

Warming-induced ocean thermal expansion, melting ice and changes in land water storage cause sea-level rise. Thermal expansion and melting ice have contributed about 75% of global sea-level rise since the early 1970s (IPCC, 2014). Sea-level rise exacerbates coastal flooding as it increases the vulnerability of coastal areas to floods in different parts of the world (French et al., 1995; Scott et al., 2012; Iwamura et al., 2013; Bhattachan et al., 2018; Knutson et al., 2020).

Despite several past disagreements on the reliability of model predictions of climate change impacts on tropical cyclones (Broccoli and Manabe, 1990; Evans and Allan, 1992; Bengtsson et al., 1996) recent studies agree on the use of high-resolution global models to predict climate change impacts on tropical cyclones (Knutson et al., 2010, 2020; Walsh et al., 2016). Relative to the end of the 20th century, a 2°C global temperature increase is projected to cause a 1 to 11% increase in the intensity of average global tropical cyclones and a 6 to 34% decrease in storm frequency by 2100 (Knutson et al., 2010, 2020). Overall, changes in storm intensity and frequency have been shown to greatly impact North and Central America, Australia, East and West Africa, Asia and South America (Ward et al., 2016). They have caused socio-economic damage and loss of human lives (Nordhaus, 2006), deteriorated the living conditions in some marine ecosystems and coastal communities (French et al., 1995).

3.2. River flows, sediment and nutrient loads

The impact of global warming on river flow regime is highly variable depending on the location. On a global scale, under SRES-A1B scenario Arnell and Gosling (2013) projected increases in mean annual runoff in Canada, high-latitude eastern Europe and Siberia by 2050 with respect to 1961–1990 averages. They also predicted declines in central Europe, around the Mediterranean, the Mashriq, central America and Brasil. Likewise, relative to 1950–1999 means, severe drought is predicted to be prevalent in North-central America from 2050 to 2099 under SRES-A1B scenario due to median declines in precipitation by 5 to 10% and runoff by 10 to 30% (Hidalgo et al., 2013). In South-western Australia, relative to averages from 1975 to 2007, a median decline by 25% in runoff resulting from a median decline by 8% in rainfall is predicted to occur by 2030 under future global temperature increases of 0.7°C, 1.0°C and 1.3°C (Silberstein et al., 2012).

Precipitation has been predicted to increase by 14 to 20% within 100km of tropical-cyclone activity (Knutson et al., 2010, 2020). Increased precipitation associated with tropical cyclones effectively generates runoff (Devlin et al., 2012; Darby et al., 2013) and contributes about 32% of the suspended sediment load draining into the Mekong Delta (Darby et al.,

2016). During high flow events, large loads of nutrients and sediments from adjacent agricultural catchments drain into the GBR (Brodie et al., 2010, 2011; Devlin et al., 2012). Consequently, current mean annual suspended sediments increased 5.5 times, nitrogen increased 5.7 times and phosphorus increased 8.9 times since European settlement (Kroon et al., 2012). On the other hand, in Mekong Delta, 33.0 ± 7.1 megatonnes of an estimated 52.6 ± 10.2 megatonnes decline in suspended sediment load was caused by shift in tropical-cyclone activity (Darby et al., 2016).

These changes have the potential to alter marine biogeochemistry and consequently marine ecosystems, and can be manifested in eutrophication, hypoxia and sedimentation. Sediment loads from rivers influence the structure and maintenance of deltas, the turbidity and nutrient concentrations of coastal waters (Sklar and Browder, 1998). Increased sediment and nutrient loads from terrestrial runoff have been shown to impact coral health on the GBR and enhance the abundance of crown-of-thorns starfish (Wolanski and De'ath, 2005). In Bohai Sea, increased nutrient loads from rivers increased the frequency and area of red tide events, and the diversity of dominant phytoplankton species (Wang et al., 2019). On the other hand, in Chilika Lagoon, riverine nutrient loads and detritus have been shown to support fisheries (Bonthu et al., 2016).

3.3. Oceanic transport processes

Oceanic transport processes comprising ocean currents, stratification and upwelling are important factors influencing marine ecosystems as they transport plants, animals, heat and nutrients around the oceans. Changes in ocean currents in response to future climate change vary across locations. For instance, between the 1990s and 2060s, Sun et al. (2012) project declines in the transport of Leeuwin Current (15%) and Indonesian Throughflow (20%), and increases in East Australian Current core transport (12%) and extension (35%) under SRES-A1B. Further, Hogg et al. (2015) reported the intensification of Southern Ocean eddy field in recent decades, with largest trends observed in the Indian ($18.3 \pm 5.1 cm^2 s^{-2}$ decade^{-1}) and Pacific ($14.9 \pm 4.1 cm^2 s^{-2}$ decade^{-1}) regions of the Southern Ocean.

Ocean stratification is projected to largely increase by the end of the 21st century, relative to the end of the 20th century under SRES-A2 scenario (Capotondi et al., 2012; Hordoir and Meier, 2012). Temperature changes have been identified as the largest contributor to stratification increases on a global scale, with the largest effect in the tropics (Capotondi et al., 2012). However, salinity was reported to have the largest influence on stratification increases in the Arctic, North Atlantic and Northeast Pacific due to Arctic freshening and increased salinity in subtropical North Atlantic and in the Mediterranean Sea (Capotondi et al., 2012).

Increased greenhouse gas emissions have been suggested to increase coastal upwelling intensity (i.e. the eastern boundary upwelling systems (EBUS)) (Bakun, 1990; Snyder et al., 2003; Bakun et al., 2015; Wang et al., 2015). The EBUS – one of the most productive marine ecosystems in the world – are projected to expand poleward due to increased temperatures (Bakun et al., 2015). However, under global warming, open ocean upwelling is projected to weaken while coastal upwelling remains unchanged (Hsieh and Boer, 1992). This is due to

the weakening of upwelling bands in equatorial and subpolar zones, and downwelling bands in subtropical zones.

These changes in oceanic transport processes will have implications on the dispersal of species larvae, distribution of nutrients and marine organisms, and nutrient cycling in marine ecosystems.

3.4. Water temperature

Global warming influences ocean temperature and will affect marine ecosystems. Temperature is arguably the most important physical variable that structures marine ecosystems. It influences the growth, composition and abundance of plankton communities, the abundance and distribution of fish, the growth and photosynthesis of seagrasses, mangroves, kelp and coral health. Extreme temperature increases caused by climate change alter marine ecosystems and the services they provide. A summary of temperature effects on marine ecosystems is shown in Figure 1. Temperature effects on plankton communities, corals, seagrasses, microbes, mangroves and kelp are detailed further below.
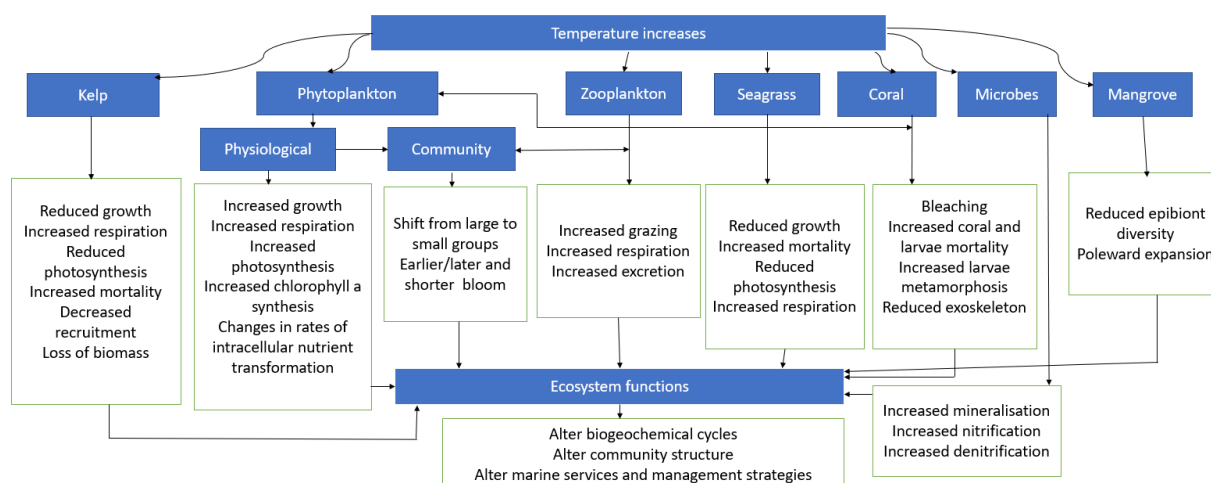

Figure 1: Summary of the responses of plankton, seagrasses, corals, microbes, mangroves and kelp to temperature increases.

3.4.1. Phytoplankton physiological responses

Phytoplankton, the most important organism in marine food chains is sensitive to temperature increases. Some experiments have shown that growth rate, nitrogen fixation rate and photosynthetic rate increase with increasing temperature, peak at an optimum temperature T_{opt}, and decrease afterwards (Figure 2c) (Breitbarth et al., 2007; Boyd et al., 2013; Fu et al., 2014). Respiration of phytoplankton in temperate regions increased with increasing temperature (i.e. from 0 to 30°C), while gross photosynthesis increased below 10°C, peaked between 10°C and 15°C and decreased at higher temperatures (Andersson et al., 1994).

Growth rate of polar diatoms increased by 25% with a temperature increase of 3°C and decreased rapidly with a further 1°C increase in temperature (Boyd et al., 2013). Temperate

(a) Exponential response curve.

(b) Saturating response curve.
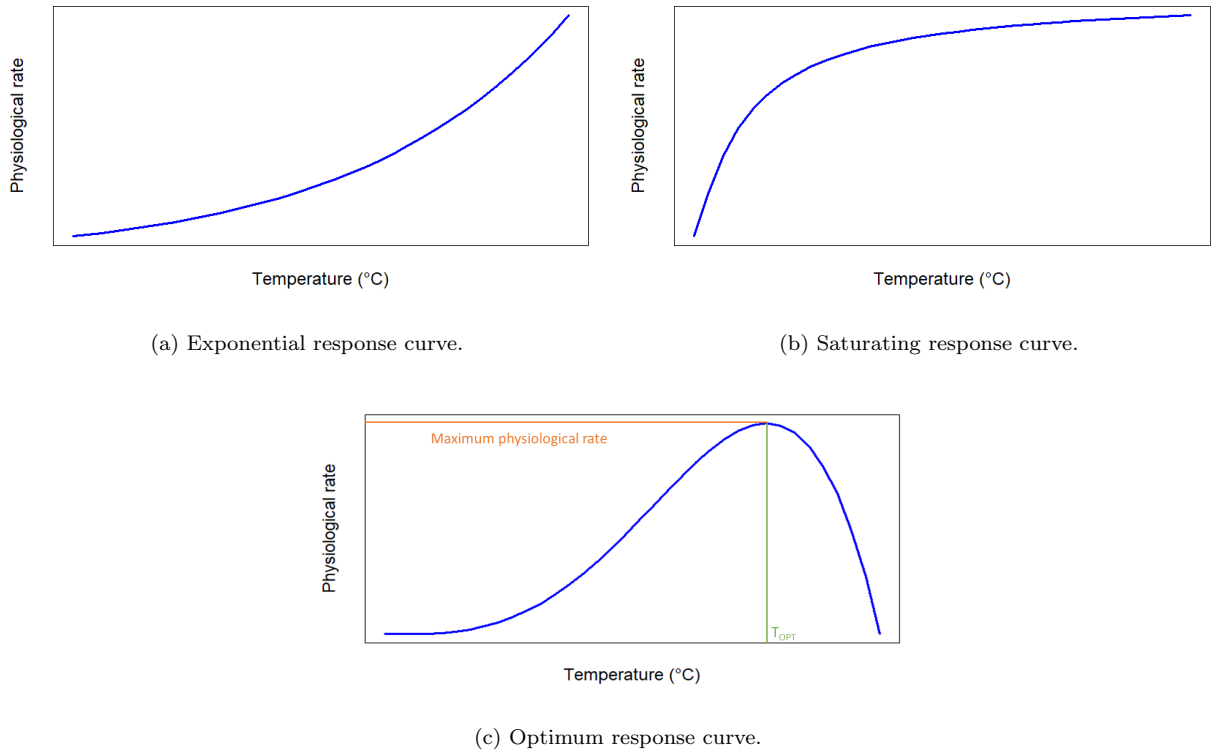

(c) Optimum response curve.

Figure 2: Temperature response curves.

diatom species experience a four-fold increase in growth rates with increasing temperature and no growth at temperatures above 20°C (Boyd et al., 2013). Maximum growth rates for polar and temperate phytoplankton species range between 0.3 d^{-1} and 1.4 d^{-1} (Boyd et al., 2013).

Tropical phytoplankton species have higher thermal tolerance than polar and temperate species as their thermal limits range between 18 and 34°C (Breitbarth et al., 2007; Boyd et al., 2013; Fu et al., 2014). *Trichodesmium* – a nitrogen fixing cyanobacterium – attained maximum growth of about 0.2 d^{-1} to 0.3 d^{-1} (Bell et al., 2005; Breitbarth et al., 2007; Boyd et al., 2013) at temperatures between 24 and 28°C (Bell et al., 2005; Breitbarth et al., 2007; Boyd et al., 2013; Fu et al., 2014) and gradually declined to zero at 35°C (Breitbarth et al., 2007; Boyd et al., 2013). Maximum nitrogen fixation by *Trichodesmium* (0.13 mmol N mol POC^{-1} h^{-1}) occurred at 27°C (Breitbarth et al., 2007), while maximum photosynthesis occurred at $\approx$ 26°C (Fu et al., 2014). *Crocosphaera*, another nitrogen fixer has been reported to have a higher thermal tolerance, with thermal limits ranging from 22°C to 34°C and optimum temperature at $\approx$ 28°C and 30°C (Boyd et al., 2013; Fu et al., 2014). Furthermore, the dinoflagellate *A. sanguinea* attained maximum growth at 25°C with an upper temperature limit between 30°C and 33°C, and a lower temperature limit between 10°C and 15°C (Boyd et al., 2013). A three-fold increase in dinoflagellate *P. donghaiense* growth rate was reported to occur between 15°C and 20°C, and $\approx$ 15% decrease at 30°C

(Boyd et al., 2013). Although tropical phytoplankton have higher thermal limits than polar and temperate species, they are highly sensitive to increasing temperature changes since they live close to or at optimum temperatures.

Ocean warming alters the phenology of phytoplankton in different ways depending on local conditions. Warming-induced increased growth and photosynthetic rates caused an earlier peak of phytoplankton spring bloom by 1–1.4 d$^{\circ}$C^{-1} in the temperate-climate Kiel Fjord on the edge of the Baltic Sea (Sommer et al., 2007; Sommer and Lewandowska, 2011). However, in the northern Red Sea, a tropical marine ecosystem, phytoplankton blooms have recently started late ($\approx$ 1–4 weeks), had a shorter duration ($\approx$ 4 weeks) and finished earlier ($\approx$ 4 weeks) (Gittings et al., 2018). This has been attributed to increased stratification and lower heat fluxes. The observed changes have implications on phytoplankton biomass.

The sensitivity of phytoplankton to pCO$_2$ is influenced by temperature. Elevated temperatures enhance growth and photosynthesis, and modulate the sensitivity of growth, photosynthesis and calcification of calcifying algae to pCO$_2$ increases (Sett et al., 2014). Likewise, the sensitivity of phytoplankton to temperature is influenced by other environmental factors, including light. Laboratory experiments for a mixed phytoplankton community conducted in conditions of light saturation and limitation, and weakly limiting nutrients have shown that maximum growth rate increases with temperature when light is saturated, while light limitation was found to reduce T$_{opt}$ by $\approx$ 5°C (Edwards et al., 2016).

Temperature increases stimulate changes in intracellular nutrient transformation and can be represented as an optimum response function (Figure 2c) (Gao et al., 2000). Regardless of growth habitat, nitrate assimilation in multiple phytoplankton species cultured in nutrient-rich conditions and different light treatments exponentially increased at temperatures below 10°C, was optimised between T$_{opt}$ of 10 and 20°C and decreased at temperatures above this range (Gao et al., 2000).

These observations suggest that many phytoplankton species have similar response curves to increasing temperature with distinct thermal tolerance and limits depending on location and species. Therefore, it is important to understand the ecological impact of these changes as they contribute to the oceans nitrogen and carbon inventories, bloom formation and to reef-building corals. These observed traits would be useful in modifying the parameterisation of biogeochemical models at the species level.

3.4.2. Phytoplankton community responses

The composition of phytoplankton communities changes as temperature varies. At higher temperatures, phytoplankton community composition shifts from large phytoplankton groups to small phytoplankton groups (Carpenter, 1973; Andersson et al., 1994; Hare et al., 2007; Keys et al., 2018), whereas large phytoplankton groups dominate when temperatures are low (Lassen et al., 2010).

At low temperatures, there is often reduced stratification and enhanced vertical mixing, hence elevated nutrient concentrations (Behrenfeld et al., 2006). At high temperatures, there is increased stratification and reduced vertical exchange, hence low nutrient concentrations (Schmittner, 2005; Behrenfeld et al., 2006). The dominance of small phytoplankton groups at higher temperatures (Falkowski and Oliver, 2007) might be attributed to their small cell size

which results in higher surface area to volume ratio (Litchman et al., 2007). This attribute enables enhanced nutrient uptake by small phytoplankton under low nutrient concentrations.

3.4.3. Zooplankton responses

Zooplankton are fundamental in shaping phytoplankton structure through grazing and facilitate energy transfer from primary producers to upper trophic level consumers in the food chain (Truong et al., 2017). In addition, they supply organic matter through excretion and mortality which provides a food source for detrital feeders and is remineralised by bacteria to release dissolved nutrients that can be taken up by phytoplankton (Morais et al., 2017).

Increasing temperatures have been observed to increase respiration, excretion and zooplankton grazing rates (Ikeda et al., 2001; Ikeda, 2014; Alcaraz et al., 2014; George et al., 2015), although Alcaraz et al. (2014) reported declines above a threshold. Respiration and excretion rates of zooplankton from polar to tropical waters (-1.7°C to 30°C) have been shown to depend on body mass and temperature (Ikeda et al., 2001; Ikeda, 2014) as they increase with increasing temperatures (Ikeda, 2014). The rate at which meso- and macro-zooplankton metabolic rates increase for a 10°C temperature rise (i.e. Q_{10}) ranges between 1.8 and 1.9 (Ikeda, 2014). Microzooplankton grazing rate increased from 0.15 ± 0.03 d^{-1} during the beginning of the spring bloom to 0.62 ± 0.11 d^{-1} during the peak and end of the bloom in the Long Island Sound (George et al., 2015).

Alcaraz et al. (2014) suggest that thermal thresholds and the balance between carbon loss and carbon gain are important in predicting warming impacts on zooplankton. They reported maximum grazing and respiration rates of Arctic *Calanus glacialis* at temperatures 2.5°C and 6°C, respectively, and that based on the balance between energetic gains and losses, the thermal threshold for *C. glacialis* survival is 6°C.

Although some experiments suggest increases in zooplankton physiological rates with increasing temperature (Ikeda et al., 2001; Ikeda, 2014; George et al., 2015), declines have been reported when temperature exceeds a thermal threshold in the Arctic (Alcaraz et al., 2014). Since tropical species live close to their thermal limits, extreme temperature increases could have similar implications for tropical zooplankton physiology. However, there is limited literature on warming effects on tropical zooplankton physiology. Thus, more work needs to be done to understand the physiological responses of tropical zooplankton to ocean warming for improved model parameterisations.

3.4.4. Coral responses

Corals provide habitats for many marine organisms through their reef-building ability. The symbiosis between reef-building corals and dinoflagellates is essential to coral calcification and coral reef growth. However, warming has disrupted this symbiotic relationship and has led to more frequent and widespread mass coral bleaching events (Hughes et al., 2017).

Corals respond to temperature variations following an optimum response curve (Figure 2c) (Castillo and Helmuth, 2005; Rodolfo-Metalpa et al., 2014; Jurriaans and Hoogenboom, 2019) and their thermal responses vary among locations and between species (Warner et al., 1996; Jurriaans and Hoogenboom, 2019). For example, in the Gulf of Honduras, Southern

Belize, *Orbicella annularis* (formerly *Montastrea annularis* and most abundant species in the Caribbean) photosynthetic and respiration rates are maximum at 33°C and decline to zero at 35°C (Castillo and Helmuth, 2005). Similarly, in the Mediterranean Sea, *O. annularis* photosynthesis and respiration are maximal at temperatures in the range $24 - 26°C$ and $25 - 27°C$, respectively (Rodolfo-Metalpa et al., 2014).

Long-term exposure $(2 - 3$ days) of several coral species widespread and abundant in tropical western Atlantic Ocean and the Caribbean Sea, namely *O. annularis*, *Agaricia lamarcki*, *Agaricia agaricites* and *Siderastrea radians* from the Discovery Bay, Jamaica to elevated temperatures between 30°C and 36°C decreased their symbiont photosynthetic efficiency (Warner et al., 1996). Complete disruption of photosynthesis in highly sensitive *O. annularis* and *A. lamarcki* occurred at 32°C and 34°C, respectively, whereas the photosynthetic efficiencies of *A. agaricites* and *S. radians* declined less (Warner et al., 1996). Short-term exposure of *Acropora spp.* (*Acropora intermedia* and *Acropora valenciennesi*) and *Porites cylindrica* from three locations in the GBR, namely Orpheus Island, Lizard Island and Heron Island to temperature increase and decrease of 5°C above the mean summer temperature showed that coral thermal performance varies with species and with latitudes, and the variation in coral symbiont types could be responsible for the observed differences in coral thermal performance (Jurriaans and Hoogenboom, 2019). Coral symbionts were shown to acclimatise better than coral hosts as their thermal optimum is closer to environmental temperatures and are likely to support coral hosts during extreme temperature events (Jurriaans and Hoogenboom, 2019). *Acropora spp.* and *P. cylindrica* are abundant and widespread in the Indo-Pacific Ocean (Wallace and Rosen, 2006).

Coral thermal tolerance is influenced by the duration of thermal stress (Hughes et al., 2018) and other environmental factors such as light intensity (Jokiel and Coles, 1990; Brown, 1997; Anthony et al., 2007). Bleaching, which correlates with coral respiration, is exacerbated by high light intensity (Jokiel and Coles, 1990; Anthony et al., 2007) causing coral mortality (Anthony et al., 2007) and declines in hard coral cover (Guest et al., 2016; Hughes et al., 2018). Increased mortality of *A. intermedia* from the GBR was reported to occur by the second half of a six-week exposure to $31 \pm 0.5°C$ temperature (Anthony et al., 2007). After the unprecedented 2016 and 2017 bleaching events on the GBR (Hughes et al., 2017, 2018), temperature-sensitive species of corals began to die immediately when exposed to temperatures above 3–4 degree-heating weeks in the GBR, and a further eight-month exposure to 6 degree-heating weeks shifted coral community assemblages (Hughes et al., 2018). As a consequence, coral calcification and production on Lizard Island in the GBR reduced by about 4–5% (McMahon et al., 2019). In general, short-term exposure (1–2 days) of corals to temperature increases of about 3–4°C above their thermal tolerance and long-term exposure (> 1 week) to increases of about 1–2°C can induce bleaching (Jokiel and Coles, 1990).

Coral larvae *Porites astreoides* experienced increased metamorphosis (7%) and mortality (30%) rates, decreased photosynthetic rate ($\approx 50\%$) when exposed to high temperature 33°C (Edmunds et al., 2001). These observed changes are likely to reduce recruitment. Relative to ambient temperature (25°C), elevated temperature (29°C) reduced coral larvae *Pocillopora damicornis* respiration rates by 32%, rubisco protein expression 2.6 times and photochemical efficiency by $\approx 49\%$ when compared to that of adult corals (Putnam et al.,

2013). This suggests that coral larvae are more sensitive to temperature than adult corals and are physiologically more suited to changing temperatures.

In response to increasing temperatures *O. annularis* skeletal extension rate decreased, whereas skeletal density increased and for each 1°C increase calcification rate increased by $\approx 0.57 \mathrm{gcm}^{-2}\mathrm{year}^{-1}$ (Carricart-Ganivet, 2004). However, extreme temperature increases at 23.7°C in the Gulf of Mexico and 25.5°C in the Caribbean Sea cause zero calcification (Carricart-Ganivet, 2004).

These findings highlight the variability of coral thermal tolerance with respect to species, locations and duration of thermal stress. They assert that tropical and subtropical corals are highly susceptible to bleaching as they live close to their thermal limits during summer. Further, thermal stress reduces the autotrophic ability of coral larvae and symbionts, thereby deteriorating coral health and reducing coral recruitment.

3.4.5. Seagrass responses

Seagrasses are ecologically important as they are primary producers and provide habitats for many marine organisms. Growth rates of seagrasses are limited by light intensity and temperature. Temperature influences seagrass dynamics as their thermal adaptation and tolerance affect distribution, productivity and biomass dynamics. Short-term exposure of seagrasses to extreme temperatures has been shown to reduce growth rate and increase mortality (Collier and Waycott, 2014) and heat waves have been associated with massive loss of seagrass habitats in the tropics (Arias-Ortiz et al., 2018), and tropical temperate transition zones (Kendrick et al., 2019). At the critical temperature threshold of 40°C seagrass growth reduced and mortality followed 2 – 3 days after temperature increased to 43°C in the GBR (Collier and Waycott, 2014).

Within the limits of physiological tolerance photosynthetic rates of seagrasses increased with increasing temperature (Evans et al., 1986; Marsh Jr et al., 1986; Bulthuis, 1987; Masini et al., 1995; Collier and Waycott, 2014; Weisse et al., 2016; Collier et al., 2017). Temperature responses of seagrasses vary among species and across locations. In the GBR, the subtropical and temperate species *Zostera muelleri* photosynthesis has been found to reach a maximum at 31°C, whereas tropical species *Halodule uninervis* and *Cymodocea serrulata* attained maximum photosynthesis at 35°C which rapidly declined to zero between 44 and 45°C (Collier et al., 2017).

The maximum photosynthetic rates of *Zostera marina L.* and *Ruppia maritima L.* in the subtropical Chesapeake Bay, USA decreased at temperatures above 19°C and 23°C, respectively (Evans et al., 1986). In Great Harbour, Massachusetts, net photosynthesis of *Zostera marina L.* was optimised at temperature between 25 and 30°C (Marsh Jr et al., 1986). Masini et al. (1995) found the T_{opt} for net photosynthesis of *Posidonia sinuosa* in (Mediterranean climate) Princess Royal Harbour, Western Australia to range between 18 and 23°C. Dark respiration rates increased exponentially under temperatures between 5 and 30°C (Marsh Jr et al., 1986; Pérez and Romero, 1992). Further, low light intensity has been shown to limit the photosynthetic capacity of seagrasses under temperature increases (Bulthuis, 1987; Masini et al., 1995).

These results show that regardless of latitude and species, seagrasses follow an opti-

mal temperature response curve. However, their thermal tolerances vary with latitude and among species as tropical seagrass species prefer higher temperatures than temperate and subtropical species. In general, short-term and long-term exposure of seagrasses to temperature increases above their thermal limits reduce their photosynthetic capacity and they are likely to suffer irreparable damage.

3.4.6. Microbial community responses

Marine microbes are fundamentally important in the health and productivity of marine ecosystems. They transform organic matter to nutrients through decomposition, transform nutrients into usable forms for marine plants and serve as a food source for some marine organisms. Marine microbes are also influenced by temperature. Marine microbial community responses to temperature increases could have positive or negative feedbacks to changing carbon and nitrogen cycles, and species that carry out important biogeochemical processes may be affected. Nitrogen mineralisation, nitrification and denitrification rates have been shown to follow an optimum response curve to temperature (Hansen et al., 1981; Thamdrup and Fleischer, 1998; Rysgaard et al., 2004). In one study of Arctic sediments, nitrogen mineralisation was found to be maximised at 20°C and decrease when temperatures are above 20°C (Thamdrup and Fleischer, 1998). In the same study, nitrification was found to increase with increasing temperatures below 8–16°C and rapidly decline for temperatures above this range (Thamdrup and Fleischer, 1998). Denitrification rates in Arctic sediments were found to be maximal at 24°C while anaerobic ammonia oxidation reached a maximum at 12°C (Rysgaard et al., 2004). We have not found studies reporting temperature response of microbial processes in tropical marine ecosystems.

3.4.7. Mangrove responses

Mangrove forests are found along the coast of tropical and subtropical oceans. Mangroves stabilise shorelines, protect coastal communities (Gedan et al., 2011) and sequester atmospheric carbon (Donato et al., 2011). They are one of the most productive ecosystems as they are sources of income, food and fuel for human communities and they provide nesting and nursery grounds for fish and invertebrates (Ewel et al., 1998; Aburto-Oropeza et al., 2008). Temperature greatly impacts mangroves as it limits the latitudinal distribution of mangroves. The minimum air temperature at which many mangroves are latitudinally limited is 16° C (Saenger, 2013) and leaf temperature between 22 and 30° C is optimal for CO_2 assimilation of tropical *Rhizophoraceae* species (Andrews et al., 1984). The 20°C winter isotherm of seawater coincides with the distributional limits of mangroves (Duke et al., 1998).

Short term exposure (2–24 hours) of *Avicennia germinans* (*Avicennia* is the most cold-tolerant genus) in three distinct life stages (dispersal, stranded, and seedling stages) to temperatures 5.7, 2.5 and -6.5° C reduced their survival, -6.5°C at 24 hours exposure had the greatest reducing effect on survival and dispersal had the greatest survival (Pickens and Hester, 2011). This shows that mangrove seedlings do not thrive in very low temperature conditions. *A. germinans* seedling photosynthetic rate was shown to be optimal (i.e., between 7.5 and 9.4 μmol cm^{-1}s^{-1}) at the range 24–25° C and zero between 39 and 42° C

under low and high nutrient conditions (Reef et al., 2016). *A. germinans* is widespread in coastal wetlands in the Caribbean and Gulf of Mexico.

Field studies indicate the expansion of mangroves into salt marshes on subtropical and temperate shorelines including, North America (Comeaux et al., 2012; Osland et al., 2013), Australia (Rogers et al., 2005; Straw and Saintilan, 2006), New Zealand (Morrisey et al., 2010; Stokes et al., 2010), China (Durango-Cordero et al., 2013) and Mozambique (De Boer, 2002). The expansion of mangroves into salt marshes corresponds to the expansion of temperature thresholds to the North and South Poles and sea-level rise (Saintilan et al., 2014). A moderate increase of ocean temperature by 1.2° C increased the overall cover of algal epibionts of mangrove roots by 24% but reduced epibiont diversity by 33% due to the occurrence of warming-induced shorter, weedy algal turfs (Walden et al., 2019).

These findings suggest that although continued temperature increases will enhance the poleward extension of mangrove forests it will modify the quality of mangrove habitats.

3.4.8. Kelp responses

Kelp species mostly occur along the coastlines of the world's temperate regions. They form structurally complex beds or forests which are one of the most diverse and productive ecosystems in the world (Steneck et al., 2002; Graham et al., 2016; Smale, 2020). Ocean temperature primarily determines the distribution of kelp. Elevated temperatures have been shown to reduce the growth of kelp due to direct effects of temperature on photosynthesis (Davison, 1991; Andersen et al., 2013). The maximum photosynthetic rate, photosynthetic efficiency and respiration of Norwegian *Saccharina latissima* were constant at 10 and 15° C, but at 20° C, maximum photosynthetic rate and photosynthetic efficiency reduced whereas respiration greatly increased (Andersen et al., 2013). Simonson et al. (2015b) exposed three dominant species in Nova Scotia (*Agarum clathratum* and *S. latissima* and *Laminaria digitata*) to four temperature treatments (11, 14, 18 and 21° C) for three weeks. They reported mortality in all species at 18 and 21° C, with mortality and tissue loss occurring at 21° C within two weeks exposure. *A. clathratum* growth rates reduced at 18° C after three weeks exposure. After one week exposure to 21° C, the strength and extensibility of *S. latissima* and *L. digitata* reduced by 40–70% although all species experienced reduced strength at 18° C after three weeks exposure. Simonson et al. (2015b) identified *A. clathratum* as the least vulnerable to warming-induced tissue weakening and loss. However, elevated temperature had no effect on kelp quality as food source for the gastropod mesograzer *Lacuna vincta* and the invasive bryozoan *Membranipora membranacea*, thereby exacerbating the direct temperature effects on kelp causing increased kelp biomass loss (Simonson et al., 2015a).

The interactive effects of temperature, nutrients, pCO_2 and competitive species have been reported to alter kelp ecosystem (Connell and Russell, 2010; Moy and Christie, 2012). A fourteen-week experimental study involving the removal of turfs from a phase-shifted system indicated the inhibition of kelp recruitment by algal turfs (Connell and Russell, 2010). Relative to ambient temperature (17° C), elevated temperature (20° C) and pCO_2 enrichment increased the abundance of algal turfs, thereby reducing kelp abundance (Connell and Russell, 2010). All juveniles of the perennial kelp *Ecklonia cava* (dominant from central to southern Japan) exposed to nutrient-enriched seawater at temperatures 20, 26, 28 and 30°

C survived, whereas mortality occurred in nutrient-deplete conditions at all temperatures (Gao et al., 2016). *E. cava* photosynthetic rate peaked at 28° C and decreased greatly at 30° C under nutrient-replete conditions, but was constant at 20 to 28° C in non-enriched conditions (Gao et al., 2016). Further, increasing temperatures from 20 to 30° C decreased growth rate under nutrient enrichment, while growth rate remained constant at 20 and 26° and decreased at 28° C under non-enriched conditions (Gao et al., 2016). Overall, photosynthetic and growth rates were greater in nutrient-enriched seawater than in nutrient-deplete conditions at temperatures between 20 and 28° C (Gao et al., 2016). However, Muth et al. (2019) showed that regardless of nutrient levels, increasing temperatures from 12 to 18° C reduced kelp recruitment in the eastern Pacific.

Over the past 40–60 years in Nova Scotia, ocean warming reduced mean kelp biomass by 85–99% and caused a shift from kelp beds to rocky reefs dominated by invasive algal turfs (Filbee-Dexter et al., 2016). Between 2004 and 2009 in the Skagerrak region along the coast of southern Norway, large-scale loss of *S. latissima* occurred leading to filamentous, ephemeral macroalgae dominance (Moy and Christie, 2012). This large-scale community shift is mainly attributed to rising temperature and eutrophication.

These findings suggest that rising temperature is a major contributor to the decline of kelp ecosystems. Continued loss of kelp forests will have implications for coastal marine production and management.

3.5. Ocean acidification

Ocean acidification caused by increased pCO_2 inhibits the ability of marine calcifiers to form shells and skeletons (Orr et al., 2005; Hoegh-Guldberg et al., 2007; Fabry et al., 2008; Chan and Connolly, 2013), affects their growth, reproduction and survival rates (Kroeker et al., 2013), and may enhance the dissolution of existing shells and skeleton material (Feely et al., 2004; Orr et al., 2005; Andersson et al., 2009; Kroeker et al., 2013).

3.5.1. Phytoplankton responses

Phytoplankton are carbon fixers, thus they influence the carbon pump of oceans. Increased seawater CO_2 concentrations has been shown to increase photosynthesis, increase primary production of calcifying phytoplankton and likely alter phytoplankton community composition (Tortell et al., 2008; Yang and Gao, 2012; Grear et al., 2017). Coccolithophore species *Emiliania huxleyi* – the most cosmopolitan species – and *Gephyrocapsa oceanica* – the most abundant species in tropical and subtropical oceans (Bendif et al., 2015) – have been shown to have pCO_2-dependent optimum-curve responses for growth, photosynthesis and calcification rates (Sett et al., 2014). Temperature modulates the optimum response of these processes. Optimum $[pCO_2]$ of *E. huxleyi* and *G. oceanica* for growth, photosynthesis and calcification increased to $\approx$ 600 and 1300 ppm pCO_2, $\approx$ 835 and 1535 ppm pCO_2, and $\approx$ 550 and 875 ppm pCO_2 when temperature increased to 20 and 25°C, respectively.

In various contexts, elevated pCO_2 concentrations (800 and 1000 ppm) increased carbon fixation by 25%, dark respiration by 35% (Yang and Gao, 2012), phytoplankton biomass by 6.5-fold (Keys et al., 2018) and growth rate by $\approx$ 10–20% (Tortell et al., 2008). Elevated pCO_2 (1000 ppm) increased the Southern Ocean bloom-forming *Chaetoceros debilis* growth

rate by 63%, but had no effect on other bloom-forming species such as *Phaeocystis antarctica*, *Pseudo-nitzschia subcurvata* and *Fragilariopsis kerguelensis* (Trimborn et al., 2013). Cellular particulate inorganic and organic carbon (PIC and POC) concentrations increased by 80% and 90% at 600 ppmV pCO_2, and a further 150 ppmV pCO_2 increase caused 48% and 45% increase in PIC and POC concentrations (Iglesias-Rodriguez et al., 2008). Likewise, *Trichodesmium* nitrogen fixation increased by 60% when pCO_2 increased from 180 to 1400 ppmV and intracellular nutrient concentrations (i.e. POC and PON) increased by 33% when pCO_2 increased from 380 to 1400 ppmV (Eichner et al., 2014). In contrast, Böttjer et al. (2014) found no significant effect on nitrogen fixation by short-term (1–3 days) exposure of natural occurring nitrogen fixers in North Pacific subtropical gyre to elevated pCO_2 ($\approx$ 1000 ppm).

There is mixed evidence on elevated pCO_2 effects on phytoplankton community composition. Bermúdez et al. (2016); Keys et al. (2018) found that temperate phytoplankton community composition shifted towards smallest size fractions due to pCO_2 increases while Tortell et al. (2002) found the opposite in phytoplankton assemblages in the Southern Ocean. The dominance of small-sized phytoplankton can be attributed to increased growth rate of small-sized phytoplankton caused by elevated pCO_2 (Grear et al., 2017). Rising pCO_2 from ambient to 1981 ppm reduced essential polyunsaturated fatty acids (PUFA) in North Sea phytoplankton and the observed nanophytoplankton PUFA reduction caused $\approx$ 10% reduction of dominant copepod *Calanus finmarchicus* PUFA (Bermúdez et al., 2016).

The findings described above suggest that phytoplankton is most likely to benefit from ocean acidification, although a reduction in phytoplankton fatty acids will reduce the nutritional quality of phytoplankton available for zooplankton and other grazers.

3.5.2. Zooplankton responses

Ocean acidification has been found in some studies to have little or no direct effect on zooplankton (McConville et al., 2013; Hildebrandt et al., 2014). Short-term exposure (4 days) of copepod species *Centropages typicus* and *Temora longicornis* to elevated pCO_2 (750 ppm) had no effect on egg production and hatching success (McConville et al., 2013). Similarly, elevated pCO_2 3000 ppm had no effect on Arctic copepods *C. glacialis* and *C. hyperboreus* (Hildebrandt et al., 2014). However, exposing pelagic copepods to about 98,000 ppm for a day increased copepod mortality in subarctic to subtropical waters (Watanabe et al., 2006). Copepods living in deep waters were shown to be more sensitive than shallow-living copepods, and deep-living copepods in subarctic and transitional waters were shown to have higher pCO_2 tolerance than subtropical copepods (Watanabe et al., 2006).

In tropical coral reefs located in Papau New Guinea, rising pCO_2 leading to average pH reduction from 8 to $\approx$ 7.8 pH reduced demersal zooplankton biomass (by a factor of three), while zooplankton community composition and fatty acid composition remained unchanged (Smith et al., 2016). Demersal zooplankton biomass reduction could be attributed to the shift from branching corals to massive bouldering corals due to progressing ocean acidification. This observation highlights the importance of in situ experiments in understanding ocean acidification effects on zooplankton as they are likely to produce results different to results obtained from laboratory experiments.

We found little information on tropical zooplankton responses to ocean acidification. More experiments are needed to understand the short- and long-term effects of ocean acidification on tropical zooplankton species.

3.5.3. Coral responses

Corals are likely to experience direct effects of increased pCO_2 as they build their skeletons from calcium carbonate. Elevated pCO_2 (635 ppm) enlarged the body size of *P. damicornis* larvae by $\approx 10\%$ (Putnam et al., 2013). *P. damicornis* larvae was shown to favour skeletal growth at the expense of asexual budding when exposed to 896 and 1681 ppm pCO_2 (Jiang et al., 2015). Combined effects of elevated pCO_2 (≈ 1100 ppm) and temperature ($2°C$ above ambient) decreased respiration by $\approx 30\%$ and recruitment of *Dendropoma cristatum* larvae by $\approx 60\%$ (Alessi et al., 2019). Coral *Stylophora pistillata* calcification decreased by 50% when exposed to increased pCO_2 (734 and 798 ppm) and temperature at $28°C$, but remained constant at $25°C$ (Reynaud et al., 2003). Increased pCO_2 (750 ppm) increased coral *Acropora pulchra* biomass by 31% and 38% at $29.8°C$ and $27.2°C$ under light saturation (Comeau et al., 2014). This supports the influence of irradiance on the responses of reef-building corals to elevated pCO_2. *P. damicornis* and *S. pistillata* are common in the Indo-Pacific Ocean.

Across the globe, there is concern that the interacting effects of ocean acidification and rising temperatures will cause a decline in calcification of coral species. For example, across the GBR, a 11.4% decline in calcification of massive *Posites* from 1990 to 2005 has been confirmed (De'ath et al., 2009, 2013). Between 390 and 750 ppm pCO_2 coral diversity, recruitment and abundance of structural corals declined, but coral cover remained unchanged due to the dominance of *Posites* over structural corals despite its low calcification (Fabricius et al., 2011). Further, in the eastern tropical Pacific *P. damicornis* extension declined by approximately 33% from 1974 to 2006 (Manzello, 2010).

These findings suggest that although the effects of pCO_2 increases on corals at their early life stages vary, they could have major consequences on their ecological functions and coupled with thermal stress pCO_2 effects on corals are exacerbated.

3.5.4. Seagrass responses

Ocean acidification has been shown to have positive effects on seagrass (Palacios and Zimmerman, 2007; Fabricius et al., 2011; Ow et al., 2015; Takahashi et al., 2016) due to the potential ability of seagrass to increase its productivity with ocean acidification (Burnell et al., 2014; Borum et al., 2016). Long-term (one year) exposure of *Z. marina* to 16–1123 μM pCO_2 under light-limited and saturating light conditions did not change shoot production and leaf photosynthesis (Palacios and Zimmerman, 2007). However, under saturating light conditions, rising pCO_2 enhanced seagrass productivity as below-ground biomass, vegetative proliferation and reproduction increased (Palacios and Zimmerman, 2007). Short-term (45 days) exposure of *Z. marina* to 3673 μM pCO_2 caused a reduction in light requirements for survival and growth, and a three-fold increase in leaf photosynthesis and shoot production (Zimmerman et al., 1997). Similarly, a two-week exposure of warm water species *Cymodocea serrulata*, *Halodule uninervis* and *Thalassia hemprichii* to rising pCO_2 (442–1204 ppm)

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increased net production and gross photosynthesis to respiration ratio in all species, and reduced light requirements for growth and survival in *C. serrulata* and *H. uninervis* (Ow et al., 2015).

In the GBR, Fabricius et al. (2011) showed that long-term enrichment of pCO_2 from 390 to 750 ppm caused an eight-fold increase in seagrass cover. Likewise, at three shallow volcanic CO_2 vents in Papua New Guinea, pCO_2 enrichment resulting to decreased average pH from 7.9 to 7.5 increased seagrass cover three times and seagrass biomass 5 times, with varying seagrass community composition (Takahashi et al., 2016).

These results suggest that continued ocean acidification could enhance the survival and growth of seagrass in coastal waters by reducing light requirements and enhancing productivity, but due to the varying seagrass community composition it could alter seagrass community structures.

3.5.5. Microbial responses

For heterotrophic bacteria, pCO_2 increases had direct positive effects such as increased growth, photosynthesis and reduced respiration. These changes could affect their ecological functions in marine ecosystems. A five-day exposure of two bacterial isolates, *Rhodobacteraceae* and *Flavobacteriaceae*, from the Mediterranean Sea to 1000 ppmV pCO_2 had positive effects on their metabolic rates (Teira et al., 2012). *Rhodobacteraceae* photosynthetic rate increased, and *Flavobacteriaceae* growth efficiency and photosynthetic rate increased, while respiration rate reduced (Teira et al., 2012). *Rhodobacteraceae* contribute about 20% of coastal bacterioplankton community (Buchan et al., 2005), while *Flavobacteriaceae* is abundant in eutrophic waters (Alderkamp et al., 2006).

Relative to pH 8, nitrification rates reduced by 50% at pH 7, reduced by $\geq 90\%$ at pH 6.5 and was inhibited at pH 6 in deep sea waters (Huesemann et al., 2002). This shows that pCO_2 increases could cause an accumulation of ammonia in bottom waters and when transported into the euphotic zone could alter phytoplankton abundance and community composition structure.

3.5.6. Mangrove responses

Elevated atmospheric CO_2 effects on mangroves are influenced by other environmental factors such as salinity, nutrient availability and water use (Lovelock et al., 2016). A fourteen-week exposure of two Australian mangroves *Rhizophora apiculata* and *R. stylosa* to a two-fold increase in ambient atmospheric CO_2 (340 μl L^{-1}) increased growth under low saline conditions but had no effect on growth under high saline conditions (Ball et al., 1997). The observed growth increase is caused by enhanced photosynthetic water use efficiency, increased net assimilation rate and increased leaf area ratio (Ball et al., 1997). Relative to 400 ppm pCO_2, elevated pCO_2 (800 ppm) increased *A. germinans* seedling maximum photosynthetic rate, T_{opt} for photosynthetic rate and the temperature at which the photosynthetic rate is zero (Reef et al., 2016). Thereby causing increased growth in above-ground biomass and root volume under high and low nutrient conditions, respectively (Reef et al., 2016). Similarly, an eighteen-month exposure of *A. germinans* to 365 and 720 μl L^{-1} CO_2 concentrations increased its growth and biomass under high nitrogen concentrations, but when

grown with cordgrass *Spartina alterniflora*, the seedling growth reduces (McKee, 2006). This indicates that competition from other species limits seedling growth under elevated CO_2 conditions. Mangrove seedlings of *R. mangle* exposed to ambient (350 μl L^{-1}) and double-ambient CO_2 conditions for a year experienced increased growth and biomass and increased branching activity due to CO_2 enrichment (Farnsworth et al., 1996). In general, CO_2 enrichment increased mangrove seedling growth by 12–47% (Lovelock et al., 2016). On the other hand, elevated CO_2 was shown to have no effect on *R. mangle*, *A. germinans* and *Conocarpus erectus* net productivity but reduced the productivity of *Laguncularia racemosa* (Snedaker and Araújo, 1998). Increased CO_2 increased the transpiration efficiency, reduced the stomatal conductance and transpiration of all four species (Snedaker and Araújo, 1998).

Relative to ambient pCO_2 (350 ppm), elevated pCO_2 (500 ppm) had no effect on the total cover of algal epibiont on mangrove roots but its interacting effect with a 1.2° C temperature increase reduced epibiont diversity and increased the total algal epibiont cover (Walden et al., 2019).

These findings suggest that CO_2 enrichment will enhance mangrove production, but the composition and structural complexity of mangrove communities will most likely be altered due to the species-specific responses to the interacting effects of CO_2 enrichment and other biotic and abiotic factors.

3.5.7. Kelp responses

Kelp canopy effectively removes inorganic carbon from water column during photosynthesis and accumulates fixed carbon in its biomass. Seasonal carbon storage and increased photosynthetic material are provided by dense kelp canopy for more carbon uptake. Ocean acidification has been shown to have little or no effect on kelp (Fernández et al., 2015; Leal et al., 2017; Mora-Soto et al., 2020; Fernández et al., 2021). Reducing the pH from 8 to 7.59 had no effect on the photosynthesis and growth of giant *Macrocystis pyrifera*, but the combined effects of pCO_2, nutrient availability and temperature could change *M. pyrifera* physiological responses to pCO2 enrichment (Fernández et al., 2015). *M. pyrifera* is the most widely distributed kelp species in the world's temperate shorelines (Mora-Soto et al., 2020). Relative to pH 8.01 and 8.4, low pH 7.2 and 7.65 did not affect the development of *M. pyrifera* and *Undaria pinnatifida* in south-eastern New Zealand (Leal et al., 2017). pCO_2 enrichment of juvenile *M. pyrifera* had no effect on their photosynthesis and growth but it increased the gene expression of nitrate reductase (Fernández et al., 2021). However, increased mortality and germination rates of *M. pyrifera* spores occurred due to the interacting effects of temperatures (13 and 18° C) and pCO_2 (400 ppm and 1800 ppm) (Gaitán-Espitia et al., 2014).

These findings indicate that ocean acidification is not a major threat to kelp health but the interacting effects of ocean acidification and other environmental factors could have adverse effects on kelp ecosystems.

3.6. Adaptation of marine organisms to changes in temperature and ocean acidification

The potential ability of marine organisms to adapt and acclimate to environmental stressors may reduce the severity of detrimental effects of a changing environment. Long-term

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acclimation (e.g. 1–2 weeks or a decade) of phytoplankton to high temperatures has been shown to improve their thermal tolerance. These improvements include reduced respiration rates, increased optimum temperatures for growth and photosynthesis (Staehr and Birkeland, 2006; Padfield et al., 2016; Schaum et al., 2017), increased growth rate and cellular pigment content, decreased cell size and Chl a-specific light absorption (Staehr and Birkeland, 2006). Accordingly, when compared to phytoplankton in ambient conditions, warm-adapted phytoplankton competes better in warm conditions and loses its competitive fitness in ambient conditions (Schaum et al., 2017).

Z. muelleri has been identified as the most thermal tolerant seagrass species after a seven-week exposure of different tropical species, namely *Cymodocea serrulata* and *Halodule uninervis* to increasing temperatures and pCO_2 under saturating light conditions (Collier et al., 2018). *Z. muelleri* maximum net production was positive at 15°C to 35°C, while rapid declines in growth, production and shoot density exacerbated by high pCO_2 at 35°C were reported in other species.

Enhanced thermal tolerance of heat-evolved strains of coral microalgal endosymbiont at 31°C increased the bleaching tolerance of coral host larvae when symbiosis is established (Buerger et al., 2020).

Epigenetic effects have the ability to buffer the impacts of changing environmental conditions by generating phenotypic plasticity. Increased DNA methylation likely reduced ocean acidification effects on coral, *S. pistillata* by contributing to its phenotypic acclimation (Liew et al., 2018). Offsprings of individuals grown in warm temperatures have been shown to grow better in warm temperatures. Warmer egg production temperature of *Acartia* copepod induced positive maternal effects which increased the egg hatching rate in warmer temperatures (Vehmaa et al., 2012).

At the ecosystem level, the low connectivity of coral reefs in Nikko Bay due to the long residence time of the bay water enables local adaptation of these coral reefs to ocean acidification (Golbuu et al., 2016).

4. How well are climate change impacts represented by marine ecosystem response models?

4.1. Model performance assessment

Model performance indicates how well model results agree with observational datasets. Model evaluation provides modellers the needed confidence in model performance. To this end, 107 out of the 131 studies reviewed reported metrics comparing predicted and measured results. Seventy-six studies had parameter values fine-tuned to better match observations (i.e. calibration), but only nine studies were validated using independent datasets. This is consistent with the findings of previous reviews of biogeochemical model assessment (Arhonditsis and Brett, 2004; Robson, 2014). Although these models have varying complexity, evaluation was mostly done by comparing model results of physical, chemical and biological variables against historical observational data.

The physical variables most commonly assessed were salinity (twelve studies), water temperature (fourteen studies) and water level (sea surface elevation) (five studies), while

the most common biogeochemical variables analysed included concentrations of chlorophyll a (Chl a) (twenty-three studies), dissolved oxygen (DO) (twelve studies), dissolved inorganic carbon (DIC) (seven studies), nitrate and phosphate (NO_3 and PO_4) (fifteen studies), total alkalnity (TA) (seven studies), net primary production (NPP) (eight studies), export fluxes (three studies) and pH (four studies). The biomass of lower and higher trophic level species, and the annual catch of fisheries were also assessed for model performance in fourteen studies.

Multiple metrics were used to assess model performance in twenty studies. These metrics include the standard deviation (SD), the root mean square error (RMSE), average absolute error (AAE), average error (AE), the modelling efficiency (MEF), the robustness index, percent model agreement, Spearman and Kendall tau-b correlation coefficients (Holzwarth and Wirtz, 2018; Lachkar et al., 2018; Irby et al., 2018; Pilcher et al., 2018; Fulton et al., 2018; Bauer et al., 2018; Bryndum-Buchholz et al., 2019). However, Suprenand and Ainsworth (2017) calibrated model parameters with trophic vulnerabilities due to insufficient observational data, although they are less suited for time series fitting when observations are available. Travers-Trolet et al. (2014) calibrated their model with an automatic method involving evolutionary algorithms based on the selection of the best set of model parameters that simulate model results (biomasses) that are closest to observed biomasses. Automatic calibration is more thorough and less labour-intensive than manual calibration, but is more likely to obtain unrealistic parameter sets unless parameter ranges and parameter priors are specified carefully (e.g., (Robson et al., 2018)), and requires greater computational resources.

Multiple metrics are used for thorough model performance assessment because they capture different aspects of model performance (Stow et al., 2009). For example, AAE, AE and RMSE measure accuracy, i.e. they measure the difference between model results and observations, while MEF evaluates both accuracy and precision, but is less sensitive to lack of correlation and should be used with a correlation metric. Olsen et al. (2016) recommend the use of at least four metrics, namely MEF, RMSE, AAE, and Spearman rank correlation for effective model performance assessment.

4.2. Time period of simulations

The long-term aspects of global climate change prompted sixty-one studies to continuously run their models from the past to the future with dates ranging between 1850 - 2100 (Meier et al., 2017; Lefort et al., 2015; Patara et al., 2013; Vancoppenolle et al., 2013; Lehodey et al., 2010) and 1950 - 2100 (Richon et al., 2019; Carozza et al., 2019; Dutkiewicz et al., 2013). However, sixteen models considered twenty-year or ten-year runs of present and future climate conditions to save computational cost (Hodgson et al., 2018). Nine studies ran their models for at most two years under future conditions. In particular, Guyondet et al. (2015) and (Irby et al., 2018) considered a model run in isolation for a year (2050) of projected future conditions, while Herrmann et al. (2013) considered 7 one-year simulations under future conditions. Thirty-eight studies performed hindcast runs (Pilcher et al., 2018) and six studies ran future simulations for over a thousand years (Yamamoto et al., 2018). Marshall et al. (2017) ran simulations for 100 years, but looped a single year ROMS oceanography 100 times. This was done to reduce the computational cost, control interannual variability of oceanic conditions and isolate the impacts of distinct drivers of change.

Depending on model formulation, long and continuous runs could allow the simulation of cumulative climate impacts and assessment of intermediate climate change conditions. However, short runs comparing current with future conditions have lower computational costs, therefore they are suitable for high resolution modelling and multiple scenarios examination.

4.3. IPCC Scenarios

IPCC scenarios describe future dynamics of GHG emissions, air pollutant emissions and land use, and are used to assess how causes of future emissions influence future emission outcomes and examine the associated uncertainties. Descriptions of IPCC scenarios can be found in (Nakicenovic et al., 2000; Watson et al., 2001; Pachauri and Reisinger, 2008; IPCC, 2014). Only sixty-two of the 131 selected studies used IPCC scenarios. Among these sixty-two studies, forty-three used a single scenario and nineteen used multiple IPCC scenarios. Twenty-seven studies dynamically downscaled IPCC climate change predictions with regional ocean models such as the Regional Ocean Modelling System (ROMS) to get daily local predictions (Carozza et al., 2019; Laurent et al., 2018) and one study considered statistical downscaling (Brown et al., 2016). Seven studies forced experiments with prescribed atmospheric CO_2, increased by 1% per year to double or quadruple its initial concentration and constant afterwards (Park et al., 2015; Yamamoto et al., 2018) for future predictions. Eleven studies used prescribed atmospheric CO_2 from observational data (Wallhead et al., 2017; Van Oostende et al., 2018) to force experiments for hindcast runs.

The use of only one IPCC scenario provides limited information regarding uncertainties, but has a lower computational cost than using multiple scenarios. Downscaled climate predictions are suitable for policy decisions as they offer better temporal and spatial resolutions. Downscaling involves the use of information from broad-scale ($\approx$ 200km grids) General Circulation Models (GCMs) to predict climate change impacts on regional scales ($\approx$ 10–50km) (Queensland Water Modelling Network). Dynamical downscaling is the use of high-resolution regional models to simulate broad-scale climate change processes on regional or local scales. Dynamical downscaling allows explicit representation of physical principles that influence climate conditions, has high computational cost and is sensitive to large-scale biases (Queensland Water Modelling Network). On the other hand, statistical downscaling uses statistical techniques to relate local climate observations to GCM outputs and produce new environmental conditions. Statistical downscaling is cost-effective, but is more likely to produce incorrect results than dynamical downscaling due to the ability of climate change to alter the statistical relationships, or large-scale climate features used as predictors are not well captured by GCMs or have strong biases (Queensland Water Modelling Network).

4.4. Scenario Analysis

Most studies compared scenarios of baseline reference of natural and current conditions against a group of scenarios representing perturbed conditions. This comparison isolates the impacts of the perturbations.

4.5. Meteorological conditions

4.5.1. Air temperature

Twelve studies represented changes in meteorological conditions as projections of climate models under high air temperatures. Parameters used in two of these studies showed direct increases in air temperature (Guyondet et al., 2015; Laurent et al., 2018). Laurent et al. (2018) represented changes in meteorological conditions as projections of a climate model forced with 3°C warmer air temperature and 10% river discharge increase. The 3°C increase in air temperature was projected by the same model used for the future run under the same IPCC scenario. Likewise, a 4°C increase in air temperature and a 10% increase in river discharge were used to force the 2050 scenario run in (Guyondet et al., 2015). This approach is simple but has the potential to overestimate or underestimate climate change impacts.

4.5.2. Wind speed

Changes in wind speed/stress were considered in only five studies. Jiang and Xia (2018) interpolated wind data from the National Center for Environmental Prediction/North America Regional Reanalysis (NCEP/NARR) and directly increased/decreased the magnitude of Southerly winds on the shelf for wind scenarios. In two studies, monthly and daily wind stress climatology were obtained from satellite data. In particular, Lachkar et al. (2018) forced their model with satellite data under nine wind stress scenarios by directly increasing and decreasing wind stress seasonally and annually, while Mogollón and R. Calil (2018) ran future model runs under increased winds scenario by directly increasing the zonal and meridional wind stress components. These studies found that changes in wind speed impact marine ecosystems. Increased wind speed reduced the residence time in coastal regions, increased phytoplankton production and nutrient export, and expanded offshore plumes (Mogollón and R. Calil, 2018; Jiang and Xia, 2018). Lachkar et al. (2018) identified the summer monsoon wind as the major driver of change in the size and intensity of the Arabian Sea oxygen minimum zone (OMZ). Strong monsoon winds expand the OMZ due to increased oxygen consumption resulting from increased productivity. Further, changing Indian monsoon influences the biological pump and the nitrogen cycle on a longer timescale, as intensified winds increased N_2O production, thereby exacerbating climate change.

Changes in cloud cover, storm intensity and storm frequency were not considered as forcings for the biogeochemical models in any of the studies reviewed. This means that the current state of the art in biogeochemical modelling of climate change impacts considers neither the effects of changes in incident light on photosynthesis, nor the effects of storms on vertical mixing, sediment resuspension nor shear stress, which can directly damage benthic habitats.

4.6. River flows, sediment and nutrient loads

Of the 131 studies reviewed, forty-nine studies considered the effects of modified river discharge as boundary conditions and forty examined changes in nutrient loads. Changes in river discharge were modelled using four main approaches, and changes in nutrient loads

using five main methods (Table 2). Providing more and better observations of river discharge/nutrient loads will improve the accuracy of hindcast model predictions and model assessments. Although the use of fixed percent increase or decrease in river discharge/nutrient loads data based on climate predictions eliminates complexities and is cost-effective, it can produce unreliable results. Likewise, using statistical models to determine input river discharge/nutrient loads is cost-effective and can produce unreliable results as the effects of underlying physical processes are not taken into account. However, the application of a hydrological model under climate change scenarios to produce input river discharge/nutrient load time series produces more reliable projections but requires high computational cost.

4.7. Ocean transport processes

None of the modelling studies included in the literature reviewed explicitly considered changes in ocean stratification, upwelling or ocean currents as forcing factors. However, thirteen studies used global or downscaled Earth System Model outputs to force biogeochemical models (Vancoppenolle et al., 2013; Hodgson et al., 2018; Park et al., 2015; Kwiatkowski et al., 2019) and may have implicitly taken the effects of these ocean transport processes into account.

4.8. Water temperature

Fifty-five studies simulated changes in water temperature in response to changes in meteorological conditions represented as IPCC climate change projections from global climate models. Five studies directly increased water temperature based on future climate predictions. Fulton et al. (2018) applied 0.2°C, 0.5°C, 1.0°C and 2.0°C water temperature increases simulated under RCP scenarios at the end of 2050 and Irby et al. (2018) directly applied a 1.75°C increase in water temperature by mid-century. Three studies directly applied the time series of monthly water temperature from observational data (Lachkar et al., 2018; Holzwarth and Wirtz, 2018; Shen et al., 2019). Direct increase of water temperature by Irby et al. (2018) is consistent with temperature predictions from downscaled global climate models (Muhling et al., 2018), but it is greater than observed temperature and slightly lower than the temperature predictions from a high resolution climate model (Saba et al., 2016). This approach reduces the complexity and computational cost of creating downscaled climate predictions but has the potential to produce misleading results by overestimating or underestimating the impacts of warming. Therefore, for better accuracy, changes in water temperature should ideally be dynamically simulated when developing scenarios for biogeochemical modelling.

4.9. Ocean acidification

As mentioned in Section 3.5, increased CO_2 ocean uptake alters carbonate chemistry which directly affects marine calcifiers and indirectly affects their predators. Six studies considered effects of changes in pCO_2 as ocean acidification effects on marine biota. They predict declines in primary production (Yool et al., 2013), fish and invertebrates growth (Cornwall and Eddy, 2015), the biomass of low pH sensitive benthic biota and the abundance of demersal fish, sharks and epibenthic invertebrates that feed on these benthic biota

Table 2: Summary of the approaches used to model the impacts of changes in river discharge and nutrient loads on marine ecosystems.

Consideration	Approach	Advantages/Disadvantages	Number of studies using this approach	Citations
Changes in river discharge	Application of past river discharge datasets.	Computationally cost-efficient. Suitable for hindcast runs and model validation. Limited observational datasets.	23	(Ruiz et al., 2013), (Guyennon et al., 2015), (Laurent et al., 2017), (Stråat et al., 2018), (Holzwarth and Wirtz, 2018).
	Fixed percent increase or decrease in river discharge data based on climate predictions.	Computationally cost-efficient. Eliminates complexity and uncertainties associated with climate model runs such as model and forcing incompatibilities. May overestimate/underestimate the impacts of changes in river discharge.	11	(Tanaka et al., 2013), (Guyondet et al., 2015), (Wakelin et al., 2015), (Etemad-Shahidi et al., 2015), (Brown et al., 2016).
	Use of a statistical model to determine input river discharge.	Based on the relationship between observations of inputs and outputs of the modelled system. Does not require detailed information on physical processes. Computationally cost-efficient. Can omit important factors influencing river discharge changes.	5	(Allin et al., 2017), (Bauer et al., 2018).
	Application of a hydrological model under climate change scenarios to obtain input river discharge.	Requires detailed information on physical processes, thus provides an understanding of hydrological processes affecting river discharge behaviour. Captures the impacts of climate variability. Most accurate in simulating river discharge changes. Large computational cost. Existence of complexity and uncertainties associated with climate model runs.	10	(Lazzari et al., 2014), (Glibert et al., 2014), (Fernandes et al., 2015), (Feng et al., 2015), (Ryabchenko et al., 2016).
Changes in nutrient loads	Application of past river nutrient loads datasets.	Suitable for hindcast runs and model validation. Limited observational datasets.	17	(Herrmann et al., 2013), (Bianucci et al., 2015), (Meier et al., 2017), (Laurent et al., 2017), (Van Oostende et al., 2018).
	Fixed nutrient loads or fixed nutrient concentrations.	Allows the manifestation of climate change impacts. May overestimate or underestimate the impacts of climate change on riverine nutrient loads.	2	(Glibert et al., 2014), (Jiang and Xia, 2018).
	Fixed percent increase or decrease of nutrient loads.	Computationally cost-efficient. Can overestimate/underestimate the impacts of changes in nutrient loads.	8	(Hardman-Mountford et al., 2013), (Guyondet et al., 2015), (Wakelin et al., 2015), (Ryabchenko et al., 2016).
	Synthesis of input nutrient loads using a statistical model	Captures statistical features of nutrient load variability. Computationally cost-efficient. Can omit important factors affecting changes in nutrient loads.	3	(Allin et al., 2017), (Bauer et al., 2018).
	Application of a hydrological model under climate change scenarios to produce input nutrient load time series.	Captures the impacts of climate variability. Most accurate in simulating nutrient load changes. Large computational cost. Existence of complexity and uncertainties associated with climate model runs.	10	(Lessin et al., 2014), (Meire et al., 2013), (Lazzari et al., 2014), (Fernandes et al., 2015), (Irby et al., 2018).

(Marshall et al., 2017; Fay et al., 2017). Van Oostende et al. (2018) project a shift to a pelagic-oriented marine ecosystem.

4.10. Adaptations of biota and ecosystems to climate change

The adaptation of ecosystems to climate change was modelled in three studies as phytoplankton adaptation to varying stoichiometry (Glibert et al., 2014; Kwiatkowski et al., 2019) and as the alignment of whale distribution to changing prey (krill) distributions (Tulloch et al., 2019).

Twelve studies modified their model algorithms to simulate changes in responses in changed-climate conditions. Tulloch et al. (2018, 2019) introduced a climate-growth parameter and a predator-prey interaction term to explore krill response to food availability and physical changes, and the effects of prey availability on the survival of baleen whales, respectively. Kwiatkowski et al. (2019) considered varying stoichiometry of phytoplankton and the habitat capacity model was incorporated into Ecospace to describe the response of functional groups to changing environmental drivers (Bauer et al., 2018). Irby et al. (2018) introduced temperature dependence to rates for phytoplankton/zooplankton growth, nitrification, detrital solubilisation and remineralisation, while optimum, minimum and maximum temperatures of species were converted to species temperature response functions (Serpetti et al., 2017). These functions were centred on the optimum temperature and thermal tolerance of species. Finally, pteropods were considered as individual functional groups to allow the investigation of pteropods as indicators of trophic shifts under climate change (Suprenand and Ainsworth, 2017).

4.11. Sea-level rise

Five studies considered sea-level rise (Etemad-Shahidi et al., 2015; Brown et al., 2016; Wang et al., 2017; Meier et al., 2017; Irby et al., 2018). In these studies, sea level was directly increased in scenario runs based on projected sea-level rises. Direct increase of sea level instead of the use of runs with continuous sea-level rise enables the study of equilibrium conditions without overlying long-term trends.

Depending on location, sea-level rise was found to increase salinity, residence time, sea water intrusion, the salinity intrusion depth, stratification and phosphate concentration. Increased residence time and sea water intrusion increased Chl a concentration and decreased total suspended solids (TSS), respectively, thereby enhancing phytoplankton growth (Wang et al., 2017; Meier et al., 2017). Further, increased stratification amplified hypoxia in bottom waters (Meier et al., 2017; Irby et al., 2018). On the other hand, Etemad-Shahidi et al. (2015) suggest that sea-level rise is likely to reduce warming in the lower part of the estuary because of enhanced inflow of cold bottom ocean waters.

4.12. Human activities

The impacts of climate change on marine ecosystems can be amplified by human activities and it is sometimes difficult to disentangle the impacts of multiple drivers of change. A combination of well-managed marine protected areas where human activities are controlled (Rilov et al., 2020) and statistical modelling (Castro-Sanguino et al., 2021) can be used

to separate the impacts of climate change and anthropogenic stressors. Currently, oceans have active fishing vessels and exploited species are overfished, thereby reducing fish stock (Pauly and Zeller, 2016). Untreated sewage discharge and industrial waste from highly populated, industrialised cities, and nutrients from agricultural land use increase riverine nutrient loads and chemicals. River flow capture, use and diversion for water management in highly urbanised areas have greatly modified river discharge, riverine sediment and nutrient loads causing coastal ecosystem alterations (Cloern et al., 2016; Elliott et al., 2019), which are enhanced by climate change-related impacts (Elliott et al., 2019).

Therefore, to effectively model the responses of marine ecosystems to impacts of climate change it is important to consider the direct and indirect effects of population growth, resource demands and use over model projection time frames. To this end, twenty-nine studies considered the impacts of changes in fishing efforts, nutrient loads, land-based and marine-based management practices, and fishing vessel activities alongside climate change impacts (Tian et al., 2015; Bauer et al., 2018; Holzwarth and Wirtz, 2018; Carozza et al., 2019). They found that intense fishing reduced the abundance of high trophic species and increased the abundance of low trophic species. They suggest that sustainable land use and effective management policies could help improve marine ecosystem functions under future climate change. Finally, increased nutrient loads enhanced hypoxia in bottom waters, while reduced nutrient loads expanded fishing habitats (Bauer et al., 2018).

4.12.1. Other forcing factors

Thirty nine studies obtained atmospheric forcing from observational data (Lachkar et al., 2018; Mogollón and R. Calil, 2018; Laurent et al., 2018) and existing reanalysis datasets, while other studies obtained atmospheric forcing data from climate model outputs (Barange et al., 2017; Nakamura et al., 2018). Klein et al. (2018) forced their model with climatological Chl a data from SeaWiFs within the model domain. Four studies obtained tidal forcing from a tidal model (Wakelin et al., 2015; Brown et al., 2016; Shen et al., 2019) and observed changes in greenhouse gases and aerosol concentrations were used to force the climate model in (Richon et al., 2019). Tanaka et al. (2013) scaled surface radiation by 10% and assumed a 10% decrease in water mixing for future climate predictions. Seven studies forced ecosystem models with simulated primary production (Suprenand and Ainsworth, 2017; Piroddi et al., 2017; Stäbler et al., 2019). Ortega-Cisneros et al. (2018) forced the Atlantis model with fish mortality rates to easily construct multiple scenarios and compare results with the Ecopath with Ecosim and Ecospace (EwE) model. The integration of simulated primary production eliminates IPCC scenario complexities associated with data accessibility and model output reliability.

5. What has been neglected? Where to from here?

It is important to note that the limits of the distribution and productivity of phytoplankton (the most important marine organism in the food chain) and other marine organisms depend on their physiological tolerance to extreme temperatures and elevated pCO_2. More experiments need to be carried out by observational scientists to provide information needed

for model parameterisation on the physiological responses of marine organisms to climate change impacts, particularly in tropical waters. Marine modellers need to interact more with observational scientists to ensure that models adequately represent available understanding of marine ecosystems.

At present, the representation of climate change impacts on marine response models is missing some key factors. Future models need to include important marine ecosystem parameters that are modified by climate change. For instance, changes in cloud cover, storm intensity and frequency, ocean stratification, upwelling and ocean currents were not considered as forcings in the reviewed literature. Few studies considered sea-level rise and changes in wind speed. It has been shown that reduced sea ice cover resulting from reduced cloud cover could increase SST (Liu et al., 2009). Also, warming and sea-level rise have been shown to affect storm intensity and frequency, and exacerbate coastal flooding (Iwamura et al., 2013; Bhattachan et al., 2018). Therefore, some important aspects of climate change could be omitted by excluding these changing environmental factors since they have been shown to affect marine ecosystems.

Better observational datasets are needed for accurate predictions of marine ecosystem responses to climate change impacts and for model assessment. Limited observational datasets hinder the effective assessment of models since for better model evaluation and uncertainty analysis calibration datasets need to be independent of validation datasets (Flynn and McGillicuddy, 2018). Improved collection of detailed and long-term observational datasets would help improve the assessment, accuracy and reliability of marine ecosystem response model predictions.

A good number of studies considered IPCC scenarios, but few studies considered the impacts of climate change under multiple IPCC scenarios. Future studies should where possible include multiple IPCC scenarios and utilise ensemble modelling approaches to capture essential effects of climate change in marine ecosystems and for better uncertainty analysis.

Some studies coupled ecosystem/biogeochemical models with physical-ocean-atmosphere models with reasonable computational efficiency (Richon et al., 2019; Hodgson et al., 2018; Mogollón and R. Calil, 2018). Regional climate models were coupled with hydrological models to represent changes in river discharge and nutrient loads as boundary conditions (Fernandes et al., 2015; Feng et al., 2015; Ryabchenko et al., 2016). Coupling regional models with hydrological models at catchment scales captures climate variability and provides information on underlying hydrological processes. Future modelling studies should continue to follow this modelling practice for improved accuracy of model predictions.

Finally, the adaptation of marine organisms to changing environmental conditions has so far been considered by very few modelling studies and should be a priority for future model development.

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Supporting Information

Additional Supporting Information can be found in the supporting information for this article.

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